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Abstract
Ecologists have become increasingly aware of the combined effects of habitat disturbance and climate change on the establishment and proliferation of invasive species. Long-term data on the population of the invasive American Shad Alosa sapidissima in the U.S. portion of the Columbia River basin provide an opportunity to examine how habitat disturbances affect the abundance and spatial distribution of an invasive species in a heavily modified environment. After the establishment of American Shad in the Columbia River in the late 1800s, the drainage was transformed from its natural lotic state to a series of reservoirs, with concomitant changes to discharge and temperature regimes, which are confounded by climate change. As the Columbia River was dammed, American Shad extended its range and increased in abundance. A large and rapid increase in spawning population abundance (recruits per spawner = 63) followed completion of The Dalles Dam in 1957, which inundated Celilo Falls, a natural barrier to upriver American Shad migration. Regressions revealed that the annual percentage of American Shad migrating upstream from McNary Dam varied with water temperature and discharge ($R^2 = 0.72$), but not population density. When Atlantic coast rivers were dammed, however, American Shad lost spawning habitat and declined in abundance. Understanding the rapid colonization of the Columbia River by American Shad may reveal ways to help American Shad recolonize rivers where they are native. Understanding the roles of water temperature and discharge may allow us to project effects of climate change on the future distribution and abundance of American Shad in the Columbia River basin. Our results suggest that dam construction and alterations to the temperature and discharge regimes of the Columbia River have contributed to the increase in abundance and spatial distribution of American Shad. These changes might have improved the reproductive success of American Shad by providing access to additional spawning grounds and creating suitable juvenile rearing conditions.

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Biological invasions result from a sequence of stages including introduction, establishment, dispersal, and impact (Williamson 1996; Kolar and Lodge 2001; Sakai et al. 2001). The spread of nonindigenous species constitutes a serious threat to global biodiversity (Vitousek et al. 1996; Simberloff et al. 2005; García-Berthou 2007), second only to the effects of habitat loss in the endangerment of native species (Wilcove et al. 1998). Initially, populations of nonindigenous species may be small, but once established, they may increase in abundance and distribution to dominate ecosystems (Waldeck et al. 2003), disrupt community trophic structure (Deegan and Buchsbaum 2005), alter species compositions of ecosystems (Chapin et al. 1997), and threaten the persistence of indigenous taxa (Wilcove et al. 1998). Ecologists are becoming increasingly aware of the effects that anthropogenic habitat disturbances and climate change can exert on the proliferation of invasive species (Hierro et al. 2005; Davis 2009; Walther et al. 2009). Although, to become established, nonindigenous species must respond rapidly to changes in the selective regimes imposed by the colonized system (Hänfling 2007), alterations to the environment that reflect conditions in their native range may aid this process. Therefore, identifying the abiotic factors responsible for the increased abundance and spatial distribution of invasive species is crucial for mitigating threats posed to native biota.

The Columbia River basin (Figure 1) is home to more than 350 nonindigenous species (Sanderson et al. 2009). Because the river has been extensively altered by anthropogenic influences, it provides an opportunity to study the effects of habitat disturbance on the proliferation of nonindigenous species. Dam construction in support of hydroelectric power development, irrigation needs, flood control, and navigation has transformed the once free-flowing Columbia River into hundreds of reservoirs, with concomitant changes to water temperature and discharge regimes (Pradeep and Jay 2005; Waples et al. 2007). These changes, confounded by regional climate change (Pradeep and Jay 2005; Battin et al. 2007), bear ecological consequences for other migratory fishes (Dauble et al. 2003; Waples et al. 2007).

The Columbia River basin contains approximately 30 non-native fish species (Waldeck et al. 2003; Sanderson et al. 2009), but the effects of these species on the ecosystem remain largely unknown (see also Levin et al. 2002). The most abundant non-native fish is the anadromous American Shad *Alosa sapidissima* (Waples et al. 2007). Though native to the Atlantic coast of North America—ranging from southern Labrador to northern...
Florida—American Shad rapidly dispersed after their introduction to the Sacramento River, California, in 1871 (Green 1874). The species was first observed in the Columbia River in 1876 (Smith 1896, but see Jordan 1916; reviewed in Hasselman et al. 2012a). Since then, American Shad in the Columbia River basin have dramatically increased in abundance, raising concern because of their potential impacts on native fishes and ecosystem function (Hasselman et al. 2012b). More than 4 million adult American Shad were annually counted passing upstream of Bonneville Dam (river kilometer [rkm] 234) from 2003 to 2006, and from 1977 to 2008 adult American Shad outnumbered all adult native salmonids (hatchery and wild combined). Adult American Shad are counted at fishways installed at Bonneville Dam and other dams on the lower main stems of the Columbia and Snake rivers. All of these fishways, with the exception of that at Priest Rapids Dam in the mid-Columbia River (Figure 1), allow American Shad to successfully pass upstream.

Specific information on the conditions suitable for American Shad spawning and juvenile survival in the Columbia River basin is lacking. However, in their native range, American Shad spawning is associated with moderate water temperature (13–26°C) and current velocity (30–90 cm/s), shallow waters (<5 m water depth), and adequate dissolved oxygen (>5 mg/L) (Klauda et al. 1991; Beasley and Hightower 2000; Harris and Hightower 2011). American Shad spawn over a variety of substrates (Stier and Crance 1985; Beasley and Hightower 2000). Although survival of juvenile American Shad in their native range has been associated with the distance that adults migrate and the availability of suitable prey in upstream reaches (Limburg 1996a, 1996b, 2001), variations in river discharge and temperature during early larval development are usually considered important regulators of year-class strength and recruitment to the spawning stock (Marcy 1976; Leggett 1977; Shoubridge and Leggett 1978; Crecco and Savoy 1987).

Given the dominant influences of water temperature and discharge on American Shad recruitment in their native range, we sought to understand how dam construction and associated changes to water temperature and discharge regimes (confounded by climate change) might have influenced the proliferation and spatial distribution of American Shad in the Columbia River basin. By understanding the factors contributing to the rapid colonization of the Columbia River by American Shad, we may discover ways to aid American Shad on the East Coast of the United States to recolonize rivers where they are native and of increasing conservation concern (Limburg and Waldman 2009; Hasselman and Limburg 2012). Furthermore, understanding the roles of water temperature and discharge may allow us to project how climate change, which is expected to cause future alterations to temperature and discharge regimes, may influence the future abundance and spread of American Shad on the Columbia River. In this study, we (1) characterize the growth of the American Shad spawning population in response to increases in available contiguous reservoir habitat as a result of dam construction, and (2) demonstrate how the spatial distribution of the spawning run within the Columbia River basin varies with alterations to discharge patterns and water temperature regimes. We then discuss possible factors responsible for the patterns we observed, and discuss future research needs and management implications.

METHODS

Study Area

The study area included the main-stem Columbia River upstream of Bonneville Dam (rkm 234) and main-stem Snake River. American Shad return to the Columbia River to spawn in locations that extend to Priest Rapids Dam (rkm 639) on the mid-Columbia River and Lower Granite Dam (rkm 173) on the Snake River (Figure 1). The study area is contained within the Columbia River basin, which drains a watershed of 671,000 km² (Ebel et al. 1989) and extends into seven U.S. states and one Canadian province (Waples et al. 2007). The drainage is regulated by more than 200 dams (Ebbesmeyer and Tangborn 1992).

Adult American Shad Data


River Data

Columbia River data.—To examine the effects of environmental conditions on American Shad abundance and distribution in the Columbia River basin, we obtained the following habitat data from the USACE: (1) available contiguous reservoir surface area (km²) from Bonneville Dam through McNary Reservoir (i.e., Lake Wallula) on the upper Columbia River and through Lower Granite Reservoir on the Snake River (Figure 1); (2) daily water temperature measured at Bonneville Dam as reported in annual USACE fish passage reports from 1949 to 2012 (available from www.nwp.usace.army.mil/Missions/Environment/fishdata.aspx [September 2012]); (3) change in cumulative active storage capacity (CRWMG 2002). We also obtained summer discharge data from the U.S. Geological Survey (USGS) at The Dalles USGS gauge station 14105700 (available from waterdata.usgs.gov/nwis [September 2012]). Contiguous reservoir surface area is used as a measure of areal habitat of American Shad in the Columbia River, and it consists of flowing water because the dams that create the reservoirs that American Shad inhabit are “run of the river.” In this study, “available contiguous reservoir habitat” refers to the available contiguous reservoir surface area (km²).
Data Analysis

Adult population abundance.—To illustrate the trend of abundances of adult American Shad, we plotted the times series of adult American Shad passing Bonneville Dam. Because American Shad counts at Bonneville Dam were often lower than the counts at The Dalles Dam after 1971 (possibly due to American Shad passing undetected through the Bonneville Dam navigation lock), the number of American Shad passing Bonneville Dam was estimated as the maximum of The Dalles and Bonneville dams adult American Shad counts (adjusted count; ADJ). To show the effect of adjusting the American Shad counts, we compared the ADJ counts with the actual counts (unadjusted count; UNADJ) at the Bonneville Dam fish ladders. Assuming that the adult shad passing The Dalles Dam must have also passed Bonneville Dam, the ADJ count was a more accurate estimate of the true spawning population passing Bonneville Dam. The ADJ and UNADJ time series of counts were strongly correlated over the years 1938–2012 ($r = 0.98$, $SE = 0.02$) and over 1970–2012 ($r = 0.97$, $SE = 0.04$). We calculated correlation separately for 1970–2012 because, after 1970, The Dalles Dam American Shad count exceeded the Bonneville Dam count in most years, and thus this period was one of maximum difference between the ADJ and UNADJ counts.

Recruits per spawner.—As an index of population growth, we developed crude estimates of yearly recruits per spawner. We estimated spawners as the count of adult American Shad passing Bonneville Dam, and estimated recruits as the average estimated count of adult American Shad passing Bonneville Dam 3–6 years later. We chose a 3–6 year time frame because this covered the age range of the bulk of spawning adults reported in previous studies (Wendler 1967; Petersen et al. 2003). We used an unweighted average for recruits instead of weighting by the age-specific percentages reported in Wendler (1967) or Petersen et al. (2003), because age structure is likely to vary widely among samples and return years. As an alternative to equal weighting, we estimated recruits by weighting the number of subsequent spawners according to the Petersen et al. (2003) age structure data, but we found that it produced minute differences in the estimated series of recruits per spawner (data not shown). A more refined estimate of recruitment would only be possible with yearly age structure data for Columbia River American Shad since adult counts began in 1938; however, such data do not exist. We calculated recruits per spawner using both the ADJ and UNADJ counts at Bonneville Dam. The two resulting log$_e$(recruits per spawner) series were strongly correlated over brood years (BYs) 1938–2006 ($r = 0.98$, $SE = 0.02$) and over BYs 1970–2006 ($r = 0.92$, $SE = 0.06$).

To determine the effect of increasing available contiguous reservoir habitat on adult American Shad abundance, we plotted the time series of log$_e$(recruits per spawner) and compared it with the time series of available contiguous reservoir surface area (km$^2$) upstream from Bonneville Dam. To test whether the recent (i.e., 2005–2011) decline in American Shad abundance was unusual, we compared recent recruits per spawner observations to the frequency distribution of recruits per spawner over the entire data series beginning in 1938.

Adult upriver distribution.—To characterize the upriver distribution of adult American Shad on the Columbia and Snake rivers, we used American Shad counts at Bonneville, The Dalles, John Day, and McNary dams on the Columbia River, and Ice Harbor, Lower Monumental, Little Goose, and Lower Granite dams on the Snake River. Using the yearly American Shad counts retrieved from the USACE database, we calculated the average number of American Shad passing each dam from 1980 to 2012. We used this time period because Lower Granite Dam was not completed until 1975, and beginning in 1980 allowed invasion upstream from the dam to proceed for about a generation before the average upstream distribution was calculated. For greatest accuracy, we used the ADJ Bonneville count for this analysis.

Adult upriver distribution versus river covariates.—To test for a linear relationship between upriver adult American Shad distribution and water temperature, we regressed the percentage of American Shad migrating to points above McNary Dam ($y_i$), against the average May–August water temperature at Bonneville Dam ($x_{1i}$) from 1970 to 2012, using least-squares regression. We used May–August data because Bonneville Dam counts show that most of the American Shad (99.99%) pass Bonneville Dam during this period (USACE 2010). Although water temperature was measured at the Bonneville Dam, water temperature fluctuations at Bonneville Dam reflected fluctuations at other locations in the main-stem Columbia River (Yearsley et al. 2001). Acknowledging that water temperature is related to discharge, we also regressed upriver distribution against average May–August discharge at The Dalles USGS gauge station ($x_{2i}$) from 1970 to 2012. Lastly, we regressed $y_i$ against both $x_{1i}$ (water temperature) and $x_{2i}$ (discharge), using multiple linear
regression. The number of American Shad passing Bonneville Dam was excluded as a covariate in these regressions because its correlation with upriver adult American Shad distribution was not significantly different from zero ($r = 0.12, \text{SE} = 0.16$).

To compare the fits of alternative models, we calculated the Akaike information criterion (AIC) of each model. Models with lower AIC values indicated a better fit to the data (Akaike 1973). We tested for lag-1 autocorrelation in residuals by using an autoregressive process of order 1 (Box et al. 1994). To determine whether multicollinearity might be an issue in the multiple linear regression (Belsley 1991), we calculated the Pearson correlation coefficient for the covariates water temperature and discharge. We used the ADJ Bonneville count for this analysis.

**River covariate trends.**—To illustrate the change in Columbia River discharge as storage capacity increased, we plotted time series of discharge measured at The Dalles USGS gauge station and storage capacity (1880–2012) on the same graph. We also demonstrated the change in the temperature distribution at Bonneville Dam during 1954–1963 and 2003–2012 by plotting daily averages for these periods. To illustrate how temperature during these periods differed for a river in the American Shad’s native range, we also plotted mean daily temperature of the Delaware River, measured at Trenton, New Jersey, during these same time periods. In addition, to show diverging trends, we plotted time series of annual average May–August temperatures for the Columbia River (1949–2012) and Delaware River (1954–2012). For each temperature data set, we tested for a trend using a Mann–Kendall test (Mann 1945). Because the Columbia River temperature data set exhibited serial dependence, we applied the Mann–Kendall test with a block bootstrap approach using 10,000 bootstrap replications and a block size of 5 years (Lahiri 2003).

**RESULTS**

**Data Analysis**

**Adult population abundance.**—The number of American Shad at Bonneville Dam peaked at 6 million in 2005 (Figure 2). In 2010, American Shad passing Bonneville Dam declined to approximately 1.2 million fish (ADJ); a lower count (ADJ) has not been observed since 1982.

**Adult population growth.**—After completion of The Dalles Dam (rkm 308) in 1957, the estimated number of adult American Shad passing Bonneville Dam increased dramatically (Figure 2). After construction of The Dalles Dam, recruits per spawner peaked at 63 (ADJ and UNADJ) [log$_e$(recruits per spawner) = 4.14] in BY 1959 (Figure 3). The geometric mean number of recruits per spawner during BYs 1956–1962 was 9.77 (ADJ and UNADJ) [average log$_e$(recruits per spawner) = 2.5]. The available contiguous reservoir habitat increased by 38 km$^2$ after The Dalles Dam was constructed. A larger increase of 383.1 km$^2$ in available contiguous reservoir habitat occurred with the completion of John Day Dam in 1968, and the number of recruits per spawner peaked at 2.79 (ADJ) [log$_e$(recruits per spawner) = 1.03] in BY 1971. The geometric mean of recruits per spawner over BYs 1968–1974 was 1.95 (ADJ) [average log$_e$(recruits per spawner) = 0.67], considerably less than the geometric mean recruits per spawner corresponding to the completion of The Dalles Dam (Figure 3). The recent decline in shad numbers yielding recruits per spawner (ADJ) of 0.246 [log$_e$(recruits per spawner) = −1.40] in BY 2005 was rare in the entire data set; only one previous observation of recruits per spawner was less than or equal to 0.246, and that was in BY 1945 (Figure 3).
TABLE 1. Average number of American Shad passing main-stem dams on the Columbia and Snake rivers (1980–2012); rkm = river kilometer, n = number of observations, Mean = sample mean, SE = standard error of sample mean.

<table>
<thead>
<tr>
<th>Dam</th>
<th>rkm</th>
<th>n</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Columbia River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bonneville</td>
<td>234</td>
<td>33</td>
<td>2,413,782</td>
<td>224,102</td>
</tr>
<tr>
<td>The Dallesa</td>
<td>308</td>
<td>31</td>
<td>2,435,378</td>
<td>232,583</td>
</tr>
<tr>
<td>John Day</td>
<td>351</td>
<td>24</td>
<td>1,114,825</td>
<td>116,280</td>
</tr>
<tr>
<td>McNary</td>
<td>470</td>
<td>33</td>
<td>665,279</td>
<td>79,748</td>
</tr>
<tr>
<td>Snake River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ice Harbor</td>
<td>538</td>
<td>33</td>
<td>91,617</td>
<td>17,107</td>
</tr>
<tr>
<td>Lower Monumental</td>
<td>589</td>
<td>24</td>
<td>39,658</td>
<td>11,393</td>
</tr>
<tr>
<td>Little Goose</td>
<td>635</td>
<td>15</td>
<td>17,265</td>
<td>6,491</td>
</tr>
<tr>
<td>Lower Granite</td>
<td>695</td>
<td>33</td>
<td>5,364</td>
<td>1,443</td>
</tr>
</tbody>
</table>

aThe Dalles Dam has a larger mean count than Bonneville Dam because shad counts at The Dalles Dam were halted after 2010 and Bonneville Dam counts were relatively low during 2011–2012.

Adult upriver distribution.—Declines in passage counts of adult American Shad with upstream distance were apparent in both the lower Columbia and the Snake rivers (Table 1). On average, 28% of the adult American Shad passing Bonneville Dam traveled an additional 236 km to pass McNary Dam, while 6% of the adult American Shad that passed Ice Harbor Dam traveled an additional 157 km upstream to pass Lower Granite Dam.

Adult upriver distribution versus river covariates.—The results of the regression analyses using percent adult American Shad penetrating upstream of McNary Dam as the response variable and mean May–August discharge and mean May–August water temperature as the explanatory variables are summarized in Tables 2 and 3. The regression containing both water temperature and discharge and their interaction had the lowest AIC value and highest coefficient of determination ($R^2$). The overall fit for each regression was significant ($P < 0.001$). Mean May–August water temperature was a significant predictor of upriver American Shad distribution ($P < 0.001$) (Figures 4a, 5a). The slope of the regression was 8.79 (SE = 1.48) and indicated that when average May–August water temperature rose by 1°C, approximately 9% more of the American Shad counted at Bonneville Dam migrated to points upstream from McNary Dam. Mean May–August discharge was also a significant predictor of upriver distribution of American Shad ($P < 0.001$) (Figures 4b, 5b) and explained 12% more of the variation in the percent American Shad passing McNary Dam than did the mean May–August temperature. The slope of the regression was −4.09 (SE = 0.59) and indicated that lower proportions of the American Shad spawning population migrated to spawning areas upstream from McNary Dam in years with higher mean May–August discharge. In the multiple linear regression, which contained both mean May–August river temperature and mean May–August discharge, the slopes of mean May–August river temperature, mean May–August discharge, and their interaction were each significant ($P < 0.001$). Thus, despite the correlation between the two predictor variables, mean May–August water temperature and mean May–August discharge, in the multiple linear regression ($r = −0.65$, SE = 0.12), regression coefficient estimates were all significant. Correlation

TABLE 2. Regression results for percentage of American Shad penetrating upstream from rkm 470 plotted with times series of (a) mean May–August water temperature measured at Bonneville Dam and (b) mean May–August discharge.

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>$R^2$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>43</td>
<td>0.00</td>
<td>321.2</td>
</tr>
<tr>
<td>Temperature</td>
<td>40</td>
<td>0.42</td>
<td>301.6</td>
</tr>
<tr>
<td>Discharge</td>
<td>40</td>
<td>0.54</td>
<td>291.5</td>
</tr>
<tr>
<td>Temperature + Discharge</td>
<td>39</td>
<td>0.72</td>
<td>272.2</td>
</tr>
<tr>
<td>(Temperature × Discharge)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

FIGURE 4. Time series of the percent of American Shad penetrating upstream from rkm 470 plotted with times series of (a) mean May–August water temperature measured at Bonneville Dam and (b) mean May–August discharge.
TABLE 3. Regression coefficient estimates for alternative models. Temperature is mean May–August river temperature, and Discharge is mean May–August discharge. In the regression, temperature is in units of °C and discharge is in units of 1,000 m³/s; SE = standard error, t = standardized regression coefficient estimates, P = probability of obtaining a test statistic at least as extreme as the one observed, Phi = autocorrelation coefficient. Temperature × Discharge = regression coefficient of the product of mean May–August water temperature and mean May–August discharge.

<table>
<thead>
<tr>
<th>Model</th>
<th>Coefficient</th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>Intercept</td>
<td>26.98</td>
<td>1.49</td>
<td>18.07</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temperature</td>
<td>Intercept</td>
<td>−126.28</td>
<td>25.94</td>
<td>−4.87</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>8.79</td>
<td>1.48</td>
<td>5.93</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Phi</td>
<td>0.44</td>
<td>0.14</td>
<td>3.02</td>
<td>0.0044</td>
</tr>
<tr>
<td>Discharge</td>
<td>Intercept</td>
<td>53.26</td>
<td>4.03</td>
<td>13.20</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Discharge</td>
<td>−4.09</td>
<td>0.59</td>
<td>−6.94</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Phi</td>
<td>0.27</td>
<td>0.16</td>
<td>1.70</td>
<td>0.0975</td>
</tr>
<tr>
<td>Temperature + Discharge</td>
<td>Intercept</td>
<td>−368.36</td>
<td>77.91</td>
<td>−4.73</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>23.93</td>
<td>4.43</td>
<td>5.41</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Discharge</td>
<td>56.99</td>
<td>11.53</td>
<td>4.94</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Temperature × Discharge</td>
<td>−3.49</td>
<td>0.67</td>
<td>−5.24</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Figure 5. Least-squares line fits of the percent of American Shad penetrating upstream from rkm 470 versus (a) mean May–August water temperature or (b) mean May–August discharge, 1970–2010.

Figure 6. Contours of the predicted percentage of American Shad penetrating upstream from rkm 470 from the multiple linear regression model. Solid dots represent observed values of mean May–August river temperature and mean May–August discharge.

between predictor variables (or multicollinearity) can produce nonsignificant regression coefficients when predictor variables are important (Belsley 1991). The negative estimate of the interaction coefficient indicates that as average May–August temperature increases, the effect of discharge on upriver distribution of American Shad becomes stronger. At higher temperatures, the temperature contours bunch closer together (Figure 6), increasing the effect of an increment in mean May–August discharge on upriver distribution of American Shad.

When all the time series used in the regressions were detrended using a least squares fit to year (Shumway and Stoffer...
FIGURE 7. (a) Daily water temperatures on the Columbia River over the past 60 years compared with those of the Delaware River. (b) Time series of average May–August water temperatures on the Columbia River and Delaware River. Solid lines represent 5-year running averages.

2000), the overall model fits continued to be significant ($P < 0.001$). Thus, trends in the data series do not drive the statistical relationships between upriver American Shad distribution and the river covariates of mean May–August temperature and mean May–August discharge (see Figure 4).

River covariate trends.—Annual average May–August water temperatures at Bonneville Dam have increased over the last 64 years, approaching those of the Delaware River (Figure 7). The Mann–Kendall tests for trend showed that the upward trend in the Columbia River annual average May–August water temperature data was statistically significant ($P = 0.004$), but no statistically significant trend existed in the Delaware River annual average May–August water temperature ($P = 0.482$). In the Columbia River, the 5-year running average of annual average May–August water temperature increased by 1.3°C between the periods 1949–1953 and 2008–2012. This increase in average May–August water temperature coincided with the rapid increase in active storage in the Columbia River basin and decrease in average May–August discharge (Figure 8).

FIGURE 8. Columbia River basin active storage capacity and average May–August discharge since the 1880s.

DISCUSSION

A central tenet of invasive species ecology is that habitat disturbance can facilitate the establishment and proliferation of nonindigenous species (Gray 1879; Hierro et al. 2005). An example is the transformation of a naturally lotic system into a series of reservoirs, which act as stepping stones for dispersal of nonindigenous species (Havel et al. 2005). Our study demonstrates that the growth of the Columbia River American Shad spawning population upriver from Bonneville Dam coincides with dam construction. Furthermore, the upriver spatial extent of the adult American Shad spawning population is strongly related to alterations of discharge and water temperature regimes.

The spawner–recruit data developed in this study helped determine the effect of opening new habitat on population growth of adult American Shad, and places the recent decline of Columbia River American Shad in context. The greatest increase in the adult American Shad count at Bonneville Dam (63 recruits per spawner) occurred after the completion of The Dalles Dam, which inundated Celilo Falls, a natural barrier to American Shad migration (Wendler 1967; Gregory et al. 2002; Hasselman et al. 2012a). Inundation of Celilo Falls allowed adult American Shad to migrate farther up the Columbia River. Note that a much smaller increase in the adult American Shad count at Bonneville Dam (three recruits per spawner) occurred after the completion of John Day Dam, even though this dam created more available contiguous reservoir habitat than did The Dalles Dam. We suspect that there are two important reasons for this. First, construction of John Day Dam did not remove a natural barrier to American Shad upstream migration, while construction of The Dalles Dam did. We would expect that
the construction of a dam that removed a natural barrier upstream would have a larger effect on American Shad abundance than would the construction of a dam that did not remove a barrier. Second, American Shad abundance decreased sharply, by about 70% between Bonneville Dam and McNary Dam (Table 1), with upstream river migration distance. Thus, we expect that an increase in habitat upstream of John Day Dam would have less net effect on American Shad abundance than an increase in habitat downstream of John Day Dam, which includes the habitat created by the construction of The Dalles Dam.

Inundation of Celilo Falls allowed access to not only mainstream Columbia River habitat, but also to large upstream tributaries such as the Deschutes and Umatilla rivers. Although American Shad use upriver main-stem habitat in the Columbia River, the extent to which American Shad use upstream Columbia River basin tributaries, perhaps for spawning, is unknown. Downstream from Bonneville Dam, American Shad are known to use the following tributaries: Willamette River (Foster and Boatner 2002); Sandy River (Wendler 1967); John Day River near Astoria, Oregon, in the Columbia River estuary; and tributary streams to Youngs Bay (Robinson 1974). Wendler (1967) noted that with the exception of these rivers and the Snake River, few American Shad have been observed in Columbia River basin tributaries.

Studies that map the spawning and rearing habitat suitability of the Columbia River basin are lacking. Such studies may help us understand the rapid population growth of American Shad that occurred after they were able to access new upstream spawning and rearing habitat. Atlantic coast American Shad studies show that spawning locations are related to substrate, depth, water velocity, and dissolved oxygen (Klauda et al. 1991; Beasley and Hightower 2000; Harris and Hightower 2011). These studies show that American Shad spawn in shallow areas (<5 m depth) in which water flows over coarse substrates. Shallow, flowing areas are available in the reservoirs of the lower Columbia and lower Snake rivers, where dams are run of the river. On the Columbia River, systematic studies of substrate, water temperature, water velocity, pH, and dissolved oxygen, which are all factors used to define habitat requirements for American Shad (Klauda et al. 1991), are not available. However, we were able to identify a few habitat studies of the John Day Reservoir that, when taken together, allowed us to identify ranges for these habitat factors (Gilbreath et al. 2000; Cross and Twichell 2004; Tiffan et al. 2006). Mapping of substrate in the John Day Reservoir showed that 10% of the total reservoir floor consisted of gravel beds free of fine sediment (Cross and Twichell 2004), which would be suitable for American Shad. Measurements by Gilbreath et al. (2000) in John Day Reservoir demonstrated that dissolved oxygen ranged from 8.4 to 12.8 mg/L, which is greater than the value of 5 mg/L known to be suitable for survival of American Shad at the egg, juvenile, and migrating adult stages (Klauda et al. 1991). Gilbreath et al. (2000) found that temperatures in the John Day Reservoir ranged from 10°C to 22°C during June–August, which lies within the temperature range of 13–26°C known to be suitable for development and survival of American Shad eggs (Klauda et al. 1991). Tiffan et al. (2006) found that water velocities at two stations within the John Day Reservoir varied by discharge and distance from shore, and ranged from 0 to 30 cm/s, which is lower than velocities thought to be optimal for American Shad spawning and egg incubation (30–90 cm/s), but within the range optimal for larvae (6–30 cm/s) and juveniles (6–75 cm/s). However, these stations were not located near the tailrace of McNary Dam (located at the upstream end of John Day Reservoir), where water velocities from the shore to midchannel can range from 0 to 100 cm/s (Faler et al. 1988).

This suggests that there are areas within the McNary Dam tailrace that contain water velocities optimal for American Shad spawning and egg incubation. Measurements of pH levels in the John Day Reservoir (7.7–8.6) by Gilbreath et al. (2000) meet the criteria for egg (>6.0) and larval stages (>6.7) (Klauda et al. 1991) of American Shad in their native range.

The recent large decline in American Shad counts at Bonneville Dam (Figure 2) is not unprecedented. Similar low values of recruits per spawner occurred during the 1940s (Figure 3). The decline, however, is rare and not understood (Pearcy and Fisher 2011). Pearcy and Fisher (2011) showed that fish counts at Bonneville Dam are correlated with abundance estimated by sampling over the continental shelf. This suggests there was an actual decline in population abundance of American Shad in the Columbia River, not simply a redistribution to areas downstream from Bonneville Dam. In 2012, over 2 million adult shad were observed passing Bonneville Dam, suggesting a resurgence in the spawning population. Our lack of understanding of the recent dramatic decline of American Shad abundance from 6 million in 2005 to 1 million in 2011 in the Columbia River basin reveals two critical needs: (1) statistical tests relating the time series of number of recruits per spawner to important biotic and abiotic factors and (2) information on cause and effect. Statistical and causative relationships will help fisheries managers understand not only the recent population decline, but also population variations throughout the entire record of counts. Statistical tests for relationships would include important abiotic factors (e.g., Pacific Decadal Oscillation [PDO], coastal upwelling index, temperature), as well as biotic factors (e.g., zooplankton abundance in reservoirs, estuary, ocean). Changes in temperature, discharge, and available habitat have probably influenced recruits per spawner of American Shad, but other factors that influence recruits per spawner are also possible, including oceanic factors. Examples include the Oregon Production Index, which was found to be negatively correlated with American Shad counts, and the PDO, which recently has switched to a cool–wet phase (Pearcy and Fisher 2011). Causal information might include surveys of prey abundance in reservoirs and stomach contents of rearing juveniles (Haskell et al. 2006), as well as parasite loads and associated mortality rates of American Shad (Shields et al. 2002; Hershberger et al. 2010).
We found that adult American Shad abundance declines with upriver distance above Bonneville Dam (Table 1), and the decline is greater with lower water temperature and higher discharge (Figure 4). The cause for the decline in abundance with upriver distance is unknown. Both energy costs and prey abundance (for juvenile American Shad) may be important factors in determining migration distance. Selection may favor American Shad that spawn in reservoirs with sufficient prey for their young. Energy used by adults to migrate a greater distance upstream is not available for reproduction and decreases the energy reserve necessary for iteroparity (Leggett et al. 2004; Castro-Santos and Letcher 2010). Petersen et al. (2003) estimated that 32% of American Shad in the Columbia River basin are repeat spawners. Energy costs could also be increased by migration delays at dams (Castro-Santos and Letcher 2010). If energy cost of migration explains variation in upriver distribution, higher discharge would increase energy costs of migration, discouraging longer migrations, especially at high temperatures when energetic costs of locomotion are greatest (Glebe and Leggett 1981). Indeed, by focusing on the region of the contour plot where the average May–August temperature and discharge observations are concentrated, we found that a higher fraction of American Shad migrated beyond McNary Dam when average May–August discharge was low, and the effect of average May–August discharge was greatest at high average May–August water temperatures (Figure 6).

The availability of prey resources for juvenile shad in different reservoirs also could play an important role in the upstream distribution of adults. Although adults feed little during their spawning migration in freshwater, prey sources for larval and juvenile shad are important for survival (Stier and Crance 1985; Limburg 1996b). American Shad may choose spawning locations that increase opportunities for their young to find suitable prey, which are unevenly distributed in the Columbia River. Haskell et al. (2006) found that prey abundance for juvenile American Shad was greater in the John Day Reservoir than in the McNary Reservoir (upriver from John Day Reservoir) largely because John Day Reservoir had twice the mean retention time of McNary Reservoir, with conditions more favorable for zooplankton abundance. Therefore, if American Shad spawned in the McNary Reservoir instead of the John Day Reservoir (downstream of McNary Dam), there would be less suitable prey available to their young.

The decline of American Shad with upriver distance may also be related to fish ladder design and the hydraulic conditions experienced by adults. American Shad migration depends upon appropriately designed fishways to pass migration barriers (Moffitt et al. 1982; Quinn 1994). When a fishway at John Day Dam went into operation in 1968, American Shad were reluctant or unable to pass through the submerged orifices in the ladders (Monk et al. 1989). The resultant “traffic jam” of American Shad became problematic because it delayed passage of Pacific salmon. It was discovered that American Shad used surface weirs but not submerged orifices to move upstream and downstream (Haro and Kynard 1997). Modifications of John Day Dam ladders in 1972 reduced water velocity and created surface passage weirs (“slot-type” weirs); fish ladders at Bonneville Dam were similarly modified in 1973 (Perkins and Smith 1973). The American Shad population grew when these ladder modifications were made in the early 1970s, reaching a maximum of 3.7 recruits per spawner (ADJ) in BY 1974 (Figure 3). The fisheries agencies used the inability of American Shad to migrate through the submerged orifices of Priest Rapids Dam fishways as a strategy to block further invasion of upstream habitat by this species (FERC 2006).

Why focus on water temperature and discharge? Our results suggest that average May–August water temperature and discharge affect the extent of the upriver spawning migration. In turn, upriver extent of the spawning migration may have consequences for juvenile American Shad growth and survival (Limburg 1996a, 1996b), recruitment, and, ultimately, fitness. From Atlantic coast studies, we know that water temperature and discharge affect year-class strength of American Shad populations (e.g., Crecco and Savoy 1984). Therefore, to understand the spread and increase in abundance as well as possible future population increases, it is important to understand how and why Columbia River water temperature and discharge have changed and how they are expected to change in the future.

Construction of dams has altered the Columbia River food web to support increases in abundance of American Shad. The Columbia and Snake rivers have been converted from lotic to lentic ecosystems (ISAB 2011), with the exception of the Hanford Reach in the mid-Columbia River. This alteration has shifted food sources from benthic or terrestrial in origin (e.g., caddisflies, mayflies, stoneflies) to planktonic (e.g., copepods, cladocerans) (ISAB 2011). This change in prey base might have favored juvenile American Shad, which are planktivorous (Haskell et al. 2006). Haskell et al. (2006) found that zooplankton made up 99% of the juvenile American Shad diet during their out-migration (August–November). Yearly zooplankton abundances fluctuate with water temperature and discharge in both the John Day and McNary reservoirs (Haskell et al. 2006). These fluctuations in prey abundance probably influence juvenile American Shad survival (Crecco and Savoy 1985) and consequently population growth. Therefore, an important area for future research is to test whether prey abundance is a significant predictor of number of recruits per spawner, which is a measure of population growth.

The shift from free-flowing to reservoir habitats in the Columbia River basin may hold evolutionary implications for American Shad. It is unlikely American Shad in their native range have experienced lentic conditions similar to those of the Columbia River basin during their evolutionary history (Baxter 1977). The lentic condition of the Columbia River basin may hold evolutionary implications for American Shad (ISAB 2011), and demography (Rottiers et al. 1992).
Impoundments like those of the Columbia River basin may be an important evolutionary driver acting on aquatic biodiversity (Haas et al. 2010). Because evolutionary adaptations may facilitate future establishment and spread of invasive taxa (Allendorf and Lundquist 2003), understanding the life history variation exhibited by American Shad is important for effective management of their population in the Columbia River basin.

To understand the true impact of American Shad on native taxa in the Columbia River basin, it is essential to know the species’ distribution throughout the entire Columbia and Snake rivers, not just in the main-stem Columbia River upstream from Bonneville Dam. If the observed pattern of decreasing adult American Shad abundance with upriver distance applies to areas downstream from Bonneville Dam, then the American Shad passing Bonneville Dam could represent a small fraction of the entire spawning population. Furthermore, yearly counts of shad in tributaries downstream (and upstream) from Bonneville Dam do not exist. An important area of future research is mark–recapture experiments to estimate the abundance of the adult American Shad population spawning downstream from Bonneville Dam.

The status of American Shad in the Columbia River versus the Atlantic coast of the United States reveals an irony (Hinrichsen and Ebbe Meyer 1998; Gregory and co-authors 2002). As the Columbia River was dammed, American Shad extended their in-river range and increased in abundance. As rivers on the Atlantic coast were dammed, American Shad lost spawning habitat and declined in abundance (e.g., St. Pierre 1994, 2003). Several factors other than dam construction have contributed to declines in American Shad populations on the Atlantic coast, including overfishing, pollution, and land development (Rulifson 1994; Bilkovic et al. 2002; Limburg et al. 2003). As a result, catch levels on the Atlantic coast dropped from 30,000 metric tons at the turn of the 20th century to 600 metric tons by 1996 (Greene et al. 2009). Several measures have been used in an attempt to restore Atlantic coast American Shad populations, including use of American Shad hatcheries (Hendricks 2003). To aid recovery of American Shad populations in their native range, the development of effective fishways is needed (Moffitt et al. 1982; Quinn 1994; Weaver et al. 2003; Katopodis 2005). Perhaps there are lessons from fishway designs and operations used to successfully pass American Shad on the Columbia River that can assist in this effort. American Shad on the Columbia River have demonstrated that spawning populations can increase in abundance without hatchery inputs when fishways are effective and other sources of mortality are held in check.

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Comparing Effects of Transmitters within and among Populations: Application to Swimming Performance of Juvenile Chinook Salmon

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Comparing Effects of Transmitters within and among Populations: Application to Swimming Performance of Juvenile Chinook Salmon

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Abstract

The sensitivity of fish to a transmitter depends on factors such as environmental conditions, fish morphology, life stage, rearing history, and tag design. However, synthesizing general trends across studies is difficult because each study focuses on a particular performance measure, species, life stage, and transmitter model. These differences motivated us to develop simple metrics that allow effects of transmitters to be compared among different species, populations, or studies. First, we describe how multiple regression analysis can be used to quantify the effect of tag burden (transmitter mass relative to fish mass) on measures of physiological performance. Next, we illustrate how the slope and intercept parameters can be used to calculate two summary statistics: $\theta$, which estimates the tag burden threshold above which the performance of tagged fish begins to decline relative to untagged fish; and $k$, which measures the percentage change in performance per percentage point increase in tag burden. When $\theta = 0$, $k$ provides a single measure of the tag's effect that can be compared among species, populations, or studies. We apply this analysis to two different experiments that measure the critical swimming speed ($U_{\text{crit}}$) of tagged juvenile Chinook Salmon Oncorhynchus tshawytscha. In both experiments, $U_{\text{crit}}$ declined as tag burden increased, but we found no significant threshold in swimming performance. Estimates of $\theta$ ranged from $-0.6\%$ to $2.1\%$ among six unique treatment groups, indicating that swimming performance began to decline at a relatively low tag burden. Estimates of $k$ revealed that $U_{\text{crit}}$ of tagged fish declined by $-2.68\%$ to $-4.86\%$ for each $1\%$ increase in tag burden. Both $\theta$ and $k$ varied with the tag's antenna configuration, tag implantation method, and posttagging recovery time. Our analytical approach can be used to gain insights across populations to better understand factors affecting the ability of fish to carry a transmitter.

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A conservative guideline for tag burden (percentage of tag mass in air to fish mass in air) is 2% (Winter 1996). However, numerous studies suggest that a tag burden exceeding 2% may not affect particular aspects of physiological performance. For example, some studies have shown significant negative effects of the transmitter when tag burden exceeds 4–5% (Adams et al. 1998a, 1998b), whereas others have failed to detect an influence of the transmitter at similar or higher tag burdens (Brown et al. 1999, 2006, 2010; Angela et al. 2004). Variation among studies suggests that the ability of a fish to carry a tag of given relative size may depend on species, life stage, rearing history (e.g.,...
Given the numerous factors that influence sensitivity of fish to transmitters, synthesizing general trends across studies is difficult because each study focuses on a particular performance measure, species, life stage, and transmitter model. Specifically, we identified two important knowledge gaps in the literature. First, variation among populations in their sensitivity to a transmitter implies that the maximum allowable tag burden should vary by population: the more sensitive a population is to a given tag, the lower should be the maximum tag burden. However, a common measure of sensitivity that would allow comparison of findings across studies is lacking. Second, setting a maximum allowable tag burden implies a threshold below which there is no effect of the tag. Yet, few studies have been conducted in such a manner so as to quantify the existence of a threshold. Does performance decline continuously in direct proportion to tag burden (Figure 1A)? Or is there a breakpoint in the relationship between tag burden and performance (Figure 1B)? Zale et al. (2005) failed to observe a threshold and showed that swimming stamina and growth of Cutthroat Trout *Oncorhynchus clarkii* declined continuously with increasing tag burden. In contrast, Brown et al. (2010) visually identified a tag burden threshold based on the intersection of growth and survival trend lines of tagged and untagged fish. Hall et al. (2009) used regression classification trees to quantify a tag burden threshold in survival. Beyond these studies, empirical evidence provides little support for either hypothesis because few studies have explicitly tested for the existence of a threshold (also noted by Jepsen et al. 2005).

These considerations were motivated by a study we conducted in 2005 to estimate critical swimming speed ($U_{\text{crit}}$) of seaward-migrating juvenile Chinook Salmon *O. tshawytscha* from the Columbia River. For this study, our primary goals were to (1) identify the tag burden threshold at which $U_{\text{crit}}$ of tagged fish begins to decline relative to untagged fish and (2) measure the additional effect of an external antenna over and above the influence of tag burden. We were then interested in comparing these findings to our past research (Adams et al. 1998b), but direct comparison was hampered by differences in fish size, tag size, tag type, fish source, and environmental conditions between studies. These differences compelled us to develop simple metrics that would allow us to compare findings among studies, species, or populations. Specifically, our goal was to develop two metrics that could be estimated from linear regression analysis: (1) a tag burden threshold and (2) a population’s sensitivity to a transmitter. We then reanalyzed the data from Adams et al. (1998b) and compared thresholds and sensitivities among studies to gain insights about the relative effect of transmitters on these disparate populations.

**METHODS**

Fish collection, tagging, and swimming performance.—Our study was conducted at John Day Dam on the Columbia River, 347 river kilometers from the Pacific Ocean. By conducting the study at John Day Dam, juvenile Chinook Salmon used in our experiment experienced similar handling, tagging, and environmental conditions as fish used in large-scale telemetry studies at dams of the Columbia and Snake rivers. The study was conducted from 27 June to 11 August 2005, and encompassed the 19th to 78th percentile of the seaward migration of subyearling Chinook Salmon passing John Day Dam. We measured critical swimming speeds of three treatment groups: untagged fish, fish surgically implanted with a dummy radio tag, and fish...
surgically implanted with a dummy acoustic tag. Dummy transmitters were supplied by Lotek Engineering (Newmarket, Ontario) (Table 1). In addition to the lack of an antenna, acoustic tags were 0.08 g heavier in air and 0.04 g heavier in water than radio tags (Table 1).

Actively migrating Chinook Salmon were obtained from the juvenile bypass facility at the dam, which samples fish that are diverted away from turbines and around the dam. Fish used in our study were of unknown origin, but consisted of both hatchery-reared and naturally produced salmon emigrating from the Snake and Columbia rivers and their tributaries. Fish were randomly sampled and assigned to one of four size-classes that were based on the tag burden associated with a 0.5-g tag: (1) >6.5% tag burden (<90 mm FL, <7.7 g), (2) 4.5–6.5% tag burden (90–102 mm FL, 7.7–11.1 g), (3) 2.5–4.5% tag burden (102–123 mm FL, 11.1–20.0 g), and (4) <2.5% tag burden (>123 mm FL, >20.0 g). We stratified sampling by size-class to ensure adequate sample sizes over a range of tag burden, but these strata were not included in the analysis. Rather, tag burden was included as a continuous covariate in the analysis. Rather, tag burden was included as a continuous covariate in the analysis. All fish were anesthetized using buffered tricaine methanesulfonate (MS-222) at a dosage of 60 mg/L, and 1 min after losing equilibrium, fish were weighed to the nearest 0.1 g and measured to the nearest 1 mm FL. For tagged fish, transmitters were surgically implanted using methods similar to Adams et al. (1998a), except that the 4-mm incision was closed with two simple interrupted stitches.

Immediately after tagging, each fish was allowed to recover for 10 min in a 19-L bucket containing 7 L of water and supplied with bottled oxygen. Each fish was then held for 19–32 h in a perforated 19-L bucket, which was submerged in an outdoor insulated holding tank (3,100 L) supplied with continuous flow of ambient river water.

Two Blážka-type respirometers with 0.5-hp variable speed motors were used to measure the critical swimming speeds of subyearling Chinook Salmon. The inside diameter of both respirometers was 8.5 cm, but one was slightly shorter (35 cm, volume = 1.65 L) than the other (38.5 cm, volume = 1.95 L). Water velocity of each respirometer was measured using Pitot tubes and Bernoulli’s equation (Vogel 1994) at a range of motor speeds. Water velocity was then related to motor speed with a linear regression equation. After the posttagging recovery period, fish were placed in the respirometer using a water-to-water transfer by gently pouring the contents of a holding bucket into the swimming chamber. Fish were acclimated for 30 min at a water velocity of 2.0 body lengths per second (BL/s). We used the ramp _U_\text{crit} protocol established by Jain et al. (1997) to measure critical swimming speed of juvenile salmon. Under this protocol, water velocities were increased continuously (i.e., “ramped”) at constant rate of 0.18 BL/min from acclimation velocity to approximately 75% of the expected fatigue velocity. After the ramp interval, water velocity was then increased by 0.5 BL/s every 15 min until the fish fatigued, defined as failure to swim after three repeated stimulations by an electrified screen. Critical swimming speed was calculated using the standard formula _U_\text{crit} = _V_\text{p} + \frac{(t_t)}{(t_f)}(_V_\text{r} - _V_\text{p}), where _U_\text{crit} is critical swimming speed measured in centimeters per second, _V_\text{p} is the water velocity at which the fish fatigued, _t_t_ is the amount of time the fish swam at the fatigue velocity, _V_\text{r} is the maximum velocity at which the fish swim the entire interval, and _t_f_ is the prescribed time interval (15 min) for each velocity (Brett 1964).

The expected fatigue velocity was established during preliminary swimming trials conducted before the beginning of the study. For the three smallest size-classes, water velocity was ramped from 2 to 5 BL/s. Because relative _U_\text{crit} (BL/s) typically decreases with increasing fish size (Beamish 1978), the largest size-class was ramped from 2 to 4 BL/s. When water temperature exceeded 22.5 °C during the last 4 d of the study, final ramp velocities were reduced to 4 BL/s and 3 BL/s, respectively, for the three small and the largest size-classes. In practice, final

<table>
<thead>
<tr>
<th>Tag type</th>
<th>M ass in air (g)</th>
<th>M ass in water (g)</th>
<th>Volume (mL)</th>
<th>Density (g/mL)</th>
<th>Antenna length (cm)</th>
<th>Antenna mass in air (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio tag</td>
<td>0.42</td>
<td>0.24</td>
<td>0.18</td>
<td>2.33</td>
<td>18</td>
<td>0.028</td>
</tr>
<tr>
<td>Acoustic tag</td>
<td>0.50</td>
<td>0.28</td>
<td>0.22</td>
<td>2.27</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
ramp velocities averaged 66.8% (SE = 1.0%) of the observed fatigue velocity.

Model development.—To compare swimming performance of tagged fish among different species, populations, or studies, we expressed \( U_{\text{ crit}} \) in terms of the tag effect (\( \delta \)), tag burden threshold (\( \theta \)), and sensitivity to the tag (\( k \); Figure 1B). The effect of a transmitter, \( \delta \), is typically measured as the difference in some performance measure between tagged and untagged fish (Figure 1). To facilitate comparison among populations, we expressed this difference in relative terms and as a function of tag burden:

\[
\delta_B = \frac{U_{\text{crit},B} - U_{\text{crit},0}}{U_{\text{crit},0}}, \tag{1}
\]

where \( \delta_B \) is the proportional change in performance of a tagged fish with tag burden \( B \) (\( U_{\text{crit},B} \)) relative to an untagged fish (\( U_{\text{crit},0} \)). When the tag effect is directly proportional to tag burden (Figure 1A), this difference can be expressed as

\[
\delta_B = k \frac{W_t}{W_r} = kB, \tag{2}
\]

where \( W_t \) is the weight of the tag in air, \( W_r \) is the weight of the fish, \( W_t/W_r = B \) is the tag burden, and \( k \) is the constant of proportionality measuring the percentage change in performance per percentage point increase in tag burden.

In contrast, under the threshold hypothesis (Figure 1B), \( \delta_B \) is zero up to some threshold tag burden, \( \delta \), beyond which the tag’s effect on performance is proportional to the increase in tag burden above the threshold:

\[
\delta_B = \begin{cases} 
  k (B - \theta) & \text{for } B > \theta \\
  0 & \text{otherwise} 
\end{cases},
\]

This formulation is attractive because \( \delta, k, \) and \( \theta \) have an intuitive interpretation and are comparable among populations: \( \theta \) measures the tag burden below which the tag effect disappears, \( k \) characterizes the sensitivity of a given population to a transmitter on a scale relative to the performance of untagged fish, and \( \delta \) measures the relative magnitude of the tag’s effect at different tag burdens. Thus, for two populations with different sensitivities to a transmitter, the population with a larger absolute value of \( k \) will experience a larger change in performance at any given tag burden above the threshold. For example, for a population with \( k = -1 \) and another with \( k = -3 \), both with a 2% tag burden threshold (\( \theta = 0.02 \)), increasing the tag burden from 2% to 7% will reduce performance by 5% and 15%, respectively, for each population. This example shows how different populations or species can have the same tag burden threshold but a different response to the transmitter when the threshold is exceeded. Furthermore, \( k \) and \( \theta \) can be estimated directly from standard linear regression models, allowing performance of tagged fish to be assessed on both absolute and relative scales within a single statistical analysis.

To estimate \( k \), we first expressed the \( U_{\text{crit}} \) of tagged fish as a function of \( U_{\text{crit}} \) for untagged fish by setting equation (1) equal to equation (2) and solving for \( U_{\text{crit},B} \):

\[
U_{\text{crit},B} = U_{\text{crit},0} + U_{\text{crit},0}kB \tag{3}
\]

and

\[
U_{\text{crit},B} = \beta_0 + \beta_1 \frac{W_t}{W_r}, \tag{4}
\]

where \( \beta_0 = U_{\text{crit},0} \) is the intercept and \( \beta_1 = U_{\text{crit},0}k \) is the slope of the regression of \( U_{\text{crit},B} \) on tag burden. Given estimates of the slope and intercept, \( k \) can be estimated as

\[
\hat{k} = \frac{\hat{\beta}_1}{\hat{\beta}_0}, \tag{5}
\]

and its SE obtained using the Delta method (Seber 1982). Here, \( k \) measures the slope of the linear regression in relative units and represents the percentage change in swimming performance of tagged fish relative to untagged fish per 1% increase in tag burden.

To estimate \( \theta \), a treatment effect is included in the regression model,

\[
U_{\text{crit},B} = \beta_0 + \beta_1 \frac{W_t}{W_r} + I_{\text{tagged}}\beta_2, \tag{6}
\]

where \( I_{\text{tagged}} \) is an indicator variable resolving to 1 for tagged fish and 0 for untagged fish, and \( \beta_2 \) estimates the difference in intercepts between tagged and untagged fish. Estimates of \( \beta_2 \) near zero support the hypothesis that the effect of the tag is directly proportional to the tag burden (Figure 1A). In contrast, positive estimates of \( \beta_2 \) support the threshold hypothesis because there will be some nonzero tag burden at which swimming performance of tagged fish equals that of untagged fish (Figure 1B). The threshold can be estimated by setting \( U_{\text{crit},B} = U_{\text{crit},0} \) in equation (6) and solving for tag burden:

\[
\hat{\theta} = \frac{\hat{\beta}_2}{\hat{\beta}_1}. \tag{7}
\]

Alternatively, when data points fall both above and below the threshold, break-point regression models could be used to quantitatively estimate the tag burden threshold (Muggeo 2003).

Data analysis.—We applied the multiple regression model described above to data from the 2005 study, but also included other factors of interest in the model. One goal was to compare swimming performance of fish implanted with an acoustic (lacking an antenna) or radio tag (with an antenna). The presence of an antenna may increase the effect of the tag over and above the influence of tag burden on swimming performance. Furthermore, the effect of the antenna on swimming performance could
increase with decreasing fish size (i.e., increasing tag burden). This process would appear as a difference in slopes between fish with radio tags and those with acoustic tags, which we tested by adding an interaction term between treatment (i.e., no tag, acoustic tag, radio tag) and tag burden to the multiple regression model.

We also included other factors in the model that were not of primary biological interest but might have influenced interpretation of the results. Since we used two respirometers, we included this effect as a class factor in the model. We also included water temperature as a continuous covariate in the model because water temperature is known to affect swimming performance (Brett 1967). Our primary goal was to ensure that these factors did not interact with tag burden or treatment, which could affect interpretation of the primary factors of interest. Therefore, we included all possible two-way interactions in the multiple regression model. Terms in this model were assessed using standard ANOVA techniques. We eliminated all nonsignificant interaction terms and then conducted ANOVA on all remaining terms in the model.

To compare findings from the 2005 study to our previous work (Adams et al. 1998b), we fit the multiple regression model shown in equation (6) to all unique tag groups from the 2005 and 1998 studies. This allowed us to compare \( k, \theta, \delta \) among six unique tag groups from both studies. Briefly, Adams et al. (1998b) measured critical swimming speeds of juvenile Chinook Salmon implanted with 1-g radio tags having a 31-cm antenna. The goal was to compare two tag implantation methods (gastric and surgical) and evaluate short-term (1 d after tagging) versus long-term tag effects (21 d after tagging). Fish used in the 1998 study were of hatchery origin and were larger, on average, than fish in the 2005 study (mean weight = 23.3 g, range = 9.6–44.7 g). Further details on this study can be found in Adams et al. (1998b).

Our model assumes \( U_{\text{crit}} \) of untagged fish is constant with respect to mass \( (w) \) because \( k \) is estimated from the mean \( U_{\text{crit}} \) of untagged fish (see Figure 1 and equations 4 and 5). For the 2005 study, we found no significant relationship between \( U_{\text{crit}} \) and mass of untagged fish (slope = 0.19 cm s\(^{-1}\) g\(^{-1}\), \( F_{1,53} = 0.44, P = 0.51 \)). Similarly for the 1998 study, we found no significant relationship between \( U_{\text{crit}} \) and mass of untagged fish (for the 1-d group: slope = 0.17 cm s\(^{-1}\) g\(^{-1}\), \( F_{1,42} = 3.17, P = 0.08 \); for the 21-d group: slope = 0.07 cm s\(^{-1}\) g\(^{-1}\), \( F_{1,46} = 0.41, P = 0.52 \)). Although absolute \( U_{\text{crit}} \) typically increases with fish size (Beamish 1978), our findings indicate that \( U_{\text{crit}} \) of untagged fish changed little with size, probably due to the relatively small range in fish size.

**RESULTS**

**The 2005 Study**

We observed considerable variation in swimming performance among individuals, with \( U_{\text{crit}} \) ranging from 44.6 to 98.4 cm/s (3.6–10.8 BL/s; Figure 2A, B). Although substantial variation remained unexplained \( (R^2 = 0.226) \), we found a significant effect of tag burden on \( U_{\text{crit}} \) \( (F_{1,161} = 33.97, P \leq 0.0001) \). The intercepts for radio- and acoustic-tagged fish were not significantly different from the mean \( U_{\text{crit}} \) of untagged fish \( (F_{1,161} = 0.49, P = 0.612) \), providing little evidence for a tag burden threshold (Figure 2A, B). Furthermore, we found no significant difference in slopes between radio- and acoustic-tagged fish \( (F_{1,153} = 0.30, P = 0.585) \), suggesting no detectable effect of the antenna. None of the other interaction terms were statistically significant. For the remaining effects in the model, we found no significant difference in \( U_{\text{crit}} \) between respirometers \( (F_{1,161} = 0.49, P = 0.851) \). We found a significant effect of water temperature on \( U_{\text{crit}} \) \( (F_{1,161} = 0.03, P = 0.046) \), but the effect was small \( (1.1 \text{ cm s}^{-1} \text{°C}^{-1}) \), explained little variation \( (\text{partial } r^2 = 0.020) \), and did not interact with any other variable.

Parameter estimates from the multiple regression model applied to each tag group (equation 6) provided insight into the magnitude of the tag’s effect on \( U_{\text{crit}} \). The intercept term, \( \beta_0 \), estimated a mean \( U_{\text{crit}} \) of 73.8 cm/s (7.0 BL/s) for untagged fish (Table 2; Figure 2A, B). The estimated tag burden threshold \( (\delta) \) was close to zero for both tag types, indicating that the decline in swimming performance was directly proportional to tag burden (Table 2). The slope terms for tag burden \( (\beta_1) \) were negative for both acoustic-- and radio-tagged fish, showing that \( U_{\text{crit}} \) declined with increasing tag burden (Table 2; Figure 2A, B). Although the slopes were not significantly different due to high variation among individuals, the magnitude of the slope for radio-tagged fish \( (−2.6 \text{ cm/s per 1% tag burden}) \) was larger than for acoustic tagged fish \( (−2.1 \text{ cm/s per 1% tag burden}) \). These findings provide some empirical evidence that the radio tag might have had a larger negative effect on swimming performance (Table 2; Figure 2). Expressed relative to untagged fish, estimates of \( k \) show that \( U_{\text{crit}} \) declined by 3.58% for each 1% increase in tag burden for radio-tagged fish and by 2.88% per 1% tag burden for acoustic-tagged fish, suggesting higher sensitivity of fish to the radio tag (Table 2).

High variability in \( U_{\text{crit}} \) might have led to low statistical power to detect a tag burden threshold or a difference in slopes of radio- and acoustic-tagged fish. Therefore, we used a parametric bootstrap procedure (Efron and Tibshirani 1993) to determine the effect size needed to yield 80% power. Our analysis had 80% power to detect a 5-cm/s difference between the intercepts of tagged and untagged fish, which translates to a 1.9% tag burden threshold for radio-tagged fish and a 2.3% tag burden threshold for acoustic-tagged fish (i.e., \( \delta = 0.019 \) and 0.023, respectively). Thus, we had high statistical power to detect a relatively small tag burden threshold, lending further support to our finding that the tag’s effect on \( U_{\text{crit}} \) was directly proportional to tag burden. In contrast, to detect a difference in slopes between radio- and acoustic-tagged fish with 80% power, we found that the antenna would have had to reduce the slope by an additional 1.35 cm/s per 1% tag burden. In other words, the antenna effect would have had to account for 40% of the total tag effect to have a high probability of detecting the additional effect of the antenna over
FIGURE 2. Critical swimming speed as a function of tag burden for six treatment groups of juvenile Chinook Salmon from two studies. Treatment groups are labeled by tag implantation method (surgical or gastric), postimplantation recovery time (1 or 21 d), and type of dummy transmitter (acoustic or radio tag). The horizontal line shows the mean $U_{\text{crit}}$ of untagged fish, the heavy line shows the regression fit to tagged fish (projected to the origin) and thin lines about the regression line display 95% CIs.
and above the effect of tag burden. We observed that the slope for radio-tagged fish was 0.52 cm/s per 1% tag burden less than that for acoustic-tagged fish, indicating the antenna comprised about 20% of the total tag effect. Although the difference in slopes is in the direction expected based on findings of Murchie et al. (2004), we had insufficient statistical power to detect such a difference.

Reanalysis of Adams et al. (1998b)

Critical swimming speed measured by Adams et al. (1998b) was considerably lower and less variable than in the 2005 study, but the relationship between \( U_{\text{crit}} \) and tag burden was similar between studies (Figure 2). The mean \( U_{\text{crit}} \) of untagged fish (\( \beta_0 \)) averaged 51.8 cm/s (4.1 BL/s) and 51.5 cm/s (4.2 BL/s) for the 1-d and 21-d groups, respectively (Figure 2C-F; Table 2). The slopes for all groups were significantly less than zero, indicating that \( U_{\text{crit}} \) declined with increasing tag burden (\( F_{1, \geq 80} \geq 22.2, P < 0.0001; \) Table 2). Furthermore, for three of the four groups, the intercept of tagged fish (\( \beta_1 \)) was not significantly different from the mean \( U_{\text{crit}} \) of untagged fish (\( F_{1, \geq 80} \leq 1.8, P > 0.188 \)), providing little evidence for a tag burden threshold. For gastrically tagged fish in the 21-d group, the intercept for tagged fish was significantly different than the mean \( U_{\text{crit}} \) of untagged fish at a significance level of \( \alpha = 0.10 \), but not at \( \alpha = 0.05 \) (\( F_{1, 83} = 3.96, P = 0.05002 \)).

Comparing the 2005 Study to Adams et al. (1998b)

Direct comparison of regression slopes between studies is hampered by differences in baseline \( U_{\text{crit}} \) of untagged fish in each study. For example, the estimated slope for gastrically tagged fish with a 1-d recovery period (−2.11 cm/s per 1% tag burden) was nearly identical to the slope for acoustic-tagged fish (−2.12 cm/s per 1% tag burden; Table 2). Although their absolute response to tag burden was similar, their response relative to untagged fish differed because untagged fish from the Adams et al. (1998b) study had considerably lower \( U_{\text{crit}} \) than did the 2005 study. Estimates of sensitivity (\( k \)) showed that \( U_{\text{crit}} \) of gastrically tagged fish with a 1-d recovery period declined by 4.08% for each 1% increase in tag burden, whereas \( U_{\text{crit}} \) of acoustic-tagged fish from the 2005 study declined by only 2.88% per 1% tag burden. This example illustrates how expressing the change in performance relative to untagged fish allows tag effects to be compared across studies.

Across all treatment groups, gastrically tagged fish showed higher sensitivity to the transmitter than did surgically tagged fish from both studies, although confidence intervals for all groups overlapped (Table 2). These findings suggested that swimming performance of gastrically tagged fish declined more quickly as tag burden increased, compared with surgically tagged fish. Estimates of \( k \) for surgically tagged groups ranged from −2.68% to −3.58% per 1% increase in tag burden, whereas for gastrically tagged fish, \( k \) ranged from −4.08% to −4.86% per 1% tag burden. In addition, for Adams et al. (1998b), the magnitude of \( k \) decreased with recovery time for surgically tagged fish, but increased with recovery time for gastrically tagged fish (Table 2). Estimates of the tag burden threshold (\( \theta \)) were close to zero or slightly positive in both studies. All estimates of tag burden threshold were \( \leq 2.1% \), indicating that swimming performance began to decline at relatively low tag burdens.

By using estimates of both \( k \) and \( \theta \), the mean proportional decline in swimming performance as a function of tag burden (i.e., \( \beta_2 \) in equation 3) can be compared across studies. The decline in swimming performance ranged from 0% to 7.5% for a 2% tag burden, from 9% to 17% for a 5% tag burden, and from 17% to 29% for an 8% tag burden (Figure 3). Gastrically tagged fish had both the highest tag burden threshold and the highest sensitivity to the tag (Figure 3, lines E and F). Consequently, at a 2% tag burden, gastrically tagged fish showed the least decline in swimming performance among groups, but they showed the largest decline in performance when tag burden exceeded 8% because \( \beta_2 \) declined more quickly with tag burden than it did in the other groups. Over the range in tag burden, the lowest tag effect occurred for the radio-tagged fish with a 21-d recovery period in the Adams et al. (1998b) study (Figure 3, line D), whereas the largest tag effect occurred for the radio-tagged fish with a 1-d recovery period in the Adams et al. (1998b) study (Figure 3, line C). For these groups, sensitivity was similar, but tag burden thresholds differed such that \( \beta_0 \) for the 21-d

<table>
<thead>
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<th>Study</th>
<th>Tag type</th>
<th>Recovery time (d)</th>
<th>Method</th>
<th>Parameter</th>
<th>( n )</th>
<th>( \beta_0 )</th>
<th>( \beta_1 )</th>
<th>( \beta_2 )</th>
<th>( k )</th>
<th>( \theta )</th>
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<td>Surgical</td>
<td>Parameter</td>
<td>111</td>
<td>73.8 (71.1, 76.6)</td>
<td>−263.9 (−454.8, −73.1)</td>
<td>1.6 (−6.0, 9.2)</td>
<td>−3.58 (−6.16, −0.99)</td>
<td>−0.006 (−0.021, 0.033)</td>
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<tr>
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<td>Acoustic</td>
<td>1</td>
<td>Surgical</td>
<td>Parameter</td>
<td>112</td>
<td>73.8 (70.9, 76.7)</td>
<td>−212.3 (−374.0, −50.5)</td>
<td>1.5 (−6.4, 9.4)</td>
<td>−2.88 (−5.07, −0.68)</td>
<td>0.007 (−0.028, 0.042)</td>
</tr>
<tr>
<td>1998</td>
<td>Radio</td>
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<td>Surgical</td>
<td>Parameter</td>
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<td>51.8 (50.2, 53.4)</td>
<td>−163.5 (−282.5, −44.6)</td>
<td>−0.6 (−6.1, 5.0)</td>
<td>−3.16 (−5.46, −0.86)</td>
<td>−0.003 (−0.035, 0.028)</td>
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<tr>
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<td>Radio</td>
<td>21</td>
<td>Surgical</td>
<td>Parameter</td>
<td>83</td>
<td>51.5 (49.9, 53.0)</td>
<td>−138.2 (−255.3, −21.0)</td>
<td>2.2 (−4.5, 8.8)</td>
<td>−2.68 (−4.96, −0.41)</td>
<td>0.016 (−0.030, 0.061)</td>
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<tr>
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<td>Radio</td>
<td>1</td>
<td>Gastric</td>
<td>Parameter</td>
<td>84</td>
<td>51.8 (50.3, 53.3)</td>
<td>−211.1 (−316.6, −105.6)</td>
<td>3.6 (−1.7, 8.9)</td>
<td>−4.08 (−6.12, −2.04)</td>
<td>0.017 (−0.009, 0.043)</td>
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<tr>
<td>1998</td>
<td>Radio</td>
<td>21</td>
<td>Gastric</td>
<td>Parameter</td>
<td>86</td>
<td>51.5 (50.2, 52.8)</td>
<td>−250.3 (−336.8, −163.9)</td>
<td>5.2 (0.1, 10.3)</td>
<td>−4.86 (−6.55, −3.18)</td>
<td>0.021 (−0.001, 0.042)</td>
</tr>
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</table>

TABLE 2. Parameter estimates (95% CI) for the regression model describing the effect of tag burden on \( U_{\text{crit}} \) for six treatment groups of juvenile Chinook Salmon from two studies. Parameter definitions are: \( \beta_0 \) = mean \( U_{\text{crit}} \) of untagged fish, \( \beta_1 \) = slope of \( U_{\text{crit}} \) on tag burden for tagged fish, \( \beta_2 \) = difference in intercepts between tagged and untagged fish, \( k \) = sensitivity of fish to the tag estimated as the percentage change in \( U_{\text{crit}} \) per percentage point increase in tag burden, \( \theta \) = tag burden threshold below which \( U_{\text{crit}} \) of tagged fish is the same as untagged fish. \( \beta_1 \) has units of cm/s per unit increase in tag burden, whereas \( \beta_2/100 \) has units of cm/s per 0.01 increase in tag burden.
recovery group was consistently 7–9 percentage points less than that for the 1-d recovery group over the range of tag burden (Table 2; Figure 3). Our findings illustrate how \( k \), \( \theta \), and \( \delta_B \) provide useful metrics for comparing the effects of transmitters among disparate species, populations, or studies.

**DISCUSSION**

Most controlled laboratory studies investigating tag effects have been narrowly focused on a particular species, population, size range of fish, transmitter configuration, implantation procedure, or performance metric. While the intent of such studies is to provide information to guide specific field applications of telemetry, such narrow focus makes direct comparison across studies difficult. We encountered just this dilemma when we studied difficult. We encountered just this dilemma when we

![Figure 3: Proportional change in swimming performance of tagged juvenile Chinook Salmon relative to untagged fish as a function of tag burden for six treatment groups from two studies. Lines (A) and (B) are for a study conducted in 2005 and analyzed in this paper. Lines (C) and (F) are from a reanalysis of Adams et al. (1998b).](image)

We observed that \( U_{\text{crit}} \) of radio-tagged fish declined more quickly with tag burden (\( k = -3.58\% \) per 1% tag burden) than \( U_{\text{crit}} \) of acoustic-tagged fish (\( k = -2.88\% \) per 1% tag burden; Table 2). Although not statistically significant, this difference was the direction expected based on the added drag of an external antenna. In our study, the difference in fish sensitivity to the radio and acoustic tag suggests that the antenna comprised about 20% of the total tag effect. In other studies, the magnitude of an antenna’s effect on swimming performance will depend on its mass per unit length and its total length, which together will influence the relative antenna size with respect to the tag and fish. For example, Murchie et al. (2004) found that \( U_{\text{crit}} \) decreased by 0.68% for every 1-cm increase in antenna length for Rainbow Trout \( O. \) mykiss having a mean tag burden of 2.2%. However, Murchie et al. (2004) used antenna material that weighed 0.254 g per 30 cm of length, whereas the antenna material used in our study weighed only 0.047 g per 30 cm, about one-fifth that used by Murchie et al. (2004). Equating tagging parameters between studies, an 18-cm antenna at a 2.2% tag burden was expected to reduce \( U_{\text{crit}} \) by 12.2% in Murchie et al.’s (2004) study and by 7.9% in our 2005 study. Thus, the smaller antenna effect observed in our study is consistent with a lighter antenna material that comprised a smaller fraction of the tag’s mass. Although minimizing an antenna’s length and mass reduces its effect on swimming performance, other negative effects of external antennas such as antenna tangling (Adams et al. 1998b; Murchie et al. 2004), antenna fouling (Thorstad et al. 2001), and wound healing at the antenna exit location (Bauer and Loupal 2007) should also be considered when assessing the effect of radio tags versus acoustic tags.

We observed considerable variation in swimming performance among individuals in our 2005 study. Variation was induced by a negative relationship between ambient water temperature and \( U_{\text{crit}} \), but temperature explained only a small fraction of the total variation. Population-level variability in swimming performance is a more likely explanation for high variation observed in our 2005 study. Fish collected for this study originated from a number of natal tributaries in the Columbia and Snake rivers. Furthermore, both hatchery- and wild-origin fish were used in our study because it was not always possible to distinguish hatchery from wild fish based on visual marks alone (e.g., a clipped adipose fin). Intraspecific variation in swimming performance can be influenced by rearing origin (i.e., hatchery versus wild; Peake et al. 1997; Pedersen et al. 2008) and mean water velocity of home streams (Nelson et al. 2003, 2008; Williamson et al. 2012). These factors probably contributed to variation in \( U_{\text{crit}} \) since individuals in our study originated from numerous unknown source populations. In contrast, fish used in Adams et al. (1998b) came from a single source population and were reared in circular tanks under uniform conditions, probably contributing to low variability among individuals relative to the 2005 study. Our findings indicate that variability in effects of transmitters on wild populations of fish is probably underappreciated (but see Zale et al. 2005 for a discussion of this topic).
Mean $U_{\text{crit}}$ of untagged fish in our 2005 study (7.0 BL/s) was substantially higher than that observed in other studies measuring swimming performance of juvenile Chinook Salmon (4.0–4.5 BL/s: Adams et al. 1998b; Anglea et al. 2004; Brown et al. 2006). The most likely explanation is that exercise training differed among studies and affected swimming performance. Our study was conducted using actively migrating juvenile salmon that were tested soon after capture, under ambient environmental conditions. These fish could have migrated up to 500 km from natal tributaries or hatcheries, which represents a considerable exercise training regimen that likely improved their endurance swimming ability (Davison 1997; Nelson et al. 2008). In contrast, fish from the other studies were probably less physically fit because they were either reared or held in tanks for an extended period prior to study. Although Brown et al. (2006) collected fish from the upper Columbia River at Rocky Reach Dam, swimming performance could have declined over time because fish were held in captivity for 2.5–4.5 weeks before testing. For example, Nelson et al. (2008) showed that swimming performance of Blacknose Dace Rhinichthys atratulus declined over time when fish collected from streams were held under low-velocity conditions in tanks.

Although $U_{\text{crit}}$ in our 2005 study was higher than observed in other studies, estimates of $k$ allowed us to directly compare findings to our previous work. For surgically tagged fish, sensitivity varied relatively little between studies, with $k$ ranging from −2.68% to −3.58% per 1% increase in tag burden. Some of this variation was likely due to differences in the antenna and recovery time among surgical treatment groups. In contrast, gastrically tagged fish showed higher sensitivity, with $k$ ranging from −4.08% to −4.86% per 1% increase in tag burden. Gastrically tagged fish might have been more sensitive because the antenna trailed from the mouth, alongside the fish. In contrast, for surgically tagged fish, the antenna exited the posterior end of the body cavity and was more aligned with the longitudinal axis of the fish. These findings provide new insights about the how the method of implantation can affect swimming performance of fish with radio tags.

In our 2005 study, we were also concerned that posttagging handling stress due to a short recovery period (1 d) could have lowered $U_{\text{crit}}$, resulting in an estimated tag-burden threshold near zero. Reanalysis of A dams et al. (1998b) provided some support for this hypothesis. Estimates of $\delta$ were near zero for surgically tagged fish tested 1 d after tagging, but increased to 1.6% for fish tested 21 d after tagging, causing $U_{\text{crit}}$ to be seven to nine percentage points higher across the range of tag burden (Figure 3, lines C and D). For gastrically tagged fish, in which the implantation procedure was less invasive and required less handling, recovery time appeared to have less influence on $\delta$ (Table 2). These findings indicate that handling effects might have reduced $U_{\text{crit}}$ of surgically tagged fish 1 d after tagging, leading to lower threshold estimates relative to those in other treatment groups.

We were surprised to find weak evidence for a tag burden threshold, given findings of other studies that have evaluated swimming performance of tagged juvenile Chinook Salmon (Adams et al. 1998b; Anglea et al. 2004; Brown et al. 2006). In our study, all estimates of a threshold were <2.1% and none were significantly different from zero despite having sufficient statistical power to detect a threshold. With respect to tag burden effects on swimming performance, each of the other studies implied an acceptable range of tag burden based on lack of significance in mean $U_{\text{crit}}$ among treatment groups: 3.2–10.0% for Brown et al. (2006), 1.6–6.7% for Anglea et al. (2004), and 2.2–5.6% for Adams et al. (1998b). However, none of these studies explicitly included tag burden as a covariate in statistical analyses, making it impossible to quantify a tag burden threshold at which performance begins to decline. For example, Adams et al. (1998b) found no significant difference in mean $U_{\text{crit}}$ between untagged and surgically tagged fish that were >120 mm FL (2.2–5.6% tag burden), 21 d after tagging. In contrast, when we explicitly included tag burden as a covariate, our reanalysis of their data estimated that $U_{\text{crit}}$ for this treatment group declined from 1.6% to 10.7% relative to untagged fish as tag burden increased from 2.2% to 5.6% (Figure 3, line D).

Telemetry field studies often establish minimum fish-size or tag-size criteria for tagging by setting an upper limit on tag burden (Liedtke and Wargo-Rub 2012). Our findings illustrate how such tag burden limits may be overly optimistic if they are based solely on inferences drawn from performance metrics that have been averaged over the range of tag burden. Instead, our analysis explicitly quantified how swimming performance declined with tag burden, providing information necessary for establishing tag burden limits. Zale et al. (2005) drew similar conclusions. They found that growth and swimming stamina of Cutthroat Trout declined continuously with tag burden despite a lack of significant differences in mean performance metrics between tagged and untagged groups. Furthermore, they found no obvious tag burden threshold above which performance declined sharply. Given a lack of a clear threshold in their study and ours, we suggest that tag burden limits be based on “acceptable” declines in laboratory performance metrics that would be unlikely to affect biological inferences drawn from field studies. For example, in our study, a 5% decline in swimming performance was associated with a tag burden ranging from 1.2% to 3.4%, depending on treatment group, whereas a 10% decline corresponded to tag burden ranging from 2.8% to 5.3% (Figure 3). Such an approach would allow each study to better weigh the costs of increasing tag burden against the benefit of information gained using telemetry techniques.

In the absence of a threshold in swimming performance (i.e., $\delta = 0$), $k$ provides a single measure that quantifies the magnitude of the tag’s effect and is comparable across different populations, species, and studies. Two populations with the same value of $k$ will have the same relative response to the transmitter (i.e., the same $\delta$) at any given tag burden regardless of differences in tag size or fish size between the populations. In contrast, a population with a higher absolute value of $k$ will be more sensitive to the transmitter, resulting in a larger relative effect of the transmitter at any given burden (i.e., larger $\delta$; Figure 3). In our
analysis, k ranged from $-2.86\%$ to $-4.86\%$ per 1% increase in tag burden, with the magnitude of k varying due to the presence of an antenna, the method of tag implantation, and posttagging recovery time. The sensitivity of a given study population to a transmitter depends on factors such as environmental conditions, fish morphology, life stage, habitat preference, rearing history, and tag design. Such factors have, in part, driven variability in recommendations for maximum tag burden among studies. However, few generalities have arisen about the relation between tag burden and performance of a given population, how such relations differ among populations, and how these differences affect maximum allowable tag burdens. Our approach can be used to gain insights across populations to better understand factors that influence the ability of fish to carry a transmitter.

Our analysis showed how a tag burden threshold and the sensitivity to the transmitter can be estimated from standard linear regression analysis. These parameters form the basis for comparing findings among disparate populations or studies. We selected $U_{critical}$ because it is a convenient index of physiological performance that is commonly used to assess effects of transmitters (Adams et al. 1998b; Brown et al. 1999, 2006; Robertson et al. 2003; Anglea et al. 2004; LaCroix et al. 2004; Murchie et al. 2004; Chittenden et al. 2009). We recognize, however, that other performance measures (e.g., respiration, growth, or survival rates) may exhibit a different relationship with tag burden. Indeed, a suite of performance measures is often used for establishing upper limits of tag burden (e.g., Chittenden et al. 2009). Toward this end, our analytical techniques could be applied to many physiological performance measures to estimate a tag burden threshold and sensitivity to the transmitter. The ability to directly compare findings across studies for a suite of performance measures would improve our understanding of transmitter effects on fish.

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Trophic Niche and Diet Overlap between Invasive White Perch and Resident White Bass in a Southeastern Reservoir

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NOTE

Trophic Niche and Diet Overlap between Invasive White Perch and Resident White Bass in a Southeastern Reservoir

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Abstract

The White Bass Morone chrysops is a popular sport fish that appears to be negatively affected by invasions of White Perch M. americana and often declines or disappears from invaded systems. In 2008, the first discovery of White Perch in Lake James, North Carolina, provided a rare opportunity to investigate trophic overlap between White Perch and a robust population of White Bass near the onset of invasion. We investigated the potential for resource competition between White Perch and White Bass by assessing their relative abundance (CPUE), trophic position, niche size, diet breadth, and diet overlap across 2 years. White Perch were more abundant than White Bass and had wider diet breadth and trophic niche size across seasons. White Perch also occupied lower trophic positions than White Bass, indicating that White Bass maintain a more piscivorous diet. However, diet and stable isotope analysis showed a high overlap between juvenile White Bass and all sizes of White Perch. Thus, juvenile White Bass may be susceptible to competition with White Perch where resources are limited. Therefore, biologists should take steps to prevent White Perch introductions into systems with popular White Bass fisheries.

The White Perch Morone americana is a highly successful invasive species in lakes and reservoirs across the United States (Zuerlein 1981; Boileau 1985; Feiner et al. 2012), and White Perch invasions have been associated with declines in many native species (Hergenrader and Bliss 1971; Hurley and Christie 1977). The White Bass M. chrysops is a popular sport fish that appears to be especially affected by White Perch invasions, often declining or disappearing from invaded systems (e.g., Gopalan et al. 1998; Madenjian et al. 2000; Harris 2006). White Bass and White Perch rely on similar food resources throughout their ontogeny (Priegel 1970; Voigtlander and Wissing 1974; Prout et al. 1990; Wong 2002), although White Bass become primarily piscivorous as adults (Muth and Busch 1989; Hartman 1998) while adult White Perch continue to consume some zooplankton and benthic invertebrates (Gopalan et al. 1998; Wong 2002; Harris 2006). Previous studies have found moderate to high diet overlap between White Perch and juvenile White Bass (Gopalan et al. 1998; Madenjian et al. 2000; Kuklinski 2007). We suggest, therefore, that interspecific competition for resources may be driving White Bass declines in invaded systems.

Recently, two North Carolina reservoirs, Lake Norman and Lake Hickory, experienced drastic declines in formerly abundant White Bass populations in the years following unintentional White Perch introductions (K. J. Hining, NCWRC, and B. J. McRae, NCWRC, personal communications) causing concern among biologists about the potential for declines in other systems. During routine North Carolina Wildlife Resources Commission (NCWRC) sampling in 2008, 35 White Perch were captured in Lake James, North Carolina. Subsequent sampling...
revealed that the White Perch population had probably been introduced circa 2005, only 3 years prior to their detection (Feiner et al. 2012). Before 2005, Lake James supported a large, recreationally popular fishery for White Bass stemming from an original stocking event in 1961 (Besler et al. 2004; Yow 2005). The early detection of White Perch in Lake James gave us a unique opportunity to study the trophic interactions of White Perch and White Bass near the onset of invasion and collect information that is lacking in the literature to date. This study sought to determine the potential for resource competition between resident White Bass and newly introduced White Perch. Specifically, we (1) described the current population characteristics of White Perch and White Bass, including relative abundance and diet, and (2) determined the degree of diet and niche overlap between these two fish species throughout their ontogeny. Studying these interactions early in the invasion allowed us to gain clearer insights into the potential effects of White Perch on White Bass before the bass population declined or their trophic status changed in response to potential competitive interactions (sensu Connell 1980).

METHODS

Field sampling.—Lake James is an oligotrophic 2,634-ha reservoir that was impounded in 1923 by Duke Power Company. The lake has 242 km of shoreline, a mean depth of 13.5 m, and a maximum depth of 43 m (Besler and Taylor 2002; NCDENR 2008). White Perch and White Bass were collected for analyses from Lake James by a combination of electrofishing, nearshore gill nets, and offshore gill nets in April, July, and October 2009, and in April and July 2010 (see Feiner et al. 2012, 2013 for details). Each species was separated into three size bins based on length frequency analysis of previous data: small (<120 mm TL White Perch and <150 mm TL White Bass), medium (121–180 mm TL White Perch and 151–300 mm TL White Bass), and large (>180 mm TL White Perch and >300 mm TL White Bass). The relative abundances of White Perch and White Bass were estimated by calculating the CPUE as fish captured per electrofishing-minute or fish caught per net-night. Fish used for stable isotope analysis were all collected in July 2010. At each site, benthic invertebrates, including chironomid and ceratopogonid larvae, were collected to serve as the benthic baseline for stable isotope analysis using a Ponar dredge, and filter-feeding Asian clams Corbicula spp. were collected by hand to serve as the pelagic baseline.

Diet and stable isotope analysis.—Diet composition was quantified using methods described in Feiner et al. (2013). Diet items were grouped into categories based on location in the water column, size, and importance in the diet; categories were: zooplankton, benthic invertebrates, Diptera pupae, Chaoborus larvae, crayfish, fish, terrestrial invertebrates, and “other” (rare or nonfood items). Diet overlap was assessed among species and size-classes with Schoener’s index (Schoener 1968; Wallace 1981), calculated as

\[ D = 1 - 0.5 \left( \sum_{i=1}^{s} |X_i - Y_i| \right), \]  

where \( D \) is the level of overlap from 0 to 1, \( S \) the number of food categories, \( X_i \) the average percent weight (%W) of diet category \( i \) in the diets of species size-class \( X \), and \( Y_i \) the %W of diet item \( i \) in species size-class \( Y \). Overlap was considered ecologically significant when \( D \) was greater than 0.6 (Wallace 1981). Diet breadth was evaluated using Levin’s index (Levin 1968, standardized by Hurlbert 1978) as follows:

\[ B = \frac{1}{S-1} \left( \frac{1}{\sum_{i=1}^{5} X_i^2} - 1 \right), \]  

where \( B \) is a measure of diet breadth from 0 to 1 for species \( X \), \( S \) is the number of prey categories, and \( X_i \) is the %W of prey item \( i \) in species \( X \).

Diet, while useful for elucidating seasonal and ontogenetic diet shifts (e.g., Ginter et al. 2011), only represent a “snapshot” of resource use due to their fast turnover rate (6–12 h in White Perch; Parrish and Margraf 1990). Therefore, stable isotopes were used to corroborate the results of the diet analysis. Naturally occurring stable isotope ratios of carbon (\( \delta^{13}C \), representing benthic versus pelagic sources: France 1995) and nitrogen (\( \delta^{15}N \), representing relative trophic position: Fry 2006) have been widely used in aquatic ecology to study the effects of introduced species on native food webs (e.g., Vander Zanden et al. 1999) and provide a space- and time-integrated view of that consumer’s dietary resources (Perga and Gerdeau 2005; but see Guzzo et al. 2011). All stable isotope samples were prepared and processed at the Cornell Stable Isotope Laboratory, Ithaca, New York (for details see Feiner et al. 2013). The \( \delta^{13}C \) values of each fish were normalized for differing lipid content (Post 2002), and trophic position of each species size-class was determined using a two-member mixing model (Vander Zanden et al. 1999) assuming no trophic fractionation of \( \delta^{13}C \) (Post 2002; Vander Zanden and Vadeboncoeur 2002). Differences in \( \delta^{13}C \), \( \delta^{15}N \), and trophic position among species and size-classes were statistically evaluated using Kruskal–Wallace tests because our data were not normally distributed. Pairwise differences were determined using M ann–Whitney U -tests with Bonferroni-adjusted P -values.

The structure of each population’s trophic niche was evaluated using \( \delta^{13}C - \delta^{15}N \) biplots and six metrics (Layman et al. 2007), each bootstrapped 10,000 times: \( \delta^{13}C \) range (CR), represents the extent of basal resources used by a species; \( \delta^{15}N \) range (NR) indicates the ability of a species to forage at different levels of the food web; mean distance to centroid (CD) indicates the level of trophic diversity of the population; standard deviation of nearest neighbor distance (SDNND) represents the level of trophic evenness; and mean nearest neighbor
distance (MNNDb) indicates the spread or clustering of individuals in niche space (see Jackson et al. 2011 for detailed methodology). Niche size and the amount of pairwise niche overlap were quantified by determining the standard ellipse area corrected for small sample size (SEAc) for each species and size-class (Jackson et al. 2011, 2012). Differences in niche size were evaluated using Bayesian inference to estimate the posterior distribution of the standard ellipse area (SEAB; Jackson et al. 2011, 2012). All analyses were run in statistical package R (R Core Team 2012), and stable isotope niche metrics were evaluated using the statistical package siar in R (Parnell and Jackson 2011).

RESULTS

Relative Abundance

White Perch CPUE via shoreline electrofishing was higher than White Bass CPUE in every season sampled (Figure 1). In the nearshore gill nets, White Perch were more abundant than White Bass in summer 2009 and spring and summer 2010, and White Bass were more abundant in spring and fall 2009 (Figure 1). Except for White Perch in summers of 2009 and 2010, catch was generally very low in the offshore gill nets, and there were no strong trends in the abundances of either species in those samples (Figure 1).

Diet Composition and Overlap

In spring, summer, and fall 2009, all sizes of White Perch and small White Bass fed mostly on Diptera pupae and benthic invertebrates, leading to high levels of diet overlap in all comparisons (Table 1; Figure 2). Medium and large White Bass also ate Diptera pupae and significantly overlapped with White Perch in spring 2009, but switched to piscivory in summer and fall, leading to low overlap values. Not enough White Bass were caught in spring 2010 to reliably assess diet composition and overlap. In summer 2010, all size-classes of White Perch consumed mostly invertebrates (though large White Perch also consumed 36% fish), while all sizes of White Bass were almost completely piscivorous, resulting in no significant diet overlap (Table 1; Figure 2). White Perch generally had higher diet breadth than did White Bass in fall 2009 and summer 2010, while White Bass had higher diet breadth in spring 2009 (Figure 3). Medium and large White Perch exhibited the widest diet breadth across seasons, while medium and large White Bass exhibited among the smallest diet breadths due to their near-exclusive piscivory in summer and fall. Diet breadth for both small White Perch and White Bass was generally low and seasonally variable.

Stable Isotope Analysis

Stable isotope analysis revealed that White Perch and White Bass in Lake James occupied slightly different trophic positions throughout their ontogeny and within the fish community (Table 2; Figure 4). There were significant differences among species in δ13C, δ15N, and trophic position (Kruskal–Wallis test: χ² = 26.06, 41.73, and 34.84, respectively; P < 0.001 for all three tests). Small White Perch were heavily reliant on benthic resources compared with the other species and size-classes and were significantly enriched in δ13C relative to medium White Bass (Mann–Whitney U-test: P = 0.011), large White Bass (P = 0.006), and large White Perch (P = 0.008; Table 2). All other species and size-classes appeared to use relatively similar proportions of benthic and pelagic food sources (Figure 4). In contrast, White Bass appeared to feed at a slightly higher trophic position than all sizes of White Perch throughout their ontogeny (Table 2; Figure 4). Small (P ≤ 0.008) and medium (P ≤ 0.50) White Perch δ15N values were significantly depleted compared with those for all sizes of White Bass, whereas large
**White Perch** $\delta^{15}N$ values were lower than those of medium ($P = 0.041$) and large White Bass ($P = 0.011$). Within species, there was no difference in the $\delta^{15}N$ values of White Bass ($P \geq 0.177$), while small White Perch had lower $\delta^{15}N$ values than large White Perch ($P = 0.002$). These differences largely translated to differences in trophic position between species. Small White Perch fed at a significantly lower trophic position than all sizes of White Bass ($P \leq 0.011$), while medium ($P = 0.014$) and large ($P = 0.011$) White Perch were at a lower trophic position than large White Bass. Within species, there were no differences in White Bass ($P \geq 0.177$) or White Perch ($P \geq 0.119$) trophic positions (Table 2).

Standard ellipse areas indicated that White Perch generally exploit a larger niche than White Bass throughout their ontogeny (Table 2; Figure 4). Medium White Perch had a much larger SEA$_c$ than any other species or size-class, while White Bass
TABLE 1. Schoener's index (D) of diet overlap between small, medium, and large White Perch (<120, 121–180, and >180 mm TL) and White Bass (<150, 151–300, and >300 mm TL) across seasons in Lake James, North Carolina. Values in bold italic text indicate ecologically significant overlap (D > 0.60). Dashes (-) indicate sample sizes for each season and size-class that were deemed inadequate for calculation of Schoener's index.

<table>
<thead>
<tr>
<th>Species and size-class</th>
<th>Small White Perch</th>
<th>Medium White Perch</th>
<th>Large White Perch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring 2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small White Perch</td>
<td>0.61</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>Medium White Perch</td>
<td>0.65</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>Large White Perch</td>
<td>0.59</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Summer 2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small White Perch</td>
<td>0.75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medium White Perch</td>
<td>0.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large White Perch</td>
<td>0.67</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall 2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small White Perch</td>
<td>0.93</td>
<td>0.03</td>
<td>0.10</td>
</tr>
<tr>
<td>Medium White Perch</td>
<td>0.82</td>
<td>0.10</td>
<td>0.17</td>
</tr>
<tr>
<td>Large White Perch</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Spring 2010</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small White Perch</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Medium White Perch</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Large White Perch</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Summer 2010</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small White Perch</td>
<td>0.08</td>
<td>0.00</td>
<td>0.13</td>
</tr>
<tr>
<td>Medium White Perch</td>
<td>0.20</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td>Large White Perch</td>
<td>0.49</td>
<td>0.36</td>
<td>0.48</td>
</tr>
</tbody>
</table>

pelagic resource use in White Perch, as evidenced by larger CRb values. Small and medium White Perch also had higher CDb and SDNNDb values, indicating increased variation and more uneven resource use among individuals (Table 2). Similar to our diet overlap analyses, there was trophic overlap between small W. hite Bass and both medium (33.3% of White Bass SEAc) and large (16.9%) W. hite Perch, but little overlap between W. hite Perch and larger sizes of White Bass (Figure 4).

DISCUSSION

Our study is the first to directly quantify the trophic niche, seasonal and ontogenetic diet shifts, and potential diet and trophic overlap between sympatric populations of White Bass and invasive White Perch. We were able to assess the

TABLE 2. Sample size (n), mean (SD in parentheses) of TL (mm), $\delta^{13}$C values, $\delta^{15}$N values, trophic position, bootstrapped means of carbon range (CRb), nitrogen range (NRb), mean distance to centroid (CDb), SD of nearest neighbor distance (SDNNDb), mean nearest neighbor distance (MNNDb), and standard ellipse area corrected for small sample size (SEAc) of small, medium, and large size-classes of White Perch (<120, 121–180, and >180 mm TL) and White Bass (<150, 151–300, and >300 mm TL) in Lake James, North Carolina, as determined by stable isotope analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>White Perch</th>
<th>White Bass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small</td>
<td>Medium</td>
</tr>
<tr>
<td>n</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>TL</td>
<td>62 (4.68)</td>
<td>145 (17.29)</td>
</tr>
<tr>
<td>$\delta^{13}$C</td>
<td>-23.88 (1.77)</td>
<td>-24.58 (2.83)</td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>10.75 (0.47)</td>
<td>11.09 (1.27)</td>
</tr>
<tr>
<td>Trophic position</td>
<td>3.18 (0.14)</td>
<td>3.26 (0.41)</td>
</tr>
<tr>
<td>CRb</td>
<td>5.92</td>
<td>11.84</td>
</tr>
<tr>
<td>NRb</td>
<td>1.81</td>
<td>4.78</td>
</tr>
<tr>
<td>CDb</td>
<td>1.61</td>
<td>2.41</td>
</tr>
<tr>
<td>SDNNDb</td>
<td>0.38</td>
<td>1.06</td>
</tr>
<tr>
<td>MNNDb</td>
<td>0.44</td>
<td>1.44</td>
</tr>
<tr>
<td>SEAc</td>
<td>2.57</td>
<td>11.63</td>
</tr>
</tbody>
</table>
potential for competition between species at the initial stages of the White Perch invasion before White Bass declines could change the nature of their interactions, which allowed us to address a potential factor driving White Bass declines in invaded systems. White Perch trophic niche and resource use in Lake James show strong overlap with that of juvenile White Bass (<150 mm TL), indicating that the potential for competition for prey with White Perch could play an important role in the declines of White Bass populations. It is also important to note that small White Bass had high trophic overlap with all sizes of White Perch, which was driven by a shared heavy reliance on benthic invertebrates; in effect, this could mean that juvenile White Bass were exposed to competition with the entire White Perch population if resources are limited. In contrast, there was little evidence for trophic overlap between White Perch and larger sizes of White Bass, the latter of which may escape potential resource competition as adults. Thus, if resources were limited, potential diet competition between White Perch and White Bass would have the greatest impact on the juvenile life stages of White Bass.

Our results support and extend previous research into the diets of White Bass and White Perch. Kulkin (2007) found evidence for moderate diet overlap between White Perch and White Bass less than 200 mm TL in an Oklahoma reservoir and recommended that this interaction be the focus of future monitoring and research in that system. Gopalan et al. (1998) found biologically significant diet overlap between age-0 White Perch and White Bass in Lake Erie, in addition to documenting a decline in age-0 White Bass abundance concurrent with the rapid expansion of the White Perch population. Citling this and evidence of heavy egg predation by White Perch in Lake Erie, Madenjian et al. (2000) concluded that reductions in observed White Bass recruitment were most likely the result of high rates of White Perch competition and predation. In other species, interspecific competition has resulted in decreased growth (Hanson and Leggett 1985; Seiler and Keeley 2009), increased mortality (Keeley 2001), and reliance on less suitable forage items (Hanson and Leggett 1986). These results, in conjunction with our findings, suggest a similar mechanism could be limiting juvenile White Bass growth or survival in invaded systems.

Resource overlap is only one part of the larger equation that comprises true competition. Resources must be limited and competing species must forage in the same habitat to meet the formal definition of competition (Tilman 1982). While we did not measure resource availability in this study, Lake James is a cool, unproductive reservoir relative to most southeastern U.S. systems, which makes it more likely that resources are limited at certain times of the year than in more productive systems. Further, White Bass and White Perch were sampled in similar habitats during this study, and moronid fishes in general can occupy similar habitats in other reservoir systems (Van Den Avyle et al. 1983). Because of similar morphology and habitat use, it is plausible that these two species face competitive interactions when resources are limited.

Assuming resource limitation, heavy reliance of both species on benthic prey, coupled with limited scope of diets, may result in especially intense competition during early ontogeny of White Bass and White Perch. White Perch were also in higher abundance than White Bass across all seasons, which could increase their impact on White Bass juveniles (Britton et al. 2010). With increasing size, White Bass niche size and diet breadth remained low, while the niche size and diet breadth of White Perch increased, indicating White Bass may be more limited in their choice of prey throughout their ontogeny while White Perch exhibit a more generalized feeding strategy (Hergenrader and Bliss 1971; Couture and Watzin 2008; Feiner et al. 2013). This trend has also been observed in Lake Erie, where White Perch foraged more effectively and switched to benthic invertebrates when zooplankton abundance decreased, but White Bass did not
switch and suffered from decreased body condition (Gopalan et al. 1998). If White Perch foraging is more plastic during periods of limited resources, they could have a competitive advantage over White Bass, which appear less able to switch away from preferred food sources.

In some cases our sample sizes were relatively small, and small sample sizes tend to bias diet overlap indices toward non-significant values (Randal and Myers 2001). However, in the cases where our sample size was smallest (e.g., medium White Bass in spring 2009, small White Bass in fall 2009) we still found significant diet overlap in most comparisons. In other cases (e.g., White Bass in summer 2010) we found no overlap, but White Bass diets were consistently piscivorous and congruous with other studies (e.g., Hartman 1998). With respect to our stable isotope results, trophic niche width using SEA with Bayesian inference is unbiased to variations in sample size and allows for more robust comparisons of niche structure across populations (Jackson et al. 2011). Additionally, our results from stable isotope analysis corroborated our conclusions from the diet overlap analyses that White Perch and juvenile White Bass exhibit significant trophic overlap in Lake James. Therefore, we believe our results are robust to sample size biases.

The high degree of diet, habitat use, and trophic overlap between White Perch and White Bass in this study indicates that resource competition, especially among juveniles, could be a factor contributing to the declines in White Bass populations observed in systems invaded by White Perch. These results, in conjunction with evidence from other studies, led us to predict that systems invaded by White Perch may lose their White Bass fisheries. Our conclusions raise questions about the best methods to mitigate the potential impact of White Perch invasions. For systems where White Perch have already been introduced, control or eradication efforts through manual removals or stocking of potential predators have been unsuccessful (Vrtiska et al. 2003; Gosch and Pope 2011). Therefore, we recommend that biologists concentrate on education and regulatory efforts to stop further introductions of White Perch in any effort to protect and maintain White Bass fisheries (Johnson et al. 2009).

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REFERENCES


Colonization of Steelhead in a Natal Stream after Barrier Removal

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Colonization of Steelhead in a Natal Stream after Barrier Removal

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Abstract

Colonization of vacant habitats is an important process for supporting the long-term persistence of populations and species. We used a before-after experimental design to follow the process of colonization by steelhead Oncorhynchus mykiss (anadromous Rainbow Trout) at six monitoring sites in a natal stream, Beaver Creek, after the modification or removal of numerous stream passage barriers. Juvenile O. mykiss were collected at monitoring sites by using a backpack electrofisher. Passive integrated transponder tags and instream tag reading stations were used in combination with 16 microsatellite markers to determine the source, extent, and success of migrant O. mykiss after implementation of the barrier removal projects. Steelhead migrated into the study area during the first spawning season after passage was established. Hatchery steelhead, although comprising more than 80% of the adult returns to the Methow River basin, constituted a small proportion (23%) of the adult O. mykiss colonizing the study area. Adult steelhead and fluvial Rainbow Trout entered the stream during the first spawning season after barrier removal and were passing the uppermost tag reader (12 km upstream from the mouth) 3–4 years later. Parr that were tagged in Beaver Creek returned as adults, indicating establishment of the anadromous life history in the study area. Population genetic measures at the lower two monitoring sites (lower 4 km of Beaver Creek) significantly changed within one generation (4–5 years). Colonization and expansion of steelhead occurred more slowly than expected due to the low number of adults migrating into the study area.

Direct removal of or damage to habitat threatens 50% of species in the United States (Richter et al. 1997). Small barriers, such as diversion dams and culverts, adversely impact aquatic fauna and are more numerous and widely distributed across the landscape than are larger main-stem dams (Moyle and Williams 1990; Sheer and Steel 2006). As numerous species of fish have declined over the last several decades, extensive efforts have been made to remove or modify these barriers to allow the passage of target fish species (Bernhardt et al. 2005). These management actions are aimed at reconnecting unoccupied habitats to re-establish populations that collectively will increase production of threatened or endangered species. Few studies have collected data during the fish colonization process in stream environments (Bernhardt et al. 2005), and oftentimes such...
studies are opportunistic, occurring after unpredictable cata-

crophic events like volcanic eruptions (Leider 1989) or the re-

lease of toxic chemicals (Demarias et al. 1993).

Barrier removal projects create opportunities to study the coloni-

zation of species or the re-establishment of migratory life histories by using the before–after treatment experimental design (Kiffney et al. 2009; Anderson et al. 2010). The rate of colonization will be dependent on the species’ dispersal capability as well as the density and distance of the unoccupied habitat to candidate source populations (Gaggiotti et al. 2004). Barrier removal projects that have been implemented in streams with populations of target species downstream of the structure have proven successful in allowing rapid, volitional colonization by fish when passage is restored (Kiffney et al. 2009; Anderson et al. 2010).

Trout and salmon are typically the target species for restora-

tion actions due to their threatened and endangered status in the USA (McClure et al. 2003); however, salmonid systems are largely supported by spawners homing to natal streams and by the development of local adaptations, which can appear to hinder population expansion and colonization processes. Several salmonid species have multiple life history strategies that co-occur in the natal streams, such as resident (stream-rearing), fluvial (river-rearing), and anadromous (ocean-rearing; Behnke 1992). These various life history strategies are known to provide demographic and genetic support to species in variable or unstable environments, and interbreeding between the life history types is widely documented (Parker et al. 2001; Docker and Heath 2003; Araki et al. 2007; Christie et al. 2011). Barrier removal is often targeted toward increasing population distribution and abundance of the anadromous life history form, which has severely declined due to extensive impacts from harvest, hydromodification of several small irrigation dams in Beaver Creek, a natal tributary to the Methow River, Washington. We were particularly interested in the process of colonization by O. mykiss because this species has complex and co-occurring life history strategies combined with potentially large hatchery effects. Migratory O. mykiss and other species of fish were allowed to naturally colonize the newly accessible habitat. Individual migrations and movements were monitored with PIT tags and tag readers. Because the different life history types interbreed, the PIT tag information was used to identify the life history of individuals during the study. The objectives of our study were to (1) identify the source and abundance of anadromous, hatchery, and fluvial adult migrants during the first 4 years after barrier removal; (2) identify whether there were detectable changes in measures of population genetics and, if so, identify the basin areas where the changes occurred; and (3) determine whether the anadromous life history was successfully established by identifying the adult returns of parr that were produced after barrier removal in Beaver Creek.

STUDY AREA

The Methow River basin is located on the east side of the Cas-

cade Mountain Range in north-central Washington. The Methow River, a tributary of the Columbia River, is located about 843 km upstream from the estuary. Beaver Creek is a third-order natal tributary that flows westward into the Methow River 57 km upstream from the river’s mouth (Figure 1). The Beaver Creek basin is 290 km², with basin elevations ranging from 463 to 1,890 m and streamflows that ranged from 0.05 to 4.7 m³/s during the study (Martens and Connolly 2010). The upper portion of the Beaver Creek basin is forest land that is managed by state or federal agencies. The lower portion of the basin is irrigated, privately owned farmland and ranch land. Fish access into Beaver Creek was disconnected due to water withdrawal and associated structures for more than 100 years (Martens and Connolly 2010). Resident O. mykiss were the most abundant species of salmonid throughout the Beaver Creek basin prior to implementation of the barrier removal projects. Steelhead were present downstream from the lowest diversion dam (Martens and Connolly 2010). From 2000 to 2004, seven small
irrigation diversion dams (1.0–2.0 m high) were modified into rock vortex weirs that allow fish passage (Ruttenberg et al. 2009; Martens and Connolly 2010). The downstream-most irrigation diversion was a 2.0-m-high, concrete diversion dam that was modified to allow fish passage after the fall of 2004. Access to Beaver Creek by migratory steelhead/Rainbow Trout was restored for the spring 2005 spawning season.

Hatchery Releases

The Grand Coulee Fish Maintenance Project was established to mitigate for the construction of Grand Coulee Dam on the Columbia River during the 1930s. Hatchery activities were implemented to replace lost production of anadromous salmon and steelhead that were blocked from reaching upstream tributaries after the dam was constructed. The Wenatchee, Entiat, Methow, and Okanagan rivers, which are located downstream of Grand Coulee Dam, are utilized to rear and release salmon and steelhead for this extensive hatchery mitigation program. The state of Washington also manages a hatchery program to mitigate for other hydropower facilities on the Columbia River.

The steelhead stock used in all these hatcheries originated from collections on the Columbia River at Rock Island Dam, located downstream of Wenatchee, Washington. The broodstock was established from returning adults at this dam because these adults were assumed to be migrating to the major tributaries upstream (e.g., Wenatchee, Entiat, Methow, and Okanagan rivers) and other tributaries upstream of Grand Coulee Dam (Chapman et al. 1994). The original broodstock was later used to establish local broodstocks in each of the basins. In recent years, the Methow River and Wenatchee River hatchery broodstocks have been managed as demographically independent stocks.

Currently, state and federal hatchery programs in the Methow River basin release 450,000–550,000 steelhead smolts per year. Returning adult steelhead are spawned, and the eggs are reared at Wells Hatchery (river kilometer 830.1) on the Columbia River downstream from the Methow River mouth. Current practices include intentional breeding between hatchery and naturally produced adults, and progeny from these crosses are primarily released in the Methow River basin (Snow et al. 2011). Hatchery *O. mykiss* are released as age-1 smolts in the Methow and Chewuch rivers upstream from the town of Winthrop, Washington. All hatchery-origin steelhead are marked with an internal tag (e.g., PIT tag), an external tag (e.g., elastomer tag), a fin clip, or a combination of these. Hatchery-origin adults comprised the majority of the adult returns to the Methow River basin. During our study (2005–2008), the percentage of hatchery fish among steelhead returns ranged from 82% in 2008 to 91% in 2005 (Snow et al. 2011).

METHODS

Fish collections and movements.—Adult *O. mykiss* were captured in Beaver Creek using a picket weir installed 1.3 km upstream from the creek’s mouth (Figure 1). This location was chosen for its accessibility and stream channel topography. The trap captured fish that were moving upstream or downstream; it was operated from March 20 to May 9, 2005; May 14 to December 5, 2005; February 13 to May 1, 2006; June 27 to November 27, 2006; February 24 to March 30, 2007; May 25 to November 29, 2007; February 24 to March 3, 2008; July 11 to July 30, 2008; and September 2 to December 10, 2008. Gaps in weir collection during May and June were due to high streamflows and debris that washed out the weir. In 2008, the weir was not operated during August because data from previous years indicated little downstream movement by juveniles during that month. Stream icing during December and January prevented trap operation. The date of capture, direction of movement, FL (mm), weight (g), sex, and population origin (wild or hatchery) were recorded for adult trout.

Juvenile *O. mykiss* were sampled at six sites on Beaver Creek (Figure 1): one site downstream of the lowest diversion dam (DS Dam); one site between the various diversion dam modifications (UBR1); and four sites (UBR2, CMP, UBR4, and South Fork Beaver Creek [SFB]) upstream from the diversion dam modifications (Figure 1). Prior to barrier removal, age-1 and older (age-1+) juvenile *O. mykiss* were sampled in the
stream during fall 2004 or summer 2005. After barrier removal, age-1+ juvenile *O. mykiss* were sampled during the summer or fall of 2008 and 2009. The 4–5 years between the before and after collections represent approximately one generation for *O. mykiss*.

Juvenile *O. mykiss* were collected by using a backpack electrofisher (Smith-Root Model LR-24). Trout were measured to determine FL (nearest mm) and were weighed (nearest 0.01 g) using a digital scale (Ohaus Scout Pro SP 400). Juvenile and adult *O. mykiss* were scanned for PIT tags and coded wire tags and were inspected for any other external tags (e.g., fin clips, elastomer tags, etc.). If the trout did not have a PIT tag, a tag (12.5 mm, full duplex, 134.2 kHz) was inserted into the dorsal sinus cavity for adult trout or into the body cavity for juvenile trout larger than 65 mm. A tissue sample was removed from the caudal fin of each juvenile and adult and was stored in a 95% solution of nondenatured ethanol.

Movements of tagged juvenile and adult *O. mykiss* were monitored using a network of in-stream tag reading stations in Beaver Creek (Figure 1) and at dams and passage facilities on the main-stem Columbia River. McNary Dam, located at river kilometer 470 on the Columbia River, was the upstream-most juvenile counting location used during this study. Tagged juvenile *O. mykiss* that were detected at or downstream of this location were considered to be smolts with downstream migrations exceeding 400 km.

The PIT tag reading stations located on Beaver Creek provided information on adult migration into the study area. One multi-antenna, multiplex PIT tag reading station and two single-antenna PIT tag reading stations were operated in Beaver Creek (described by Connolly et al. 2008; Martens and Connolly 2010). Briefly, the multiplex unit was operated with a Digital Angel Model FS-1001 transceiver connected to six custom-made antennas and a DC power source. The antennas were arranged in three arrays across the streambed, with each array having two antennas that extended across the streambed to provide redundancy and complete coverage at most streamflows. This configuration allowed us to determine the direction of movement and increased the probability of detection. The single-antenna interrogation stations were operated using a 2001F-isodi Digital Angel PIT tag reader that was powered by a 12-V battery connected to a single custom-made antenna. The downstream-most single-antenna PIT tag reading station was operated from September 27, 2004, to December 2, 2008. The multiplex tag reading station has been operating since July 20, 2004. The upper single-antenna PIT tag reading station was operated from August 1, 2004, to November 12, 2008.

Migratory life history (anadromous or fluvial) of the adult *O. mykiss* was identified from the PIT tag detections. Fluvial Rainbow Trout left Beaver Creek and were not detected at any of the Columbia River facilities. Some of these fish returned in successive years. Steelhead were detected at main-stem Columbia River dams at river kilometer 470 or farther downstream during their upstream migration, downstream migration, or both. Hatchery-origin *O. mykiss* were identified from PIT tags, coded wire tags, fin clips, or other marks.

Laboratory methods.—Tissue samples from Wells Hatchery brood years 2005 and 2006 (hatchery × hatchery crosses) were provided by the Washington Department of Fish and Wildlife. Sixteen microsatellite markers were used to identify individuals. Thirteen of these markers are standardized across the Columbia River basin and are summarized by Stephenson et al. (2009). Additional primer sets analyzed were Omen102 (Olsen et al. 2000), Omm1036, and Omm1046 (Rexroad et al. 2002).

The DNA was isolated from ethanol-preserved fin clips by using QiaGen DNAeasy tissue extraction kits in accordance with the manufacturer’s standard protocols. Sixteen microsatellite loci were amplified by PCR in three multiplex reactions using Qiagen Multiplex PCR Master Mix in 96-well plates on GeneAmp PCR System 9700 Thermal Cyclers (Applied Biosystems, Foster City, California). The PCR products were run on an Applied Biosystems 3730 Genetic Analyzer. Peaks were scored using GeneM apper version 3.7 (Applied Biosystems) and were labeled by following the Steven Phelps allele nomenclature (SPAN) convention (Stephenson et al. 2009). Forward primers were fluorescently labeled (Applied Biosystems).

Amplication (PCR) consisted of 5-µL reactions containing 2.5 µL of Qiagen Multiplex PCR Master Mix, five or six primer sets, and water, added to 2 µL of DNA extract that was dried down in a 96-well plate. Cycling conditions included initial denaturation for 15 min at 95°C, followed by 28 cycles for 30 s at 94°C, 90 s at 51°C (multiplex A) or 57°C (multiplexes B and C), and 60 s at 72°C, followed by a final cycle for 30 min at 60°C. Multiplex A consisted of Oki23, Oke4, Oneu14, Ssa289, and Ssa408; multiplex B included Ot4s, Omy7, Ogo4, One102, Omm1046, and Ssa407; and multiplex C contained Ot100, Omy1011, Omy1001, Ot3s3, and Omm1036. Amplication products were diluted with 10 µL of DNA-grade water and 1 µL of each dilution added to 10 µL of LIZ-formamide solution (30 µL of LIZ600 to 1 mL of formamide). Completed runs were analyzed automatically with GeneM apper, followed by manual analysis of all peaks for verification. All homozygous results were checked for small-allele dropout and large-allele dropout. Peaks were also visually checked for conformity to expected profiles. Laboratory error rates for the 13 standardized loci were less than 2% (Stephenson et al. 2009). Duplicate samples indicated that laboratory error rates were less than 1% for our study.

Statistical analysis.—Detection efficiency at the middle (i.e., multiplex) reader was calculated according to the methods of Connolly et al. (2008; n = 29) based on joint probability among the three antenna arrays at this station. Because detection efficiencies for adult steelhead at this reader are high (99.9%), detection efficiencies at the lower tag reader and the weir could be calculated by using a joint probability from detection counts for tagged adult *O. mykiss* that entered Beaver Creek and were recorded as passing the middle tag reading station (n = 22; Lady et al. 2003; Connolly et al. 2008). Specifically, site detections
expected heterozygosity was also calculated in GENEPOP. GENEPOP version 4.0.10 (Raymond and Rousset 1995). Equilibrium and linkage disequilibrium were performed using.

The before-after analysis relies on the assumption that temporal genetic diversity is stable so that a detectable response can be attributed to the treatment. To test the temporal stability of the genetic diversity and variation, we used pairwise comparisons between consecutive years. Therefore, pairwise comparisons between the before and after samples were used to detect changes due to the barrier removal treatments. Whereas pairwise comparisons between consecutive years were used to test the frequency of statistical significance due to non-treatment-related factors (e.g., finite sampling). Before-after comparisons were tested twice against different years for three of the six sites to confirm the significance and repeatability of the before-after comparisons (Table 1).

Prior to statistical tests, full siblings were identified and removed from the data set by using ML-RELATE (Kalinowski 2006); this was done to avoid bias in measuring site-based population genetic measures. Exact tests of Hardy–Weinberg equilibrium and linkage disequilibrium were performed using GENEPOP version 4.0.10 (Raymond and Rousset 1995). Expected heterozygosity was also calculated in GENEPOP. Unbiased estimates of allelic richness and private alleles were calculated using HP-RARE (Kalinowski 2005). Exact tests of the genetic differentiation index $F_{ST}$ were performed using ARLEQUIN version 3.5 (Excoffier and Lischer 2010). All comparisons were adjusted for multiple comparisons by using a Bonferroni correction (Rice 1989).

We used STRUCTURE version 2.3.3 (Pritchard et al. 2000) to estimate the proportion of hatchery admixture for each $O$. mykiss collected at each site and year in comparison with the sample of known-hatchery-origin steelhead from Wells Hatchery ($n = 99$). Allele frequencies from the two hatchery brood years were not statistically different and were combined for our analysis. STRUCTURE is a Bayesian-based model that clusters individuals according to allelic frequencies while minimizing linkage disequilibrium and deviation from Hardy–Weinberg equilibrium. The model allows for admixture between population groups. The admixture model in STRUCTURE was run by using 10,000 iterations for burn-in and 100,000 iterations with a Markov-chain Monte Carlo resampling algorithm as described by Pritchard et al. (2000). The number of populations ($K$) was set to 2. All other settings were run using default values. Ten independent runs were made for each site, and the run with the lowest log likelihood was selected as the best run for estimation of hatchery admixture. The average of the percent hatchery admixture was calculated for each site and collection year.

### RESULTS

Weir captures of $O$. mykiss in Beaver Creek during 2005 and 2006 appeared to be high; only two individuals in 2005 and

<table>
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<th>AR</th>
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<th>$F_{ST}$</th>
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**Temporal tests**

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one individual in 2006 were known to be missed in our sample based on tag detections. However, the weir was not operational for the entire spawning seasons of 2007 and 2008, reducing our ability to capture and count the wild steelhead that entered the stream during those years (Figure 2). Based on the pattern of steelhead detections and captures, capture efficiency for the weir was estimated at 20% ($CV = 45\%$) for 2005–2008. Attempts to examine years independently failed due to low sample sizes; however, the count data indicated that capture efficiencies during 2005 and 2006 were higher than estimated (Figure 2). Detection efficiency was estimated as 67% ($CV = 0.29\%$) at the lower tag reader and 99.9% ($CV = 0.09\%$) at the middle reader.

Numerous hatchery steelhead were detected at the tag readers in Beaver Creek during the study years, and the counts based on tags would be biased toward hatchery steelhead due to hatchery evaluation programs in the basin during these years. Between 2003 and 2005, tagging of juvenile hatchery steelhead increased from 25% to over 50% in the hatchery programs. The total percentage of tagged hatchery steelhead during these years ranged from 50% to 60% (Washington Department of Fish and Wildlife and U.S. Fish and Wildlife Service, unpublished data). These tagged steelhead returned as adults from 2004 to 2007. A total hatchery returns into Beaver Creek were primarily comprised Wells Hatchery releases into the Methow River basin; however, one hatchery stray from the Wenatchee River, Washington, and one wild stray from the Tucannon River, Washington, were also detected. The increase in tagged hatchery adults in Beaver Creek during the 2007 spawning season was due to the release of a high number of hatchery smolts in spring 2005. The 2005 release year had the highest proportion of tagged hatchery fish in state and federal hatchery programs, which could explain the increase in hatchery tag returns during 2007. Nearly all of the adult hatchery steelhead that returned to Beaver Creek in 2007 had spent 1 year rearing in the ocean.

Fluvial Rainbow Trout were particularly numerous during 2006, with nearly three times the number of adult migrants than in the other years of our study (Figure 3). Over the four study years, 34 individual fluvial Rainbow Trout larger than 200 mm were documented during the spawning run in Beaver Creek. Males were the largest proportion (67%) of this life history type; females and fish of unknown sex represented 6% and 18%, respectively. Individual fluvial Rainbow Trout were documented as entering Beaver Creek up to four consecutive years, with 32% of the individuals entering the creek in multiple years. Data from tag readers located on Beaver Creek indicated that adult steelhead migrated farther upstream past the tag reader at stream kilometer 12 in Beaver Creek during the latter 2 years of the study (2007 and 2008; Figure 4).

Parr that were tagged at sites upstream from the diversion dams were detected as smolts at Columbia River dams during
all years of the study. Of the tagged parr that were released during 2004 at UBR1, 12% were detected during downstream migration on the Columbia River. These data provide definitive evidence that juvenile *O. mykiss* from this reach were expressing an anadromous life history prior to barrier treatment; however, none of these parr returned as adults. The percentage of parr tagged at UBR1 that were detected as smolts after barrier removal varied annually, with no apparent trend (8% in 2005; 5% in 2006; 6% in 2007; 8% in 2008; 6% in 2009; and 14% in 2010). Among the parr that were tagged at sites further upstream (i.e., UBR2, CMP, UBR4, and SFB), 1–2% were detected as smolts on the Columbia River; these rates remained constant during the study period, indicating no change in life history at these sites. None of the parr that were tagged at the four upper sites returned as adults.

Between 2007 and 2011, 38 adult steelhead that were tagged as parr in Beaver Creek during previous years were detected as migrating upstream in the Columbia River. Most (68%) of these adults were last detected on the Columbia River or at a tag reader at the mouth of the Methow River downstream from spawning sites in the basin. Eight adults (21%) were detected in Beaver Creek (*n = 1* in 2007, *3* in 2008, and *4* in 2009), and four adults (33%) were detected in other tributaries (Twisp River and upper Methow River). These tagged returns demonstrated that steelhead progeny from early colonizers in the basin successfully homed back to Beaver Creek; however, one-third of these adults were detected in Methow River basin tributaries other than Beaver Creek.

The total number of alleles detected at each locus ranged from 7 to 28, and the average allelic richness by site and collection date ranged from 4.9 to 7.2 (Table 1). Expected heterozygosity and average allelic richness were similar to values documented for *O. mykiss* in other studies (Heath et al. 2002; Narum et al. 2004, 2006, and 2008; Nielsen et al. 2009). We did not detect significant departures from Hardy–Weinberg equilibrium or significant linkage disequilibrium in the juvenile samples from Beaver Creek sites. Tests on the Wells Hatchery samples did not detect any significant departures from Hardy–Weinberg equilibrium, but linkage disequilibrium was detected at six pairs of loci. There was no discernible pattern to these locus pairs.

The genetic diversity parameters indicated some changes in the before–after comparisons, with the temporal tests remaining stable for expected heterozygosity and allelic richness. The average number of private alleles did vary across the comparisons (Table 1). The STRUCTURE output indicated that Wells Hatchery admixture in the samples decreased from downstream to upstream sites in Beaver Creek (Figures 5, 6). The Wells Hatchery practices include intentional interbreeding of hatchery and wild steelhead that return to Wells Dam. Therefore, contributions of nonhatchery alleles are evident in the Wells Hatchery brood samples. In the comparison of before and after data sets, the proportion of hatchery admixture decreased at the DS Dam site. In the before–after comparisons for sites upstream from the diversion dams, the proportion of hatchery admixture generally increased after barrier removal; the exception was the uppermost site on Beaver Creek (UBR4), where the proportion of hatchery admixture decreased after barrier removal. Pairwise Wilcoxon rank tests examining hatchery admixture for the before–after comparisons were significant for both comparisons at UBR1 (2004 versus 2008, and 2004 versus 2009; *P < 0.003*) and for only one comparison at the SFB site (2005 versus 2008; *P = 0.02*); the other comparisons were not significant. Proportion of hatchery admixture was fairly consistent in the temporal comparisons (2008 versus 2009) except for SFB, where hatchery admixture declined. None of the pairwise Wilcoxon rank tests for temporal comparisons of hatchery admixture proportion were significant (*P > 0.05*).

Comparisons of genetic differentiation (*F*\textsubscript{ST} and allele frequency) showed significant differences at the two downstream-most sites in the basin (Table 1). Both comparisons demonstrated significant differences, indicating consistency across these measurements and supporting the conclusion that population genetics changed at UBR1 after barrier removal. Interestingly, the DS Dam site showed a significant change even though it was
FIGURE 6. Output from STRUCTURE, showing population admixture in Rainbow Trout/steelhead sampled at the upstream-most three monitoring sites in Beaver Creek (Figure 1). Wells Hatchery steelhead were used as a reference for the hatchery population (hatchery × hatchery crosses; brood years 2005 and 2006). Each individual is represented by a bar on the plots (black shading = proportion hatchery alleles; gray shading = proportion wild alleles). Hatchery samples were provided by the Washington Department of Fish and Wildlife.

accessible prior to the barrier removal treatments. The genetic differentiation tests for the uppermost site, UBR4, were significant when comparing 2004 and 2008 but were not significant for the comparison between 2004 and 2009; the significance could be a result of finite sampling or nonrandom mating or tissue collections. The temporal tests comparing FST or allele frequencies in consecutive years were not significant (Table 1).

DISCUSSION

After the initial number of adult *O. mykiss* migrated into Beaver Creek in 2005, the number of adults did not increase in the subsequent 3 years after barrier removal. Counts of wild and hatchery steelhead declined from 2005 to 2007 and then increased slightly. The adult steelhead counts at Wells Dam as reported by Snow et al. (2011) were highly correlated with our weir and tag reader counts of adult steelhead entering Beaver Creek (r = 0.91), indicating that our counts are following a similar trend. Fluvial Rainbow Trout constituted a variable portion of the run. These adults reproduced with the steelhead and should be considered part of the population (Weigel 2013).

Kiffney et al. (2009) found rapid colonization and steadily increasing abundances of *Coho Salmon* *O. kisutch* during the first 4 years after dam passage was restored; however, abundances of *Chinook Salmon* *O. tshawytscha* in that same study declined during the first and second years before increasing during the third and fourth years. Abundances of both *Coho Salmon* and *Chinook Salmon* in the Kiffney et al. (2009) study were substantially higher than the abundance of *O. mykiss* in our study. However, the distance colonized by adult *Coho Salmon* in the Kiffney et al. (2009) study was similar to that of *O. mykiss* in our study within 4 years after passage was restored. Demarias et al. (1993) found that recolonization by Virgin Chub *Gila seminuda* extended as far as 30 km in the Virgin River, Utah, 29 months after an accidental release of rotenone. The rate of colonization is mediated by abundance, distance, and connectivity to source populations; therefore, different species and locations may vary in response to connectivity projects or disturbance events. Wild steelhead and Rainbow Trout constituted 77% of the adults entering Beaver Creek. Abundances of wild steelhead returning to the Methow River basin are low, which likely impacts the number of adults entering Beaver Creek and could slow the population response to barrier removal.

Few hatchery steelhead entered Beaver Creek, despite high proportions of hatchery steelhead in the returns to the Wells Dam. Leider (1989) also found that the proportion of hatchery steelhead differed between a hatchery counting site lower in the basin and a natal tributary. Hatchery fish may return to release locations or to the hatchery site near the release location. In addition, other survival differences (e.g., selective harvest) may affect the proportion of hatchery fish between the ladder at Wells Dam and the natal tributaries. The counts of hatchery-produced steelhead entering Beaver Creek appeared to increase in 2007; however, tagged hatchery steelhead vastly outnumbered the tagged wild steelhead in the basin, so without a fully operational weir it is impossible to determine the proportion of wild steelhead that could have entered the stream. Year-to-year variability in population sizes, survival rates, overlapping generations, and numbers of tagged steelhead in the basin precludes our ability to provide a valid estimate of steelhead that were missed at the weir based on these tag counts. Fluvial Rainbow Trout were not tagged by other fisheries sampling programs, and our efforts only tagged those fluvial individuals that were captured at the weir; therefore, the total population size and proportion tagged are also unknown for this life history.

Several parr that were tagged in Beaver Creek returned as adults in 2007–2011, indicating that the complete life cycle of the anadromous life history was established in the newly opened habitat. Some straying of these returning adult steelhead occurred during the study, but 66% of these adults returned to the natal area. All of the strays detected in the Methow River basin were recorded in tributaries upstream from Beaver Creek. Steelhead were found to stray into tributaries upstream from
their natal tributary after the volcanic eruption on Mount St. Helens, Washington (Leider 1989). An additional steelhead that were tagged as parr in Beaver Creek were last detected while migrating upstream in the Columbia River or at the mouth of the Mchow River; these adults were not detected again as entering a natal tributary, and their fate is unknown. They either died, entered another stream undetected, or returned to Beaver Creek downstream from the lowest tag reader. The rate of straying by steelhead from Beaver Creek (33%) was substantially higher than that documented in other studies (7.7%; see Hendry et al. 2004 and citations therein). Our data do not indicate why this high straying rate was observed, but it could be part of the early colonization process prior to establishing a viable population and associated local adaptations. Although the straying rate in our study is only based on four adult strays from Beaver Creek, we consider this to be a conservative estimate of straying because there are many basin locations where strays would go undetected.

The temporal stability of population genetic measures is important to identify when attempting to detect a treatment effect. Population genetic measures can vary due to genetic drift from finite population sizes (Allendorf and Luikart 2007). Therefore, some tests could show significant differences that are unrelated to the treatment. Similar to results of other studies, our populations were temporally stable over short-term comparisons. Similar tests of collections ranging from less than 1 year apart to 5 years apart found that only 1 of 21 comparisons was significantly different (Heath et al. 2002; Narum et al. 2004, 2006; Nielsen et al. 2009). Therefore, we can expect fewer than 5% of temporal tests to be significant due to random or unmeasured effects.

Steelhead/Rainbow Trout from the two downstream-most sites (DS Dam and UBR1) showed significant differences in allele frequency and $F_{ST}$ values. We did not expect to see a change at the DS Dam site because it was accessible to migratory steelhead/Rainbow Trout prior to the barrier treatments. Interestingly, there was also a reduction in the proportion of hatchery admixture at the DS Dam site after barrier removal. This shift in genetic parameters at the DS Dam site may be due to (1) individual trout moving downstream from upstream sites for rearing or (2) the mixing of anadromous or fluvial O. mykiss with the resident individuals occurring upstream from the diversion dams. The reduction in hatchery admixture could result from the higher contribution of the wild O. mykiss spawning in the newly opened habitat.

The UBR1 site had the greatest shift in $F_{ST}$, allele frequencies, and hatchery admixture, which were significantly different before versus after treatment. The increase in hatchery admixture is interesting since the hatchery steelhead that colonized the stream during 2005 and 2006 produced very few offspring (Weigel 2013). However, resident O. mykiss can adopt the anadromous life history, and gene flow into the hatchery from the populations upstream of Wells Dam is high. Therefore, the hatchery admixture is also tied to the anadromous life history through hatchery brood practices. Additionally, parr from UBR1 were exhibiting an anadromous life history prior to modification of the diversion dams. Life history is plastic in O. mykiss and can be related to growth or genetics. It is uncertain whether a few adult steelhead were accessing this site prior to barrier removal or whether this site was converting more parr to smolts due to favorable growing conditions. Nevertheless, these data indicate that monitoring of juvenile tag migrations alone may not clearly indicate whether the anadromous life history is established in newly opened stream habitats.

The sites further upstream did not show changes in population genetics when comparing before and after treatment samples. Tag data indicate that few spawners migrated to these upper reaches during the first 4 years after barrier removal. The UBR4 site showed a significant change in $F_{ST}$ and allele frequencies in the comparison of 2004 with 2008 samples but not in the comparison of 2004 with 2009 samples. Since the pairwise comparisons were not similar across the different years, we felt that the significant comparison did not indicate clear genetic changes due to the treatment. Similarly, the SFB site had an increase in allelic richness and private alleles in the comparison of 2005 and 2008 samples but not in the comparison of 2005 and 2009 samples. These shifts in population genetic measures could be the result of genetic drift from a finite number of breeders, nonrandom mating, or finite sampling; the shifts may also be attributable to the presence of a few new migrants in 2008 that did not migrate into this area in 2009.

Although it is possible that the genetic shifts at Beaver Creek sites could be due to increased migration among resident O. mykiss from the monitoring sites, the tag data indicated that adult steelhead moved higher into the basin during the study. Additionally, the increases in the proportion of hatchery admixture and the significant changes in population genetics indicate that movements by resident individuals are unlikely to explain the observed results. Furthermore, barriers in streams may allow passage downstream but prevent passage upstream, thus allowing for migration and gene flow in the downstream direction. It is also likely that the resident sites produce a small number of anadromous or fluvial out-migrants that can navigate downstream over the diversion dams. However, if this was the case, then significant changes in allele frequencies would not be expected.

In summary, adult steelhead entered Beaver Creek during the first spawning season after barrier removal and parr from the initial brood years returned to Beaver Creek, indicating that the complete life cycle of steelhead was established. In addition, tag movement data indicated that adult steelhead were moving to the upper monitoring sites during the third and fourth years after barrier removal. Hatchery steelhead represented a small proportion (23%) of these colonizing adults, despite high abundances of fish from hatchery releases by local fishery management programs. A abundance of adult O. mykiss did not increase during the 4 years of weir operation. Because hatchery fish did not comprise a majority of the run into Beaver Creek
and because hatchery fish are expected to have substantially reduced reproductive success (Miller et al. 2004; Araki et al. 2007), the low numbers of wild steelhead entering the Methow River basin are likely limiting colonization of Beaver Creek by this life history type. Colonization and expansion of steelhead were slower than expected, with adult steelhead beginning to expand into the upper basin sites during the later years of the study. Monitoring of the population and colonization process should continue until the anadromous life history attains stable distribution and abundance in the basin. Additionally, as the colonization process continues, relationships such as the relative abundances of hatchery steelhead entering the stream may shift.

ACKNOWLEDGMENTS
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Summer Habitat Use by Lake Sturgeon in Manistee Lake, Michigan

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Summer Habitat Use by Lake Sturgeon in Manistee Lake, Michigan

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**Abstract**

The Lake Sturgeon *Acipenser fulvescens* is targeted for rehabilitation across its range, but little is known about habitat use by Lake Sturgeon during periods other than the spawning period. Insight into habitat use during nonspawning periods for these long-lived fish is crucial to our understanding of this species and its recovery. Our goal was to characterize summer habitat use by Lake Sturgeon in Manistee Lake, Michigan, a drowned river mouth complex. Fish were tagged and relocated in the lake by using telemetry in 2003–2005. The lake was divided into 18 sampling sections, and abiotic and biotic variables with potential influences on habitat use were quantified in each section during May–July in 2003 and 2004. Lake Sturgeon were found in the lake during May–July and primarily occupied habitats near the wetland complex and shipping channel in the northern portion of the lake. Water depth, temperature, dissolved oxygen level, Secchi depth, and densities of chironomid larvae, dreissenid mussels, burrowing mayflies *Hexagenia* spp., and amphipods differed among sampling sections. Similarities between Lake Sturgeon relocation sites and the sampling sections were analyzed with Penrose distance statistics. Abiotic and biotic variables in the southern and central portions of the lake were most similar to those at sampling sections where Lake Sturgeon were relocated. The difference between southern and central sampling sections and the sections where fish were relocated suggests that habitat use was influenced by additional factors that were not monitored. Future efforts to conserve Lake Sturgeon populations should include habitat management during nonspawning periods.

Lake Sturgeon *Acipenser fulvescens* are native to the Great Lakes, Mississippi River, and Hudson Bay drainages of central North America (Harkness and Dymond 1961), but abundances across the species' historic range are greatly reduced due to exploitation and habitat modification resulting from dam construction, logging, and other industrial activity (Harkness and Dymond 1961; Tody 1974; Hay-Chmielewski and Whelan 1997). Because of this decline, the state of Michigan listed the Lake Sturgeon as threatened, and this species is a priority for rehabilitation by state, federal, and tribal natural resource agencies (Hay-Chmielewski and Whelan 1997; Hill and McClain 1999; LRBOI 2008; Hayes and Caroffino 2012). An understanding of Lake Sturgeon habitat use during spawning and nonspawning seasons will allow rehabilitation efforts to focus on the long-term viability of the species (Beamesderfer and Farr 1997; Holey et al. 2000; Secor et al. 2002).

Adult Lake Sturgeon are known to exhibit complex movement patterns (Rusak and Mosindy 1997; Borkholder et al. 2002; Smith and King 2005; Adams et al. 2006). Outside of spawning migrations, some Lake Sturgeon move seasonally among habitats (Rusak and Mosindy 1997; Borkholder et al. 2002; Knights et al. 2002), with individuals of many populations exhibiting sedentary winter behavior (Rusak and Mosindy 1997; Borkholder et al. 2002). In river systems where downstream postspawn movements are unrestricted by dams, Lake Sturgeon can move hundreds of kilometers (Harkness and Dymond 1961; Priegel and Wirth 1971; Auer 1999) or can reside year-round in the river while using core areas for activity (Kettle...
River [unimpounded], Minnesota: Borkholder et al. 2002; Mississippi River [impounded]: Knights et al. 2002). Lake Sturgeon in Lake Winnebago, Wisconsin, moved extensively within home basins, but their travel away from these relatively limited areas was infrequent except during spawning periods (Priegel and Wirth 1971). Variation among movement strategies implies differences in preferred spawning, feeding, and overwintering habitats, which may be geographically distant depending on the system in which a particular sturgeon population resides.

Drowned river mouth lakes are a common feature along Great Lakes shorelines, including the eastern shore of Lake Michigan (Jude et al. 2005). These features form when an embayment is separated from the Great Lakes by sand deposition from wind, waves, transport by a river, or a combination of these processes (Dorr and Eschman 1971). Some of the drowned river mouth lakes are connected to large rivers suitable for spawning and have hosted or currently host remnants of Lake Sturgeon populations that were abundant prior to their collapse in the late 1800s (Tody 1974; Hay-Chmielewski and Whelan 1997). Drowned river mouth complexes bordering Lake Michigan offer a diverse array of habitats that are potentially suitable for Lake Sturgeon, allowing access to the river, lake, and Lake Michigan.

Few studies have focused on habitat preferences of adult Lake Sturgeon, and none has focused on habitat use in drowned river mouth complexes. Habitat selection by other sturgeons (Acipenseridae) is influenced by both abiotic and biotic factors, including environmental variables and food availability (e.g., Bramblett and White 2001; Erickson et al. 2002; Fox et al. 2002; Harris et al. 2005). Habitat use by Lake Sturgeon has been linked to substrate composition in rivers (Knights et al. 2002; Werner and Hayes 2004) and in lakes (Hay-Chmielewski 1987; Boase et al. 2011). Lake Sturgeon generally occupy habitats with depths less than 10 m and with silt, mud, gravel, or sand substrate (Harkness and Dymond 1961; Rusak and Mosindy 1997; Haxton 2003; Trested et al. 2011). Benthic macroinvertebrates (including Diptera, Ephemeroptera, and Trichoptera larvae and Mollusca) that are commonly found in Lake Sturgeon diets are often associated with these substrate types (Rusak and Mosindy 1997; Hay-Chmielewski 1987; Boase et al. 2011). Lake Sturgeon prefer habitats with reduced velocities and potentially higher productivity, such as transitional habitats between rivers and lakes (Engel 1990; Knights et al. 2002; Boase et al. 2011). Drowned river mouth lakes provide diverse habitats that may encompass abiotic and biotic variables of importance for Lake Sturgeon, including periods other than the spawning season.

The goal of the present study was to characterize habitat use by adult Lake Sturgeon in Manistee Lake, Michigan, a drowned river mouth complex. Our objectives were to (1) document residence of Lake Sturgeon in Manistee Lake during summer, (2) quantify abiotic and biotic variables throughout the lake that could influence Lake Sturgeon habitat use, and (3) model the relationship between these abiotic and biotic variables and habitat use by Lake Sturgeon. Knowledge of habitat use by adult Lake Sturgeon will aid in identification of habitats to be restored and protected for further rehabilitation of Lake Sturgeon populations.

**STUDY SITE**

Manistee Lake (Figure 1) is a 3.80-km² drowned river mouth with a maximum depth of 15 m and a mean depth of 7 m; the lake is fed by the Big Manistee and Little Manistee rivers in Manistee County, situated in the northwest corner of Michigan’s Lower Peninsula (Rediske et al. 2001; see Chiotti et al. 2008 for a description of the Manistee River and its watershed). The Manistee River system supports a stable adult population of Lake Sturgeon (Hayes and Caroffino 2012) and is listed as a high-suitability river system for Lake Sturgeon rehabilitation due to suitable habitat below Tippy Dam, a hydroelectric facility located 47 km upstream from Manistee Lake (Hay-Chmielewski and Whelan 1997). Lake Sturgeon reproduce in the Manistee River below Tippy Dam, as demonstrated by the collection of eggs and larvae (Chiotti et al. 2008).

The size of the spawning population during the study period was estimated to be 33–66 individuals (Lallaman et al. 2008). Manistee Lake has been impacted by industrial activity, including manufacturing of paper products, lumber processing, salt brine extraction, metal smelting, and related maritime shipping practices since the 1840s; in addition, lake sediments are contaminated with hydrocarbons and other chemicals, with...
LAKE STURGEON HABITAT USE

the exception of northern Manistee Lake and the area adjacent to the Little Manistee River (Rediske et al. 2001). Northern Manistee Lake also has a diverse benthic macroinvertebrate assemblage consisting of both pollution-tolerant and pollution-intolerant species, whereas the remaining areas of the lake have only pollution-tolerant species (Rediske et al. 2001). The lake was divided into 18 sampling sections for habitat assessment analyses (Figure 1). The number and location of the sections were determined after preliminary habitat sampling in 2003.

METHODS

Lake sturgeon capture.—Lake Sturgeon were captured in Manistee Lake by using gill nets at the mouth of the Manistee River (Figure 1) during 2003–2005 (27 March to 26 June 2003, 27 March to 1 June 2004, and 1 April to 28 May 2005; see Lallaman et al. 2008 for netting details). Lake Sturgeon were removed from the gill nets and placed in a holding tank. Total length (nearest 0.5 cm) and weight (nearest 0.5 kg) were recorded. Sex and spawning status of each Lake Sturgeon was determined by cutting a small (4–6-cm), ventral incision anterior to the pelvic girdle (Gunderson 2001; Lallaman et al. 2008) and then examining for either testes or eggs. Established conservative criteria were used to identify males and females as either nonspawning or spawning individuals in a given year. Males with white testes in either a prespawn or postspawn state were considered sexually mature (Rusak and Mosindy 1997; Bruch et al. 2001). Females with large (~4-mm), brown eggs (Rusak and Mosindy 1997; Bruch et al. 2001) were considered to be in a prespawn state; females with spongy, pink tissue where eggs would have been in a prespawn female were considered to be in a postspawn state (Bruch et al. 2001).

Telemetry tags (Sonotronics Model ART-15 combination acoustic/radio tags in 2003; Sonotronics Model CT-05 or CT-82-21 acoustic tags in 2004 and 2005) were inserted into the incision that was made for the spawning status assessment. Telemetry tags weighed 10–12 g, were 80–105 mm long with no external antenna, and had a guaranteed battery life of 14–18 months. Tags were programmed to transmit a unique aural sequence of approximately 1-s pings consisting of three or four numbers (ranging from 1 to 9), with a ∼2-s delay in between each number. Tags transmitted within the range of 69–83 kHz and had an approximate detection range of 1,000 m. Individuals were recognized by using the unique aural codes and the range of frequencies. The radiotelemetry capability of the ART-15 tags was not used during this study. Ten milligrams of oxytetracycline per kilogram of body weight were injected at the incision site. The incision was cleaned, closed with two to four absorbable sutures, and sealed with Nexaband surgical glue or Nexacare Liquid Bandage spray (Hay-Chmielewski 1987; Chapman et al. 1996; Fox et al. 2000). Lake Sturgeon were placed in the lake or into a water tank to recover after surgery. During recovery, a 3-cm section of the base of the pectoral fin ray was removed for age estimation (Cuerrier 1951; Wilson 1987; Rossiter et al. 1995; Collins and Smith 1996). Lake Sturgeon were released near the original capture location once they had fully recovered (i.e., were swimming upright).

Lake telemetry.—Daily in Manistee Lake during April-August 2003–2005, Lake Sturgeon with transmitters were actively tracked and relocated with a unidirectional hydrophone (Sonotronics DH-4 attached to a Sonotronics USR-96 telemetry receiver) attached to a 3.2-cm, polyvinyl chloride pipe. The receiver’s frequency was set in the middle of its range (usually about 75 kHz), and automatic frequency scanning was turned off. The hydrophone was lowered approximately 1 m into the water and was slowly rotated 360° to assess whether any tags were located nearby. If tags were detected, the individual tag that was closest to the boat (i.e., the tag with the strongest signal) was qualitatively determined. The operator would then tune to the individual frequency of the tag in question in order to hear that tag more clearly. The hydrophone was turned to the direction in which the signal was strongest (i.e., to determine a direction of travel), and the number of aural pulses was counted to determine the identity of the tagged individual. The boat was then driven toward the direction of the strongest signal, stopping periodically (every 20–500 m, depending on perceived signal strength) to allow the operator to listen and re-assess the direction of travel. When the signal was found to be equally strong in all horizontal directions, the cone of the hydrophone was pointed downward to the lake bottom. When the signal was stronger downward relative to the other directions (i.e., it was directly under the boat), the Lake Sturgeon was considered to have been relocated. Generally, ultrasonic transmitters can be located within less than 3–4 m (Winter 1983). The appropriate sampling section and GPS coordinates (Garmin GPS 12XL) were recorded when a Lake Sturgeon was relocated. Tracking typically started in the north end of Manistee Lake adjacent to the wetland complex and proceeded south, with stops made approximately every 700 m. Except during active tracking of a signal, the boat generally stayed in the middle of the lake when searching for signals. The field crew typically checked the Manistee shipping channel and Lake Michigan within 1 km of the river mouth upon completing the survey of the lake’s south end. Telemetry was terminated for the day after all possible Lake Sturgeon had been relocated or after the entire lake and shipping channel had been surveyed for tags. Lake Sturgeon were tracked in the Manistee River on their spawning runs, but those data are not reported herein. Fall, winter, and early spring telemetry were inconsistently performed due to safety issues (i.e., unstable ice and dangerous weather) as well as logistical concerns. Relocations that were recorded from May to August 2003–2005 are reported here.

Residence time was defined as the number of days for which an individual Lake Sturgeon was relocated within the study area. Residence times are conservative estimates because Lake Sturgeon may have been present in the lake before and after the tracking sessions. The proportion of relocations recorded for each Lake Sturgeon in a section was determined for May, June,
Habitat assessment.—Habitat use (i.e., habitat features that were used by Lake Sturgeon; Hall et al. 1997) and availability (i.e., habitat features that were accessible to Lake Sturgeon; Hall et al. 1997) were assessed during 15–27 May, 22–25 June, and 28–31 July 2003 and during 25–28 May, 24–29 June, and 22–27 July 2004; habitat use and availability were not measured in 2005. Potentially important habitat features for Lake Sturgeon (e.g., water depth, m; benthic temperature, °C; benthic dissolved oxygen, mg/L; Secchi depth, m; and benthic macroinvertebrate densities, individuals/m²) were measured each time a Lake Sturgeon was relocated during these time periods. We also randomly measured the same habitat features in each lake sampling section (n = 3–6) during each sampling period (Figure 1); these data were considered to represent habitat availability (Hall et al. 1997). Water depth was measured with a sonar depth finder that was adjusted for the depth of the transducer. Temperature and dissolved oxygen were recorded at the water surface and lake bottom with a YSI 650 temperature/dissolved oxygen meter. Secchi depth was measured with a 10-cm-diameter Secchi disk.

Benthic macroinvertebrates were collected with a 590-cm³ Ekman dredge; these collections were obtained at every Lake Sturgeon relocation in 2003 and with every fifth Lake Sturgeon relocation in 2004. Benthic macroinvertebrate samples (n = 3–6) were also collected randomly from each section in May–July of 2003 and 2004. The benthic macroinvertebrate samples were washed in a 500-µm-mesh screen bucket to remove fine sediments, and remaining materials were frozen or preserved in a 90% solution of ethanol. In the laboratory, samples were washed in a 500-µm sieve to remove fine sediments. The macroinvertebrates were separated from the substrate, identified to the lowest possible taxon, and enumerated (Thorp and Covich 1991; Merritt and Cummins 1996; McCafferty 1998). Benthic macroinvertebrate data were log transformed to meet the assumptions of normality. Temporal (i.e., month) and spatial (i.e., section) differences for each abiotic and biotic variable were examined with univariate analyses (GLM procedure in SAS, with Bonferroni correction for multiple tests; SAS 2008).

Substrate samples (n = 3 per lake sampling section) were also collected with a 590-cm³ Ekman dredge in August 2003 to examine differences in substrate composition among sampling sections. Samples were transported to the laboratory and immediately frozen at −20 °C. Substrate samples were thawed, and a subsample (~20–50 mL) was sieved into the following particle sizes: less than 63 µm; 63–124 µm; 125–249 µm; 250–499 µm; 500 µm to 2.0 mm; and over 2.0 mm (King 1982). The sieve contents were dried at 60 °C until a constant mass was reached (typically 24 h). Additional subsamples were used to determine the percent organic composition of the sediment. Subsamples were dried to a constant mass, weighed, and combusted in a Fisher Scientific Isotemp muffle furnace for 24 h at 550 °C (King and Cummins 1989). The subsamples were reweighed, and the ash-free dry mass was calculated to determine the percent organic material composition. Differences in the percent composition of particle size (multivariate ANOVA; GLM procedure in SAS) and the percent organic material composition of the substrate (ANOVA with Tukey’s tests; GLM procedure in SAS) among sampling sections were explored.

Penrose distance statistics (Manly 1986) were used to model the similarity of abiotic and biotic habitat features among lake sampling sections and Lake Sturgeon relocations. The Penrose distance statistic is dimensionless and does not imply an actual probability of occupancy by Lake Sturgeon. Like the Mahalanobis distance method, the Penrose distance statistic is interpreted as a suitability and probable use of a particular area (Manly et al. 2002; Kolowski and Nielsen 2008). Both methods incorporate the means of the variables included in the model as well as habitat use (Manly et al. 2002), but the Penrose distance statistic is less computationally complex. The Penrose distance (PD) for lake sampling section i was calculated as

\[ PD_i = \sum \frac{(\mu_{ki} - \mu_{kj})^2}{\sigma_k^2} \]

where p is the number of habitat variables, \( \mu_{ki} \) is the mean value of variable k in sampling section i, \( \mu_{kj} \) is the mean value of variable k at Lake Sturgeon relocation j, and \( \sigma_k^2 \) is the variance of variable k (Manly 1986). Correlation analyses were used to test for independence of the variables prior to conducting the regressions; r-values less than 0.50 indicated independence (CORR procedure in SAS). The habitat variables were standardized because they were measured on different scales, which could result in some variables contributing disproportionately to the Penrose distance statistic (Manly 1986). Data were standardized to the mean and variance, resulting in values ranging from 0 to 1. Correlations between Penrose distances and each habitat variable were tested to determine the relative importance of each variable in relation to Penrose distances across the study area (CORR procedure in SAS; Nielsen and Woolf 2002; Kolowski and Nielsen 2008). Penrose distances between the minimum and median values indicated lake sampling sections with the highest similarity in abiotic and biotic habitat features to those of Lake Sturgeon relocations.

RESULTS

Lake Telemetry

Locations of 15 individual Lake Sturgeon in Manistee Lake were monitored in 2003 (n = 10), 2004 (n = 10), and 2005 (n = 7) after the spawning run in the Manistee River concluded (Table 1). Ten males were tracked for two or three consecutive years; only two of the males were assumed to have spawned in consecutive study years. One female was tracked in Manistee
TABLE 1. Lake Sturgeon TL (cm) and estimated age (years) at tagging, sex and spawning status, and residence time during years when the fish were tracked in Manistee Lake, Michigan, 2003–2005. Age and sex could not be determined for all fish sampled. “Spawned” indicates that the Lake Sturgeon was assumed to have spawned in the Manistee River prior to being tracked in the lake; “present” indicates that the fish was assumed to not have spawned in a given year but was still present in the lake; and “—” indicates that the fish was not captured or relocated in the lake during the given year. Residence time for each fish was calculated as the difference between the first and last dates of relocation via telemetry in Manistee Lake. The plus symbol indicates calculated residence times that may have been lower than actual residence times (i.e., because the Lake Sturgeon was still present in Manistee Lake at the conclusion of the field season). Lake Sturgeon were identified by their unique telemetry signal sequence.

<table>
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<th>Fish number</th>
<th>TL (cm)</th>
<th>Age (years)</th>
<th>Sex</th>
<th>Spawning status</th>
<th>Residence time (d)</th>
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FIGURE 2. Mean (+SE) proportion of Lake Sturgeon telemetry relocations that were recorded in each sampling section (see Figure 1) in Manistee Lake, Michigan, during May–July 2003–2005.

The proportion of Lake Sturgeon relocations differed among lake sections (F<sub>17, 899</sub> = 28.69, P < 0.0001); the lake section × month interaction (F<sub>34, 899</sub> = 1.66, P = 0.01) and the lake section × month × year interaction (F<sub>68, 899</sub> = 1.65, P = 0.001) were significant (Figure 2). Some individuals were located in southern sections of the lake during sampling; however, the majority of Lake Sturgeon relocations occurred in northern sections near the wetland complex (Figure 2). Sections 12, 14, 15, 16, and 18 generally had more Lake Sturgeon relocations than the other sampling sections (Figure 2).

Habitat Assessment

Habitat available to Lake Sturgeon differed among lake sampling sections (P < 0.0001 for water depth, temperature, dissolved oxygen concentration, and Secchi depth). Water depths in the sampling sections varied from 0.2 to 14.0 m across the lake in 2003 and 2004 (Figure 3a); many of the shallowest sites were adjacent to the Manistee River and the wetland complex associated with the river mouth. Benthic water temperatures in Manistee Lake ranged from 13.2°C to 25.9°C; the lowest temperatures were recorded during May sampling events (Figure 3b). Mean dissolved oxygen concentrations decreased over the sampling period each year (from ~8-10 mg/L in May to ~5.5 mg/L in July; F<sub>2, 408</sub> = 616.58, P < 0.0001; Figure 3c). In general, the lowest dissolved oxygen concentrations were found at the south end of the lake. Secchi depths were approximately 2 m during each sampling period, and Secchi depths were shallower in the lake’s north end adjacent to the wetland complex (Figure 3d).

With the exception of fingernail clams (Sphaeriidae), densities of benthic macroinvertebrates varied among lake sampling sections (P < 0.0001). Chironomid larvae were consistently found in every sampling section (Figure 4a-f), and mean densities ranged from 48.4 individuals/m<sup>2</sup> (SE = 28.0; section 2, June 2003) to 2,776.4 individuals/m<sup>2</sup> (SE = 1,458.7; section 14, May 2004). Dreissenid mussels were primarily found in central Manistee Lake (sections 8-15; Figure 4a-f). Similarly, burrowing mayflies Hexagenia spp. were usually found in the wetland complex at the north end; fingernail clams were also found in the wetland complex, but their densities did not differ among sampling sections or through time (Figure 4a-f). A miliolid was almost always found in the wetland complex, although amphipod densities fluctuated greatly among sampling sections (Figure 4a-f). Isopods, oligochaetes, gastropods, and phantom midges Chaoborus spp. (Diptera), which were found at very low densities, comprised the majority of the remaining benthic macroinvertebrates in the samples. Interestingly, three larval species were captured in one Ekman grab in section 17 during July 2003.

The percent composition of substrate particle size did not differ among sampling sections (P > 0.14). Mean percent organic composition was lower in sections 5 and 17 than in sections 1, 2, 3, 4, and 11 (F<sub>17, 35</sub> = 4.73, P < 0.0001). Lake Sturgeon were captured in one Ekman grab in section 17 during July 2003.

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FIGURE 3. Box plots of (a) water depth (m), (b) benthic water temperature (°C), (c) dissolved oxygen concentration (mg/L), and (d) Secchi depth (m) for measures of habitat availability in lake sampling sections (open bars) and habitat use by Lake Sturgeon (shaded bars) in Manistee Lake during May–July in 2003 and 2004 (dashed line within each box = monthly mean; solid line in box = median; ends of box = first and third quartiles; whiskers = 95% confidence interval; black circles = outliers).
(mean = 30.18 individuals/m², SE = 3.74) for fingernail clams; and 0.00–12,300.24 individuals/m² (mean = 111.61 individuals/m², SE = 46.79) for amphipods (Figure 4g–l).

Penrose distance models were created for Lake Sturgeon relocations by using six habitat variables (water depth, dissolved oxygen, temperature, and densities of chironomid larvae, Hexagenia spp., and amphipods); these variables were uncorrelated and differed among lake sampling sections in univariate analyses. The sampling sections with the highest similarity to habitat at Lake Sturgeon relocation sites were located in the southern and central portions of Manistee Lake (Figure 5). Water depth and densities of chironomid larvae, Hexagenia spp., and amphipods were significantly correlated with the Penrose distance statistic values (Figure 6). Habitats that were most similar to Lake Sturgeon relocation sites were deeper and had lower densities of chironomid larvae, Hexagenia spp., and amphipods relative to the rest of the lake (Figure 6).

DISCUSSION

The majority of the Lake Sturgeon in this study used Manistee Lake for extensive periods during the summer—and potentially the entire year—regardless of whether the individual fish had spawned in a given year. Lake Sturgeon spawn in the Manistee River (Lallaman et al. 2008) and then move downriver, as has been observed in other Lake Sturgeon populations (e.g., McKinley et al. 1998; Auer 1999; Boase et al. 2011). The Lake Sturgeon then enter Manistee Lake, a drowned river mouth characterized by a wetland complex and a more polluted southern arm, and may move into Lake Michigan. Lake Sturgeon

![Habitat availability](image1)

![Habitat use](image2)

**FIGURE 4.** Mean densities (individuals/m²; log(x + 1) transformed) of chironomid larvae, dreissenid mussels, burrowing mayflies Hexagenia spp., fingernail clams, and amphipods: (a)-(f) as measures of habitat availability in lake sampling sections and (g)-(l) as measures of habitat use by Lake Sturgeon in Manistee Lake during May–July in 2003 and 2004.
Lake Sturgeon are often found, and they constitute a preferred prey item of Lake Sturgeon in other systems (Harkness and Dymond 1961; Hay-Chmielewski 1987; Chiasson et al. 1997). Small crustaceans, such as fingernail clams, have also been reported to occur in diets of both juvenile and adult Lake Sturgeon (Harkness and Dymond 1961; Jackson et al. 2002). Sampling sections that were least similar to Lake Sturgeon relocation sites (i.e., those with greater Penrose distances) had higher densities of chironomid larvae, Hexagenia spp., and amphipods; however, Penrose distance is a measure of suitability and probable use, and it incorporates a number of variables, including important abiotic factors such as water depth. The productive wetland complex is likely a critical habitat for both juvenile and adult Lake Sturgeon given the abiotic and biotic features of this habitat.

Although Lake Sturgeon were found primarily near the wetland complex in northern Manistee Lake, sampling sections in southern and central Manistee Lake were more similar to Lake Sturgeon relocation sites. This may indicate that additional factors not examined in this study also influence habitat use by Lake Sturgeon. For example, habitat use has been associated with substrate type in several studies (Hay-Chmielewski 1987; Boase et al. 2011; Trested et al. 2011). The selection of substrate type is often linked with access to prey (e.g., Hay-Chmielewski 1987; Boase et al. 2011), suggesting that the substrate increases the presence of prey or feeding efficiency. However, there were no differences in substrate size and very few differences in substrate composition among the sampling sections. Although substrate samples for the habitat use assessment were not collected at Lake Sturgeon relocations, the inclusion of substrate size and composition in the Penrose distance statistics would not have significantly altered the outcome given the similarity of substrate composition among the lake sampling sections. Additionally, Lake Sturgeon habitat use and movement rates have been linked to water flow (e.g., Borkholder et al. 2002; Knights et al. 2002; Trested et al. 2011). Transitional areas in which currents change from fast to slow may affect habitat features, such as substrate composition and prey availability (Knights et al. 2002), or may provide some other habitat cue for Lake Sturgeon. Given the positive correlation between movement rates and discharge (Borkholder et al. 2002), water flow in northern Manistee Lake at the juncture of the river delta and shipping channel may be a factor influencing Lake Sturgeon habitat use, although this variable was not included in our assessment. Similarly, a subset of Lake Sturgeon in Lake St. Clair also remained in lake areas near the delta of the St. Clair River (Boase et al. 2011). Another possibility is that Lake Sturgeon are selecting habitat on a finer scale than was measured in this study.

Alternatively, Lake Sturgeon use of sampling sections that were deemed more similar to the fish relocation sites may have occurred during times when the habitat use assessment was not being actively conducted. Lake Sturgeon have exhibited a wide range of summer movement rates, from 0.02 to 0.8 km/d (Hay-Chmielewski 1987; Gerig et al. 2011; Adams et al. 2006), suggesting that they easily could have moved among our
FIGURE 6. Relationships between Penrose distance statistics and measures of habitat availability in Manistee Lake: (a) water depth (m); (b) dissolved oxygen (mg/L); (c) benthic water temperature (°C); and densities (individuals/m²) of (d) chironomid larvae, (e) burrowing mayflies Hexagenia spp., and (f) amphipods. Biotic data were $\log(x + 1)$ transformed for analyses. Spearman’s rank correlation coefficients ($R_s$) and $P$-values are given for each correlation.
sampling ranges in Manistee Lake were similar to previous estimates for Lake Sturgeon in other systems (i.e., home range = 15.28-46.25 km²; Haxton 2003; Adams et al. 2006), then Lake Sturgeon would have the potential to use the entire lake. However, Lake Sturgeon were consistently found in the same sampling sections even when relocated at different times of the year, and annual mean home ranges varied from 0.50 to 0.84 km² (Damstra 2007). Although telemetry studies provide information on fish locations, factors that are critical for survival are difficult to determine without manipulative studies (Rogers and White 2007).

A combination of abiotic features and prey availability likely drives habitat use by Lake Sturgeon, making it difficult to identify one or two factors that determine habitat use (Hay-Chmielewski 1987; Boase et al. 2011; Gerig et al. 2011). Inclusion of other variables (e.g., current and flow data in lacustrine habitats) in future studies of Lake Sturgeon habitat use may further elucidate their use of wetland habitats. As the ecosystem of Manistee Lake recovers from its former and current industrial uses, Lake Sturgeon may increase their use of the southern end, especially the area adjacent to the mouth of the Little Manistee River. Continued protection of the northern wetland complex is necessary for the viability of this population. The incidental capture of larval Lake Sturgeon in the wetland complex is further evidence of Manistee Lake’s importance for the future viability of the population. Future management of Lake Sturgeon populations should consider habitat conditions during all life stages, including summer habitat use.

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REFERENCES


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Using a Stream Network Census of Fish and Habitat to Assess Models of Juvenile Salmonid Distribution

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Using a Stream Network Census of Fish and Habitat to Assess Models of Juvenile Salmonid Distribution

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Abstract
We censused juvenile salmonids and stream habitat over two consecutive summers to test the ability of habitat models to explain the distribution of juvenile Coho Salmon Oncorhynchus kisutch, young-of-the-year (age-0) steelhead O. mykiss, and steelhead parr (age ≥1) within a network consisting of several different-sized streams. Our network-scale habitat models explained 27, 11, and 19% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively, but strong levels of spatial autocorrelation were typically present in the residuals. Explanatory power of base habitat models increased and spatial autocorrelation decreased with the sequential inclusion of variables accounting for the effects of stream size, year, stream, reach location, and a tertiary interaction term. Stream-scale models were highly variable. Fish–habitat associations were rarely linear and ranged from negative to positive; the variable accounting for location of the habitat within a stream was often more important than the habitat variables. The limited success of our network-scale models was apparently related to variation in the strength and shape of fish–habitat associations across and within streams and years. These results indicate that there are several potential limitations to extrapolating models to broader areas based only on spatially limited surveys.

Stream habitat models can be a useful tool for predicting the density and distribution of salmonids (Fausch et al. 1988; Railsback et al. 2003; Rosenfeld 2003). The models assume that fish selectively occupy habitats (e.g., pools) with particular characteristics (e.g., depth), and if the fish–habitat associations are known, the density and distribution of fish can be predicted based on the quantity and distribution of those habitats (Beecher et al. 1993; Knapp 1999; Van Horne 2002). The utility of a model therefore depends on the strength and consistency of the surrogate for fish distribution: the fish–habitat associations. For single reaches or streams, habitat models may effectively predict fish density and distribution by using a few habitat variables, but models generally perform poorly when applied broadly to several streams because of variation in fish–habitat associations within streams and between streams and years (Fausch et al. 1988; Dunham and Vinyard 1997; Gibson et al.

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Nonetheless, models that are derived from a subsample of reaches or streams are commonly expanded to unsampled areas to predict fish distributions at larger scales that are more relevant to recovery and restoration, such as the stream network (Fausch et al. 2002). A potential concern with this approach is that agreement between models and the actual distribution of fishes is rarely tested at the stream network scale, so the extent and effects of variability in fish–habitat associations on larger-scale predictions remain poorly understood.

One challenge to evaluating how well stream habitat models predict fish distribution at the network scale is a lack of spatially extensive and continuous data. Salmonid and stream habitat data have traditionally been collected for a single species or life stage in short reaches (e.g., 100–1,000 m) located at widely spaced intervals in one stream or similarly sized streams, often during only a single year (Fausch et al. 2002). Although this approach is typically based on logical sampling designs, it presents three problems for model predictions at more extensive scales. First, the distribution of salmonids is often patchy, and sampling of short and sparsely located reaches could miss aggregations, voids, and the upper and lower limits of fish presence, thereby misrepresenting large-scale distribution patterns (Torgersen et al. 2012) and potentially confounding model predictions (Dunham and Vinyard 1997; Angermeier et al. 2002). Second, focusing on a single species or life stage may miss important variability in assemblage patterns because different salmonid species and age-classes may use different parts of a network (Gibson et al. 2008; Reeves et al. 2011; Brenkman et al. 2012; Kanno et al. 2012). Lastly, fish–habitat associations can vary extensively between different stream sizes, different streams, reach locations within streams, and years (Fausch et al. 1988; Dunham and Vinyard 1997; Rosenfeld et al. 2000). Sparse sampling of reaches or streams in only a single year may therefore oversimplify fish–habitat associations and underestimate the potential influences of space and time on model effectiveness (Clinchy 2002; Isaak and Thurow 2006; Torgersen et al. 2012).

One way to address some of these limitations is to collect continuous data (i.e., census) over long sections (e.g., 40–70 km) of a stream for multiple species of salmonids (Torgersen et al. 2006; Brenkman et al. 2012; Reeves et al. 2011; Kanno et al. 2012) to more closely match the scale at which (1) salmonids carry out their freshwater life cycle (Riemann and Dunham 2000) and (2) managers make decisions (Beechie and Bolton 1999). A census of several streams of varying sizes seems particularly applicable to evaluating how network-scale patterns in fish and habitat distribution match stream habitat model predictions. To date, however, most studies that have censused fish and stream habitat have focused on associations between salmonids and habitat along the longitudinal profiles of individual medium to large streams (Torgersen et al. 1999, 2006; Brenkman et al. 2012) or small streams (Gresswell et al. 2006; Reeves et al. 2011; Kanno et al. 2012). Few studies have used census data to test how well habitat characteristics predict the density and distribution of salmonids across a network of both smaller and larger streams over multiple years, but results for adult salmonids have provided novel insights into the extent to which space, time, and the space × time interaction can potentially influence fish distribution models at larger scales (Isaak and Thurow 2006).

Census data could also be used to evaluate the extent and effects of spatial autocorrelation (Torgersen et al. 2008, 2012), which occurs when measurements in adjacent areas are more similar to each other than measurements in distant areas (Legendre 1993). The phenomenon can inflate apparent explanatory power and increase the chance of type I errors (false positives; Legendre et al. 2002). The patchy distributions of salmonids and their associations with habitat are prone to spatial autocorrelation that may violate assumptions about the independence of survey reaches (Dunham and Vinyard 1997; Dunham et al. 2002), but this problem is rarely accounted for when modeling aquatic organisms (e.g., Segurado et al. 2006).

Stream habitat models are commonly applied to draw inferences about juvenile salmonids that spend long periods in freshwater, such as Coho Salmon Oncorhynchus kisutch and steelhead O. mykiss (anadromous Rainbow Trout). These two species co-exist in many networks, and their associations with habitat are well studied (Everest et al. 1985; Bisson et al. 1988; Bjornn and Reiser 1991) and have been extensively modeled (Porter et al. 2000; Rosenfeld et al. 2000; Sharma and Hilborn 2001; Burnett 2001), although more so for juvenile Coho Salmon than for steelhead. However, censuses of both species and stream habitat in the same network are limited to long but disjunct sections of river in a single year (Scarnecchia and Roper 2000) and a single-thread small stream over multiple years (Reeves et al. 2011), with each study reporting somewhat contrasting findings. Furthermore, we are not aware of previous research using census data to test how stream size, stream, location, and year influence the ability of stream habitat models to explain the distribution and density of juvenile Coho Salmon and steelhead at the network scale. Such tests are needed, however, to understand the level of uncertainty that might be expected by managers and scientists when using a model to predict the density and distribution of salmonids across several streams.

In this study, we tested the ability of habitat models to explain the network-scale distribution of juvenile Coho Salmon and two size-classes of juvenile steelhead. To accomplish this, we censused stream habitat characteristics and juvenile salmonids in over 60% of the linear stream kilometers available to anadromous salmonids in the Calawah River, Washington, during two summers. The objectives were to (1) determine how well models consisting of several instream habitat characteristics predicted juvenile salmonid distribution at the network scale; (2) test for spatial autocorrelation and the effects of stream size, stream, reach location within a stream, and year on network-scale models; and (3) test the extent to which juvenile salmonid distribution at the stream scale is a function of individual habitat characteristics or of the location of the habitat within the stream. The high-resolution data set provided a unique opportunity to assess the strength and consistency of fish–habitat associations across
multiple streams. We discuss the results and their implications for stream habitat modeling and stream conservation actions.

METHODS

Survey Site and Salmonid Populations

The Calawah River basin (196 km²) is a tributary of the greater Quillayute River basin, which is part of the temperate rainforest that stretches across the western side of the Olympic Peninsula (Figure 1). The main-stem Calawah River is formed by the South Fork (SF) Calawah River and North Fork (NF) Calawah River. Elk Creek flows into the main-stem Calawah River, whereas the Sitkum River, Hyas Creek, and Lost Creek drain into the SF Calawah River. The streams are variable in channel length and width, with "rivers" being longer and larger than "creeks" (Tables 1, 2). The NF Calawah River was unique because an extensive section of stream (∼12 river kilometers [RKM]) naturally goes dry during the summer, and we considered sections at either end separately because of the differences in width and slope; hereafter, these sections are referred to as the lower and upper NF Calawah River. The stream network is large enough to contain numerous tributaries with differing characteristics and exceptional bank-to-bank water clarity for snorkeling, yet it is small enough (wetted width < 25 m) to be adequately surveyed by a small crew (diver and bank walker) within a relatively short period of time (∼3 weeks).

The Calawah River supports naturally spawning populations of summer and winter steelhead, fall and summer Chinook Salmon O. tshawytscha, fall Coho Salmon, resident Rainbow Trout, Coastal Cutthroat Trout O. clarkii clarkii, and a small number of Chum Salmon O. keta and river-type Sockeye Salmon O. nerka. We focused on enumerating juvenile Coho Salmon and steelhead because (1) they are the most abundant species, (2) they have extended freshwater rearing periods, and (3) respective associations with stream habitat may vary between species and within size-classes (e.g., age 0 versus age 1; Everest et al. 1985; Bjornn and Reiser 1991). Little information exists on juvenile Coho Salmon or steelhead in this network, but adult steelhead spawn primarily in the larger main-stem Calawah, SF Calawah, Sitkum, and lower NF Calawah rivers, while fall Coho Salmon spawn primarily in the creeks and throughout the entire NF Calawah River (Quileute Tribe and Washington Department of Fish and Wildlife, unpublished annual steelhead redd surveys, 1995–2003).

Data Collection

Extent of surveys.—Our goal each summer was to census fish and stream habitat across all stream habitats that were available to juvenile anadromous salmonids in the SF Calawah River, NF Calawah River, Sitkum River, Elk Creek, Hyas Creek, and Lost Creek (Figure 1). Surveys in small and large streams (except for Elk Creek, Lost Creek, and the SF Calawah River) ended at the uppermost falls constituting a barrier to anadromous salmonids. We continued surveys for a minimum of 1.5 km upstream of assumed barrier falls to confirm a lack of anadromous salmonids. The upper 0.7 km of Elk Creek and the upper 0.4 km of Lost Creek were not surveyed because depths were consistently too shallow for snorkeling (<0.2 m deep). The upper SF Calawah River inside the Olympic National Park was not sampled because the habitat is in pristine condition, whereas the vast majority of areas outside the park drain a mosaic of commercial timberlands in various stages of growth and harvest (Smith 2000), and such variation in land use patterns would potentially

Juvenile salmonid surveys.—We used snorkel surveys to census the distribution and abundance of salmonids in all habitat units greater than 0.2 m in depth (Dolloff et al. 1993; Thurow 1994). All units were sampled by the same experienced diver and habitat recorder to reduce bias associated with multiple surveyors (Hankin and Reeves 1988; Thompson and Mapstone 1997). Salmonids were classified based on species and size (estimated FL) as juvenile Coho Salmon, young-of-the-year trout (hereafter, age-0 steelhead; <70 mm), and age-1 and older steelhead parr (hereafter, steelhead parr; 70–200 mm; J. McMillan, unpublished data); larger parr (>200 mm) that could have matured as resident Rainbow Trout (e.g., McMillan et al. 2007) were excluded. We classified age-0 trout as steelhead, but we acknowledge that some of the small trout were presumably Coastal Cutthroat Trout; however, at that size it is difficult to distinguish the species (Thurow 1994). Thus, we assumed that most (>85%) of the age-0 fish were steelhead offspring based on comparisons of adult abundance estimates for both species (WDFW 2012; J. R. McMillan, unpublished data).

Stream habitat surveys.—We identified habitat units as pools and nonpools according to Bisson et al. (1982), and we measured characteristics that were important for juvenile Coho Salmon and steelhead habitat use, including habitat unit depth, wetted habitat unit width, habitat unit gradient (Everest et al. 1985; Bjornn and Reiser 1991), and stream valley width (Burnett et al. 2007). Wetted width and length of each habitat unit were measured across a single transect, with width being measured at a spot that was approximately average for the unit (Hankin and Reeves 1988). We measured habitat unit gradient with a laser range finder and a stadia rod, and maximum depth was measured at the single deepest location. Stream channel (i.e., bankfull) depth and width as well as floodprone width (stream width at a discharge twice that of the maximum bankfull depth) were measured with a laser range finder, and the valley width index (VWI) was then calculated as floodprone width divided by bankfull width (Grant and Swanson 1995).

Statistical Analyses

Stream habitat and salmonid variables.—We used the habitat-unit-scale data to generate response and predictor variables at the reach scale for 2002 and 2003. First, working upstream from the mouth, we delineated each small stream into approximately 200-m reaches and each large stream into approximately 1,000-m reaches (Table 1); these reach lengths are similar to those used in traditional noncensus studies (Fausch et al. 2002). Because we did not use block nets and fish may have moved between units to avoid the diver (Peterson et al. 2005), aggregation of the data into reaches also reduced the potential for fish movement to influence habitat associations at smaller scales. We also aggregated data into reaches because fish use different habitat units within a given area to survive, grow, and develop over the course of a year (e.g., habitat complementation; Nagermeier and Schlosser 1989; Schlosser and Nagermeier 1995), making longer stream reaches more inclusive of the surrounding habitat potential. Reach lengths varied slightly because we placed the upstream boundary of each reach at natural breaks in habitat units rather than artificially dividing a unit (and its fish) into partial units to achieve uniformity. Second, for each reach and year, we calculated the weighted mean of five habitat metrics, including the percentage of the reach length in pool habitat, mean habitat unit depth, mean wetted width, mean unit gradient, and mean VWI (Table 2). We then calculated the number of juvenile Coho Salmon, age-0 steelhead, and steelhead parr per linear meter of stream (our measure of density) to represent

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<td>6.4</td>
<td>102/14/109/14</td>
<td>211 ± 26</td>
</tr>
<tr>
<td>Upper North Fork</td>
<td>Small</td>
<td>3.0</td>
<td>114/14/103/14</td>
<td>211 ± 23</td>
</tr>
<tr>
<td>Elk Creek</td>
<td>Small</td>
<td>3.5</td>
<td>75/15/66/12</td>
<td>202 ± 31</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Stream</th>
<th>Length (km)</th>
<th>n units/reaches</th>
<th>Mean reach length (m)</th>
<th>% of stream &lt;0.2 m deep</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Fork</td>
<td>Large</td>
<td>24.8</td>
<td>94/10/81/10</td>
<td>982 ± 308</td>
</tr>
<tr>
<td>Calawah River</td>
<td>Large</td>
<td>13.0</td>
<td>114/12/125/12</td>
<td>1,056 ± 150</td>
</tr>
<tr>
<td>Lower North Fork</td>
<td>Large</td>
<td>15.9</td>
<td>242/12/326/16</td>
<td>1,016 ± 135</td>
</tr>
<tr>
<td>Calawah River</td>
<td>Large</td>
<td>2.9</td>
<td>173/23/167/23</td>
<td>223 ± 26</td>
</tr>
<tr>
<td>Sitkum River</td>
<td>Small</td>
<td>6.4</td>
<td>102/14/109/14</td>
<td>211 ± 26</td>
</tr>
<tr>
<td>Upper North Fork</td>
<td>Small</td>
<td>3.0</td>
<td>114/14/103/14</td>
<td>211 ± 23</td>
</tr>
<tr>
<td>Elk Creek</td>
<td>Small</td>
<td>3.5</td>
<td>75/15/66/12</td>
<td>202 ± 31</td>
</tr>
</tbody>
</table>
TABLE 2. Descriptions and expected influence of variables considered in generalized additive models for predicting the density (fish/linear meter) of juvenile Coho Salmon, age-0 steelhead, and steelhead parr (age ≥1).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Expected influence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream habitat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent pool (%)</td>
<td>(Length of reaches consisting of pool habitat)/(reach length)</td>
<td>Influences availability of slow-water habitats&lt;sup&gt;a,b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>Habitat unit depth × (unit length/reach length)</td>
<td>Influences extent of vertical cover and habitat area&lt;sup&gt;a,b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mean width (m)</td>
<td>Habitat unit width × (unit length/reach length)</td>
<td>Influences available habitat area&lt;sup&gt;a,b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Stream channel gradient (%)</td>
<td>Rise over run for entire reach length (Habitat unit VWI × unit length)/(reach length)</td>
<td>Influences stream velocity and substrate size&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mean valley width index (VWI)</td>
<td></td>
<td>Influences availability of secondary streams&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Time, size, stream, and space</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>Year in which sampling was conducted</td>
<td>Fish–habitat associations may vary annually&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>Stream size</td>
<td>Small (wetted width &lt; 7 m) or large (wetted width &gt; 7 m) streams</td>
<td>Fish–habitat associations may vary by stream size&lt;sup&gt;e,f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Stream</td>
<td>Geographically distinct tributary or stream section</td>
<td>Fish–habitat associations may vary by stream&lt;sup&gt;e,f&lt;/sup&gt;</td>
</tr>
<tr>
<td>River kilometer</td>
<td>Longitudinal location of reach midpoint within each stream</td>
<td>Accounts for spatial autocorrelation in the model&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Bisson et al. 1988.
<sup>b</sup>Bjornn and Reiser 1991.
<sup>c</sup>Montgomery et al. 1999.
<sup>d</sup>Grant and Swanson 1995.
<sup>e</sup>Fausch et al. 1988.
<sup>f</sup>Dunham and Vinyard 1997.
<sup>g</sup>Segurado et al. 2006.

reach-scale variation in distribution (Table 3). The caveat to the density estimate is that we were unable to enumerate salmonids via snorkeling in units with depths less than 0.2 m, and age-0 steelhead often use shallow habitats (Bjornn and Reiser 1991).

Modeling approach.—We used generalized additive models (GAMs; Wood 2011) to examine correlations between juvenile salmonid density and the five stream habitat variables (Table 4). Generalized additive models offer a flexible approach to modeling that requires minimal assumptions about the shape of the relationships and allows for a range of possible error distributions and links (Efron and Tibshirani 1991). Results of other studies using GAMs (e.g., Knap and Preisler 1999; Stoner et al. 2001) suggest that the approach has considerable utility in the development of models to predict fish distributions based on habitat characteristics because the shape of the response is rarely known prior to the analysis. We used the GAM function implemented in R (R Development Core Team 2011) with the mgcv package (Wood 2001). The default smoothing function, thin-plate penalized regression splines, and smoothing parameter estimation method (generalized cross validation criterion) were used (Wood 2003). We assumed normally distributed errors with the identity link, and we examined the model residuals to check this assumption.

Network-scale models.—We first fit GAMs at the scale of the entire stream network to examine the ability of a common set of five stream habitat variables (Table 4) to explain variation in the density (i.e., fish per linear meter) of juvenile Coho Salmon, age-0 steelhead, and steelhead parr. We then gradually added complexity to the model by first allowing the habitat variable relationships to vary by stream size and then adding year, stream, the reach location × stream interaction, and lastly the location × stream × year interaction.

The habitat portion of the model is either expressed as a sum of smoother terms (where $s =$ smooth function),

$$
\text{Density (fish/m)} = \beta_0 + s_1(\% \text{ pool}) + s_2(\text{mean depth}) + s_3(\text{mean width}) + s_4(\text{mean slope}) + s_5(\text{mean V WI}),
$$

or as a sum of smoother terms that vary by stream size (see Table 4),

$$
\text{Density (fish/m)} = \beta_0 + s_1(\% \text{ pool [stream size]}) + \ldots
$$

Here, the term $s_1(\% \text{ pool [stream size]})$ indicates separate relationships (smooths) for each level of the stream size factor (i.e., small stream or large stream). This is analogous to a fixed interaction term in a standard linear model. In all cases, the habitat variable relationships were limited to smooths of four
TABLE 3. Analysis of deviance results for generalized additive models constructed for the entire Calawah River stream network, with iterative influences of stream size, time, stream, and space and their interaction on the base habitat model; the model deviance, df, delta Akaik's information criterion (ΔAIC), $R^2$ values, and Moran's I-statistic (a measure of spatial autocorrelation in model residuals; see M methods) for 2002 and 2003 are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Deviance</th>
<th>df</th>
<th>ΔAIC</th>
<th>$R^2$</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Coho Salmon</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null model</td>
<td>160.0</td>
<td>1.0</td>
<td>247</td>
<td>0.00</td>
<td>0.56</td>
<td>0.68</td>
</tr>
<tr>
<td>Habitat</td>
<td>112.7</td>
<td>9.3</td>
<td>193</td>
<td>0.27</td>
<td>0.54</td>
<td>0.58</td>
</tr>
<tr>
<td>Habitat × stream size</td>
<td>96.7</td>
<td>13.8</td>
<td>171</td>
<td>0.35</td>
<td>0.58</td>
<td>0.38</td>
</tr>
<tr>
<td>(Habitat × stream size) + year</td>
<td>90.9</td>
<td>14.8</td>
<td>161</td>
<td>0.39</td>
<td>0.54</td>
<td>0.33</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × stream</td>
<td>67.3</td>
<td>20.3</td>
<td>111</td>
<td>0.53</td>
<td>0.22</td>
<td>0.25</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × (location × stream)</td>
<td>50.8</td>
<td>31.0</td>
<td>76</td>
<td>0.63</td>
<td>0.25</td>
<td>0.14</td>
</tr>
<tr>
<td>(Habitat × stream size) + (location × stream × year)</td>
<td>28.3</td>
<td>51.7</td>
<td>0</td>
<td>0.76</td>
<td>0.04</td>
<td>-0.19</td>
</tr>
<tr>
<td><strong>Age-0 steelhead</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null model</td>
<td>44.7</td>
<td>1.0</td>
<td>113</td>
<td>0.00</td>
<td>0.25</td>
<td>0.52</td>
</tr>
<tr>
<td>Habitat</td>
<td>38.0</td>
<td>9.4</td>
<td>97</td>
<td>0.11</td>
<td>0.20</td>
<td>0.40</td>
</tr>
<tr>
<td>Habitat × stream size</td>
<td>34.9</td>
<td>16.4</td>
<td>94</td>
<td>0.16</td>
<td>0.16</td>
<td>0.33</td>
</tr>
<tr>
<td>(Habitat × stream size) + year</td>
<td>30.8</td>
<td>17.0</td>
<td>70</td>
<td>0.25</td>
<td>0.18</td>
<td>0.26</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × stream</td>
<td>24.9</td>
<td>20.4</td>
<td>34</td>
<td>0.38</td>
<td>0.11</td>
<td>0.12</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × (location × stream)</td>
<td>23.5</td>
<td>28.2</td>
<td>38</td>
<td>0.39</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>(Habitat × stream size) + (location × stream × year)</td>
<td>16.4</td>
<td>45.2</td>
<td>0</td>
<td>0.53</td>
<td>-0.25</td>
<td>-0.10</td>
</tr>
<tr>
<td><strong>Steelhead parr</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null model</td>
<td>3.6</td>
<td>1.0</td>
<td>263</td>
<td>0.00</td>
<td>0.24</td>
<td>0.71</td>
</tr>
<tr>
<td>Habitat</td>
<td>2.8</td>
<td>9.5</td>
<td>230</td>
<td>0.19</td>
<td>0.27</td>
<td>0.70</td>
</tr>
<tr>
<td>Habitat × stream size</td>
<td>2.0</td>
<td>18.2</td>
<td>180</td>
<td>0.39</td>
<td>0.11</td>
<td>0.68</td>
</tr>
<tr>
<td>(Habitat × stream size) + year</td>
<td>1.8</td>
<td>19.6</td>
<td>167</td>
<td>0.43</td>
<td>0.07</td>
<td>0.65</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × stream</td>
<td>1.4</td>
<td>23.3</td>
<td>112</td>
<td>0.58</td>
<td>0.19</td>
<td>0.43</td>
</tr>
<tr>
<td>(Habitat × stream size) + year × (location × stream)</td>
<td>1.3</td>
<td>32.7</td>
<td>116</td>
<td>0.58</td>
<td>0.16</td>
<td>0.40</td>
</tr>
<tr>
<td>(Habitat × stream size) + (location × stream × year)</td>
<td>0.6</td>
<td>49.2</td>
<td>0</td>
<td>0.78</td>
<td>-0.30</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Density (fish/m)

$$= \beta_0 + s_1(\% \text{ pool [stream size]}) + s_2(\text{mean depth [stream size]}) + s_3(\text{mean width [stream size]}) + s_4(\text{mean slope [stream size]}) + s_5(\text{mean VVI [stream size]}) + s_6(\text{location [stream - year]}).$$

Here, the dimension of the location smooth is constrained to five. For each model, we calculated the deviance, the df, the delta Akaik's information criterion (ΔAIC; Burnham and Anderson 2002), and the $R^2$ (proportion of total variability in fish density that was explained by the model). Evaluation of model performance was based primarily on ΔAIC.

Spatial autocorrelation is a common statistical property in ecological data that poses problems because correlated data violate the assumption of independence, which is a key assumption for parametric statistical tests (Legendre 1993; Legendre et al. 2002). To account for this, we quantified the degree to which the individual models explained the spatial structure in fish density among reaches by calculating Moran’s I-statistic for the model residuals. Moran’s I-values of 0–0.20, 0.21–0.50, 0.51–0.70, and 0.71–1.0 indicate that spatial autocorrelation is absent, weakly positive, moderately positive, or strongly positive, respectively, and vice versa if values are negative for negative spatial autocorrelation (Legendre et al. 2002).

Stream-scale models.—Next, we fit GAMs at the stream scale to test the extent to which juvenile salmonid distribution was a function of individual habitat characteristics in comparison with
the location of the habitat (i.e., stream reach) within the stream. First, we fit GAMs for each stream and each habitat variable individually to investigate the potential for variation in fish-habitat associations among streams. Second, we evaluated the effect of space within a stream by adding a reach location term to each model (e.g., Legendre et al. 2002). We used P-values and R² for each variable (e.g., Fausch et al. 1988) to compare and contrast the relative effects of each habitat variable versus reach location. Year was included as a main effect (NA = not applicable because fish abundance was too low for modeling).

Due to the continuous spatial sampling design, we recognize the danger of overfitting and type I error; therefore, the R² values should be viewed as upper bounds of any potential fish-habitat associations at the network and stream scales. By entering location in the GAMs as a smoother term (e.g., Knapp and Preisler 1999), we allowed for fish-habitat associations and the effects of reach location to be compared in a common framework.

RESULTS

Extent of Census, Stream Habitat, and Juvenile Salmonids

We censused stream habitat and juvenile Coho Salmon and steelhead across 52.5 km of stream habitat in 2002 and 54.6 km in 2003, which accounted for slightly more than 60% of the linear stream network that was accessible (total of ~84 linear kilometers of stream) to juvenile salmonids during summer (Figure 1; Table 1). Cumulatively, we sampled 95% and 93% of the linear length of stream in 2002 and 2003, respectively, and only in a few streams did shallow depths (depth < 0.2 m) preclude sampling of more than 10% of the habitat (Table 1). Close bank observation suggested that few fish used shallow habitats in the small streams, whereas age-0 steelhead were rare to abundant in such habitats within the large streams.

Habitat characteristics were highly variable (Figure 2). Large streams were generally deeper and had narrower VWIs than small streams; variation in mean depth and mean width was greater in large streams than in small streams, while variability in mean VWI was generally greater in small streams (Figure 2). In addition, variation in habitat metrics between streams was generally greater than variation between years within a given stream (Figure 2). Owing to this complexity, no two streams displayed the same habitat characteristics.

All salmonids co-existed and were present up to anadromous barriers throughout most of the stream network (Figure 3a–c). Coho Salmon and age-0 steelhead generally were found at the highest densities, and steelhead parr typically exhibited the lowest densities (Figure 2). Densities within streams were similar among years for all three salmonid groups, with the upper and lower NF Calawah River being the clear exception (Figure 2). Coho Salmon and age-0 steelhead displayed similar distributions that were mostly continuous, although

<table>
<thead>
<tr>
<th>Variable</th>
<th>Elk Creek</th>
<th>Hyas Creek</th>
<th>Lost Creek</th>
<th>Upper North Fork Calawah River</th>
<th>Lower North Fork Calawah River</th>
<th>South Fork Calawah River</th>
<th>Sitkum River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent pool</td>
<td>0.48</td>
<td>0.09</td>
<td>0.58</td>
<td>0.21</td>
<td>0.14</td>
<td>0.15</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>M ean depth</td>
<td>0.35</td>
<td>0.00</td>
<td>0.36</td>
<td>0.06</td>
<td>0.39</td>
<td>0.36</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>M ean width</td>
<td>0.33</td>
<td>0.41</td>
<td>0.09</td>
<td>0.09</td>
<td>0.10</td>
<td>0.16</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.52</td>
<td>0.45</td>
<td>0.04</td>
<td>0.36</td>
<td>0.36</td>
<td>0.21</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>M ean VWI</td>
<td>0.38</td>
<td>0.27</td>
<td>0.05</td>
<td>0.84</td>
<td>0.06</td>
<td>0.05</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>RKM</td>
<td>0.74</td>
<td>0.53</td>
<td>0.60</td>
<td>0.67</td>
<td>0.54</td>
<td>0.60</td>
<td>Indiv. w/RKM</td>
</tr>
<tr>
<td>Coho Salmon</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent pool</td>
<td>0.07</td>
<td>0.22</td>
<td>0.20</td>
<td>0.32</td>
<td>0.08</td>
<td>0.26</td>
<td>0.47</td>
</tr>
<tr>
<td>M ean depth</td>
<td>0.26</td>
<td>0.11</td>
<td>-0.04</td>
<td>0.40</td>
<td>0.20</td>
<td>0.10</td>
<td>0.47</td>
</tr>
<tr>
<td>M ean width</td>
<td>0.12</td>
<td>0.36</td>
<td>0.01</td>
<td>0.15</td>
<td>0.14</td>
<td>0.15</td>
<td>0.43</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.07</td>
<td>0.37</td>
<td>0.16</td>
<td>0.01</td>
<td>0.01</td>
<td>0.08</td>
<td>0.55</td>
</tr>
<tr>
<td>M ean VWI</td>
<td>0.30</td>
<td>0.00</td>
<td>0.07</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.72</td>
</tr>
<tr>
<td>RKM</td>
<td>0.63</td>
<td>0.22</td>
<td>0.34</td>
<td>0.15</td>
<td>0.23</td>
<td>0.43</td>
<td>0.28</td>
</tr>
<tr>
<td>Age-0 steelhead</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent pool</td>
<td>0.19</td>
<td>0.65</td>
<td>0.25</td>
<td>0.41</td>
<td>0.00</td>
<td>NA</td>
<td>0.32</td>
</tr>
<tr>
<td>M ean depth</td>
<td>0.12</td>
<td>0.67</td>
<td>0.02</td>
<td>0.31</td>
<td>0.04</td>
<td>NA</td>
<td>0.33</td>
</tr>
<tr>
<td>M ean width</td>
<td>0.28</td>
<td>0.11</td>
<td>0.03</td>
<td>0.29</td>
<td>0.12</td>
<td>NA</td>
<td>0.33</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.23</td>
<td>0.68</td>
<td>0.02</td>
<td>0.11</td>
<td>0.03</td>
<td>NA</td>
<td>0.35</td>
</tr>
<tr>
<td>M ean VWI</td>
<td>0.07</td>
<td>0.65</td>
<td>0.10</td>
<td>0.23</td>
<td>0.04</td>
<td>NA</td>
<td>0.54</td>
</tr>
<tr>
<td>RKM</td>
<td>0.36</td>
<td>0.63</td>
<td>0.15</td>
<td>0.63</td>
<td>NA</td>
<td>0.35</td>
<td>0.18</td>
</tr>
</tbody>
</table>

TABLE 4. Coefficient of determination (R²) and statistical significance (values in bold indicate P < 0.05) of individual habitat variables and reach location (river kilometer [RKM]) in generalized additive models for each stream (2002 and 2003 combined) when modeled individually (Indiv.) and with RKM (w/RKM). Year is included as a main effect (NA = not applicable because fish abundance was too low for modeling).
age-0 steelhead were skewed further towards the headwaters (Figure 3a, b) and Coho Salmon densities were higher in small streams (Figure 2). Steelhead parr had the patchiest distribution and were skewed farthest upstream, with a density spike in the headwaters that changed locations from 2002 to 2003 (Figure 3c). In addition, the distribution patterns within streams did not necessarily match what was found at the network scale, as Coho Salmon were sometimes patchier and distributed further upstream than both age-classes of juvenile steelhead and vice versa (Figure 3a–c).

Network-Scale Models

Associations between stream habitat and juvenile salmonids.—Generalized additive models using the five stream habitat variables explained 27, 11, and 19% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively (Table 3). We also found weak levels of spatial autocorrelation in model residuals for both size-classes of steelhead in 2002, moderate levels for age-0 steelhead in 2003 and for Coho Salmon in both years, and strong levels for steelhead parr in 2003 (Table 3). The shape of the salmonid response to individual habitat characteristics was typically curvilinear and differed between species and between the steelhead age-classes in some cases (Figure 4). For example, Coho Salmon were positively associated with percent pool habitat, while age-0 steelhead and steelhead parr were not (Figure 4). Furthermore, Coho Salmon had a negative association with channel gradient while steelhead did not, and the curve for steelhead parr peaked at a greater depth than that for Coho Salmon and smaller age-0 steelhead (Figure 4). All salmonids responded similarly to mean VWI (positive) and mean width (negative).

Effect of stream size, time, stream, and reach location.—We found strong effects of stream size, year, stream, and reach location on the network-scale distribution models (Table 3). Sequential inclusion of each variable consistently reduced deviance and improved explanatory power (Table 3). Consequently, the best model for all salmonids was the full model, which included a reach location effect that was allowed to vary by stream and year; this model explained 76, 53, and 78% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively (Table 3). The reach location × stream × year interaction term produced the greatest single improvement in deviance and explanatory power among models and salmonids except for one instance with steelhead parr (Table 3). Inclusion of the reach location variable and its interactions in the full model also accounted for the spatial autocorrelation in model residuals for Coho Salmon in both years and for age-0 steelhead and steelhead parr in 2003. Spatial autocorrelation was weak to nonexistent for age-0 steelhead and steelhead parr in 2002, so the location variable had less of an effect.

Stream-Scale Models

Stream habitat variable consistency and explanatory power.—Single habitat variables explained as much as 70% of the variability in salmonid density in individual streams when reach location within a stream was not considered (Table 4). On average, however, explanatory power tended to be quite low,
FIGURE 3. Density depicted in 200-m bins (fish/200 linear meters) for (a) juvenile Coho Salmon, (b) age-0 steelhead, and (c) steelhead parr (age ≥ 1) across the Calawah River stream network in 2002 and 2003.

FIGURE 4. Nonparametric response of juvenile Coho Salmon, age-0 steelhead, and steelhead parr (age ≥1) densities as a function of percent pool habitat (% pool), mean depth (m), mean stream channel gradient (%), mean wetted width (m), and mean valley width index (VWI) for all streams combined. Dashed lines indicate ± 2 SEs for the smoothed parameter.
and no single variable was significant across all of the streams for a given species (Table 4). Although it was low in general, the consistency of fish–habitat associations was highest for Coho Salmon, with all variables (except for mean width) having a significant effect and $R^2$ values being greater than 20% for three of the seven streams (Table 4). For steelhead parr, only percent pool habitat was significant and this variable had an $R^2$ of at least 20% for two streams; for age-0 steelhead, the mean depth, stream channel gradient, and mean VWI achieved $R^2$ values greater than 20% for two streams (Table 4).

Part of the inconsistency in fish–habitat relationships was related to the shape of the response. For example, the response of steelhead parr to percent pool habitat ranged from strongly positive to strongly negative, even among streams of similar sizes, whereas the effect of mean depth was generally positive for steelhead parr in small streams and negative for those in large streams (Figure 5). In fact, outside of mean depth and mean VWI, response curves for age-0 steelhead and steelhead parr generally ranged from strongly negative to strongly positive without a clear pattern between streams of similar sizes (Figure 5). Fish–habitat associations appeared to be more consistent for Coho Salmon, especially with percent pool habitat, but that variable was still not significant for three of the seven streams, and $R^2$ values were below 10% for three streams and below 25% for five streams (Table 4). The association of Coho Salmon with stream channel gradient was also typically negative, while other responses were inconsistent.

Effects of longitudinal location of habitat.—Location of the survey reach (RKM) was significant for 50% of all streams (for all salmonids combined) and had the highest $R^2$, often by a large margin, for 45% of those streams (Table 4). The effects were most pronounced for Coho Salmon, with RKM being significant for five of the seven streams and having the highest $R^2$ value for four streams, compared with two streams for age-0 steelhead and three streams for steelhead parr (Table 4). River kilometer also influenced the significance of habitat variables. In Hyas Creek, mean wetted width, stream channel gradient, and mean VWI were individually significant for juvenile Coho Salmon but not when RKM was included (Table 4). The patterns were similar for age-0 steelhead and steelhead parr; consequently, RKM was the only significant variable in the Hyas Creek models and in the upper NF Calawah River models for Coho Salmon and steelhead parr.

**DISCUSSION**

**Network-Scale Models**

Expansive spatial coverage and a census of a wide variety of streams over multiple years allowed us to test stream habitat models in a way that would not have been possible with traditional sampling schemes. Nonetheless, the fish–habitat associations we reported were generally consistent with prior knowledge, albeit often nonlinear. Percent pool habitat had a positive influence on density of juvenile Coho Salmon, and
channel habitat and fish data to predict the distribution of spawning Chinook Salmon over a 9-year period and found that inferences drawn from fewer than 3–5 years of study would have underestimated the influence of time relative to space. Thus, the effect of year in our models might have been greater had we sampled over more years.

Ultimately, the full models that accounted for the reach location × stream × year interaction achieved a high level of explanatory power. However, the full models did not necessarily tell us why large-scale patterns in salmonid distribution differed between and within streams and years. Rather, we only determined that those patterns in distribution were less related to stream habitat than to the location of the habitat within the network and each stream between years; this result is not entirely surprising because previous studies have found that habitat location can strongly influence growth and survival of juvenile salmonids (Ebersole et al. 2009; Pess et al. 2011). This may have also been the case in our study based on the distributions of the two steelhead size-classes. For example, age-0 steelhead were abundant in many stream reaches where steelhead parr were rare or absent. The young-of-the-year steelhead either survived poorly in or moved away from those areas as they got older, implying that some reaches—and even entire sections of streams, such as the lower NF Calawah River—are sources and sinks (Schlosser and Aingermeier 1995). If true, then juvenile distributions might have been more strongly influenced by other factors (e.g., food, competition, predation, and water temperature) that were not measured in our study but that affect growth, survival, and movement (Aingermeier and Schlosser 1989; Dunham and Rieman 1999; Railsback and Rose 1999; Keeler 2001).

The unexplained patterns in distribution could also have been influenced by other factors. For instance, we probably consistently undersampled age-0 steelhead; these fish may rely heavily on shallow-water habitats (Bjornn and Reiser 1991), but we were unable to snorkel habitats less than 0.2 m deep, which could have reduced explanatory power. To some degree, distributions of young-of-the-year juveniles also likely reflected differences in the abundance and location of spawning adults (Finstad et al. 2009). We could not determine this because spatially explicit data on redd locations are not available for all sections of individual streams in the Calawah River basin. However, there are escapement data for adults; estimates for adult Coho Salmon in the entire network increased marginally from 2001 to 2002 (escapement = 3,994 and 4,267 adults, respectively), and estimates for adult steelhead decreased by about the same amount (escapement = 4,413 and 3,990 adults, respectively). Thus, we documented large, stream-scale increases in the density and distribution of juvenile Coho Salmon and age-0 steelhead between years when adult abundance was similar, which suggests that egg-to-fry survival may have had a greater effect on juvenile salmonid distribution than the yearly differences in adult abundance.

We also found moderate to strong levels of spatial autocorrelation in the residuals of most network-scale models, suggesting that the survey reaches were not spatially independent.
Nonindependence can produce correlation coefficients that are biased and overly precise (Legendre et al. 2002). However, Moran’s I-values were generally reduced to negligible levels (I < ± 0.25) by including stream, reach location, and the associated interaction terms. Although this approach accounted for spatial autocorrelation, inclusion of the site-specific variables eliminated transferability to other streams (Segurado et al. 2006); consequently, our inferences are limited to the sites we sampled and the interactions with the habitat characteristics we measured. Future modeling efforts may thus consider including spatial autocorrelation into regressive models to improve predictive success (Betts et al. 2006).

Stream-Scale Models

Models for individual streams can achieve a high level of explanatory power and precision by incorporating a few habitat variables (Fausch et al. 1988). In our study, individual habitat variables for each stream explained up to 70% of the variation in salmonid density, but on average, explanatory power was low and no single variable was significant across all streams for any of the three salmonid groups. Further, the shape and direction of the responses were inconsistent. For instance, the effect of VWI on Coho Salmon and the effect of channel gradient on age-0 steelhead and steelhead Parr ranged from strong to weak and from strongly positive to strongly negative depending on the stream—something that is not often observed in fish–habitat associations (Bjornn and Reiser 1991; Burnett et al. 2007). The stream-specific responses of fish to habitat indicate that models based on multiple streams can oversimplify variability in fish–habitat associations. In our case, oversimplification of fish responses was one reason why the network-scale models struggled to effectively predict the distribution of juvenile Coho Salmon and steelhead.

The only fairly consistent response—that between Coho Salmon density and percent pool habitat—did not necessarily produce a strong correlation. Percent pool habitat explained less than 10% of the variation in Coho Salmon density for three of the seven streams and less than 22% for five of the streams. Previous habitat use studies (Bisson et al. 1988; Bjornn and Reiser 1991) and models based on traditional sampling schemes (Rosenfeld et al. 2000; Sharma and Hilborn 2001) and census data (Reeves et al. 2011) have reported stronger correlations between pools and Coho Salmon. Notably, however, the associations between Coho Salmon and pool habitat were stronger in smaller streams than in larger ones. Similarly, steelhead Parr were positively associated with depth in small streams, while the association was nonexistent to negative in large streams. This finding suggests that age-class differences in habitat use can influence distribution (Kanno et al. 2012) and that relatively small fish (e.g., juveniles) may prefer deeper water in shallower streams than in deeper streams and vice versa (Rosenfeld et al. 2011). The results underscore the idea that strong effects of stream and stream size can potentially limit how well a single model can be applied across different areas (Fausch et al. 1988; Porter et al. 2000; Rosenfeld et al. 2000, 2007). Part of the variability we found in fish–habitat associations between streams could also be related to differences in fish density rather than to actual differences in habitat selection. For example, many suitable habitats may be unoccupied at very low densities, while many potential sinks may be occupied at high densities (Van Horne 1983; Angermeier and Schlosser 1989). Additionally, Rosenfeld et al. (2005) found that density altered the habitat selection and suitability curves for juvenile Coho Salmon. In our study, the escapement goals in 2001 and 2002 for spawning Coho Salmon and winter steelhead were both easily achieved, and escapement levels were among the highest observed for the Calawah River during the period of record (1980–2012; WDFW 2012). Perhaps consequently, fish were more thoroughly distributed and habitat that would not be used in years with lesser adult abundances was selected during the years of our study, when adult abundance was higher. Overall, though, the effects of density appear to be negligible considering that we sampled several streams with a wide range of densities, but models generally performed poorly for all streams and for all species and life stages. Nonetheless, we also acknowledge that inferences based on habitat selection in nature may provide different results from stream to stream and from year to year based on organism abundance (Hobbs and Hanley 1990).

Perhaps most importantly, we found that fish–habitat associations were dramatically weakened when habitat was allowed to compete with reach location. Previous models based on traditionally collected data (Dunham and Vinyard 1997) and models using continuous data for salmonids (Isaak and Thurow 2006; Ebersole et al. 2009) and nonsalmonids (Grenouillet et al. 2004) have also noted that location within a network can influence fish distribution. Although the location variable did not allow us to identify the underlying reason for the correlation, it did allow us to determine that individual fish–habitat associations were generally weak or nonsignificant after location was included in the full model. This is important because without accounting for location, we would have had an artificially high level of certainty in many of the fish–habitat associations (Legendre et al. 2002). This type of reach effect could limit how effectively correlations drawn from a subsample of reaches can be expanded to larger scales, such as entire streams or networks, and it highlights how the interpretation of models can be biased if the surrounding context of fish and habitat is not considered (Dunham and Vinyard 1997).

Implications

Stream habitat models are commonly generated from a subsample of reaches and streams and then are widely applied to other streams and networks to predict the distribution and density of salmonids (Fausch et al. 1988; Dunham and Vinyard 1997; Porter et al. 2000; Rosenfeld 2003). This approach would have had little success in our study. Stream habitat models performed poorly until we accounted for an interaction between...
fish–habitat associations and the location of habitat within streams, the latter of which often violated assumptions about sample independence of the survey reaches and inflated effects of habitat characteristics. These results raise two cautionary points. First, fish–habitat associations that are drawn from multiple streams or from streams other than those in which the data were collected cannot be presumed to be representative of stream-scale variability across a network, so the testing of assumptions is important for establishing a level of certainty (Fausch et al. 1988; Porter et al. 2000; Van Horne 2002). Second, even if fish–habitat associations are known, accounting for the spatial and temporal context of those associations within individual streams may be necessary to effectively predict potentially dramatic troughs and aggregations in the network-scale distribution of salmonids (Dunham and Vinyard 1997; Angermeier et al. 2002; Isaak and Thurow 2006; Torgersen et al. 2012).

Uncertainty due to a lack of testing has implications for the use of stream habitat models to guide management and restoration in unsampled areas and across streams of differing sizes (Fausch et al. 1988). Steelhead parr in our study offer one example. Effects of percent pool habitat ranged from strongly negative to strongly positive between streams and were not entirely consistent within a stream, suggesting that the benefits of manipulating stream channels to create more pool habitat may vary depending on the stream, at least when only summer is considered. In addition, even when the density of steelhead parr was positively correlated with pools, the location of the habitat generally mattered more than the amount. Interactions between fish–habitat associations and space are relatively common and can influence growth and survival across a variety of scales (Ebersole et al. 2009; Pess et al. 2011). If this variability is common in networks, then restoring watershed-scale processes that regulate natural habitat formation may be more effective than manipulating short reaches and expecting the fish to exhibit uniform responses (Beechie and Bolton 1999; Feist et al. 2003).

An increasing focus on larger scales in restoration efforts, combined with strong stream and spatial effects on fish–habitat associations and nonindependence among survey reaches, poses challenges for future modeling and sampling. Our rather complete data set reveals that we know less about the influences on fish distribution than what we have been led to believe—that is, from models based on less spatially exhaustive data. Still, we were only able to detect patterns rather than identify mechanisms, and without understanding the processes it is hard to know why space was so important in our models (Clinchy et al. 2002). Nonetheless, future research that couples intensive, traditional-scale sampling of fish condition and survival with extensive censuses of fish and habitat distribution over multiple years could prove valuable for untangling patterns and processes (Dunham et al. 2002; Isaak and Thurow 2006; Ebersole et al. 2009; Torgersen et al. 2012). One possible way to accomplish this is through integrated population models that rely on repeated count data to estimate various parameters (e.g., abundance or survival) associated with population dynamics over time (Dail and Madsen 2011; Schaub and Aabø 2011). Such models are increasingly being applied to understand changes in populations of birds and mammals (Schaub and Aabø 2011), and the models may be further improved by explicitly including spatial autocorrelation (Betts et al. 2006). Such an approach could help to clarify the level of uncertainty that can be expected by scientists and managers when applying habitat models broadly across streams, locations, and times.

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Influence of Survey Design on Fish Assemblages: Implications from a Study in Chesapeake Bay Tributaries

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Influence of Survey Design on Fish Assemblages: Implications from a Study in Chesapeake Bay Tributaries

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Abstract
Aquatic resource surveys that span multiple decades provide valuable information about fish population responses to environmental and human-induced changes. Often, surveys are altered as scientific objectives change or in response to management needs. These modifications usually result in inconsistencies in the time series, which must be addressed for proper analysis of fish community data. Since 1997, juvenile fishes in Virginia tributaries of Chesapeake Bay have been captured monthly using a bottom trawl at both fixed and random sites. Previous surveys in these tributaries (1955–1996) were conducted at fixed sites only; thus, an understanding of the effect of this design change would allow us to infer fish community status through multiple decades. We compared samples from the fixed site design with those from the stratified random design in the James, York, and Rappahannock rivers and examined species composition, biodiversity, relative abundance estimates, and size distributions to understand the effects of survey design on these metrics. Catches from random sites were characterized by consistently higher species richness than those from fixed sites; biodiversity metrics varied by sampling site type (fixed versus random) and river. For most select species, we observed similar trends in relative abundance regardless of site type; however, for some species we noted differences in magnitude among years and between sampling site types. Community metrics, such as taxonomic diversity and distinctness, revealed subtle differences about fish species assemblages compared with traditional diversity metrics demonstrating that community metrics can characterize biodiversity of fishes at higher taxonomic levels. Thus, species-specific and community metrics derived from assemblage data from fixed-site surveys may not fully represent the magnitude of change in demersal fish assemblages, but can provide reliable indicators of patterns of change in abundance through time.

A quatic resource surveys that span multiple decades provide valuable information about species population responses to environmental and human-induced changes. Long-term surveys may be altered as scientific objectives change or technological advances occur, or in response to management needs (Brown et al. 2007). These modifications usually result in data exhibiting temporal inconsistencies, which must be addressed for proper analysis and interpretation of trends in abundance or changes in species composition. For example, alterations to the sampling design of research surveys (e.g., sampling frequency, site selection, gear type) may result in differences in the captured fish community (e.g., species composition, abundance, life history structure) and may therefore confound investigations of environmental or human perturbations on fish assemblages. The effects of small-scale variation on larger-scale community patterns is confounded by sampling designs that follow gradients or are stratified by habitat (Gray et al. 2009). This is particularly important in estuarine systems where habitat, time, and life history stage of fishes influence the presence and abundance of both resident and transient species (Gray et al. 2011). A s long-term data sets are increasingly used to establish baseline reference points to guide policy development in aquatic environments, it is vital that biases are known or that uncertainty resulting from a change in sampling strategy or protocol is evaluated. Here we focused on effects associated with changes in the type of sampling site selected (random versus fixed sites), rather than...
effects associated with changes in gear type or gear operation procedures on survey catchability (e.g., Stauffer 2004; Stenevik et al. 2012).

We evaluated the effects of changes in site selection on a long-term, fisheries-independent survey of juvenile fishes by characterizing differences between two concomitant and continuous time series of fixed-site samples and stratified-random samples. We asked: What differences exist in catches between fixed and random sites? What bias might we introduce in our understanding of community composition, size distributions of species, and indices of relative abundance if we analyze catches from fixed sites only? The latter question was motivated by the availability of fish catch data from 1955 to the present at fixed sites only; thus, a multidecadal series could be available for investigation. To answer these questions, we compared monthly samples from the fixed sites with those from random sites from 1997 to 2010 and examined species composition, relative abundance estimates, and size distributions of numerically dominant species to understand how alterations in site selection affect our understanding of juvenile fish assemblages in three tributaries of Chesapeake Bay.

METHODS

Virginia tributaries to Chesapeake Bay.—Three large tributaries (the James, York, and Rappahannock rivers, Virginia) empty into the lower portion of western Chesapeake Bay and serve as nursery and spawning habitats for many estuarine-dependent species of the Mid-Atlantic Bight (Murdy et al. 1997; Figure 1). The tributaries are partially mixed, coastal plain estuaries with depths generally between 5 to 10 m along the axes, but with deeper portions (>20 m) near the mouths (Kuo and Neilson 1987). The James River has a high average discharge rate (194 m$^3$/s) and encompasses the largest area at mean low water (MLW): 658.2 × 10$^4$ m$^2$ (Cronin 1971). The York River is the smallest of the three tributaries and has an average discharge rate of 31 m$^3$/s and an area of 210.9 × 10$^4$ m$^2$ at MLW, whereas the Rappahannock River is intermediate and has an average discharge rate of 47 m$^3$/s and an area of 401.5 × 10$^4$ m$^2$ at MLW (Cronin 1971). These characteristics translate into observable differences in temperature and salinity conditions among tributaries. Discharge of freshwater into the James River is four to seven times that of the Rappahannock and York rivers (USGS 2012). The high discharge rate in the James River, along with its proximity to the mouth of Chesapeake Bay, creates a large salinity gradient along the river axis that reduces the likelihood of hypoxic conditions through gravitational mixing (Kuo and Neilson 1987). However, hypoxia is routinely observed during summer in the York and Rappahannock rivers (Kuo and Neilson 1987; Long and Seitz 2009).

Brief history of the VIMS juvenile fish trawl survey.—The Virginia Institute of Marine Science (VIMS) juvenile fish trawl survey began sampling in 1955 at fixed sites extending from the head of the York River to the mouth of Chesapeake Bay. Over the ensuing decades, changes to the survey gear, vessel, and sampling design occurred, and these changes probably affected the species composition, relative abundance, and size distributions of the observed catch. The most recent change involved a sampling design modification that incorporated the addition of random sites to the existing fixed-station framework. Beginning in March 1996 and continuing to the present, stratified-random and fixed site sampling has been conducted in the James, York, and Rappahannock rivers on a monthly basis using the same gear and research vessel. This hybrid sampling design provides a monthly time series of fish catch data for comparison of the potential effects of site selection on juvenile fish recruitment and fish community structure in these estuaries since 1997 (the first full year of implementation).

Site selection.—Fixed sites were established in midchannel waters along the axis of each river and were spaced approximately every 8.0 km. Each month, eight fixed sites are sampled in the James and Rappahannock rivers and nine fixed sites are sampled in the York River (Figure 1). Fixed sites range in depth from 3.7 to 10.7 m in the James River, from 3.7 to 18.3 m in the Rappahannock River, and from 4.0 to 12.2 m in the York River.

Random sites were selected using a stratified random design where strata were defined by water depth and river zone. Depth is believed to influence fish assemblage composition and abundance (Gray et al. 2011) and is commonly used to stratify fisheries surveys (Gunderson 1993). Random stations were assigned to depth strata ranging from 3.6 to 9.1 m, 9.1 to 12.8 m, and greater than 12.8 m for the deepest areas. An additional shallow stratum (1.2 to 3.6 m) is routinely sampled during the survey; however, no fixed sites occur in this stratum and therefore data from this stratum were not included in the analysis. Due to the presence of a salinity gradient, four river zones were used as strata to ensure sampling throughout the range of available salinity from the mouth to the freshwater interface of each river. Each month, one or two sites (depending on the area of the stratum) are selected randomly from each stratum from a list of available sites, resulting in 10 random sites sampled monthly in the James and Rappahannock rivers, and nine random sites sampled monthly in the York River.

Fish collection and processing.—We used a 9.1-m, four-seam, semiballoon otter trawl with body made from 38.1-mm-stretch mesh and a 6.4-mm-mesh cod liner to collect fish in the James, York, and Rappahannock rivers from a 8.5-m research vessel. Monthly samples consisted of 5-min tows at approximately 2.5 knots at each site. For each tow, surface and bottom water temperature, depth, salinity, and dissolved oxygen were measured. The catch was sorted by species and fish were measured (FL or TL) to the nearest millimeter using an electronic measuring board. Catches of a single species exhibiting multiple modal sizes and large catches were subsampled and at least 30 individuals from each species or size mode were measured at each site. The remaining catch was counted and the size distribution of the subsampled catch was expanded proportionally to the total number captured.
FIGURE 1. Fixed sites (▲) sampled by the Virginia Institute of Marine Science juvenile fish trawl survey from 1997 to 2010 in the James, York, and Rappahannock rivers, Chesapeake Bay, Virginia. River segments (four in each river) established for selection of stratified-random sites along the salinity gradient are also shown as single lines.
Fish assemblage composition and structure.—Species composition, diversity indices, and size distributions were investigated using annual (n = 14 years) catch data from each river. Most diversity indicators, such as Hill’s N1 (the exponential of the Shannon–Wiener index) and N2 (the reciprocal of Simpson’s index), are invariant to the relatedness of species and do not describe biodiversity above the species level (e.g., genera and family level diversity). Therefore, in addition to traditional community metrics (species richness, which we compared using Spearman’s correlation, and Hill’s N1 and N2), we calculated taxonomic diversity (\(\Delta\)), taxonomic distinctness (\(\Delta^*\)), and taxonomic distinctness based on presence-absence data (\(\Delta^+\)) to characterize community structure from random and fixed sites within and among rivers (Warwick and Clarke 1995; Clarke and Warwick 1998). The purpose of using additional diversity metrics was to examine shifts in fish community composition that would be otherwise unknown using traditional metrics, such as a change in the number of taxonomic groups that are represented. Taxonomic diversity and distinctness metrics (\(\Delta, \Delta^*, \text{ and } \Delta^+\)) incorporate species taxonomic relationships, along with relative abundance in the case of \(\Delta\) and \(\Delta^*\), to produce indices that describe how close two or more related species are to one another; these indices are useful to characterize biodiversity at higher taxonomic levels. We used 10 taxonomic levels to classify fishes from Chesapeake Bay tributaries based on Nelson (2006): class, subclass, division, subdivision, superorder, order, family, subfamily, genus, and species. A path length was constructed to quantify the relationship between any two fish and is defined as 0 for two individuals of the same species, 1 for two individuals in the same genus but from different species, 2 for two individuals from the same subfamily but from different genera, and so on, continuing until all classification levels were quantified. Average taxonomic diversity (\(\Delta\)) captures the taxonomic relatedness of the sample by calculating the average path length between randomly chosen individuals from the sample (Clarke and Warwick 1998). Taxonomic distinctness (\(\Delta^*\)) quantifies taxonomic relatedness of two randomly chosen individuals conditional on them being different species and provides an index of pure taxonomic breadth. Because \(\Delta^*\) is based on presence-absence only, it may be used to examine a time series of catch data resulting from different effort, gear, vessels, and statistical design. A n important aspect of these taxonomic metrics (\(\Delta, \Delta^*, \text{ and } \Delta^+\)) is that they do not depend on sampling effort, which contrasts with other commonly used community metrics, allowing comparisons of community structure for studies with unequal sample sizes (Clarke and Warwick 1998).

The resulting two-dimensional ordination based on the Euclidean distance between similarity rankings depicts relationships among tributaries and years and was used in correlation analyses to determine the relationship between observed fish community assemblages and annual mean environmental variables measured during this study, namely, bottom water temperature, dissolved oxygen, salinity, depth, freshwater flow (USGS 2012), and the winter index of the North Atlantic Oscillation (NAO) (Clarke and Ainsworth 1993; Hurrell 1995; Austin 2002). The NAO was included because Wood and Austin (2009) found that fish recruitment in Chesapeake Bay varied on decadal and interannual scales and may be coupled with regional climate rather than river-specific environmental patterns. All multivariate community analyses were conducted using package vegan in R (R Development Core Team 2010; Oksanen et al. 2011).

Age-0 indices of relative abundance for select species.—We considered only numerically abundant species (Atlantic Croaker Micropogonias undulatus, Bay Anchovy Anchoa mitchilli, Blackcheek Tonguefish Symphurus plagiula, Blue Catfish Ictalurus furcatus, Hogchoker Trinectes maculatus, Spot Leiostomus xanthurus, Weakfish Cynoscion regalis, and White Perch Morone americana) in our examination of the effects of sampling site type on relative abundance indices and mean size of age-0 fish (Table 1). A bundance species were chosen for these analyses so that observed differences could be attributed to site type effects rather than to limitations of the data (i.e., infrequent catches). Length thresholds were used to assign fishes to age-0 for index calculations (Table 1). Catch data for these species followed lognormal distributions and zero catches comprised about 50% of the data overall. Therefore, we used a delta lognormal model to estimate abundance of age-0 fish (Kimura and Somerton 2006). A bundance was estimated for catches that occurred during months when age-0 fish were available to the gear. To estimate age-0 abundance indices for each species, we calculated the proportion of positive tows and the mean of the log-transformed positive catches. The index was estimated by multiplying the proportion of positive tows and the unweighted back-transformed mean of positive catches, adjusted by one-half of the variance to account for the bias in estimating the mean in log-space (Pennington 1983; Syrjala 2000). A bundance trends were evaluated using correlation analysis between sampling designs. Mean length of age-0 fish from fixed and random sites was compared using generalized linear models.

Within stratum comparisons.—Because random site selection is stratum-specific, we also examined the consistency between fish abundance and assemblage metrics from fixed and random sites from the same stratum. However, we noted that not all strata included a fixed station, so inferences from these analyses were restricted to strata containing both types of sampling sites, which were distributed throughout each river from the river mouth to the freshwater interface, except for the uppermost stratum in the York River where only fixed sites were sampled.
TABLE 1. Monthly length thresholds used in calculating juvenile abundance indices for eight abundant fish species captured by bottom trawl in the James, York, and Rappahannock rivers (1997–2010). Shown are maximum sizes (TL [unless indicated otherwise], mm) and months used to sample age-0 (juvenile) fish. These eight species accounted for 96.1% (by number) of all fish captured from random sites and 95.9% of those captured from fixed sites. Numbers in parentheses after the species name is the percent contribution of that species to total number caught of all species.

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<tr>
<th>Species</th>
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Correlation analyses were used to compare relative abundances and mean lengths of select species, as well as fish community metrics to understand temporal consistency between sampling site types within each stratum. Results from this analysis will help us understand the small-scale (<8 km) spatial patterns of juvenile fish abundance, community structure, and variability.

RESULTS

Fish Assemblages and Water Quality Comparisons

During the 14-year survey, 8,956 tows were completed: 2,968 in the James River, 2,998 in the York River, and 2,990 in the Rappahannock River. A few sites were not sampled in this time series due to mechanical issues with the research vessel, but such omissions represented only 0.8% of the targeted sampling. We encountered 110 fish species from random sites sampled between 1997 and 2010 (Table 2). The eight species examined in detail in this study accounted for 96.1% of the total number of fish captured at random sites (2,100,756 individuals). By comparison, 1,675,010 individuals representing 105 species were collected at fixed sites during the same period; the eight select species accounted for 95.9% of the total number collected at fixed sites. With one exception (James River, 1999), the number of species observed at random sites on an annual basis was greater than or equal to that observed at fixed sites (Figure 2). For all years combined, more species were collected in the James River (91 species from fixed sites and 95 species from random sites) compared with the York River (83 species from fixed sites and 87 species from random sites) and the Rappahannock River (68 species at fixed sites and 75 species at random sites; Table 2). Annual species richness at fixed and random sites was significantly correlated in the York (Spearman’s \( r_s = 0.79, P < 0.001 \)) and Rappahannock rivers (Spearman’s \( r_s = 0.89, P < 0.001 \)), but we found no significant correlation in species richness between sampling site types in the James River (Spearman’s \( r_s = 0.52, P = 0.06 \)). We found more unique species (\( n = 13 \)) in randomly selected sites; however, fixed sites contained eight species not observed at random sites.

Indices characterizing fish community structure varied through time and among tributaries (Figure 3). Hill’s \( N_2 \) was strongly correlated with Hill’s \( N_1 \) (\( r^2 = 0.94 \)) and therefore \( N_2 \) was not used in subsequent analyses. In the James River, fish assemblages at fixed and random sites exhibited similar temporal patterns, and all diversity metrics were significantly correlated except for the index based on...
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<td>Red Drum Sciaenops ocellatus</td>
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<td>13</td>
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<td>Silver Perch Bairdiella chrysoura</td>
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<td>4,569</td>
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<td>1,676</td>
<td>1,997</td>
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<td>Silver Seatrout Cynoscion nothus</td>
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<td>Smallmouth Flounder Eotropus microstomus</td>
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<td>Southern Kingfish Menticirrhus americanus</td>
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<tr>
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<td>Spanish Mackerel Scomberomorus maculatus</td>
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<td>4</td>
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<tr>
<td>Spot Leiostomus xanthurus</td>
<td>23,493</td>
<td>22,632</td>
<td>17,232</td>
<td>26,946</td>
<td>32,033</td>
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(Continued on next page)
### Table 2. Continued.

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<th>Species</th>
<th>James River</th>
<th></th>
<th>York River</th>
<th></th>
<th>Rappahannock River</th>
<th></th>
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<tbody>
<tr>
<td></td>
<td>Fixed</td>
<td>Random</td>
<td>Fixed</td>
<td>Random</td>
<td>Fixed</td>
<td>Random</td>
</tr>
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<td>Spotfin Butterflyfish <em>Chaetodon ocellatus</em></td>
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<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Spotfin Mojarra <em>Eucinostomus argenteus</em></td>
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<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Spottail Shiner <em>Notropis hudsonius</em></td>
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<td>13</td>
<td>952</td>
<td>1</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Spotted Hake <em>Urophycis regia</em></td>
<td>1,370</td>
<td>7,557</td>
<td>2,117</td>
<td>3,759</td>
<td>1,501</td>
<td>1,864</td>
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<tr>
<td>Spotted Seatrout <em>Cynoscion nebulosus</em></td>
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<td>9</td>
<td>14</td>
<td>36</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Star Drum <em>Stellifer lanceolatus</em></td>
<td>13</td>
<td>114</td>
<td>10</td>
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<td>0</td>
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<tr>
<td>Striped Anchovy <em>Anchoa hepsetus</em></td>
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<td>287</td>
<td>26</td>
<td>271</td>
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<td>18</td>
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<tr>
<td>Striped Bass <em>Morone saxatilis</em></td>
<td>1,773</td>
<td>1,347</td>
<td>2,531</td>
<td>1,182</td>
<td>1,777</td>
<td>973</td>
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<td>Striped Blenny <em>Chasmodes bosquianus</em></td>
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<td>0</td>
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<td>Striped Killifish <em>Fundulus majalis</em></td>
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<td>0</td>
</tr>
<tr>
<td>Striped Mullet <em>Mugil cephalus</em></td>
<td>31</td>
<td>32</td>
<td>3</td>
<td>10</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Striped Searobin <em>Prionotus evolans</em></td>
<td>83</td>
<td>78</td>
<td>10</td>
<td>27</td>
<td>7</td>
<td>53</td>
</tr>
<tr>
<td>Summer Flounder <em>Paralichthys dentatus</em></td>
<td>1,330</td>
<td>1,534</td>
<td>664</td>
<td>1,006</td>
<td>325</td>
<td>727</td>
</tr>
<tr>
<td>Tautog <em>Tautoga onitis</em></td>
<td>5</td>
<td>49</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tessellated Darter <em>Etheostoma olmstedi</em></td>
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<td>5</td>
<td>12</td>
<td>0</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Threadfin Shad <em>Dorosoma petenense</em></td>
<td>144</td>
<td>317</td>
<td>12</td>
<td>9</td>
<td>27</td>
<td>32</td>
</tr>
<tr>
<td>Weakfish <em>Cynoscion regalis</em></td>
<td>13,612</td>
<td>16,777</td>
<td>36,923</td>
<td>29,124</td>
<td>18,576</td>
<td>25,583</td>
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<tr>
<td>White Catfish <em>Ameiurus catus</em></td>
<td>1,261</td>
<td>1,228</td>
<td>3,662</td>
<td>885</td>
<td>1,647</td>
<td>705</td>
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<tr>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Windowpane <em>Scopthalmus aquosus</em></td>
<td>96</td>
<td>48</td>
<td>2</td>
<td>7</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Winter Flounder <em>Pseudopleuronectes americanus</em></td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Yellow Perch <em>Perca flavescens</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>552,979</td>
<td>763,852</td>
<td>704,943</td>
<td>633,712</td>
<td>417,088</td>
<td>703,192</td>
</tr>
</tbody>
</table>

**presence–absence, Δ⁺** (Figure 3). In the York River, only Hill’s N1 showed a significant correlation between fixed and random sites, and no community metric comparisons between fixed and random sites were significantly correlated in the Rappahannock River (Figure 3). While most fish assemblage metrics were not correlated in the York River, actual metric values were similar each year indicating that differences between station types were small. Conversely, fish assemblages from fixed sites in the Rappahannock River had higher N1 and Δ⁺ values than those from random sites each year. Only Δ⁺ showed similar community structure between station types in the Rappahannock River. Overall, fish assemblages in the Rappahannock River had lower taxonomic diversity (Figure 4), but the species that were present represented a similar taxonomic range (i.e., contained a similar number of taxonomic groups) relative to those observed in the James River, where species richness was greatest (Figure 2).

As expected, fish assemblages observed at fixed and random sites within a river are more similar to one another than they are to fish assemblages from different rivers (Figure 5). Based on results of the ordination and the correlation between assemblages and the environmental conditions observed in the rivers during 1997–2010, fish assemblages from the three rivers are well separated from one another, though some overlap between assemblages in the York and Rappahannock rivers is apparent. Because we were concerned about the influence of rare species (defined here as fewer than 100 individuals captured during the study period) on fish assemblages, we excluded rare species from the catches and reexamined fish assemblages using the same nonmetric multidimensional ordination approach. The reduced species matrix contained 55 species compared with the original 118 species. Results from the ordination and correlation analyses on both data sets (full versus reduced) indicated that the separation of the James River fish community from those in the other rivers is consistent between data sets and is largely driven by dissolved oxygen content and river flow. Though bottom water temperature, salinity, and dissolved oxygen were significantly correlated among rivers demonstrating the influence of regional climate effects, the NAO index was not associated with
INFLUENCE OF SURVEY DESIGN ON FISH ASSEMBLAGES

Changes in fish assemblages in these tributaries ($r = 0.09, P = 0.67$). River-specific differences were apparent: the James River had lower mean salinity, higher mean water temperature, and higher mean dissolved oxygen content than the York and Rappahannock rivers (Table 3). In the York River, fish assemblages were correlated with higher mean water temperature and higher mean salinity observed in this system (Figure 5). Mean annual salinity varied by sampling site type such that random sites had significantly greater mean salinities than fixed sites (Table 3). Differences in mean annual salinity between sampling site types were 1.86 psu (Rappahannock River), 2.23 psu (James River), and 4.28 psu (York River). Random sites in the James and York rivers were deeper than the fixed sites, on average, even though they were collocated in the same depth stratum, whereas in the Rappahannock River, fixed sites were deeper. The mean difference in average depth between fixed and random sites was 2.8 m in the James River, 1.9 m in the York River, and 1.5 m in the Rappahannock River; however, depth was not significantly correlated ($r = 0.19, P = 0.21$) with the species ordination.

**Fish Assemblage Correlations within Strata**

Within river strata, monthly species richness estimates from fixed sites were significantly correlated with species richness estimates from random sites; this was true for all three rivers, although correlation coefficients were weak in some cases (Spearman’s $r_s < 0.40$; Tables 4–6). Based on these correlations, monthly shifts in species richness were similar within each stratum, but the ability to predict species richness at random sites from catches at fixed sites was limited. Taxonomic distinctness and diversity metrics ($\Delta, \Delta^*, \Delta^+$) varied by stratum with some strong correlations found between fixed and random sites (Pearson’s $r > 0.60$; Table 6) and others not significantly correlated.
Although correlations among sampling site types were of variable strength, fewer than half of the comparisons of the total numbers of fish captured at fixed sites were significantly correlated with numbers captured at random sites (Tables 4–6).

Relationships between juvenile abundance indices from the two sampling site types varied by species and showed no obvious patterns (Tables 4–6). These relationships also varied among strata. For example, in the James River, juvenile abundance indices for Atlantic Croaker at fixed and random sites were significantly correlated for strata near the freshwater–saltwater interface and for strata in the lower river (Table 4: James 2, and James 4, both F1 and F2 sites). Similarly, in the Rappahannock River, juvenile abundance indices for Atlantic Croaker at fixed

Although correlations among sampling site types were of variable strength, fewer than half of the comparisons of the total numbers of fish captured at fixed sites were significantly correlated with numbers captured at random sites (Tables 4–6).

Relationships between juvenile abundance indices from the two sampling site types varied by species and showed no obvious patterns (Tables 4–6). These relationships also varied among strata. For example, in the James River, juvenile abundance indices for Atlantic Croaker at fixed and random sites were significantly correlated for strata near the freshwater–saltwater interface and for strata in the lower river (Table 4: James 2, and James 4, both F1 and F2 sites). Similarly, in the Rappahannock River, juvenile abundance indices for Atlantic Croaker at fixed

**TABLE 3.** Mean dissolved oxygen (mg/L), bottom water temperature (°C), salinity (psu), and depth (m) measured at fixed and random sites in the James, York, and Rappahannock rivers from 1997 to 2010; SE is provided in parentheses. Pearson’s correlation, r, between station types is shown. Asterisk (*) denotes a significant difference between abiotic properties at fixed and random sites (t-test, P < 0.05). Also shown are mean (SE) values for each abiotic property by river and the Pearson correlation among rivers; all correlations were significant at P < 0.05.

<table>
<thead>
<tr>
<th>River</th>
<th>Dissolved oxygen</th>
<th>Temperature</th>
<th>Salinity</th>
<th>Depth</th>
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</thead>
<tbody>
<tr>
<td>Fixed</td>
<td>Random</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>James</td>
<td>8.44 (0.15)</td>
<td>16.69 (0.20)</td>
<td>11.00 (0.46)</td>
<td>7.65 (0.04)</td>
</tr>
<tr>
<td>York</td>
<td>7.41 (0.09)</td>
<td>16.58 (0.14)</td>
<td>12.57 (0.38)</td>
<td>7.99 (0.04)</td>
</tr>
<tr>
<td>Rappahannock</td>
<td>7.43 (0.13)</td>
<td>15.87 (0.17)</td>
<td>11.95 (0.46)</td>
<td>11.07 (0.12)</td>
</tr>
</tbody>
</table>

**FIGURE 4.** Comparison between taxonomic distinctness (Δ*) and taxonomic diversity (Δ) for fixed and random sites in the James (black circles), York (green triangles), and Rappahannock (red squares) rivers.

**FIGURE 5.** The relationship among annual fish assemblages from fixed (F) and random sites (R) in the James (black letters), York (green letters), and Rappahannock (red letters) rivers from 1997 to 2010 based on nonmetric multidimensional scaling (NMDS) analysis using double square-root-transformed abundance data stress = 17.84. The NMDS scores for each river, year, and sampling site type are shown (e.g., FJ-97 = fixed stations, James River, 1997). Significant correlations between the fish community ordination and environmental properties (dissolved oxygen [DO, mg/L], r = 0.59, P = 0.001; bottom water temperature [Temp, °C], r = 0.36, P = 0.002; salinity [Sal, psu], r = 0.61, P = 0.001; and flow [m³/s], r = 0.72, P = 0.001) are shown as vectors (blue lines) with the direction indicating an increasing relationship and the length of the vector indicating the strength of the correlation. [Figure available online in color.]
TABLE 4. Monthly correlation between sampling sites within James River strata for species richness, taxonomic distinctness (Δ), taxonomic diversity (Δ*, Δ+), total number of fish, juvenile abundance indices (abundance, based on delta lognormal model), and mean length for species shown. Strata are defined by location along the river axis (3.7 ≤ S ≤ 9.1 m) and depth (D > 9.1 m). Fixed sites are identified by “F” and random sites are identified by “R”. A number follows the site designation if more than one site type occurs within a stratum. Pearson’s correlation coefficient (Spearman’s rs is shown for species richness) is shown and significance (P < 0.05) is indicated by shaded cells; NA = insufficient data for comparison.

<table>
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<tr>
<th>Stratum (depth)</th>
<th>James 1 (S)</th>
<th>James 2 (S)</th>
<th>James 2 (D)</th>
<th>James 3 (S)</th>
<th>James 4 (D)</th>
<th>James 4 (S)</th>
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<tbody>
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<td>Comparison</td>
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<td></td>
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<tr>
<td>Species richness</td>
<td>0.46 0.56</td>
<td>0.26 0.23</td>
<td>0.27 0.23</td>
<td>0.20 0.20</td>
<td>0.35 0.32</td>
<td>0.32 0.44</td>
</tr>
<tr>
<td>Δ</td>
<td>0.30 0.22</td>
<td>0.19 0.23</td>
<td>0.23 0.32</td>
<td>0.17 0.07</td>
<td>0.40 0.22</td>
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</tr>
<tr>
<td>Δ*</td>
<td>0.07 0.23</td>
<td>0.40 0.23</td>
<td>0.23 0.31</td>
<td>0.12 0.06</td>
<td>0.26 0.30</td>
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</tr>
<tr>
<td>Δ+</td>
<td>0.46 0.56</td>
<td>0.58 0.10</td>
<td>0.27 0.21</td>
<td>0.01 0.09</td>
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<td></td>
</tr>
<tr>
<td>Total fish</td>
<td>0.56 0.46</td>
<td>0.14 0.40</td>
<td>0.10 0.24</td>
<td>0.19 0.33</td>
<td>0.66 0.64</td>
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<tr>
<td>Abundance</td>
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<td>Atlantic Croaker</td>
<td>-0.17 0.14</td>
<td>0.66 0.40</td>
<td>-0.08 0.47</td>
<td>0.29 0.10</td>
<td>0.68 0.68</td>
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</tr>
<tr>
<td>Bay Anchovy</td>
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<td>-0.09 0.01</td>
<td>-0.07 0.02</td>
<td>0.02 0.06</td>
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</tr>
<tr>
<td>Blackcheek Tonguefish</td>
<td>0.64 0.24</td>
<td>0.28 0.53</td>
<td>0.19 0.19</td>
<td>-0.01 0.17</td>
<td>NA NA</td>
<td>NA</td>
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<tr>
<td>Blue Catfish</td>
<td>NA NA NA NA</td>
<td>NA 0.16 0.34</td>
<td>0.22 0.05</td>
<td>0.15 0.37</td>
<td>0.46 0.46</td>
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<td>Hogchoker</td>
<td>NA NA 0.16</td>
<td>0.50 0.67</td>
<td>-0.05 0.50</td>
<td>0.66 0.15</td>
<td>0.37 0.46</td>
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<tr>
<td>Spot</td>
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<td>-0.13 0.67</td>
<td>0.50 0.86</td>
<td>0.73 0.27</td>
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<tr>
<td>Weakfish</td>
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<td>-0.15 0.02</td>
<td>-0.24 0.18</td>
<td>0.14 0.38</td>
<td>0.22 0.70</td>
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</tr>
<tr>
<td>White Perch</td>
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<td>-0.28 0.01</td>
<td>0.02 0.20</td>
<td>0.45 0.09</td>
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<tr>
<td>Mean length</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atlantic Croaker</td>
<td>0.71 0.78</td>
<td>0.86 0.91</td>
<td>0.90 0.86</td>
<td>0.67 0.85</td>
<td>0.76 0.76</td>
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</tr>
<tr>
<td>Bay Anchovy</td>
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<td>0.58 0.82</td>
<td>0.58 0.60</td>
<td>0.63 0.45</td>
<td>0.54 0.54</td>
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<td>Blackcheek Tonguefish</td>
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<td>0.72 0.79</td>
<td>0.52 0.52</td>
<td>NA NA</td>
<td>NA NA</td>
<td></td>
</tr>
<tr>
<td>Blue Catfish</td>
<td>NA NA NA NA</td>
<td>NA 0.74 0.81</td>
<td>0.62 0.74</td>
<td>0.60 0.60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hogchoker</td>
<td>0.79 0.75</td>
<td>0.65 0.72</td>
<td>0.74 0.70</td>
<td>0.84 0.81</td>
<td>0.85 0.85</td>
<td></td>
</tr>
<tr>
<td>Spot</td>
<td>0.67 0.73</td>
<td>0.59 0.80</td>
<td>0.73 0.58</td>
<td>0.50 0.83</td>
<td>0.78 0.78</td>
<td></td>
</tr>
<tr>
<td>Weakfish</td>
<td>0.51 0.72</td>
<td>0.33 0.43</td>
<td>0.64 0.64</td>
<td>0.54 0.48</td>
<td>0.68 0.68</td>
<td></td>
</tr>
<tr>
<td>White Perch</td>
<td>NA NA 0.60</td>
<td>0.18 0.26</td>
<td>-0.06 0.26</td>
<td>0.48 0.48</td>
<td>0.41 0.41</td>
<td></td>
</tr>
</tbody>
</table>

and random sites in the lower river (Table 6: Rappahannock 1 and Rappahannock 2, both F1 and F2 sites) and a portion of the upper river (Table 6: Rappahannock 4, F2) were significantly correlated. With the exception of a single stratum (Table 5: York 1, F2), juvenile abundance indices for Atlantic Croaker at fixed and random sites in the York River were not significantly correlated. Similar results were found for other species examined; in addition, results from two or more fixed sites within a given stratum were also observed to exhibit juvenile abundance indices that were both correlated and uncorrelated with juvenile abundance indices estimated from catches at random sites within that stratum. For example, in the James River (James 4, S), juvenile abundance indices for Weakfish from one of the fixed sites (F2) was significantly correlated with the juvenile abundance indices estimated from catches at the random station, whereas juvenile abundance indices from the other fixed station in that stratum were not (Table 4). Correlation results were not adjusted for multiple comparisons, so it is possible that some of these correlations were spurious, further supporting the notion that abundance indices calculated from catches at fixed sites may not reflect relative abundance estimated from catches at randomly sampled sites for a given stratum.

Whereas juvenile abundance index comparisons between fixed and random sites were inconsistent, the size distributions of fishes within strata were similar at fixed and random sites and exhibited similar increases in mean length during the recruitment period. Within a given stratum, many of the correlations between mean length of individual species from fixed and random sites were significant and strongly positive. Differences in the spatial distribution of species among strata were also evident, with Blackcheek Tonguefish located in the lower portions of the rivers and Blue Catfish in the upper portions. Because mean length comparisons were based on monthly estimates of length and because fish might not have been captured at both sampling site types in a given month, some station type comparisons were not possible (e.g., James River, Blackcheek Tonguefish).
TABLE 5. Monthly correlations between sites in York River strata for species richness, taxonomic distinctness ($\Delta$), taxonomic diversity ($\Delta^*$, $\Delta^+$), total number of fish, juvenile abundance indices (abundance, based on delta lognormal model), and mean length for species shown. Strata are defined by location along the river axis ($3.7 \leq S \leq 9.1$ m) and depth ($D > 9.1$ m). Fixed sites are identified by “F” followed by a number if more than one fixed site occurs in a stratum and random sites are identified by “R”. Pearson’s correlation coefficient (Spearman’s $r_S$ is shown for species richness) is shown and significance ($P < 0.05$) is indicated by shaded cells; NA = insufficient data for comparison.

<table>
<thead>
<tr>
<th>Stratum (depth)</th>
<th>York 1 (D)</th>
<th>York 1 (S)</th>
<th>York 2 (S)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>Atlantic Croaker</td>
<td>0.63</td>
<td>0.47</td>
</tr>
<tr>
<td>$\Delta$</td>
<td>Atlantic Croaker</td>
<td>0.36</td>
<td>0.22</td>
</tr>
<tr>
<td>$\Delta^*$</td>
<td>Atlantic Croaker</td>
<td>0.37</td>
<td>0.12</td>
</tr>
<tr>
<td>$\Delta^+$</td>
<td>Atlantic Croaker</td>
<td>0.29</td>
<td>0.07</td>
</tr>
<tr>
<td>Total fish</td>
<td>Atlantic Croaker</td>
<td>0.73</td>
<td>0.79</td>
</tr>
<tr>
<td>Abundance</td>
<td>Atlantic Croaker</td>
<td>0.25</td>
<td>0.53</td>
</tr>
<tr>
<td>Bay Anchovy</td>
<td>Atlantic Croaker</td>
<td>0.68</td>
<td>0.83</td>
</tr>
<tr>
<td>Blackcheek Tonguefish</td>
<td>0.55</td>
<td>-0.09</td>
<td>0.77</td>
</tr>
<tr>
<td>Blue Catfish</td>
<td>NA</td>
<td>NA</td>
<td>0.98</td>
</tr>
<tr>
<td>Hogchoker</td>
<td>0.08</td>
<td>0.06</td>
<td>0.78</td>
</tr>
<tr>
<td>Spot</td>
<td>0.02</td>
<td>0.40</td>
<td>0.48</td>
</tr>
<tr>
<td>Weakfish</td>
<td>0.33</td>
<td>-0.28</td>
<td>0.48</td>
</tr>
<tr>
<td>White Perch</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Mean length</td>
<td>Atlantic Croaker</td>
<td>0.88</td>
<td>0.88</td>
</tr>
<tr>
<td>Bay Anchovy</td>
<td>Atlantic Croaker</td>
<td>0.74</td>
<td>0.70</td>
</tr>
<tr>
<td>Blackcheek Tonguefish</td>
<td>0.31</td>
<td>NA</td>
<td>0.43</td>
</tr>
<tr>
<td>Blue Catfish</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Hogchoker</td>
<td>0.91</td>
<td>0.85</td>
<td>0.53</td>
</tr>
<tr>
<td>Spot</td>
<td>0.86</td>
<td>0.82</td>
<td>0.80</td>
</tr>
<tr>
<td>Weakfish</td>
<td>0.75</td>
<td>0.68</td>
<td>0.65</td>
</tr>
<tr>
<td>White Perch</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

Age-0 Juvenile Abundance Correlations for Select Species

Relative abundance indices from fixed and random sites were significantly correlated for most species, although some notable exceptions occurred, and the magnitude of juvenile abundance indices from fixed and random sites differed for some species (Figure 6; Table 7). For example, in the James River, juvenile abundance indices for Weakfish were not correlated; however, changes in recruitment were not evident between 1997 and 2010 and the overall mean and SE of fixed-site and random-site juvenile abundance indices were similar ($t$-test: $t = 1.8952$, $df = 26$, $P = 0.0692$; fixed site mean = 14.6, SE = 1.96, and random site mean = 19.8, SE = 1.92). Conversely, patterns in Hogchoker recruitment differed between fixed and random sites in the Rappahannock River such that recruitment indices from catches at fixed sites were greater than those observed at random sites. A similar result was observed for Hogchoker in the York River with more Hogchokers captured at less-saline fixed sites than at randomly selected sites characterized by higher salinities. In the York and Rappahannock rivers, few Blue Catfish juveniles were captured at random sites compared with fixed sites, resulting in our inability to examine the effect of station type for this species in these rivers. All other species comparisons were significantly correlated; however, index values varied by species and river. For example, juvenile abundance indices for Bay Anchovy showed the greatest variation between fixed and random sites in each river.

The average length of select species was similar among sampling designs for all species except Atlantic Croaker, Blackcheek Tonguefish, and Hogchoker (Table 8). In all three cases, fixed sites had significantly smaller average lengths than those found at random sites. The different mean lengths observed for Hogchoker were not dependent on depth since lower salinities occurred in shallow, fixed sites in the York River and in deeper, fixed sites in the Rappahannock River.

**DISCUSSION**

Patterns in Species Composition between Fixed and Random Sites

We examined the potential effects of fixed and random site selection on catches of juvenile fishes and our understanding of community composition, size distribution, and indices of
TABLE 6. Monthly correlations between sites within Rappahannock River strata for species richness, taxonomic distinctness (Δ), taxonomic diversity (Δ*, Δ+), total number of fish, juvenile abundance indices (abundance, based on delta lognormal model), and mean length for species shown. Strata are defined by location along the river axis (3.7 ≤ S ≤ 9.1 m) and depth (9.1 ≤ D ≤ 12.8 m; VD > 12.8 m). Fixed sites are identified by “F” followed by a number if more than one fixed site occurs in a stratum, and random sites are identified by “R”. Pearson’s correlation coefficient (Spearman’s rs is shown for species richness) is shown and significance (P < 0.05) is indicated by shaded cells; NA = insufficient data for comparison.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Species</th>
<th>Rappahannock 1 (D)</th>
<th>Rappahannock 2 (VD)</th>
<th>Rappahannock 3 (D)</th>
<th>Rappahannock 4 (S)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F1–R</td>
<td>F2–R</td>
<td>F1–R</td>
<td>F2–R</td>
</tr>
<tr>
<td>Species richness</td>
<td>0.54</td>
<td>0.51</td>
<td>0.56</td>
<td>0.59</td>
<td>0.30</td>
</tr>
<tr>
<td>Δ</td>
<td>0.27</td>
<td>0.18</td>
<td>0.45</td>
<td>0.22</td>
<td>0.04</td>
</tr>
<tr>
<td>Δ*</td>
<td>0.22</td>
<td>0.37</td>
<td>0.60</td>
<td>0.46</td>
<td>0.07</td>
</tr>
<tr>
<td>Δ+</td>
<td>0.14</td>
<td>0.23</td>
<td>0.57</td>
<td>0.51</td>
<td>0.10</td>
</tr>
<tr>
<td>Total fish</td>
<td>0.54</td>
<td>-0.07</td>
<td>0.37</td>
<td>-0.18</td>
<td>-0.29</td>
</tr>
<tr>
<td>Abundance</td>
<td>Atlantic Croaker</td>
<td>0.52</td>
<td>0.92</td>
<td>0.83</td>
<td>0.85</td>
</tr>
<tr>
<td></td>
<td>Bay Anchovy</td>
<td>0.18</td>
<td>-0.19</td>
<td>0.06</td>
<td>-0.06</td>
</tr>
<tr>
<td></td>
<td>Blackcheek Tonguefish</td>
<td>0.65</td>
<td>0.78</td>
<td>0.26</td>
<td>0.71</td>
</tr>
<tr>
<td>Mean length</td>
<td>Atlantic Croaker</td>
<td>0.73</td>
<td>NA</td>
<td>0.63</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Bay Anchovy</td>
<td>0.75</td>
<td>0.55</td>
<td>0.58</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Blackcheek</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Tonguefish</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Blue Catfish</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Hogchoker</td>
<td>0.72</td>
<td>0.29</td>
<td>0.48</td>
<td>-0.08</td>
</tr>
<tr>
<td></td>
<td>Spot</td>
<td>0.84</td>
<td>0.54</td>
<td>0.21</td>
<td>-0.18</td>
</tr>
<tr>
<td></td>
<td>Weakfish</td>
<td>0.52</td>
<td>0.48</td>
<td>0.23</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>White Perch</td>
<td>NA</td>
<td>NA</td>
<td>0.63</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>Atlantic Croaker</td>
<td>0.73</td>
<td>NA</td>
<td>0.92</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Bay Anchovy</td>
<td>0.75</td>
<td>0.55</td>
<td>0.58</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Blackcheek</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Tonguefish</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Blue Catfish</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Hogchoker</td>
<td>0.31</td>
<td>0.50</td>
<td>0.68</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Spot</td>
<td>0.89</td>
<td>0.87</td>
<td>0.89</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>Weakfish</td>
<td>0.70</td>
<td>0.61</td>
<td>0.55</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>White Perch</td>
<td>NA</td>
<td>NA</td>
<td>0.83</td>
<td>-0.33</td>
</tr>
</tbody>
</table>

relative abundance and found important similarities and substantial differences. For example, species richness as indicated by catches from fixed sites underestimated species richness by 11–12% (or 6 to 11 species), on average, compared with estimates of species richness from random sites. The bias in species composition identified by the concurrent sampling allowed us to interpret the longer time series with appropriate caution and understanding. The negative bias of the fixed-site design for species richness is not surprising because our fixed sites were located primarily in midchannel habitats, whereas random sites were not spatially constrained within a stratum, and thus the likelihood of sampling unique habitats was higher for sites selected randomly.

Rare or unique species did not account for the differences in species assemblages found at fixed and random sites. Some species that were unique to either fixed or random sites would not be considered important members of the Chesapeake Bay estuarine fish assemblage due to their subtropical distribution and intermittent appearances in the bay (e.g., Orange Filefish Aluterus schoepfii). Other rare species found in this study are common to Chesapeake Bay yet were not well represented in our catches, because these species exhibit low catchability or availability to our survey gear. For example, large schools of Cownose Ray Rhinoptera bonasus are often observed in the bay (Smith and Merriner 1987), yet catches of Cownose Ray are rare in the VIMS juvenile fish trawl survey. That is not to say that rare species are unimportant in assessing changing community structure, but we did not observe a consistent pattern in the occurrence of rare or unique species at one type of sampling site relative to the other.

Community Composition

Fixed and random sites showed similar temporal patterns in fish community composition and taxonomic distinctness in the James and York rivers, but site types exhibited greater differences in the Rappahannock River. The Rappahannock River community captured through randomly chosen sites showed less taxonomic diversity compared with fixed sites, probably
due to the dominance of Bay Anchovy at random sites. Bay Anchovy were >3.5 times more abundant at random sites in the Rappahannock River and showed the greatest differences in relative abundance of all individual species investigated. When only presence-absence data were examined ($\Delta^+$), similar patterns in taxonomic diversity were found regardless of the site or river indicating that taxonomic distinctness, as measured at fixed sites, appears to be unbiased relative to taxonomic distinctness measured at randomly selected sites. Because $\Delta^+$ is not influenced by variation in effort or changes in sampling gear, we suggest the longer time series of catch data from Chesapeake Bay tributaries be examined using this metric; such an examination could be extended back to 1955 and thus provide a 56-year assessment of changes in taxonomic distinctness of fish assemblages in the York River and similar, though shorter, assessments in the James (47 years) and Rappahannock rivers (49 years).

Species assemblages were correlated with environmental characteristics that differed among rivers, specifically water flow, bottom water temperature, salinity, and dissolved oxygen, but were not associated with depth. Although, water depth can be an important determinant of species composition in other systems (Gray et al. 2011), the difference in water depth between sampling designs, though significant, was not an important
TABLE 7. Correlations between juvenile abundance indices from fixed and random sampling sites in the James, York, and Rappahannock rivers from 1997 to 2010; \( t \) is the test statistic, \( \text{df} \) is the degrees of freedom, \( P \) is the probability of observing a greater \( t \)-value under the null hypothesis of no difference, and \( r \) is Pearson's correlation coefficient.

<table>
<thead>
<tr>
<th>Species</th>
<th>James River</th>
<th>York River</th>
<th>Rappahannock River</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( t )</td>
<td>( \text{df} )</td>
<td>( P )</td>
</tr>
<tr>
<td>Atlantic Croaker</td>
<td>8.4</td>
<td>12</td>
<td>(&lt;0.001)</td>
</tr>
<tr>
<td>Bay Anchovy</td>
<td>2.6</td>
<td>12</td>
<td>0.023</td>
</tr>
<tr>
<td>Blackcheek Tonguefish</td>
<td>3.0</td>
<td>12</td>
<td>0.012</td>
</tr>
<tr>
<td>Blue Catfish</td>
<td>3.7</td>
<td>12</td>
<td>0.003</td>
</tr>
<tr>
<td>Hogchoker</td>
<td>0.8</td>
<td>12</td>
<td>0.438</td>
</tr>
<tr>
<td>Spot</td>
<td>9.8</td>
<td>12</td>
<td>(&lt;0.001)</td>
</tr>
<tr>
<td>Weakfish</td>
<td>1.0</td>
<td>12</td>
<td>0.321</td>
</tr>
<tr>
<td>White Perch</td>
<td>2.4</td>
<td>12</td>
<td>0.035</td>
</tr>
</tbody>
</table>

TABLE 8. Average length of age-0 fish from fixed and random sites in the James, York, and Rappahannock rivers from 1997 to 2010. Asterisk (*) indicates a significant difference in mean length between sampling designs. NA = insufficient data for comparison.

<table>
<thead>
<tr>
<th>Species</th>
<th>James River</th>
<th>York River</th>
<th>Rappahannock River</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fixed</td>
<td>Random</td>
<td>Fixed</td>
</tr>
<tr>
<td>Atlantic Croaker</td>
<td>88.3</td>
<td>92.3</td>
<td>70.8</td>
</tr>
<tr>
<td>Bay Anchovy</td>
<td>45.6</td>
<td>45.9</td>
<td>47.8</td>
</tr>
<tr>
<td>Blackcheek Tonguefish</td>
<td>81.9</td>
<td>88.0*</td>
<td>75.2</td>
</tr>
<tr>
<td>Blue Catfish</td>
<td>131.7</td>
<td>132.7*</td>
<td>120.6</td>
</tr>
<tr>
<td>Hogchoker</td>
<td>58.8</td>
<td>59.4</td>
<td>54.6</td>
</tr>
<tr>
<td>Spot</td>
<td>132.7</td>
<td>137.1</td>
<td>137.2</td>
</tr>
<tr>
<td>Weakfish</td>
<td>81.9</td>
<td>86.6</td>
<td>79.6</td>
</tr>
<tr>
<td>White Perch</td>
<td>75.2</td>
<td>74.6</td>
<td>75.1</td>
</tr>
</tbody>
</table>

factor accounting for variations in species assemblages. In an estuarine setting, fixed sites cannot control for physical aspects other than geographic position and perhaps depth (to some extent). Even depth, in the context of a long-term survey, can change with natural geophysical processes, such as sedimentation or redistribution of sediment due to storms, which can potentially alter the fish community associated with that location. As estuarine-dependent fishes respond to a suite of interacting variables that influence their spatial distribution, our understanding of community composition will be affected by biological responses to varying environmental stimuli. Abiotic factors, such as dissolved oxygen, freshwater discharge, water temperature, and salinity, vary on small temporal (hours, days) and spatial scales and this variation affects the distribution and relative abundance of species. The dynamic environmental properties typical of estuaries may override the importance of water depth, at least at the depths observed in this study.

Tributaries that empty into lower Chesapeake Bay show a latitudinal trend of decreasing species diversity as distance from the bay's mouth increases. Fish assemblages in the Rappahannock River comprise fewer species than assemblages in the York and James rivers; however, the taxonomic breadth of the Rappahannock River fish assemblage was similar to or higher than that observed for the other two rivers. Some studies examining fish assemblages suggest that biodiversity metrics at higher taxonomic levels may be redundant with conventional species diversity metrics (i.e., Hill’s N1 and N2) because these two sets of metrics are correlated (Hall and Greenstreet 1998). Rogers et al. (1999) proposed that the positive correlation between conventional diversity metrics and taxonomic relatedness metrics results when individual samples are aggregated on regional scales; however, our results show this is not the case. Hall and Greenstreet (1998) suggest one reason may be that perturbations that affect conventional diversity indices will have already altered community properties that are measured by taxonomic relatedness and propose that taxonomic distinctness metrics may therefore be more sensitive to community change than conventional diversity metrics. In contrast to Hall and Greenstreet (1998), we found that average taxonomic distinctness (\( \Delta^* \)) is not always positively correlated with species diversity, demonstrating that it is possible to have diverse species assemblages that are composed of species that are related at
higher taxonomic levels, while exhibiting low species diversity due to numeric dominance of a few species. However, in simple communities (consisting of fewer than nine species), taxonomic distinctness metrics may lead to counter-intuitive or spurious results, though how these metrics behave with more complex species assemblages is unknown (Mérigot and Gaertner 2011).

Alternatively, observed correlations among diversity metrics for fish communities may arise if the taxonomic range of the samples is restricted (compared with the benthic invertebrate community from which taxonomic relatedness indices arose). In this case, the utility of taxonomic relatedness metrics is reduced by limiting the scope in which these metrics can vary compared with conventional diversity metrics (Hall and Greenstreet 1998). However, studies of demersal fish communities indicate that taxonomic distinctness can be used to detect differences in communities that were not apparent through conventional metrics (Collie et al. 2008; Tolimieri and Anderson 2010). Our study demonstrated that differences in community structure were evident, even though our samples displayed a limited taxonomic scope, and that taxonomic indices may prove useful in discriminating subtleties in changing fish community structure.

Age-0 Juvenile Abundance Indices for Select Species

We observed similar relative abundance trends for age-0 fishes between fixed and random sites during the 14-year survey for the eight species examined in detail, supporting an extension of the analysis of juvenile abundance data collected before 1997. Whereas trends in relative abundance can be interpreted with confidence for most species examined, relative abundance during any given year should be considered with caution and on an individual species basis. For example, the 1999 Weakfish index based on samples from the random sites in the Rappahannock River was the highest observed for the time series; however, all other Weakfish indices indicated average recruitment for Weakfish that year. It is possible that more Weakfish were present in the Rappahannock River in 1999, but additional information should be obtained that would corroborate the high abundance in this river. Bay Anchovy indices were highest in the Rappahannock River random sites each year indicating that fixed sites were not representative of relative abundance for this schooling species. Indices of relative abundance that are not of the same magnitude may still be informative, as long as such indices exhibit similar temporal trends.

We found similar size distributions among sampling site designs for most of the selected species despite significant differences in depth indicating that depth differences are not important when sampling is focused on a single life history stage (i.e., juveniles). Important differences in relative abundance for Hogchoker are probably related to habitat preferences of juveniles for less saline waters (Dovel et al. 1969) and were not related to water depth. Therefore, interpretation of the longer time series based on fixed sites only will have to account for the low salinity bias of fixed sites and the potential effects on species of interest. The species we examined in detail were well represented numerically and vulnerable to the bottom trawl and, thus, provided catch data that were somewhat ideal for comparison. Even with high catch rates, we observed differences in abundance indices within individual strata as well as between station types, which demonstrates the small-scale (~10 km) patchy distribution of juvenile fishes. Fish assemblage metrics and fish species abundance and size structure would probably exhibit more pronounced differences between fixed and random sites for species with low capture rates. Differences are likely to be exaggerated if only a portion of these data are examined. Therefore, care should be taken to maintain the broad spatial extent of the survey design to avoid addressing spatially narrow questions using only a portion of the catch data (i.e., at the stratum level), as those data may not be representative due to small sample size.

It is well known that sampling sites adjacent to one another spatially tend to be more similar (i.e., positively correlated) and therefore data from adjacent sites provide less information about the variance of the characteristic of interest than noncorrelated sites (Cressie 1993; Koenig 1999). Autocorrelation is a violation of the assumption of independence that affects estimates of the variance of the mean (Kimura and Somerton 2006). Thus, in the presence of autocorrelation, effective sample size is reduced. For these survey data, estimates of relative abundance based on catch data from both fixed and random sites would be more precise (due to larger sample sizes) than estimates from fixed or random sites alone; however, such an approach may be considered susceptible to bias due to autocorrelation among catches from survey sites in close proximity. Our results suggest that autocorrelation in juvenile fish abundance in Chesapeake Bay tributaries may not be a concern at the stratum level, probably due to the patchy distribution of individuals and the short tow duration (5 min) used to capture fish in this study. Thus, we believe that the sample size within each stratum (sum of the numbers of fixed and random sites) is a true sample size that can be used to estimate the variance of the mean for each stratum, thereby providing robust confidence intervals for indices of abundance.

CONCLUSIONS

As ecosystem-based approaches to fisheries management gain favor, long-term data sets will be queried to establish reference points and targets to guide policy and evaluate management decisions. Inclusion of surveys that have implemented site-selection changes through time can be considered over a longer time series if there is agreement between the two sampling designs. Alternatively, if the two site-selection criteria produce results that are temporally correlated yet result in different values for a given metric, then examining a data set containing changes to the survey design would still be of interest though more limited conclusions could be drawn. Finally, if there is no consistent relationship between catches resulting from different
survey designs, then interpretation of a longer time series using catches from only one type of site requires caution.

In our survey, fixed sites have a low salinity bias in all three tributaries that affects the species composition of fish assemblages and relative abundance estimates of some species. We also found differences in species assemblages among tributaries that could affect population dynamics and the nursery function of these systems. Explicit understanding of the application and limitations of available data sets will benefit scientists and managers as they wrestle with uncertainty in research surveys and the need to manage resources effectively.

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Within-Day Variability in Catch Taken by Public Access Fishers during a Recreational Fishing Survey

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NOTE

Within-Day Variability in Catch Taken by Public Access Fishers during a Recreational Fishing Survey

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Abstract

Access point surveys of recreational fisheries are usually stratified into weekdays and weekend days and allocate only a single sampling assignment per day sampled; this is because most variation is thought to be due to differences in angler behavior between the week and weekend and between days. However, few estimates of within-day variability are available, and this source of error has not been adequately assessed. During a 2011 survey of the recreational fishery for blue crabs *Callinectes sapidus* in Maryland, we used a stratified two-stage design with week and weekend strata, and multiple assignments were selected randomly within sampling days to measure within-day variability. Within-day variability accounted for 85.3–98.5% of the variation in blue crab catch between July and September, whereas 1.5–14.7% of the variation was due to between-day variability; during the months examined, there was no significant effect due to week–weekend. These results suggest the use of a simple two-stage design to estimate the recreational catch of blue crabs, with sampling effort allocated to capturing within-day variability. Better management of the main sources of error can increase the precision and accuracy of catch estimates, and we recommend that recreational surveys use pilot studies to evaluate sources of variation before the study design is finalized.

Access point surveys are often used to estimate recreational catch and effort from specific water bodies that cover clearly delimited geographic areas with well-defined access sites (Pollock et al. 1994). The method is also widely used for estimating catch rate in complemented survey designs, wherein effort is estimated by using a telephone or mail survey, aerial survey, or trailer count and catch is calculated as the product of effort and catch rate. In practice, access point surveys are appropriate when targeted activity passes through a limited number of publicly accessible sites, which can be drawn up into a comprehensive list; field agents can then visit sites chosen from the list to intercept anglers returning from their trips. Although access point surveys are more expensive than telephone or mail surveys, they avoid error associated with self-reported data (e.g., misidentification of caught species, faulty recall, and prestige bias) because the unreleased catch (i.e., harvest) can be directly observed by agents. However, an issue that has received little attention is that access point surveys often do not appropriately capture all public access sources of variability.

Estimates will be most precise when a population is partitioned so that sampling units are as similar as possible (Thompson 1992). As a result, surveys are generally stratified into weekdays and weekend days. However, the two-stage sampling design that is commonly used within each of these strata does not estimate the variability associated with each stage of the design (Pollock et al. 1994). Thus, when a sampling assignment consists of a single visit to one access point for a specified period, the sampling units in the frame consist of all possible assignment periods on all days at all points in the access list over the full duration of the survey. These period–ramp sampling units are aggregated into primary sampling units (PSUs) consisting of the individual days in the frame. For example, in a survey covering 4 weeks with 10 boat ramps listed and each day divided into four 6-h assignment periods, there would be 40 sampling units in each day (4 assignment periods × 10 access points), resulting in 800 sampling units for the week stratum (40 sampling units per day × 20 possible weekdays) and 320 sampling units for the weekend stratum, or a total of 1,120 sampling units in the frame. From each stratum, PSUs are first selected by simple
random sampling without replacement, followed by selection of the sampling units within the PSUs. However, only one assignment is generally undertaken each day; as a result, within-day variability cannot be measured and variance is based on primary unit estimates (Pollock et al. 1994).

Efficient allocation of sampling effort improves precision and reduces the cost of sampling designs (e.g., Cochran 1977; Thompson 1992). For situations where most of the variation occurs within PSUs (e.g., Chittenden 1989), effort should be allocated accordingly. However, few public access surveys that measure within-day variability have been published, and the potential magnitude of this source of error has not been adequately assessed. During a 2011 survey of the recreational fishery for blue crabs Callinectes sapidus in Maryland, we intercepted recreational crabbers at public access sites to obtain estimates of catch and effort. We used a two-stage design stratified by week and weekend, and we measured within-day variability by undertaking multiple assignments on each sampling day.

METHODS

Field agents intercepted recreational fishing boats as they returned to public boat ramps between May and October 2011. We used a list of public boat ramps (n = 113) based on a registry for the Chesapeake Bay (Chesapeake Bay Program 2000). For each month, sampling was undertaken in 6-h assignments, each consisting of a visit to a single boat ramp, stratified by week and weekend, and distributed between morning (0600–1200 hours) and afternoon (1200–1800 hours) periods; thus, there were 226 potential sampling units for each day (Table 1). State of Maryland regulations limit the number of returning fishing boats outside of these periods and for the entire day on Wednesdays; therefore, these were not included in the frame. For each month, sampling days were selected randomly without replacement from all possible sampling days within the week and weekend strata. Within each day, sampling units were selected from a list consisting of period–ramp units (e.g., morning period at the Wetipquin boat ramp) to yield a stratified two-stage design.

Based on earlier surveys (e.g., Ashford et al. 2010b), we anticipated that recreational crabbing activity would be minimal during May and October. Although activity typically increases in June, crabbing in Maryland is largely confined to southern bays and estuaries and does not reach its full spatial extent until later in the summer; moreover, a large proportion of the catch consists of soft crabs in the molting process. We therefore examined within-day variability from July to September by deploying up to four agents to sample period–ramp units on each of 4 d during both the week and the weekend (Table 1). Agents arrived at the boat ramps at the selected time and used a standard questionnaire to interview returning boat parties and assess the crabs in each party’s catch. At the end of August, a state of emergency was declared due to Hurricane Irene, and we assumed that no fishing activity occurred on the two weekend sampling days that were selected during this period. Effort for each assignment was calculated as the number of crabbing boat parties that returned across the boat ramp, including (1) parties that were interviewed; (2) those that declined the interview but that were obviously crabbing; and (3) those that were obviously crabbing but that were missed because the sampler was already occupied with an interview. For each assignment, catch was calculated as the total number of blue crabs reported by all boat parties interviewed, corrected for any declined or missed interviews by using the ratio of all returning crabbing boat parties to the number of parties that completed interviews.

For week and weekend strata within month, we estimated total daily trips taken ($t_i$) for the $i$th day as (Thompson 1992)

$$t_i = \frac{M_i}{m_i} \sum_{j=1}^{m_i} t_{ij},$$

where $t_{ij}$ represents the total number of trips taken during each of $m_i$ possible period–ramp units selected from $M_i$ possible period–ramp units in each of $n$ primary units selected from $N$ within the week and weekend. The number of trips ($T$) was then estimated as

$$T = \frac{N}{n} \sum_{j=1}^{n} t_j.$$

### TABLE 1

<table>
<thead>
<tr>
<th>Month</th>
<th>PSU WK</th>
<th>PSU WE</th>
<th>Period-ramp units per day</th>
<th>Assignments</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WK</td>
</tr>
<tr>
<td>Jul</td>
<td>17</td>
<td>11</td>
<td>226</td>
<td>11</td>
</tr>
<tr>
<td>Aug</td>
<td>18</td>
<td>8</td>
<td>226</td>
<td>13</td>
</tr>
<tr>
<td>Sep</td>
<td>17</td>
<td>9</td>
<td>226</td>
<td>15</td>
</tr>
</tbody>
</table>
Variance of $T$ was estimated by

$$\text{vâr}(\hat{T}) = N(N-n)\frac{s^2}{n} + \frac{N}{n} \sum M_i (m_i - \bar{m}_i) \frac{s_i^2}{m_i},$$

(3)

where

$$s^2 = \frac{1}{n-1} \sum_{i=1}^{n} (t_i - \bar{t})^2,$$

(4)

and

$$s_i^2 = \frac{1}{m_i-1} \sum_{j=1}^{m_i} (t_{ij} - \bar{t}_i)^2;$$

(5)

$\bar{t}$ is the mean number of trips per day. Because effort was sampled independently each month and each week or weekend, total effort $T_{st}$ was estimated as

$$\hat{T}_{st} = \sum \hat{T},$$

(6)

and its variance was estimated by

$$\text{vâr}(\hat{T}_{st}) = \sum \text{vâr}(\hat{T}).$$

(7)

Similarly, to estimate catch, we used estimators for a two-stage design with random sampling at each stage within week–weekend within month. The number of blue crabs caught during the $i$th day ($\hat{c}_i$) was estimated as

$$\hat{c}_i = \frac{M_i}{m_i} \sum_{j=1}^{m_i} c_{ij},$$

(8)

where $c_{ij}$ represents the catch during the $m_i$ period-ramp units selected from $M_i$ possible period-ramp units in each of the $n$ days selected from the $N$ in the frame. The number of crabs ($\hat{C}$) was then estimated using

$$\hat{C} = \frac{N}{n} \sum_{i=1}^{n} \hat{c}_i,$$

(9)

and its variance was estimated by

$$\text{vâr}(\hat{C}) = N(N-n)\frac{s^2}{n} + \frac{N}{n} \sum_{i=1}^{n} M_i (M_i - m_i) \frac{s_i^2}{m_i},$$

(10)

where

$$s^2 = \frac{1}{n-1} \sum_{i=1}^{n} (c_i - \bar{c})^2$$

(11)

and

$$s_i^2 = \frac{1}{m_i-1} \sum_{j=1}^{m_i} (c_{ij} - \bar{c}_i)^2;$$

(12)

$\bar{c}$ is the mean catch per day. As with effort, because sampling was undertaken independently between each month and each week–weekend, total harvest $C_{st}$ was estimated by

$$\hat{C}_{st} = \sum \hat{C},$$

(13)

and the associated variance was estimated by

$$\text{vâr}(\hat{C}_{st}) = \sum \text{vâr}(\hat{C}).$$

(14)

To assess within-day variability for each month, a linear model for a nested design with three nested factors was used (Kuehl 1994: 233): week–weekend was included as a fixed factor and between-day and within-day sources of variability were considered as nested random factors. The linear model was

$$y_{hij} = \mu + \alpha_{ih} + b_i(h) + c_{ij(h)},$$

(15)

where $y_{hij}$ denotes catch sampled during the $i$th assignment of the $j$th day within week and weekend strata $h$, $\alpha_{ih}$ is the fixed effect due to week–weekend, $b_i(h)$ is the random between-day effect nested within week–weekend, and $c_{ij(h)}$ is the nested within-day effect. To test for differences between the week and the weekend, we used the $F_0$ statistic, which is calculated as $\text{MS}(A)/\text{MS}(B/A)$, where $\text{MS}(A)$ is the observed mean square due to week–weekend and $\text{MS}(B/A)$ is the observed mean square for variation due to day within week–weekend. Values for average blue crab catch per day fulfilled assumptions of normality (Kolmogorov–Smirnov test, $\alpha = 0.05$) and homogeneity of variances ($F_{\text{max}}$ test, $\alpha = 0.05$) after transformation. The transformations used were $y^{0.5}$ for July catch, $y^{0.1}$ for August catch, and $y^{0.5}$ for September catch. The estimator for the within-day variance component for each month was

$$\hat{\sigma}^2_{cb} = \text{MS}(C/B),$$

(16)

where $\text{MS}(C/B)$ is the observed mean square error for variation due to period-ramp within day. The between-day variance component was

$$\hat{\sigma}^2_{ba} = \frac{\text{MS}(B/A) - \text{MS}(C/B)}{c},$$

(17)

where $c$ is the coefficient for the day within week–weekend component of variance.
RESULTS

Between July and September 2011, 76 assignments were completed at boat ramps in the Maryland section of the Chesapeake Bay; another eight assignments occurred during Hurricane Irene (Table 1). Recreational activity targeting blue crabs was encountered during 36 (47.4%) of the 76 completed assignments, varying between 26.7% for assignments during the week in September to 80% for assignments during the weekend in July. Agents intercepted 163 recreational crabbing parties, and interviews were obtained with 143 (87.7%) of those parties. Of the 20 parties that either declined to be interviewed or were missed, 12 parties were encountered during July, and 8 of those 12 were encountered during the weekend. The monthly response rate (consisting of crabbing boat parties that agreed to be interviewed and who did not decline and were not missed) was 87.0% during July, 80.6% in August, and 95.0% in September. Blue crabs were identified correctly by all fishing parties intercepted, with no identification error.

As is expected for recreational data (e.g., Jones et al. 1995), the distribution of catch taken per boat party was heavily skewed; however, the distribution of the catch recorded per assignment was much more stable. There was a wide range of activity between months: the most active month was July, when 971,000 blue crabs were taken, whereas activity declined to 331,000 crabs in August and 219,000 crabs in September (Figure 1). However, there was no significant effect due to week–weekend during the months examined (Table 2; $F_{0,Jul} = 2.76, P = 0.14$; $F_{0,Aug} = 0.64, P = 0.46$; $F_{0,Sep} = 3.91, P = 0.09$); within-day variability was the largest source of error in all monthly catch estimates, explaining 91.6% of the variation in July catch, 85.4% of the variation in August catch, and 98.5% of the variation in September catch (Table 3). By comparison, between-day variability accounted for only 1.5–14.7% of the catch variability due to random effects.

DISCUSSION

By intercepting recreational crabbers during multiple assignments allocated to each sampling day, we found that within-day variability accounted for only 1.5–14.7% of the catch variability due to random effects.

### Table 2: Mean square error (MS) estimates for three-factor nested ANOVAs of blue crab recreational catch, with fixed effects due to week–weekend and random effects due to between-day and within-day sampling assignments for July, August, and September (SS = sum of squares).

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week–weekend</td>
<td>1</td>
<td>334</td>
<td>334</td>
</tr>
<tr>
<td>Between day</td>
<td>6</td>
<td>729</td>
<td>121</td>
</tr>
<tr>
<td>Within day</td>
<td>18</td>
<td>1,686</td>
<td>94</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>2,684</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week–weekend</td>
<td>1</td>
<td>0.456</td>
<td>0.456</td>
</tr>
<tr>
<td>Between day</td>
<td>4</td>
<td>2.854</td>
<td>0.714</td>
</tr>
<tr>
<td>Within day</td>
<td>13</td>
<td>6.002</td>
<td>0.462</td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>9.401</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Week–weekend</td>
<td>1</td>
<td>163</td>
<td>163</td>
</tr>
<tr>
<td>Between day</td>
<td>6</td>
<td>250</td>
<td>42</td>
</tr>
<tr>
<td>Within day</td>
<td>22</td>
<td>866</td>
<td>39</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>1,289</td>
<td></td>
</tr>
</tbody>
</table>

### Table 3: Variance components for random effects ($\sigma^2_{(b)}$ and $\sigma^2_{(a)}$; see equations 16 and 17) in blue crab recreational catch. Percentage of variation explained is given in parentheses.

<table>
<thead>
<tr>
<th>Component</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_{(b)}$</td>
<td>93.7 (91.6)</td>
<td>0.462 (85.4)</td>
<td>39.4 (98.5)</td>
</tr>
<tr>
<td>$\sigma^2_{(a)}$</td>
<td>8.6 (8.4)</td>
<td>0.079 (14.6)</td>
<td>0.6 (1.5)</td>
</tr>
</tbody>
</table>
variability was by far the largest source of variation in our stratified two-stage design. In contrast, between-day variation and the variation due to week–weekend were much less important. These results suggest that for the blue crab recreational fishery in Maryland, a simple two-stage design with sampling allocated between and within days would be appropriate for use in July–September. The results also indicate that because only a small amount of variation is due to between-day effects, the design could be made more efficient by allocating more sampling effort to capture within-day variability.

Moreover, evaluation of potential within-day sources of error may improve efficiency further. Aecdotal evidence indicated that the most successful fishers left and returned earlier—and holiday-makers left and returned later—than other recreational crabbers; thus, differences between morning and afternoon assignment periods may account for a large amount of variation. Boat ramps may be important, with higher levels of activity from some boat ramps being associated with good facilities and access to crabbing areas within river mouths. Tidal may contribute as well: crabbers often reported informally that they targeted the ebb or flood but not the low or high tide. Measuring the important sources of variation can facilitate designs with better allocation of sampling effort that increases the precision and accuracy of catch and effort estimates.

Improving estimates by use of access point surveys is critical because of the coverage issues and biases associated with other approaches. Recent re-assessment of the methods employed in surveys of marine recreational fisheries (NRC 2006) has focused on the use of angler license registries, which reduce wasteful sampling by increasing the number of active anglers in the frame relative to alternatives, such as lists of households in coastal counties (Ashford et al. 2009). However, the registries are rarely comprehensive, as they exclude categories like minors or veterans and they omit noncompliant anglers. Because of the lack of coverage, potential biases are difficult to assess. In complemented designs, estimates of catch rate normally rely on public access surveys, but recent evidence indicates substantial divergence in the behavior of public access and private access fishers (Ashford et al. 2010a, 2010b). The consequent risk of incorporating public access bias in the catch estimate can be addressed by using roving creel surveys (Pollock et al. 1994), but they are expensive and susceptible to length-of-stay bias. In practice, roving creel surveys also rely heavily on accurate self-reporting of access method and catch by the intercepted boat parties.

Access point surveys offer an important option for directly estimating catch and effort by public access fishers. In addition to avoiding error due to misidentification, faulty recall, and prestige bias, this approach is generally more efficient than bus route designs, particularly for spatially dispersed fisheries, because time is not lost to travel between distant sampling points. Compared with complemented designs, direct estimation avoids variability in the effort estimate when calculating catch based on effort and catch rate. Nevertheless, high levels of variability can remain, even when standard access point methods are used (Ashford et al. 2013); this is the case for the Maryland blue crab fishery because the major sources of variation are within-day, as indicated by our results. Therefore, we strongly recommend the use of pilot studies to evaluate sources of variation before a survey design is finalized. Better management of the main sources of variability can substantially increase the precision of catch estimates, hence improving efficiency and reducing the cost of recreational fishing surveys.

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Assessing Reproductive Condition in Captive and Wild Common Snook Stocks: A Comparison between the Wet Mount Technique and Histological Preparations

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Assessing Reproductive Condition in Captive and Wild Common Snook Stocks: A Comparison between the Wet Mount Technique and Histological Preparations

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Abstract
We describe oocyte development in Common Snook Centropomus undecimalis and, secondarily, present results from a comparison of the wet mount technique with histological preparations of ovarian biopsies. Potential differences in ovarian development between wild and captive broodstock were investigated. Results showed that mean oocyte diameter (µm) was not statistically different between the two groups or within each defined stage and step of reproductive condition. Histological preparations were used to validate the wet mount technique as a rapid, yet accurate, low-cost alternative for assessing reproductive condition in Common Snook. When compared with histology, the wet mount provided a precise method for determining whether female broodstock were candidates for hormone induction in aquaculture applications. However, due to the loss of fine resolution, it was not possible to identify cortical alveoli, oocyte atresia, and postovulatory follicle complexes by using the wet mount technique. Despite these limitations, findings from this study indicate that the wet mount technique may have applications in fishery biology as a noninvasive method for assessing reproductive condition in wild fish stocks.

A critical component for many studies of fish reproductive biology is an accurate assessment of the reproductive condition of individual fish. There are numerous macroscopic and microscopic methods for evaluating the gonadal condition of fish, particularly with regard to ovarian development. West (1990) reviewed some of these in detail and discussed the level of accuracy and usefulness for each. The methods in use range from histology, which can be very accurate yet time consuming, to more rapid but less certain visual evaluation based on whole-gonad appearance (Hunter and Macewicz 1985). Other methods include assessments based on the measurement of oocyte size and gonad indices (Honji et al. 2006). One additional method, the wet mount technique, assigns reproductive stage based on microscopic visual inspection of whole oocytes obtained from...
ovarian biopsies (Neidig et al. 2000; Grier 2009). In the fields of aquaculture and fisheries, a variety of these methods can be used to answer important questions about when fish have spawned or are preparing to spawn.

Fishery biologists typically gather information on fish reproductive status by sacrificing fish to score whole ovaries (García-Díaz et al. 1997). During ecological assessments, a combination of histology and gross morphological evaluations of whole gonads is used to answer questions about fecundity, size at maturity, spawning frequency, and overall reproductive health of fish stocks (Hunter and Macieczw 1985; West 1990). An understanding of fish reproductive success and population reproductive potential is critical for designing and implementing effective fisheries management strategies (Lowerre-Barbieri 2009). In fields such as aquaculture, determining the reproductive condition of captive broodstock is important for administering hormonal therapies and inducing ovulation and spawning (Mylonas et al. 2010). Determinations of oocyte development are often based on macroscopic visual inspection, which involves documenting the color and general appearance of oocytes collected from ovarian biopsies (Honji et al. 2006). In addition, microscopic methods like the wet mount technique have been utilized for quick, low-cost oocyte staging (Neidig et al. 2000; Grier and Neidig 2011). Unlike in fisheries applications, aquaculture assessments of gonadal condition must be performed at the time of the ovarian biopsy and cannot be hampered by the delay of histological processing. The fields of aquaculture and fisheries require the same information but on different temporal scales and with different levels of precision.

Although histology is recognized as the most accurate method for examining reproductive status in fish populations, it often requires sacrificing individuals for evaluation (West 1990). This is not optimal in cases where (1) fish stocks are under conservation management, with limited numbers available for sampling; or (2) fish have a high commercial value, such as broodstock that are used for spawning in aquaculture facilities. The Common Snook Centropomus undecimalis is an example of a species for which sacrificing fish to assess reproductive condition is not ideal. The Common Snook is a high-priority species for conservation as it is both ecologically and economically important in select regions of North America and South America (Avila-Lajonchère and Tsuzuki 2008; Winner et al. 2010). A long the Gulf coast of the United States, Common Snook are part of a popular recreational fishery. However, factors such as environmental change (cold kills), habitat destruction, and overfishing have left the stocks vulnerable to decline. Recent findings highlighting changes in Common Snook stock abundance and recruitment have prompted the Florida Fish and Wildlife Conservation Commission to regularly assess the condition of wild stocks (Uller and Taylor 2012). From a fisheries management perspective, noninvasive techniques for assessment of fish reproductive condition and spawning potential would be beneficial for Common Snook as well as for other species. One such technique, the wet mount, has been used for a number of years by fisheries biologists and aquaculturists as an accurate, low-cost alternative to histology. There is a variety of forms of the wet mount technique and staging, but not all forms have been properly validated for accuracy (Patiño and Sullivan 2002; Kjesbu 2009). Therefore, the aims of our study were to describe oocyte development in Common Snook and, secondarily, to evaluate the wet mount technique of staging ovarian development in comparison with histological techniques.

METHODS

Broodstock systems.—In 2009, wild adult Common Snook were caught and transported to Mote Aquaculture Research Park, Sarasota, Florida. Collected broodstock were divided between two separate, indoor, photoperiod- and temperature-controlled recirculating tank systems (tanks A and B). Tank A contained 22 males and 11 females, whereas tank B contained 18 males and 15 females. Each system consisted of a 4.57-m-diameter fiberglass tank with a total system volume of 28 m³. Temperature was controlled (±1°C) in each tank by cycling water through an individual heater/chiller unit. The filtration system included a 0.085-m³ drop filter (Aquaculture Systems Technologies), a 900-L moving bed for biofiltration, a protein skimmer, and an ultraviolet light sterilization unit. Salinities were maintained at 35‰.

Broodstock sampling.—To sample the broodstock, the tank water level was lowered and, by using two dividers made from plastic mesh stretched across a polyvinyl chloride pipe frame, the fish were gently corralled into a section of the tank. From this restricted section, individual fish were netted into a 500-L tank containing 200 L of water and were anesthetized with tricaine methanesulphonate (MS-222) at a concentration of 300 mg/L. Male and female Common Snook were then weighed (kg) and measured (FL and TL).

Sixteen broodstock sampling events took place between 2010 and 2012. During each event, a cannulation biopsy was taken from every female (n = 26 fish) by inserting a soft tubing catheter (1.0-mm inside diameter) into the gonaduct and applying a gentle suction (using a 3-mL syringe) to collect an ovarian biopsy. A small portion of the biopsy was prepared for observation as a wet mount by placing the biopsy on a glass slide and covering it with a 22 × 22-mm, number-1 glass coverslip. Oocytes from the biopsy (n = 20 oocytes/biopsy) were immediately staged and photographed. The remaining portion of the biopsy was then placed in Trump’s fixative (McDowell and Trump 1976). For light microscopy, the fixed portion was subsequently embedded in glycol methacrylate and sectioned at 6 µm on an LKB Bromma 2218 Histostage Omicrotome (LKB Bromma, Sweden). Tissue sections were stained with periodic acid–Schiff, metanil yellow, and Weigert’s hematoxylin and eosin (Quintero-Hunter et al. 1991). Both wet mounts and histological tissue sections that were collected from individual females at each sampling event were photographed by using an Olympus BX53 microscope fitted with a DP-72 digital camera.
Oocytes were measured using Olympus cellSens version 1.3 imaging software.

Capture and sampling of wild stocks.—Wild female Common Snook (n = 152) were captured from April to September over the course of 3 years (2010–2012). All fish were weighed (kg) and measured (TL and FL) at the time of collection. Ovarian biopsies obtained from individual females were prepared as wet mounts and for histology by following the same procedures as described above for captive broodstock. Oocytes were placed on ice in the field and were later staged, measured (n = 20 oocytes/biopsy), and photographed at Mote Aquaculture Research Park within 3–5 h after collection.

Oocyte staging.—For each wild and captive fish, wet mounts of ovarian biopsies were compared with histological preparations of the same biopsy. The wet mount technique and oocyte staging terminology from Grier et al. (2009) were used to identify the reproductive condition (stage and step) of each female and to determine which individuals were suitable for hormonal implantation. The same oocyte staging method was applied to classify the reproductive status of wild females. Maturation and spawning of Common Snook for aquaculture purposes have only recently been achieved. Consequently, it was important to confirm that oocyte development in fish held under captive conditions was similar to oocyte development in wild fish. Therefore, oocyte development in wild Common Snook was examined and compared with that of captive individuals. The terminology used for staging oocytes and describing oocyte development in Common Snook was adapted to the wet mount technique, wherein letters rather than numbers are used to describe oocyte development (Grier et al. 2009; Grier 2012). In the abbreviations used here, stages are indicated by uppercase letters, whereas their subdivisions (called “steps”) are indicated by lowercase letters (for example, the preovulatory step within the oocyte maturation stage/step differences in mean oocyte diameter for captive and historical preparations is by looking closely at the nucleoli within the germinal vesicle (Figure 2). Another way to clearly identify the steps of PG is by determining the oocyte diameter (Table 1). As PG progressed, the gross oocyte characteristics did not change much, despite an increase in oocyte diameter (Figure 2; Table 1). In captive broodstock, PGon oocytes were the smallest, with a mean diameter of 66.9 µm (SE = 1.2), whereas PGod oocytes were the largest at 159.2 µm (SE = 1.5; Table 1).

A number of differences were seen when photographs of PG oocyte wet mounts and histology were compared. In wet mounts, the ooplasm remained clear in PGon, PGmn, and PGpn oocytes (Figure 2a, c, and e). In histological preparations, the ooplasm was stained blue because it is basophilic (Figure 2b, d, and f). Furthermore, PGpn oocytes in the wet mounts (Figure 2e) appeared to have nucleoli randomly scattered within the germinal vesicle, whereas histologically the nucleoli were located around the periphery of the germinal vesicle (Figure 2f).

As oocyte growth progressed from PGpn to PGod, additional details reflecting the lower resolution of wet mounts relative to histological preparations became apparent, as in the “ring oocyte.” The black ring is composed of numerous small oil droplets that are not individually resolved due to the limited resolution of the wet mount technique (Figure 2g). Using light microscopy, the oil droplets are seen as clear vesicles encircling the germinal vesicle (Figure 2h). Ring oocytes are found at the initiation of oocyte development and are usually scattered among transparent PG oocytes in an earlier step of development. They are indicative of the transition from PG to secondary growth (SG) and are present in both stages.

Secondary growth.—Secondary growth includes three steps: early (SGe; Figure 3a-c), late (SGl; Figure 3d, e), and full grown (SGfg; Figure 3f, g). Within the SG stage, SGe, SGl, and SGfg can be distinguished from each other by determining the diameter of the oocyte (Table 1). In a spawning-capable female Common Snook, SGfg oocytes had a mean diameter of approximately 400 µm (Table 1).

As in PG, greater details in SG oocytes were revealed by histology than by wet mounts. Secondary growth commences upon the appearance of yolk in the form of globules scattered throughout the ooplasm (Figure 3b, c); the yolk appears as fine, clear vesicles in the wet mount ring oocytes (Figure 3b). In histological preparations, the yolk is visible as fine, distinctively stained globules in SGe, SGl, and SGfg oocytes (Figure 3c, e, and g). As oocyte growth continues, the accumulating yolk globules

**RESULTS**

**Oocyte Diameter**

Wet mount stage and step descriptions and the corresponding mean oocyte diameters are presented in Table 1. In total, 3,040 and 4,780 oocyte diameters (n = 20 oocytes/biopsy) were recorded for wild and captive fish, respectively. Mean oocyte diameter (µm) within each defined stage and step of reproductive condition was not statistically different between wild and captive fish (P > 0.05).

**Validation of the Wet Mount Technique**

Primary growth.—Primary growth (PG) oocytes, which were transparent in wet mounts, were the only oocytes present in biopsies from regressed ovaries of Common Snook (Figure 1). The PG oocyte stage includes four steps: one nucleolus (PGon; Figure 2a, b); multiple nucleoli (PGmn; Figure 2c, d); perinucleolar (PGpn; Figure 2e, f); and oil droplets (PGod; Figure 2g, h). The best way to distinguish among the steps of PG in wet mounts and histological preparations is by looking closely at the nucleoli within the germinal vesicle (Figure 2). Another way to clearly identify the steps of PG is by determining the oocyte diameter (Table 1). As PG progressed, the gross oocyte characteristics did not change much, despite an increase in oocyte diameter (Figure 2; Table 1). In captive broodstock, PGon oocytes were the smallest, with a mean diameter of 66.9 µm (SE = 1.2), whereas PGod oocytes were the largest at 159.2 µm (SE = 1.5; Table 1).

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TABLE 1. Stages and steps of Common Snook oocyte development as they appear when the wet mount technique is used; mean ± SE oocyte diameter (µm) in captive and wild Common Snook (n = 20 oocytes measured per female) and number of females sampled are also shown.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Step</th>
<th>Abbreviation</th>
<th>Wet mount stage and step descriptions</th>
<th>Captive females</th>
<th>Wild females</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Oocyte diameter</td>
<td></td>
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<td>N of fish sampled</td>
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<tr>
<td>Primary growth (PG)</td>
<td>One nucleolus</td>
<td>PGon</td>
<td>Germinal vesicle (gv) has a single nucleolus; ooplasm is transparent</td>
<td>66.9 ± 1.2</td>
<td>63.2 ± 1.1</td>
</tr>
<tr>
<td></td>
<td>Multiple nucleioli</td>
<td>PGmn</td>
<td>Spherical gv with two or more nucleoli not at the periphery; ooplasm is transparent</td>
<td>73.4 ± 0.51</td>
<td>75.6 ± 0.47</td>
</tr>
<tr>
<td></td>
<td>Perinucleolar</td>
<td>PGpn</td>
<td>The gv nucleoli are peripheral, and gv may have an undulating outline; ooplasm is transparent</td>
<td>87.6 ± 0.61</td>
<td>82.3 ± 0.69</td>
</tr>
<tr>
<td></td>
<td>Oil droplets</td>
<td>PGod</td>
<td>Oil droplets located around periphery of the gv are resolved as a black ring (ring oocyte); ooplasm is transparent</td>
<td>159.2 ± 1.5</td>
<td></td>
</tr>
<tr>
<td>Secondary growth (SG)</td>
<td>Early</td>
<td>SGe</td>
<td>Some scattered, small yolk globules appearing as clear spheres, still called ring oocytes</td>
<td>231.3 ± 2.9</td>
<td>239.8 ± 2.2</td>
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<tr>
<td></td>
<td>Late</td>
<td>SGI</td>
<td>Oil droplets masked by density of yolk globules; gv is a diffuse, clearer area in center of oocyte; ooplasm is dark and granular</td>
<td>356 ± 1.7</td>
<td>335.7 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>Full grown</td>
<td>SGfg</td>
<td>Contains dark granular ooplasm; distinguishable from SGI by oocyte diameter; oil droplets are masked by yolk globules</td>
<td>399.5 ± 1.0</td>
<td>388.2 ± 0.98</td>
</tr>
<tr>
<td>Oocyte maturation (OM)</td>
<td>Eccentric germinal vesicle</td>
<td>OM egv</td>
<td>Oil globules with black borders coalesce until a single, central oil globule is formed, displacing the germinal vesicle to an eccentric position</td>
<td>429.0 ± 1.9</td>
<td>422.6 ± 1.7</td>
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<tr>
<td></td>
<td>Germinal vesicle migration</td>
<td>OM gvm</td>
<td>Oocyte hydrates; a single oil droplet is generally present, but multiple droplets can occur; gv is not visible</td>
<td>469.1 ± 4.3</td>
<td>488.3 ± 3.9</td>
</tr>
<tr>
<td></td>
<td>Preovulatory</td>
<td>OM pov</td>
<td>Ooplasm is cleared (hydrated), with extensions of peripheral ooplasm extending into yolk; gv has broken down (is not visible)</td>
<td>501.8 ± 2.9</td>
<td>522.4 ± 2.4</td>
</tr>
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</table>

Oocyte maturation.—Oocyte maturation (OM) includes ooplasmic and germinal vesicle changes and the breaking of meiotic arrest prior to ovulation. Oocyte maturation includes three steps: eccentric germinal vesicle (OM egv), germinal vesicle migration (OM gvm), and preovulatory (OM pov; Figure 4). When using the wet mount technique, the first sign of OM (i.e., OM egv) is the coalescence of oil droplets around the central germinal vesicle (Figure 4a). When the oil droplets begin to coalesce at the beginning of OM egv, they are thereafter called “oil globules,” a terminology change that separates oocyte growth from OM (Grier et al. 2009). The dark borders of oil globules in wet mounts (Figure 4a) distinguish them from the diffuse border of the germinal vesicle that is located behind numerous spherical yolk globules, as during SG (Figure 4f). The germinal vesicle becomes displaced to an eccentric position during OM egv as the oil globules coalesce centrally. In the wet mount preparation, an eccentric germinal vesicle is the first observed polarity of the oocyte in the developing Common Snook egg (Figure 4b). Histological preparations also reveal the appearance of fluid yolk at the vegetal pole during OM egv (Figure 4c). By the completion of OM egv, there is a single, central oil globule and the germinal vesicle has become eccentric, being displaced toward the animal pole of the oocyte.
The germinal vesicle is no longer observed in wet mounts of OMgvm oocytes, when the yolk is hydrating or clearing, and one or more oil globules are observed (Figure 4d). However, in histological preparations of OMgvm oocytes, germinal vesicle migration is observed to begin when there is ooplasm between the single oil globule and the germinal vesicle (Figure 4e). Although germinal vesicle migration is not observed in wet mounts during OMgvm, oil globules and clearing yolk are observed and serve to distinguish this OM step. Germinal vesicle breakdown and the resumption of meiosis are also not observed in either the wet mounts (Figure 4d) or the histological preparations (Figure 4e, g).

In the OMpov step, the germinal vesicle has broken down; meiosis has resumed, and meiotic arrest has occurred in metaphase of the second division of meiosis. A single oil globule is present, and the ooplasm extends from the oocyte periphery into the fluid yolk, subdividing the yolk into large, fluid yolk globules (Figure 4f, g). The yolk globules are distinct in wet mounts (Figure 4f) and are outlined by basophilic ooplasm in histological preparations (Figure 4g).

**Oocyte atresia.**—Atretic oocytes were observed (Figure 5) in ovaries of captive and wild Common Snook. Oocyte atresia is not visible in wet mounts because oocytes in early atresia appear as normal SG oocytes; however, early atretic oocytes are clearly revealed in histological preparations. The germinal vesicle was never observed in atretic oocytes by using either wet mounts or histology, as it had broken down. Histologically, the salient features of early atresia in captive Common Snook include the fragmented zona pellucida, which primarily becomes clumped toward the center of the oocyte in the generally disorganized ooplasm. The ooplasm is mostly composed of scattered oil droplets and yolk globules; the latter are seen to be breaking down toward the oocyte periphery. Numerous oil droplets are scattered throughout the ooplasm.

**DISCUSSION**

Accurate assessment of fish reproductive condition and spawning potential is critical in aquaculture and fisheries. In the study of fish reproductive biology, numerous techniques and corresponding staging methods are available for documenting and interpreting gonadal development. However, not all of these techniques have been validated with very precise methods like histology, and not all of the staging descriptions use
the same terminology. Some of the staging schemes use letters (Grier et al. 2009), while others use numbers (Bromley 2003) to describe and define the development of fish oocytes. The problems encountered using different numbered staging schemes to describe oocyte growth and maturation events in fish are well documented (Mayer et al. 1990; West 1990; Patiño and Sullivan 2002; Brown-Peterson et al. 2011). The lack of generally accepted, consistent ovarian terminology has limited communication among scientists within and across research fields by making it difficult to conduct data comparisons (Grier et al. 2009; Brown-Peterson et al. 2011). Bromley (2003) highlighted the problem with the terminology used in fisheries literature by citing the incongruent staging (i.e., based on different numbered stages) used by fisheries biologists for the Plaice Pleuronectes platessa. The resulting data for Plaice could not be compared within the same fishery, thus confirming the need for validated sampling methods as well as clear and consistent definitions of oocyte growth and maturity (Blazer 2002; Parenti and Grier 2004).

Although the timing of events during gamete development may vary among species, each reproductive phase that occurs during annual reproductive cycles has specific physiological and histological markers that are conceptually universal. Variability in oocyte development may occur due to reproductive diversity among fishes (Lubzens et al. 2010). For example, in Gulf Killifish Fundulus grandis, cortical alveoli are large and well developed prior to the appearance of oil droplets but become smaller later in development (Grier et al. 2009). In Common Snook, cortical alveoli appear shortly after the PGon step. The appearance of oil droplets and the appearance of cortical alveoli in PG have been designated as transitory steps to SG (Grier 2012). Cortical alveoli cannot be observed in wet mounts due to the limited resolution of the technique. For fish that produce pelagic eggs with an oil globule, a ring of blackened oil droplets surrounds the germinal vesicle in wet mount preparations. The appearance of oil droplets around the germinal vesicle and the appearance of cortical alveoli at the oocyte periphery are events that occur nearly simultaneously during oocyte growth, as indicated histologically in Common Snook.

Within a population, fish are not spawning capable unless full-grown oocytes are present in the ovary (Brown-Peterson et al. 2011). In fish that produce pelagic eggs, the appearance of ring oocytes in wet mounts should suffice to determine reproductive condition for purposes of aquaculture and fisheries applications when histology is not used. Again, the designation “ring oocyte” is not a stage of oocyte development. Ring oocytes may encompass two stages and multiple steps of oocyte development (e.g., PGon and SGn) when yolk begins to form. The dark appearance of oil globules around the germinal vesicle is an important diagnostic criterion found during hatchery evaluations of wet mounts. The same criterion could be applied in fisheries for pelagic egg development where an oil globule is present in the egg. Oil droplets in PG and SG oocytes become oil globules during OM. By definition, this is meant to distinguish oocyte growth from OM (Grier et al. 2009). However, ring oocytes are not full-grown oocytes (i.e., SGfg). Until SGfg oocytes are present in the ovary, a fish cannot be induced to undergo maturation and ovulation by using hormones. The SGfg oocytes are easily detected using either the wet mount technique or histological processing, and oocyte diameter is a good indicator.
FIGURE 3. Micrographs of Common Snook secondary growth (SG) oocytes from wet mount preparations (a, b, d, and f) and corresponding micrographs of histological preparations (c, e, and g) are shown: (a) primary growth (PG) oocytes and SG stage, early step (SGe) oocytes, appearing as ring oocytes; (b) ring (R) oocyte with clear yolk globules in the ooplasm and over the germinal vesicle; (c) a PG stage, oil droplet step (PGod) oocyte, an SGe oocyte (with a well-defined germinal vesicle [gv], cortical alveoli [ca], yolk [y], and oil droplets [od]), and an SG stage, late step (SGl) oocyte visible in the left corner; (d) SG stage, full-grown step (SGfg) oocyte, with R, SGe, and SGl oocytes (nonspherical shape of SGfg oocytes is due to the pressure applied to the coverslip); (e) PG stage, perinucleolar step (PGpn) oocytes surround an SGl oocyte with clear oil droplets (od), yolk (y), and peripheral cortical alveoli (ca); (f) SGfg oocyte, with the germinal vesicle (gv) present as a clearer area; and (g) SGfg oocytes, with central germinal vesicles (gv) and ooplasm containing clear oil droplets (od) intermixed with yolk globules (y), and an SGe oocyte also present. [Figure available online in color.]
FIGURE 4. Oocyte maturation (OM) in Common Snook (a, b, d, and f are wet mounts; c, e, and g are histological preparations): (a) early in the OM stage, eccentric germinal vesicle step (OMegv) of oocyte development, the germinal vesicle (gv) is central and the oocyte is full of yolk globules (y), rendering it opaque, and oil globules with dark borders (og) encircle the central germinal vesicle; (b) an oocyte at the end of the OMegv step has a central oil globule (og) that has displaced the germinal vesicle (gv) to an eccentric position; (c) OMegv oocyte (more advanced than the OMegv oocyte in panel a), with multiple oil globules (og) coalescing at the center of the oocyte, displacing the germinal vesicle (gv) to an eccentric position toward the animal pole, and with yolk globules (y) that are smaller at the animal pole but are coalescing (arrowheads) at the vegetal pole; oocyte polarity is clearly established; (d) OM stage, germinal vesicle migration step (OMgvm) oocyte, showing black patchiness in the ooplasm (clearing yolk [cy]) and oil globules (og) with a dark border; (e) OMgvm oocyte at the beginning of migration, signified by ooplasm between the oil globule (og) and the germinal vesicle (gv), and fluid yolk (fy) surrounds the germinal vesicle, still having yolk globules within; (f) OM stage, preovulatory step (OMpov) oocytes, exhibiting numerous “lines” through the fluid yolk (fy) and generally a single oil globule (og); and (g) OMpov oocyte with fluid yolk (fy) and a single oil globule (og), and arrowheads indicate the extension of ooplasm through the fluid yolk. [Figure available online in color.]
The wet mount technique for ovarian biopsies has been applied in aquaculture spawning procedures, and the technique has been validated by comparison with histological preparations. In an aquaculture setting where a simple and quick method is needed to determine whether a female Common Snook is a potential candidate for hormone induction of ovulation, the microscopic evaluation of whole oocytes by using the wet mount technique will be accurate and informative. Use of the wet mount technique need not be restricted to aquaculture applications; it may also have applications in fishery biology as a tool for immediate, low-cost determination of a population's reproductive condition. Gross ovary evaluations are commonplace in fisheries science, especially when histology is not available, because gross evaluations constitute an inexpensive way to routinely monitor the reproductive state of the catch. Depending on the needs of the study, the wet mount technique can be advantageous by providing a noninvasive method of observation in situations where sacrificing the fish to determine their reproductive condition is not optimal. Although the wet mount technique has potential as a tool that can be used across research fields, it does have some limitations. In Common Snook, oocytes in early atresia appeared to be normal oocytes when viewed in wet mounts but were easily identified as atretic when using histology. Additionally, due to the loss of fine resolution, it was not possible to accurately identify cortical alveoli, oocyte atresia, and postovulatory follicle complexes by use of the wet mount technique. This limitation negates the technique's utility for evaluating spawning frequency, which is an important part of many fisheries management studies.

In conclusion, use of the wet mount technique with a tiered and adaptable staging scheme has been validated for aquacultural and field applications with Common Snook. Results indicate that use of the side-by-side comparison of the wet mount technique and histological preparations could serve as guide for researchers in aquaculture and fisheries to conduct similar validations for species of interest in addition to Common Snook.

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Abundance of Skeena River Chum Salmon during the Early Rise of Commercial Fishing

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ARTICLE

Abundance of Skeena River Chum Salmon during the Early Rise of Commercial Fishing

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Abstract
We used reported commercial catch data and historical information to estimate the abundance of Skeena River Chum Salmon *Oncorhynchus keta* during the early rise (1916–1919) in the commercial fishery to provide historical perspective for recovery plans. We applied a Bayesian analysis to address the uncertainties associated with the estimation process. Based on the historical catch of 204,000 in 1919 and an estimated harvest rate of 0.32–0.58, the estimated return of Skeena Chum Salmon ranged from 355,000 to 619,000, with the most probable single estimate being 431,000. The estimated return of Chum Salmon based on the 1916–1919 geometric mean catch of 154,000 ranged from 268,000 to 471,000, with the most probable single estimate being 325,000. Our posterior modal historical estimates are 8–11 times larger than the estimates for the contemporary period 1982–2010 and 39–52 times larger than those for the most recent period of 2007–2010. Intense harvest pressure is the single most probable factor explaining the sustained decline in Chum Salmon abundance, but other interactive factors, notably natural variations in survival, the loss of spawning and rearing habitat, and poor data quality, also are important considerations. Nonetheless, the Skeena catchment is largely pristine today, and our robust estimates of historical abundance should be of value to contemporary management and conservation agencies for the rebuilding of such severely diminished populations.

The rich ecological and cultural legacy of Canada's Pacific coast is shaped, if not defined, by wild Pacific salmon *Oncorhynchus* spp.; thus, these fish form a vital component of its future. Salmon contribute “identity” to coastal indigenous peoples (Campbell and Butler 2010; Hill et al. 2010), deliver essential nutrient subsidies to watersheds (Gende et al. 2002; Willson et al. 2004), and are important to coastal economies through nature-based tourism, harvesting, and processing (Schindler et al. 2010).

While many wild salmon stocks and species in British Columbia have been considerably diminished over the last century of intensive exploitation (see Slaney et al. 1996), a commercial mixed-stock fishery continues to harvest salmon. Recently, Sockeye Salmon *O. nerka* and Pink Salmon *O. gorbuscha* fisheries in British Columbia have acquired “sustainable” eco-certification labels from the Marine Stewardship Council (MSC; Tavel Certification 2010), and an application for Chum Salmon *O. keta* is in progress. This market-driven certification
program provides financial incentive to fishers while promising adherence to international sustainability criteria. Although the MSC certification scheme is arguably failing to protect the ecological integrity of some marine systems (Jacquet et al. 2010), it is considered one important component of salmon conservation (Conn 2011). For example, the MSC certification of Skeena River Sockeye Salmon is conditional (in part) upon the creation and implementation of recovery plans for Skeena Chum Salmon (Tavel Certification 2010) that currently are at very low abundance and vulnerable to bycatch in the mixed-stock Sockeye Salmon and Pink Salmon fisheries (Walters et al. 2008).

To be effective, recovery planning for Skeena River Chum Salmon must address the rebuilding of life history characteristics and abundance; to be legitimate, it must endeavor to compare the current levels of abundance not only with the levels that immediately preceded recovery listing but also with historical estimates of abundance. Without such a historical perspective, recovery targets may considerably underestimate the potential abundance and diversity that is required to assure the persistence of these populations.

Estimates of the historical abundance of Skeena River Chum Salmon (and British Columbia salmon stocks in general) suffer from a “shifting baseline” syndrome of information (Price et al. 2008). All too often, run-reconstruction analyses and stock status evaluations are based on abundance data that date back only to the 1950s or even the 1980s (English et al. 2006; Spilsted and Pestal 2009; Cox-Rogers and Spilsted 2012; English 2012). However, Skeena salmon abundance was considerably reduced as early as the 1920s (Pritchard 1948; Ricker and Smith 1975), and roughly one-third of the original biodiversity is estimated to have disappeared before 1950 (Walters et al. 2008). Clearly, a historical perspective is needed, and herein we show how historical information for Skeena River Chum Salmon can be used to estimate past abundance. We use a Bayesian analysis framework to estimate Chum Salmon run sizes from company records of the canned pack and other products. Thus, our primary objective is to provide an evidence-based estimate of Chum Salmon abundance returning to the Skeena River during the early rise of the industrial commercial fishery. Our analysis provides a reasonable historical estimate to underpin recovery plans.

METHODS

Our source of historical harvest records for Skeena River Chum Salmon was the extensive commercial catch data compilation for British Columbia salmon of Argue and Shepard (2005, their Table 46). These data were based primarily on the canned-pack records of salmon canneries operating at the mouth of the Skeena River beginning in 1877 (Figure 1). The first commercial harvest records for Chum Salmon date from 1901, yet the catch remained negligible until 1914 compared with all other commercially caught Skeena salmonids (Argue and Shepard 2005). A num Chum Salmon catch steadily increased from 1914 (64,000) to 1919 (204,000), then declined (with some variations) for several years, but peaked in 1926 (328,000). Before gasoline-powered vessels were introduced on the Skeena River in 1924, an oar and sail gill-net fishery prevailed (Milne 1955; Figure 2). The limited range of the row-boats confined the commercial fishery during this early period primarily to the Skeena River (Milne 1955; Wood 2008), which provides strong evidence that the vast majority of Chum Salmon caught were of Skeena origin.

We based our historical Chum Salmon abundance estimates on catch data from 1916 to 1919. This 4-year period, spanning approximately one generation (Ricker 1980; Salo 1991), represents the period when Skeena River Chum Salmon first experienced high rates of harvest but before the population showed clear signs of overharvesting. Thus, run size estimates based on the catch record for this period likely best represent the inherent capacity of the Skeena catchment to produce Chum Salmon during the period immediately prior to the continuous harvest of a large proportion of the run.

Despite the growing trend in catch during 1914–1919, Chum Salmon were incidentally caught during this period in Sockeye Salmon (the most profitable species) and Coho Salmon O. kisutch fisheries (Milne 1955; Lyons 1969). Sockeye Salmon were harvested annually between mid-June and the end of August, predominantly within the Skeena River (Milne 1955; Wood 2008). Some form of an “outside” fishery also existed, whereby a portion of fishing effort occurred within the Skeena estuary during the first 3 weeks of the Sockeye Salmon fishery (Ross 1967; Wicks 1975; Blyth 1991). The resulting catch abundance of the outside fishery was reportedly much smaller than the later “inside” fishery, when Sockeye Salmon concentrated within the Skeena River (Ross 1967; Wicks 1975; Figure 1). The Coho Salmon fishery occurred from the end of August to mid-September (Carrothers 1941; Milne 1955). Today, as we assume occurred in the past, the annual return of Skeena Chum Salmon peaks by the third week of August and the run continues into September (see Tyee Test Fishery 2012 for data).

Bayesian Estimation of Historical Run Sizes

We used the harvest rates on Skeena River Sockeye Salmon estimated by Ricker (1958, 1973) and substantiated by Wood (2008) to approximate the harvest rate on Chum Salmon during our period of evaluation (1916–1919). By considering the combined information about the harvest rate on Sockeye Salmon, the proportion of the Chum Salmon run coinciding with the Sockeye Salmon fishery, the post-Sockeye Salmon fishery for Coho Salmon, and the remaining proportion of the Chum Salmon run coinciding with the Coho Salmon fishery, we were able to place reasonable bounds on the total Chum Salmon harvest rate. This required that we estimate the following parameters: (1) ChRS, the proportion of the total Chum Salmon run that encountered (and was potentially subject to harvest during) the Sockeye Salmon fishery, (2) SH Ch, the proportion of the annual harvest rate on Sockeye Salmon to which Chum Salmon in the overlapping proportion of the Chum Salmon run (ChRS) were vulnerable, (3) SHR, the total annual harvest rate on the Sockeye.
FIGURE 1. Study area, including the Skeena River and estuary; locations of the salmon canneries that operated during 1916-1919; and the historical and current commercial fishing boundaries.
Salmon run, (4) $\text{CoHR}$, the proportion of the total harvest rate on the post–Sockeye Salmon fishery for Coho Salmon to which the overlapping proportion of the Chum Salmon run $(1 - \text{ChRS})$ was vulnerable, and (5) $\text{CoHR}$, the harvest rate on Coho Salmon during the post–Sockeye Salmon season Coho Salmon fishery. Hence, the harvest rate on Chum Salmon was estimated as

$$\text{ChHR} = (\text{ChRS} \cdot \text{SHCh} \cdot \text{SHR}) + [(1 - \text{ChRS}) \cdot \text{CoHR} \cdot \text{CoHR}].$$

(1)

We followed the general approach of Gayeski et al. (2011) to estimate the principal parameter of interest, the terminal Chum Salmon run size ($N$), from the total catch and estimates of the harvest rate applied to the total run. We employed a negative binomial likelihood based on the gamma–Poisson parameterization (see the appendix for justification) and treated the total commercial Chum Salmon catch ($C$) as a Poisson random variable in which the Poisson rate parameter ($\lambda$) is drawn from an underlying gamma distribution with a constant scale parameter ($\beta$) equal to the underlying average harvest rate ($\text{ChHR}$) and a shape parameter ($\alpha$) equal to the total run from which the catch was obtained, that is, $C \sim \text{Poisson}(\lambda)$; $\text{Bin} \sim \text{gamma}(N, \text{ChHR})$. Thus, we estimated the parameters of the negative binomial likelihood

$$P(C, \lambda, N, \text{ChHR}) = P(C | \lambda) \cdot P(\lambda | N, \text{ChHR}),$$

(2)

which is the joint probability of obtaining the catch $C$ given a Poisson distribution with rate parameter $\lambda$, and obtaining $\lambda$ from a gamma distribution with parameters $N$ and $\text{ChHR}$. In this parameterization, the expected value of the gamma is $\alpha \cdot \beta$ (in this case, $N \cdot \text{ChHR}$), which will also be the expected value of $\lambda$. Since the expected value of a Poisson-distributed random variable is also $\lambda$, the expected value of the Poisson-distributed catch $C$ will also be equal to $\lambda$, which will be the mean of the negative binomial. But unlike the Poisson distribution, the variance of the negative binomial will be greater than the mean and equal to $\alpha \cdot \beta \cdot (1 + \beta)$. Thus, the variance of the catch will be $N \cdot \text{ChHR} \cdot (1 + \text{ChHR})$. In our situation, $C$ (catch data) is a constant and $\lambda$, $\text{ChHR}$, and $N$ are the parameters to be estimated.

There is little uncertainty in the estimation of $\lambda$, since the coefficient of variation ($\text{CV} = \text{SD}/\text{mean}$) for large values of $\lambda$ (as is the case here) is very small (e.g., for $\lambda = 200,000$, the SD will be $\sqrt{200,000} = 447$, and $\text{CV} = 447/200,000 = 0.00224$). However, considerable uncertainty is involved in estimating $N$, $\text{ChHR}$, and each of the five independent parameters in equation (1) ($\text{ChRS}$, $\text{SHCh}$, $\text{SHR}$, $\text{CoHR}$, and $\text{CoHR}$), from which the aggregate Chum Salmon harvest rate, $\text{ChHR}$, is derived. We address these uncertainties by employing a Bayesian approach, placing prior distributions on all unknown parameters and using a Metropolis-within-Gibbs algorithm to sample the posterior distribution equation (3) corresponding to the negative binomial likelihood equation (2):

$$P(\lambda, N, \text{ChHR}|C) = P(C|\lambda) \cdot P(N, \text{ChHR}|\lambda).$$

(3)

The Bayes estimate of the terminal run size was obtained using the Fortran shell program Metropolis-within-Gibbs (MTG) written by the late Daniel Goodman (Environmental Statistics...
Group, Department of Biology, Montana State University, Bozeman). The MMTG implements the Metropolis-within-Gibbs algorithm, sampling a joint distribution specified by a joint log proportional density function (which for the Bayesian analysis is the joint posterior divided by a proportionality as the product of the joint prior and joint likelihood). The posterior distribution equation (3) was sampled for each of the two values of the total catch. For each estimate, 2,000,000 samples were retained using a thinning interval of 100 (i.e., every 100th sample was retained) to reduce the autocorrelation among parameter values (which results from the MCMC sampling of the posterior distribution) and to ensure thorough sampling of the entire posterior probability space. The priors and posteriors of the parameters selected for histogram display were binned into 100 equal-size bins on the x-axis to produce smooth histograms and to provide reasonably fine-scale resolution of the posterior probability densities. Histograms of the posterior distributions for the parameters contributing to the Chum Salmon harvest rate (i.e., ChRS, SHCh, SHR, 1−ChRS, CohCh, and CohR) were examined together with summary statistics for the MCMC samples to verify that the entire posterior parameter space had been properly sampled. The parameterizations of the prior distributions were based on available data regarding the conduct of the fisheries and associated gear type, the known and estimated run timings of each species, and the relative and absolute body sizes of Chum Salmon.

Justification of the Prior Distributions

The prior distributions and their parameters are listed in Table 1. To be conservative, we chose values that tended to give smaller estimates of the total Chum Salmon population size for the following priors:

The Poisson rate parameter for the distribution of the Chum Salmon catch (PLAM).—Given the assumption that the total catch of Chum Salmon is a Poisson random variable, we placed upper and lower limits on a uniform distribution of the rate parameter, PLAM, which spanned all possible values that could yield the numerical catch C. For values of C as large as those for the two time periods whose catch we evaluate, values of PLAM will lie well within plus or minus 10% of C, so we set the lower boundary at 0.9 · C and the upper boundary at 1.1 · C. This guaranteed that all possible values of the posterior probabilities of PLAM would be found.

The proportion of the total Chum Salmon run that encountered the Sockeye Salmon fishery (CHRS).—The commercial Skeena River Sockeye Salmon fishery historically closed by the end of August each year (M. Ille 1955). The majority of Chum Salmon are thought to return to the Skeena River before the end of August, but the exact proportion remains unknown. Data from the Tyee test fishery, which dates back to 1956, suggest that this proportion is somewhere between 67% and 75% of the entire annual return of Skeena Chum Salmon (Tyee Test Fishery 2012). As noted above, we reasonably assumed that this range also applies to the period of interest herein (1916–1919); thus, we placed a uniform distribution on the parameter between 0.67 and 0.75.

The proportion of the annual Sockeye Salmon harvest rate to which Chum Salmon were vulnerable (SHCH).—Although Chum Salmon were targeted by the Skeena River fishery to some extent, it is improbable that harvest rates were higher than those on Sockeye Salmon during the years of our evaluation because Chum Salmon had less market value (M. Ille 1955; Lyons 1969). Furthermore, Chum Salmon were substantially larger on average than Sockeye Salmon (i.e., 6.4 kg, compared with 2.9 kg; Auge and Shepard 2005), which made Chum Salmon less susceptible to capture in Sockeye Salmon-specific gill nets (i.e., 5.75-in [14.6-cm] mesh; M. Ille 1955) that retain fish within a narrow size range (Hamley 1975; Muir et al. 1994). Thus, the actual harvest rate on Chum Salmon likely was some fraction of the estimated Sockeye Salmon harvest rate, perhaps 50% to 60%, and certainly not more than 90%. Therefore, we placed a uniform distribution on SHCh bounded between 0.60 and 0.90.

The total annual harvest rate on the Sockeye Salmon run (SHR).—The harvest rate on Skeena River Sockeye Salmon during the period 1915–1919 has been estimated at 0.62 (Ricker 1958, 1973; Ricker and Smith 1975) and substantiated by Wood (2008). However, good as this estimate may be, it is likely that there is some degree of uncertainty surrounding it when it is applied to any single year; accordingly, we placed a uniform distribution on SHR bounded between 0.60 and 0.66.

The proportion of the total Chum Salmon run that encountered (and were potentially subject to harvest during) the post-Sockeye Salmon season Coho Salmon fishery (1−CHRS).—The sampling of this parameter was calculated deterministically by subtracting each value sampled from the prior of CHRS from 1. This is because we are estimating the proportion of the Chum Salmon run that remained after the Sockeye Salmon fishery but that were also vulnerable to the late-season Coho Salmon fishery (i.e., we assume that all Chum Salmon were either exposed to the Sockeye Salmon or Coho Salmon fishery).

<table>
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<tr>
<th>Parameter</th>
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<td>1.1 · C</td>
</tr>
<tr>
<td>ChRS</td>
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</tr>
<tr>
<td>SHCh</td>
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<td>0.90</td>
</tr>
<tr>
<td>SHR</td>
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<td>1−ChRS</td>
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<td>CohR</td>
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<tr>
<td>CohCh</td>
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<td>0.90</td>
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<tr>
<td>N: Catch/max(CHHR)</td>
<td>Catch/min(CHHR)</td>
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The proportion of the total harvest rate on the post–Sockeye Salmon season Coho Salmon run to which the overlapping proportion of the Chum Salmon run (1—CHRS) were vulnerable (CoHCh).—Chum Salmon were substantially larger on average than Coho Salmon (i.e., 6.4 kg, compared with 4.4 kg; Argue and Shepard 2005) and may thus have been less likely than Coho Salmon to be caught in the late-season gill-net fishery. Additionally, Chum Salmon were unlikely to be caught in the hook-and-line fishery that targeted Coho Salmon during our period of interest. But to be conservative in our estimates, and given the paucity of information, we placed the same distribution and limits on the harvest rate on the late-season Chum Salmon run as we did for Chum Salmon subject to the Sockeye Salmon fishery. That is, we felt that Chum Salmon were as vulnerable to the Coho Salmon fishery as they were to the Sockeye Salmon fishery (i.e., 0.60 and 0.90).

The harvest rate on the post–Sockeye Salmon season Coho Salmon fishery (CoHR).—Harvest rates on Coho Salmon were not likely higher than the harvest rates on Sockeye Salmon because Sockeye Salmon had superior market value (Milne 1955); canneries and fishermen made the majority of their money on Sockeye Salmon (Ross 1967; Lyons 1969; Wicks 1975). And although some fishermen only participated in the Sockeye Salmon fishery (Knight and Koizumi 1976), others were involved in an additional hook-and-line fishery that targeted Coho Salmon (Blyth 1991). To conservatively account for the uncertainties in fishing effort, we placed a uniform distribution on the CoHR parameter between the bounds 0.45 and 0.60.

The informative character of the prior distribution of the Chum Salmon harvest rate (CHHR).—Despite our having to employ uniform priors for five independent parameters to obtain the prior distribution for the aggregate harvest rate on Skeena River Chum Salmon, the resulting prior had a unimodal bell shape centered around 0.45. This resulted from a common property of the multiplication of several uniform distributions and yielded a considerable reduction in the uncertainty surrounding this parameter. The critical information lies in the upper and lower limits of the contributing uniform priors, which we delimit as best we could given the available historical information. Thus, even with little or no information on the shape of the component parameters of this prior, the aggregation of multiple uniform priors yielded a prior that contained considerably more information than if we had placed a uniform prior directly on CHHR.

Sensitivity of the prior for the Chum Salmon harvest rate to the limits of the component parameter distributions.—We examined the sensitivity of the distribution of CHHR to the lower and upper limits of the parameter components to determine how influential each limit of each component was to the distribution of CHHR; our methods and results are presented in the appendix. Essentially, the prior on CHHR was moderately sensitive to increases of 0.1–0.2 in the upper limits of SRH and CoHR (Tables A.1–A.2 in the appendix), values for the Sockeye Salmon and Coho Salmon harvest rates that are well above any estimates made for these fisheries. The prior on CHHR was insensitive to changes of 0.1–0.2 to the lower or upper limits of CHRS, SHCh, and CoHCh (Tables A.3–A.5).

The terminal Chum Salmon run size (N).—The only information on historical Chum Salmon abundance is the company records of canned packs and other products, which were converted to catch in pieces by Argue and Shepard (2005). Accordingly, we simply bounded the prior distribution of N broadly between the minimum and maximum values possible, given the values of the prior distributions contributing to CHHR. Given the values of our priors, the minimum value of CHHR = (0.67 · 0.60 · 0.58) + (0.33 · 0.60 · 0.45) = 0.32. The maximum value of CHHR = (0.75 · 0.90 · 0.66) + (0.25 · 0.90 · 0.60) = 0.58. Given a value for C, the lower bound on N = C/0.58 and the upper bound on N = C/0.32. The posterior distribution of N then will be bounded by these limits; this permits the sampling of the posterior of N to examine only possible values of N and thereby increases the efficiency of the MCMC algorithm.

Choice of years on which to base the estimates of historical Chum Salmon abundance.—We calculated two estimates of Chum Salmon abundance during the period 1916–1919: (1) using the single large catch year of 1919 and (2) using a 4-year running geometric mean catch for the years 1916–1919. We chose to base our estimate on the large catch of 1919 (204,000) because the fishery at that time remained predominantly within the Skeena River (Milne 1955; Wood 2008), and the resulting estimate likely best reflects the potential of the river to produce Chum Salmon before the influence of intense fishing pressure and other human stressors. We chose to base our second estimate on the catch during the time period 1916–1919 (154,000) because this is when Chum Salmon began to be retained in considerable numbers and because this represents the average generation time of Skeena Chum Salmon at the onset of intense commercial fishing (Ricker 1980; Salo 1991).

Comparison of Historical and Contemporary Run Sizes

We used run-reconstruction estimates of Chum Salmon returning to the Skeena River during 1982–2010 (see English 2012) to compare our results of historical (1916–1919) run sizes with recent abundance. Because Chum Salmon in Canada are managed within the context of conservation units (CUs; WSP 2005), we apportioned our historical Chum Salmon abundance estimate into the CUs for the Skeena River; these include those for the Skeena estuary and the lower, middle, and upper Skeena River (Holby and Ciruna 2007). We used Department of Fisheries and Ocean’s management target escapement goals for each CU to approximate the historical proportion of Chum Salmon that returned to each CU. The assigned goals and proportions are as follows: Skeena estuary (2,775; 4%), Lower Skeena (43,975; 76%), and Middle Skeena (11,000; 19%; DeMarco 1991). Given the absence of target goal data for the Upper Skeena CU, which currently may consist of only a single small spawning population (Gottesfeld and Rabnett 2008), we assumed that this CU historically represented 1% of the combined Skeena Chum Salmon abundance.
RESULTS
The prior distribution of the aggregate harvest rate on Chum Salmon during 1916–1919 ranged from 0.32 to 0.58, with the most probable value being 0.45 (Figure 3). Because the catch data fail to provide independent information on the harvest rate, the posterior distributions of ChHR are identical to the priors. Based on the historical catch of 204,000 in 1919, the estimated return of Chum Salmon to the Skeena River watershed ranged from a minimum of 355,000 to a maximum of 619,000, with a most probable (modal) single estimate of 431,000 (Table 2; Figure 4). There is a 95% probability that the terminal run exceeded 395,000 and a 5% probability that it was larger than 541,000. The estimated return of Chum Salmon based on the 1916–1919 geometric mean catch of 154,000 ranged from a minimum of 268,000 to a maximum of 471,000, with a most probable single estimate of 325,000 (Figure 5). There is a 95% probability that the run was greater than 297,000 and a 5% probability that it exceeded 408,000.

The average annual run size of Chum Salmon returning to the Skeena River estuary and watershed during the contemporary period 1982–2010 was 40,440. For the most recent 4-year period of 2007–2010, the average annual run size of Skeena-bound Chum Salmon was 8,271. The posterior modal historical estimates of the total run size of Chum Salmon returning to the Skeena during the periods 1916–1919 and 1919 are 8–11 times larger than those for 1982–2010 and 39–52 times larger than those for 2007–2010. Apportioning our historical modal Chum Salmon run size estimates for the period 1916–1919 and the peak year 1919 into separate Skeena CUs result in differences from the most recent contemporary period that range from 38- to 57-fold (Table 3).

DISCUSSION
Our objective was to provide a credible estimate of the historical return of Chum Salmon to the Skeena River watershed during the early development of the commercial fishery. We argue that our methodology and results in fact do provide such a credible estimate and that these results reveal a large discrepancy between the return of 94 years ago and those of today. There are at least four potential explanations for the discrepancy: differences in marine survival between the periods, loss of spawning and rearing habitat, overexploitation, and poor data quality.

Differences in Marine Survival
Marine climate variability at basinwide and regional scales has a well-known influence on Pacific salmon productivity (Mantua et al. 1997; Mueter et al. 2002). The ocean survival of Alaska and south-coast British Columbia salmon populations appears to exhibit a strong and consistent correlation with

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<th>Year</th>
<th>C</th>
<th>Mode</th>
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<th>Mean</th>
<th>Std.</th>
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<td>431,000</td>
<td>456,000</td>
<td>462,000</td>
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<td>395,000–541,000</td>
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<tr>
<td>1916–1919</td>
<td>154,000</td>
<td>325,000</td>
<td>344,000</td>
<td>348,000</td>
<td>34,600</td>
<td>297,000–408,000</td>
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indices of ocean productivity, such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997; Beamish et al. 2000). Similarly, consistent effects of regional sea surface temperatures (SSTs) on the survival of Pacific salmon have been observed (Mueter et al. 2002, 2005; Connors et al. 2012). For example, the relatively recent 20- to 30-year time period associated with warmer ocean temperatures on British Columbia’s south coast are thought to have contributed to the fourfold decline in the marine survival of steelhead O. mykiss (Ward 2000). Furthermore, the large and consistent decreases in Sockeye Salmon productivity in many areas along the West Coast of North America since the late 1990s may be due to similar processes (Peterman and Dornier 2012). However, we believe that it is unlikely that the large difference in abundance between historical and contemporary periods that we have estimated for Skeena River Chum Salmon can be accounted for by differences in ocean productivity. There are three reasons for this. First, the salmon populations in northern British Columbia do not appear to respond to productivity indices such as the PDO as strongly as populations further south or north (Hare et al. 1999; Hill et al. 2009). Second, even if Skeena River Chum Salmon responded strongly to such indices, the ocean conditions in the decade leading up to the large run of 1919 (as indexed by the PDO) were not distinctly favorable or vastly different from those experienced in recent years (Hare et al. 1999; Biondi et al. 2001). Finally, coastal ocean conditions (as measured by PDO or SST, both of which are admittedly indirect and statistically noisy indices) explain a small proportion of the variability in salmon productivity (i.e., recruitments per spawner) relative to other factors (Mueter et al. 2005; Connors et al. 2012).
Skeena Chum Salmon populations were already significantly reduced since the late 1980s is considered a likely factor in the steep decline of wild Chum Salmon north of Southeast Alaska (Ruggerone et al. 2010). The annual release of 2 billion Japanese hatchery-produced Chum Salmon could affect the growth of wild Chum Salmon from Alaska and British Columbia because these enhanced fish are broadly distributed throughout the North Pacific (Myers et al. 2004). Russia also releases 360 million hatchery Chum Salmon annually (Ruggerone et al. 2010), and combined with the annual release of Alaskan and Japanese hatchery Chum Salmon and Pink Salmon, could negatively affect the survival of wild Chum Salmon from the Skeena River.

Might competitive effects from the increased abundance of hatchery fish be the primary driver of the decline in the abundance of Skeena River Chum Salmon over the last century? Again, we believe not, for two reasons. First, although the annual release of billions of Japanese and Russian hatchery-produced Chum Salmon is thought to be inhibiting the recovery of wild Chum Salmon populations in Russia (Radchenko 1998; Kaeriyama et al. 2007), overharvest and perhaps freshwater habitat degradation in the southern area of the Russian Far East are considered the key factors in the overall decline of Russian wild Chum Salmon (Ruggerone et al. 2010). Second, Skeena Chum Salmon populations were already significantly reduced by the 1930s and remained low until at least 1950 (Argue and Shepard 2005), long before large-scale hatchery production commenced. We do believe, however, that the substantial increase in hatchery fish now utilizing the North Pacific may account for the large decline of Skeena Chum Salmon over the period 1982-2010.


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<tbody>
<tr>
<td>Skeena Estuary</td>
<td>13,012</td>
<td>17,080</td>
<td>800</td>
<td>308</td>
</tr>
<tr>
<td>Lower Skeena</td>
<td>247,228</td>
<td>324,520</td>
<td>34,372</td>
<td>6,531</td>
</tr>
<tr>
<td>Middle Skeena</td>
<td>61,807</td>
<td>81,130</td>
<td>5,268</td>
<td>1,432</td>
</tr>
<tr>
<td>Upper Skeena</td>
<td>3,253</td>
<td>4,270</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Salmon share a common resource pool in the North Pacific; as a result, large increases in salmon abundance can reduce survival rates (Peterman 1984; Ruggerone and Nielsen 2004; Helle et al. 2007). For example, the dramatic increase in the abundance of artificially produced (hatchery) salmon has likely increased competition in oceanic feeding grounds for wild salmon populations, leading to reduced productivity (Cooney and Brodeur 1998; Heard 1998; Zaporozhets and Zaporozhets 2004). Pink Salmon abundance in the North Pacific, which has more than doubled since the 1950s owing to hatchery supplementation (Ruggerone et al. 2010), is suspected to have had a strong negative influence on the productivity of numerous British Columbia sockeye salmon populations (Connors et al. 2012). Moreover, the large release of hatchery-produced Chum Salmon in Alaska has amounted to 360 million annually (Ruggerone et al. 2010), and combined with the annual release of Alaskan and Japanese hatchery Chum Salmon and Pink Salmon, could negatively affect the survival of wild Chum Salmon from the Skeena River.

**Loss of Spawning and Rearing Habitat**

The Skeena River is currently one of North America’s most important salmon producers (Gottesfeld and Rabnett 2008). Chum Salmon spawn mostly in the coastal portion of the watershed and commonly utilize back channels and spring brooks in the lower Skeena River and adjacent tributaries. Emergent fry may hold for several weeks in floodplain spring brooks as presmolts (J. Stanford, unpublished data). While industrial development in the watershed remains in its infancy, some habitat degradation has occurred. With relevance to Chum Salmon, several back-channel habitats in the lower Skeena River have been altered or cut off by railroad and highway construction, and logging has been extensive (Gottesfeld and Rabnett 2008). Unfortunately, the extent of spawning habitat loss or degradation for Skeena Chum Salmon has not been quantified. But data deficiency aside, we believe that the difference between our historical abundance estimate and that for the contemporary period far exceeds even the most exaggerated estimate of decline due to spawning habitat loss. For example, habitat loss for the steelhead returning to Puget Sound (a region of high-density urban and industrial development) was recently estimated to be no more than 33% (Gayeski et al. 2011). Notably, this loss in habitat was deemed negligible in the context of a 25-fold reduction in steelhead abundance. The Skeena River, by comparison, is essentially in pristine condition. Although reductions in marine productivity owing to warmer sea temperatures or oceanic competition from hatchery fish likely far outweigh the effect of freshwater habitat loss, further work is needed to assess the current levels of spawning habitat abundance and to evaluate the current potential of these habitats to produce juveniles.

**Overexploitation during the Rise of Industrial Fishing**

Declines in marine productivity and available spawning habitat have undoubtedly contributed somewhat to the current low numbers of Chum Salmon returning to the Skeena River watershed. However, intense harvest pressure is the single most probable factor in the initial decline in Chum Salmon abundance. Severe overharvesting of most species of salmon is believed to have occurred during the rise of industrial fishing on the Skeena (Gottesfeld and Rabnett 2008), and an evaluation of the historical catch data lends support to this hypothesis. With regards to Chum Salmon, the peak catch years of 1919 and 1926 coincided with peaks in fishing effort. The number of canneries...
reached a maximum during the years 1917–1919 and 1926 (Ross 1967; Lyons 1969), and the number of gill-net licenses exceeded 1,000 for the first time in 1919 (Milne 1955), surpassing the previous maximum (in 1915) by approximately 200 licenses. Despite advances in fishing technology after 1924 (e.g., gasoline-powered vessels and mechanical net-drums, which substantially increased catch efficiency) and the perpetuation of intense fishing effort (annual gill-net licenses exceeded 1,100 until 1935; Milne 1955), the overall Chum Salmon catch has generally declined since 1926 (Argue and Shepard 2005). Thus, perhaps analogous to the situation with wild Chum Salmon in Russia south of the Amur River and Japan, fishing pressure is likely to have significantly reduced the abundance of Skeena River Chum Salmon and the other anthropogenic influences discussed above now inhibit their recovery.

An additional factor that may be inhibiting the recovery of Skeena River Chum Salmon (which is exacerbated by previous fishing-induced declines in spawner abundance) is the loss of marine-derived nutrient subsidies. Some evidence suggests that spawning salmon influence juvenile salmonid growth rates and the perpetuation of future generations through carcass deposition and nutrient cycling (Gende et al. 2002). Estuaries can receive a large proportion of postspawning salmon nutrients (Cak et al. 2008), which is of particular importance for Chum Salmon that rear as juveniles in estuaries. It is plausible that the fertility of the Skeena River and estuary has declined considerably owing to the more than 100 years of intense exploitation of most Skeena salmonids and the subsequent reduction in the nutrients provided by returning salmon. A nutrient shortage may keep population sizes far below their historical levels as a result of density-dependent mortality in juveniles (Larkin and Slaney 1997; Gresh et al. 2000) and thus impede the recovery of these populations (Achord et al. 2003).

Data Quality

One concern regarding the catch data used for our historical estimate is that a portion of the Chum Salmon caught during 1916–1919 may have originated in systems other than the Skeena River. It is generally understood that Chum Salmon were incidentally harvested in the more lucrative Sockeye Salmon fishery during the period of our evaluation (Milne 1955; Lyons 1969). Some fishing effort may have occurred beyond the river and within the Skeena estuary between mid-June and the first week of July (Ross 1967; Wicks 1975; Blyth 1991). Because Chum Salmon generally do not enter the Skeena River until after the second week of July (but may have historically returned earlier), it is plausible that a proportion of the Chum Salmon caught during the outside fishery originated elsewhere. Recent gill-net catch data (1970–2009) for DFO’s statistical area 4 (a vast area that extends far beyond the mouth of the Skeena River) suggest that up to 12% of the Chum Salmon of unknown origin are caught before the second week of July (PSC 2011). The historical and contemporary run timings of Chum Salmon being equal, these data suggest that up to 12% of the total catch calculated by Argue and Shepard (2005) may not have originated in the Skeena. For the year 1919, this would amount to a maximum of 25,000 non-Skeena Chum Salmon. Importantly, this proportion was probably offset by Skeena-bound Chum Salmon caught in the Nass and Alaska fisheries that are not included in Argue and Shepard’s (2005) catch reconstructions. Catch data from the southern Southeast Alaska management area show that a total of 4.1 million Chum Salmon were caught in 1919, with an average of 3.3 million Chum Salmon being caught annually during 1916–1919; more than 57 million Chum Salmon were caught during 1919 in the combined Alaska fisheries (Byerly et al. 1999). If only 0.05% of the Chum Salmon caught in the Alaska fisheries of 1919 were of Skeena origin, the number would exceed our estimated proportion of non-Skeena Chum Salmon. We believe this provides further evidence that our historical run size estimates are conservative and more likely to underestimate than to overestimate, the true historical run size of Skeena Chum Salmon.

Contemporary estimates of Chum Salmon abundance are based on poor data quality. Chum Salmon returning to the largest Chum Salmon spawning area in the Skeena River catchment, the Ecstall River, have not been enumerated since 2002; in fact, only 5 out of 59 known spawning areas have had spawner counts in the previous decade (see English 2012). Additionally, the contemporary run-reconstruction estimates that we examined are based on numerous assumptions related to limited catch, run timing, and escapement data, all of which have inherent uncertainties (English et al. 2012). Furthermore, a significant portion of the Chum Salmon run may spawn in the main-stem Skeena River, which very often is turbid and would make detection of spawners and redds difficult. Given these data uncertainties, and because hatchery-produced Chum Salmon constitute a portion of the aforementioned contemporary estimates, the number of wild Chum Salmon annually returning to the Skeena could be either lower or higher.

Relevance for Conservation

The principal value of our terminal run size estimate is that it provides an index of the historical capacity and potential of the Skeena River system to produce Chum Salmon. Based on our geometric mean run estimate of 325,000 during 1916–1919, of which 154,000 were harvested, the Skeena River had the capacity to support at least 171,000 Chum Salmon spawners annually. This historical escapement should be of value to contemporary management, particularly in the context of the order-of-magnitude-lower abundance of Chum Salmon returning to the Skeena River in the most recent period. Admittedly, we cannot say anything about how this decline relates to the natural variability in Chum Salmon abundance over time, which may have been immense, as has recently been shown for western Alaska Sockeye Salmon (Rogers et al. 2013).

Canada’s modern conservation policy for Pacific salmon attempts to protect distinct populations (WSP 2005). Four CU’s have been identified for Skeena River Chum Salmon (Holtby
and Ciruna 2007), and our analysis suggests that currently these CUs are severely diminished compared with a century ago. Although two separate investigations have shown that Skeena Chum Salmon may represent a single large population (e.g., Beacham et al. 1987; Kondzela et al. 1994), other data suggest that at least two separate races exist in addition to the four CUs. For example, there appear to be an early run of Chum Salmon that spawns in downwelling areas of main river channels and a late run that spawns in upwelling groundwater of back channels (J. Stanford unpublished data), as has been described for Chum Salmon in Russia (Kuzishchin et al. 2010) and Alaska (Gilk et al. 2005). Given the disproportionately large harvest pressure on the early Chum Salmon run during the approximately 40-year Skeena Sockeye Salmon fishery leading up to 1916, this type of life history diversity for Skena-bound Chum Salmon may be significantly less than it was 150 years ago. Indeed, as Gottesfeld and Rabnett (2008) suggest, “Chum are probably the Skeena watershed salmon species in greatest danger of significant loss of spawning stocks and genetic diversity.”

Conservation initiatives and recovery plans for Skeena River Chum Salmon will require an evaluation of credible hypotheses about the decline in historical abundance that our estimates suggest. An assessment of this loss is necessary to identify appropriate abundance targets for recovery that will ensure the persistence of Skeena Chum Salmon. Competitive interactions with hatchery fish, loss of genetic diversity and spawning habitat, bycatch in mixed-stock fisheries, possible changes in the magnitude of marine productivity, and loss of marine-derived nutrient subsidies are all likely contributors to the historical decline in Skeena Chum Salmon. It is imperative that monitoring efforts for wild Chum Salmon returning to the Skeena watershed be vastly improved, as the continued erosion of monitoring effort handicaps fishery and conservation decisions (Price et al. 2008). Notably, “[t]he available data are not adequate to assess current [Chum Salmon] status.” (Walters et al. 2008). While there is evidence that a portion of the Chum Salmon spawning groups have been lost and others are at very low abundance, some optimism is warranted. The Skeena watershed remains a relatively intact salmon-producing system, such that recovering substantially larger wild Chum Salmon populations is a foreseeable possibility—but only if conservation measures aimed at reducing the factors inhibiting their recovery are immediately initiated.

ACKNOWLEDGMENTS

We are grateful to the Pacific Salmon Foundation for providing accessible contemporary run-reconstruction data, the Gordon and Betty Moore Foundation for funding, A. Argue for thoughtful discussions on historical catch data, and G. Knox, B. Spilsted, and two anonymous reviewers for comments that greatly improved the manuscript.

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APPENDIX: JUSTIFICATION OF THE USE OF THE GAMMA–POISSON DISTRIBUTION

The catch of migratory salmon in a gauntlet-type fishery, whereby a more or less stationary fishing fleet captures fish as they attempt to proceed upstream (such as the historical lower Skeena River commercial fishery), is not well represented as a series of independent Bernoulli trials at the fine spatiotemporal scale of an individual boat or a single fishing period for the fleet. Each salmon is not independently susceptible to the fishing gear, nor is it reasonable to think that each fish in the run has the same probability of being captured by the gear. In actuality, migrating salmon tend to be aggregated and their spatial and temporal distributions are clumped. Additionally, local conditions such as river discharge or flow, tidal stage, weather, water temperature, water clarity, moon phase, and time of day result in varying capture efficiencies for the fishing gear.

The clumped distribution that characterizes catches at fine scales likely approximates a gamma–Poisson process, which will generate a negative binomial distribution of the catches from any particular size run of fish subject to the fishing gear during any period of interest. For each such period (such as a single hour’s fishing by the fleet), the catch can be thought of as a Poisson random variable in which the rate parameter (λ) of the corresponding Poisson distribution (which is equal to the expected catch) is itself a random variable drawn from an underlying gamma distribution with the shape parameter α equal to the total run susceptible to the gear during the fishing period, and the scale parameter β equal to the underlying average harvest rate, over all similar fishing periods. In this parameterization, the expected value of λ will equal α · β with variance α · β · (1 + β).

The aggregate catch over a season will include numerous (often hundreds) of such individual catches. For a given type of gear in a given fishing area during each discrete fishing period i (such as 1 h), the expected catch (λi) will depend only on the total run of fish susceptible to the gear during each period (αi), assuming a constant season-average harvest rate (β). The additive property of independent gamma random variables with a common scale parameter β insures that for λ1 ∼ gamma(α1, β) and λ2 ∼ gamma(α2, β) the distribution of λ1 + λ2 ∼ gamma(α1 + α2, β); Gelman et al. 1995: 479). Consequently, under these conditions— and conditions that reasonably approximate them—the value of the Poisson rate parameter for the entire season (λ) will be distributed as gamma(Σ(αi), β), where Σ(αi) is the sum of all of the individual runs of fish susceptible to the gear during each discrete period of fishing i. The Poisson distribution possesses this same additive property (Gelman et al. 1995: 482), so that the seasonal catch C ∼ Poisson{gamma(Σ(αi), β)} will have the same distribution as Poisson(Σ(λi)).

In other words, the distribution of the total catch will be the same whether it is estimated from the sum of the expected catches based on estimates of the individual run sizes (if the data with which to make those estimates were available) or from estimates of the total run size over the entire season. This ensures that the inverse problem of obtaining a Bayesian estimation of the run size from the total catch plus estimates of the average seasonal harvest rate using the gamma–Poisson likelihood will derive the same advantage of additivity of the parameters of the likelihoods applicable to the fine-scale harvest. This phenomenon is a manifestation of the law of large numbers. Essentially, the same conditions hold when the individual catches, Ci, are obtained from varying harvest rates, βi, provided that the βi are drawn from an underlying probability distribution with mean equal to β when the number of individual catches is large (as was the case with Skeena River Chum Salmon during our period of interest).
Thus, at the scale of the aggregate seasonal catch (for which the estimation of historical run size takes place), the law of large numbers will result in the total catch’s being represented with reasonable accuracy from the dual process of sampling the average seasonal harvest from a gamma distribution with a shape parameter equal to the total run and a scale parameter equal to the average harvest rate, and then sampling the actual catch as a Poisson random variable with a rate parameter equal to the average harvest. The only caveat is that the period of time (e.g., weeks) over which the run is harvested must be long relative to the length of time of individual fishing events (e.g., hours) where the extra-binomial variation is concentrated, which was the case here.

At very large sample sizes, the distribution of the catch from an estimate of total run size and average harvest rate derived from a gamma–Poisson process will be well approximated by a simple binomial with the parameters total run size and average harvest rate. Consequently, the inverse problem of obtaining a Bayesian estimation of the run size from the total catch and an estimate of the average harvest rate using the binomial likelihood will also closely approximate the posterior distribution of the run size estimated using the gamma–Poisson distribution. Extensive simulations (not shown) confirm these general conclusions.

In summary, the uncertainty in our historical abundance estimate, which is due primarily to uncertainties surrounding the aggregate harvest rate at the time of the fishery, will be robustly represented by employing either the gamma–Poisson likelihood or the binomial likelihood. The gamma–Poisson will more often achieve a marginal improvement in precision at a very small additional computational cost (due to having to estimate the additional [Poisson rate] parameter), which is why we chose it for our analyses.

SENSITIVITY OF THE PRIOR ON THE CHUM SALMON HARVEST RATE TO THE LIMITS OF THE COMPONENT UNIFORM PRIOR DISTRIBUTIONS

To evaluate the sensitivity of ChHR to the lower and upper limits of the uniform distributions of the component prior distributions from which ChHR was derived, we created 21 samples (each consisting of 1,000,000 random values) of ChHR generated by randomly sampling the uniform distributions of the five underlying component uniform distributions and calculating ChHR using equation (1):

\[
\text{ChHR} = (\text{CHRS} \cdot \text{SHCh} \cdot \text{SHR}) + [(1 - \text{CHRS}) \cdot \text{CoHCh} \cdot \text{CoHR}].
\]

(1)

The 21 samples included the default parameterizations of the five component distributions. Each of the remaining 20 samples was created by changing the lower or upper limits of one of the component distributions as shown in Tables A.1–A.5. The quintile values (the minimum; 20th, 40th, 60th, and 80th percentiles; and maximum) of the cumulative distribution of each sample of 1,000,000 were calculated for comparison with the quintiles of the default parameterization. This is a limited sensitivity analysis, in which the upper or lower limit of a single component was changed while keeping all other limits at their default values. As noted in the text, the results of the evaluation of the individual limits show that the interactions among the component parameters under multiple changes to the upper and lower limits would be unlikely to have a large impact on the range and shape of the distribution of ChHR.

The caption of each table lists the lower and upper limits of the default parameterization of the uniform distribution of the component parameter being analyzed. The first row of each table shows the quintile values of ChHR under the default parameterization of all five component distributions. The next four rows show the quintile values of ChHR when the lower or upper limit of the uniform distribution of the component parameter is changed from the default value to the value indicated in the first column. For example, the third row of Table A.1 shows the change in ChHR when the lower limit on the uniform distribution of the Sockeye Salmon harvest rate is set to 0.50 instead of the default 0.58, and the default upper limit of 0.66 is retained together with the default lower and upper limits of the remaining four independent parameters.

Table A.1 shows results of reducing the lower limit on SHR from the default value of 0.58 to 0.50 and 0.40 (14% and 31%, respectively), and increasing the upper limit from the default 0.66 to 0.75 and 0.85 (14% and 29%, respectively). The reduced limits have a negligible impact on the maximum value

<table>
<thead>
<tr>
<th>SHR parameter</th>
<th>Minimum</th>
<th>20th percentile</th>
<th>40th percentile</th>
<th>60th percentile</th>
<th>80th percentile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Default</td>
<td>0.325</td>
<td>0.403</td>
<td>0.431</td>
<td>0.457</td>
<td>0.485</td>
<td>0.574</td>
</tr>
<tr>
<td>Low</td>
<td>0.253</td>
<td>0.348</td>
<td>0.379</td>
<td>0.408</td>
<td>0.445</td>
<td>0.574</td>
</tr>
<tr>
<td>High</td>
<td>0.330</td>
<td>0.422</td>
<td>0.452</td>
<td>0.481</td>
<td>0.514</td>
<td>0.635</td>
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<td>0.4</td>
<td>0.295</td>
<td>0.381</td>
<td>0.409</td>
<td>0.434</td>
<td>0.464</td>
<td>0.574</td>
</tr>
<tr>
<td>0.75</td>
<td>0.328</td>
<td>0.439</td>
<td>0.475</td>
<td>0.508</td>
<td>0.551</td>
<td>0.699</td>
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<tr>
<td>0.85</td>
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</tr>
</tbody>
</table>
### TABLE A.2. Results of the sensitivity analysis from changes made to the lower and upper limits of the total annual harvest rate on the Coho Salmon run (CoHR) from the default uniform distribution (0.45, 0.60).

<table>
<thead>
<tr>
<th>CoHR parameter</th>
<th>Minimum</th>
<th>20th percentile</th>
<th>40th percentile</th>
<th>60th percentile</th>
<th>80th percentile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Default</td>
<td>0.325</td>
<td>0.403</td>
<td>0.431</td>
<td>0.457</td>
<td>0.485</td>
<td>0.574</td>
</tr>
<tr>
<td>0.25</td>
<td>0.288</td>
<td>0.379</td>
<td>0.409</td>
<td>0.435</td>
<td>0.465</td>
<td>0.574</td>
</tr>
<tr>
<td>0.35</td>
<td>0.309</td>
<td>0.392</td>
<td>0.420</td>
<td>0.446</td>
<td>0.475</td>
<td>0.572</td>
</tr>
<tr>
<td>0.75</td>
<td>0.327</td>
<td>0.417</td>
<td>0.447</td>
<td>0.473</td>
<td>0.503</td>
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</tr>
<tr>
<td>0.90</td>
<td>0.328</td>
<td>0.430</td>
<td>0.462</td>
<td>0.490</td>
<td>0.523</td>
<td>0.653</td>
</tr>
</tbody>
</table>

### TABLE A.3. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the total Chum Salmon run that encountered the Sockeye Salmon fishery (ChRS) from the default uniform distribution (0.67, 0.75).

<table>
<thead>
<tr>
<th>ChRS parameter</th>
<th>Minimum</th>
<th>20th percentile</th>
<th>40th percentile</th>
<th>60th percentile</th>
<th>80th percentile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Default</td>
<td>0.325</td>
<td>0.403</td>
<td>0.431</td>
<td>0.457</td>
<td>0.485</td>
<td>0.574</td>
</tr>
<tr>
<td>0.50</td>
<td>0.315</td>
<td>0.400</td>
<td>0.425</td>
<td>0.449</td>
<td>0.476</td>
<td>0.572</td>
</tr>
<tr>
<td>0.60</td>
<td>0.323</td>
<td>0.402</td>
<td>0.429</td>
<td>0.454</td>
<td>0.481</td>
<td>0.573</td>
</tr>
<tr>
<td>0.85</td>
<td>0.329</td>
<td>0.405</td>
<td>0.433</td>
<td>0.461</td>
<td>0.491</td>
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<tr>
<td>0.95</td>
<td>0.328</td>
<td>0.405</td>
<td>0.436</td>
<td>0.465</td>
<td>0.497</td>
<td>0.587</td>
</tr>
</tbody>
</table>

### TABLE A.4. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the annual Sockeye Salmon harvest rate to which Chum Salmon were vulnerable (SHCh) from the default uniform distribution (0.60, 0.90).

<table>
<thead>
<tr>
<th>SHCh parameter</th>
<th>Minimum</th>
<th>20th percentile</th>
<th>40th percentile</th>
<th>60th percentile</th>
<th>80th percentile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Default</td>
<td>0.325</td>
<td>0.403</td>
<td>0.431</td>
<td>0.457</td>
<td>0.485</td>
<td>0.574</td>
</tr>
<tr>
<td>0.40</td>
<td>0.247</td>
<td>0.334</td>
<td>0.378</td>
<td>0.422</td>
<td>0.466</td>
<td>0.572</td>
</tr>
<tr>
<td>0.50</td>
<td>0.287</td>
<td>0.369</td>
<td>0.404</td>
<td>0.440</td>
<td>0.475</td>
<td>0.574</td>
</tr>
<tr>
<td>0.70</td>
<td>0.325</td>
<td>0.380</td>
<td>0.394</td>
<td>0.406</td>
<td>0.420</td>
<td>0.484</td>
</tr>
<tr>
<td>0.80</td>
<td>0.326</td>
<td>0.393</td>
<td>0.413</td>
<td>0.431</td>
<td>0.451</td>
<td>0.527</td>
</tr>
</tbody>
</table>

### TABLE A.5. Results of the sensitivity analysis from changes made to the lower and upper limits of the proportion of the total harvest rate on the post-Sockeye Salmon season Coho Salmon run to which the overlapping proportion of the Chum Salmon run were vulnerable (CoHCh) from the default uniform distribution (0.60, 0.90).

<table>
<thead>
<tr>
<th>CoHCh parameter</th>
<th>Minimum</th>
<th>20th percentile</th>
<th>40th percentile</th>
<th>60th percentile</th>
<th>80th percentile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Default</td>
<td>0.325</td>
<td>0.403</td>
<td>0.431</td>
<td>0.457</td>
<td>0.485</td>
<td>0.574</td>
</tr>
<tr>
<td>0.40</td>
<td>0.296</td>
<td>0.386</td>
<td>0.415</td>
<td>0.442</td>
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<td>0.50</td>
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<tr>
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<td>0.423</td>
<td>0.449</td>
<td>0.476</td>
<td>0.560</td>
</tr>
</tbody>
</table>
of the posterior of ChHR, and the reduction to 0.40 produces a negligible increase in the range of the central 20% of the distribution (from [0.431, 0.457] to [0.379, 0.408]). The range of the entire distribution is increased from [0.325, 0.574] to [0.253, 0.574] for the 31% reduction in the lower limit. Any such reduction in the lower limit on SHR would, of course, increase the upper limit of the posterior distribution of the terminal run.

Increasing the upper limit of the uniform distribution on SHR from the default value of 0.66 (the maximum harvest rate estimated by Ricker 1975, which was substantiated by Wood 2008) for Skeena River Sockeye Salmon throughout the period of record) to 0.75 and 0.85 (14% and 29%, respectively) has a negligible effect on the minimum value of ChHR but a noticeable and biologically significant effect on the maximum value. For example, increasing the upper limit to 0.75 increases the maximum value of ChHR to 0.635 and increasing it to 0.85 increases the maximum value to 0.70, which would produce a reduction in the lower tail of the posterior distribution of the Chum Salmon terminal run size, lowering the minimum run size from 268,000 to 220,000 for the 1916–1919 geometric mean catch of 154,000 and from 355,000 to 293,000 for the 1919 catch of 204,000. The effect of either increase on the central 20% of the distribution of ChHR is much less dramatic. For example, increasing the upper limit to 0.85 increases the central 20th percentile range from [0.431, 0.457] to [0.475, 0.508].

The results of similar changes in the lower and upper limits of the component prior for the Coho Salmon harvest rate (CoHR) are similar but smaller than those for SHR (Table A.2). Increasing the upper limit from the default of 0.60 to 0.75 increases the maximum value of ChHR from 0.574 to 0.616, which has only a small impact on the central 20% of the distribution, increasing the range from [0.431, 0.457] to [0.447, 0.473]. This would produce a small reduction in the posterior of the terminal run size. Increasing the upper limit on CoHR to 0.90 increases the maximum of ChHR to 0.653 and the central 20% to [0.462, 0.490]. This would produce a further modest reduction in the posterior of the run size.

The changes to ChHR resulting from alterations of similar magnitudes to the limits of the remaining three independent component priors are noticeably smaller (Tables A.3–A.5). Because the upper limits of both SHR and CoHCh (the proportions of the total harvest rates on Sockeye Salmon and Coho Salmon to which Chum Salmon were vulnerable) in the default parameterization were very large (i.e., 0.90), only reductions of 0.10 and 0.20 in the upper limit were evaluated and these only contribute to lowering the ChHR upper limit. Overall, the changes in the upper and lower limits shown in Tables A.3–A.5 produced negligible changes in the magnitude and range of the central 20% of the distribution of ChHR. Notably, increasing the upper limit on the proportion of the Chum Salmon run encountering the Sockeye Salmon fishery from the default of 0.75 to 0.95 (Table A.3) increases the maximum value of ChHR to 0.587 from 0.574 and produces an even smaller increase in the location and magnitude of the central 20%, to [0.436, 0.465] from [0.431, 0.457]. All of the other alterations of the lower limits, of course, serve to further reduce the values of ChHR across the entire distribution, which would result in increases of the posterior distribution of the terminal Chum Salmon run size.

**APPENDIX REFERENCES**


Experimental Assessment of the Magnitude and Sources of Lake Sturgeon Egg Mortality


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Experimental Assessment of the Magnitude and Sources of Lake Sturgeon Egg Mortality

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Abstract
Mortality during early life stages can greatly affect annual recruitment. Despite the importance to population abundance and community composition, quantitative estimates of the sources and magnitude of early life mortality in natural environments are generally lacking for many fish species. We conducted a field experiment to quantify egg mortality during incubation for Lake Sturgeon Acipenser fulvescens. Fertilized Lake Sturgeon eggs were placed in replicated exclosures in the Black River, Michigan, at a known spawning location. Incubation conditions were modified using four exclosure treatments differing in mesh size that simulated different levels of access by predators and water flow regimes (0.1–0.6 m/s). Egg mortality through 80% of the incubation period was high (average 91%) and varied significantly (75–97%) across treatments. Treatments with reduced predator access and low water velocity experienced the highest levels of cumulative egg mortality. Developmental arrest was a larger source of mortality (84%) than the combined effect of predation and scour or de-adhesion (16%). We also documented a significant treatment by time (day of incubation) interaction, indicating that although cumulative rates of mortality may not vary significantly among spawning sites, the relative contributions of different sources of mortality can vary greatly at different times during egg incubation.

Mortality during early life (EL) stages plays an important role in the population dynamics of many species (Houde 1987; Congdon et al. 1999). For example, variable rates of predation can result in large fluctuations in annual abundance (Bailey and Houde 1989). Environmental conditions experienced during early life can also have indirect effects during subsequent ontogenetic stages, affecting traits associated with survival (Vandenbos et al. 2006) and the ability of populations to adapt to changing environmental conditions (Roff 2002). Estimates of EL mortality are frequently quantified without knowledge of sources and rarely are estimates available across spatially or temporally varying environments.

Mortality during the egg and larval stages exceeds 95% for many fish species and can be a useful indicator of annual recruitment (Bouwes and Luecke 1997; Fitzsimons et al. 2007; Smith and Marsden 2009). However, because fish species exhibit...
variation in behavior and different EL history traits that can affect rates of loss (Kouft et al. 2003; Wedekind and Miller 2005), generalizing the importance of EL mortality is difficult. For example, levels of EL mortality in species providing parental care (e.g., nest construction and protection) of a few larger eggs and larvae (Taborsky and Foerster 2004) differ from those in species that provide limited or no postovulatory care for numerous smaller offspring dispersed into the environment (Winemiller and Rose 1992). Yet, because “broadcast”-spawning species deposit eggs over broad areas that are exposed to a wide variety of environmental conditions, there is opportunity to simultaneously assess numerous effects of different components of the stream environment that are likely to influence egg mortality, especially when different suites of conditions can either be controlled or varied experimentally within stream settings.

Lake Sturgeon Acipenser fulvescens are long-lived migratory fish that use river habitats for spawning in the spring (Peterson et al. 2007). Lake Sturgeon spawn in large groups (Bruch and Binkowski 2002), and spawning site selection and the timing of spawning are highly repeatable for individuals (Forsythe et al. 2012a). Lake Sturgeon reach sexual maturity later in life (10 plus years) and at a large size (Peterson et al. 2007) relative to species with a similar life history (e.g., Walleye Sander vitreus or Gizzard Shad Dorosoma cepedianum). They also do not spawn every year (Forsythe et al. 2012a). Lake Sturgeon females are highly fecund (~11,000 eggs/kg; Bruch et al. 2006) and have adhesive eggs (2.7–3.8 mm) that are broadcast over the stream bottom with no nest preparation or postspawning parental care. Eggs are negatively buoyant and adhere to substrate surfaces and interstitial spaces. The timing of spawning (Forsythe et al. 2012b) and spawning site selection by adults (Chiotti et al. 2008) contribute to embryonic mortality, which can be high during incubation (Johnson et al. 2006; Caroffino et al. 2010a). The sources of egg mortality in other sturgeon species Acipenser spp. include arrest during development, predation, and physical stream processes that dislodge eggs (Parsley et al. 2002).

While our understanding of Lake Sturgeon biology has increased over the past decade, the relative contribution of sources causing egg mortality are still lacking, and no study to date has quantified rates of egg mortality associated with different habitat features characterizing spawning sites. The objectives of this study were to (1) quantify daily rates of egg mortality during incubation and (2) partition mortality into sources that were predicted to vary temporally and among different simulated stream conditions. Describing the degree of variability in the magnitude and causes of mortality between enclosures that reflect structured variation in natural stream conditions experienced by eggs through the incubation period can inform managers of levels of inter- and intra-annual variation in recruitment expected under different natural conditions.

**METHODS**

**Study site.—** The study was conducted in the Upper Black River (UBR; Cheboygan County, Michigan), a fourth-order stream, and the largest tributary of Black Lake. The adult Lake Sturgeon population in Black Lake consists of ~1,000 sexually mature adults of which ~250 spawn annually. Lake Sturgeon access to the UBR is restricted to the 11-km reach downstream of Keber Dam, and spawning occurs in several discrete areas over 1.5 km of stream below the dam (constructed in 1949) (Forsythe et al. 2012a) from late April through early June (Forsythe et al. 2012b). The distribution of river substrate varies considerably within and among major spawning sites and is a heterogeneous mixture of sand, gravel, cobble, and boulders (mean substrate size ±1 SD, 65.2 ± 19.8 mm; see Forsythe 2010 for detailed maps). A annual drift net sampling at locations downstream from spawning areas indicates interannual variation in natural recruitment to the out-migrating larval stage (Smith and King 2005).

Many verified predator species of Lake Sturgeon eggs (Kempinger 1988; Caroffino et al. 2010b) are commonly found within Black Lake and reaches of the UBR during spawning (Cwalinski and Hanchin 2011). These include both introduced and native species of crayfish (rusty crayfish Orconectes rusticus and calico crayfish Orconectes immunis, respectively), mudpuppies Necturus maculosus, Silver Redhorse Moxostoma anisurum, Greater Redhorse Moxostoma valenciennesi, White Sucker Catostomus commersonii, and adult Lake Sturgeon. Other numerically common species found at UBR spawning locations (P. S. Forsythe, unpublished) that may consume Lake Sturgeon eggs include Rock Bass Ambloplites rupestris, Smallmouth Bass Micropterus dolomieu, darters (family Percidae), chubs (family Cyprinidae), and benthic insects such as mayfly (Ephemeroptera), dragonfly (Odonata) and stonefly (Plecoptera) larvae.

Estimating mortality and determining the sources of loss.— Egg mortality was quantified using enclosures that differed in mesh size during the spring of 2005. Enclosure compartments (0.03 m² treatments) were constructed using rebar enclosed on all sides with metal cloth of three different mesh sizes (large mesh: 5.08 cm, small mesh: 1.27 cm, and fine mesh: 2 mm; Figure 1). A fourth treatment compartment was left open. Enclosure mesh size treatments were designed to modify water flow within the enclosure while simulating different probabilities that eggs would be removed by predators or scourred by stream flow (Figure 1).

Eggs and milt were obtained from spawning adults (two males and two females on May 7, 2005), and groups of eggs were randomized across treatments and blocks to avoid systematic bias attributed to differences in hatching success between crosses. Two hundred unfertilized eggs were counted immediately after collection and placed by hand on brown circular porous filters (0.073 m²; 3M Worldwide Polishing Pads), a density observed under natural spawning conditions in the UBR (Forsythe, 2010). Filters with eggs were then placed in trays (0.01 m²) containing only river water and diluted milt (1:200 with no clay) for 10 min, a protocol similar to that used for hatchery sturgeon broodstock, where fertilization rates of up to 95% are achieved (Deng et al. 2002).
Water temperature \( (\text{using a Marsh-McBirney flowmeter at the end of the experiment}) \) was measured to ensure proper development, while simulating different probabilities that eggs would either be removed by predators or scoured by water currents.

Exclosure mesh was cleaned of debris daily to maintain water flow (and delivery of dissolved oxygen to eggs) necessary for proper development. Eight replicates were deployed simultaneously in an area of the UBR that has traditionally been used for spawning (Forsythe et al. 2012b). Exclosure mesh was cleaned of debris daily to maintain water velocity. Water flow (m/s) inside exclosures was measured using a Marsh-McBirney Model 2000 flowmeter. Water temperature \( (\text{°C}) \) was measured continuously using a single HOBO temperature logger placed in stream at the study site. Total river discharge was measured once each day at a fixed transect using the mid-section method (U.S. Geological Survey, http://hydroacoustics.usgs.gov/midsection/index.shtml). Water velocity was measured using a Marsh-McBirney Model 2000 flowmeter.

The numbers of viable and dead eggs were counted in each exclosure every 24 h by raising the entire block (stabilized on corner with rebar posts) to just under the water surface. Blocks of treatments were checked simultaneously by three independent observers (count of eggs) took \( \leq 15 \) min. We partition egg mortality into two sources: arrested development and eggs lost to predation or scour. Arrested development was based on triplicate counts (one per each of three observers) of remaining viable eggs defined as the formation of the blastodisc, thickening at the animal region pole, and evidence of cellular division as described by Dettlaff et al. (1993). Observed reductions in the numbers of eggs over 24 h were presumed lost to predation or de-adhesion (scour) from stream flow. The experiment was terminated at 120 h (\( \sim 80\% \) of total incubation based on cumulative temperature units; see Kempinger 1988) postfertilization once larvae became active inside the embryo to avoid attributing hatching to egg mortality.

Statistical analyses.—Data were analyzed using a randomized complete block design with repeated measures using a general linear mixed model with the MIXED procedure of SAS Version 9 (see SAS for Mixed Models; Littel et al. 1996). Pairwise comparisons were investigated using least square means and post hoc differences were computed using Tukey’s HSD \((\alpha = 0.05)\). Differences in average flow rates between treatments were tested separately in SAS using analysis of variance (ANOVA).

**RESULTS**

**Magnitude of Egg Mortality and Sources of Loss**

River water temperature at the study site ranged from 10.9°C to 15.6°C (mean = 13.6°C) and was observed to vary by a maximum of 3.4°C over 24 h during the period observations were taken. Total river discharge generally decreased during the experimental period and ranged from 6.4 to 8.2 m³/s, which was low relative to the seasonal average of 8.7 m³/s (range = 5.5–23.1 m³/s). Average water velocity inside exclosures increased with increasing mesh size (mean ± SD; open: 0.60 ± 0.08 m/s, large mesh: 0.30 ± 0.04 m/s, small mesh: 0.12 ± 0.02 m/s, fine mesh: 0.12 ± 0.01 m/s), and with the exception of the fine-mesh and small-mesh treatments, differences were significant \( (F_{3, 28} = 25.5, P < 0.05) \). Lake Sturgeon were observed spawning at downstream locations in the UBR from May 8 to May 12 in 2005 (see also Forsythe et al. 2012b). No adult Lake Sturgeon (or other migratory fish) were observed immediately upstream or downstream of the study area at the time blocks were set or through the 5-d incubation period. However, numerous vertebrate and invertebrate benthic predator guilds including Plecoptera (stoneflies), Ephemeroptera (mayflies), Diptera (chironomids), Decapoda (crayfish), and perciformes (e.g., darters...
Etheostoma spp.) had colonized open and large-mesh treatments across all blocks. Our estimate of total egg mortality across all treatments was 91% (N = 5793 eggs). Daily mortality rates changed significantly over the five daily observation periods (F\(_{4, 101} = 476.9, P < 0.001\)). On average, four eggs died per day during the first 48 h following fertilization, 133 eggs died per day between 48 and 72 h (2–3 d), and 20 eggs died per day between 73 and 120 h (4–5 d). However, treatment means changed at significantly different rates (Time × Treatment interaction: F\(_{12, 101} = 5.7, P < 0.001\)), with the lowest rates of loss in the open and large-mesh treatments observed between 72 and 96 h after fertilization (shown in Figure 2 as the percent of eggs surviving). No significant difference in average mortality was observed among treatments at the end of incubation (mean ± SE; fine mesh = 89 ± 22%, small mesh = 92 ± 19%, large mesh = 90 ± 21%, open = 89 ± 12%) (F\(_{3, 31} = 5.7, P = 0.374\)).

Developmental arrest was a more dominant source of total mortality (N = 4848, 84%) across treatments than egg removal (N = 946, 16%). The magnitude of each mortality source also varied through time (Figures 3A, 3B). Both sources of mortality also increased significantly over time (developmental arrest: F\(_{3, 61} = 45.1, P < 0.001\); removal: F\(_{3, 61} = 60.6, P < 0.001\)). Specifically, 100% (N = 272) of mortality was attributed to removal by scour or predators 24 and 48 h after fertilization but developmental arrest accounted for 89% of the total loss (or 29 new mortalities per day) 48–96 h postfertilization. No egg drift from exclosures was observed during this experiment or in preliminary trials where eggs were placed on buffer pads without exclosures and then raised and lowered repeatedly.

Rates of total mortality over the entire 5-day period attributed to each source were marginally associated with treatment (i.e., Treatment × Time interaction: developmental arrest: F\(_{3, 37} = 59.7, P = 0.17\); removal: F\(_{3, 61} = 45.7, P = 0.08\)). Generally, developmental arrest was a smaller component of mortality on each day as mesh size and water velocity increased. Egg removal increased with increasing mesh size (Figures 3A, 3B). Significant mean differences in the magnitude of each mortality source among treatments (based on pairwise comparison) were noted by the end of incubation (removal: F\(_{3, 43} = 3.9, P < 0.01\); development failure: F\(_{3, 43} = 4.8, P < 0.005\)) and were consistent across daily observations (Figures 3A, 3B).

**DISCUSSION**

**Developmental Arrest as a Source of Mortality**

Eighty-four percent of the total egg mortality was attributed to developmental arrest. Fertilization rates are never 100% (even in controlled hatchery settings) and so a portion of developmental arrest was likely due to unsuccessful fertilization (J. A. Crossman, unpublished) and would not have been readily detectable using visual observation until several days following fertilization. Levels of mortality attributed to developmental arrest or lack of successful fertilization were expected to have been comparable across mesh treatments. However, rates of...
developmental mortality increased with increasing treatment mesh size and decreasing water velocity.

Observations of comparatively higher rates of developmental arrest in small-mesh relative to large-mesh treatments may be attributed to differences in dissolved oxygen (DO) or stream flow. Oxygen demand of developing eggs generally increases with increasing metabolite rates and larval activity during later periods of incubation (Ninnes et al. 2006). Dissolved oxygen concentration, water current velocity, and increased turbulence from the substrate are often positively correlated (Allan 1995), and thus DO concentrations may have dropped below levels necessary to sustain egg survival. Dissolved oxygen readings were not taken inside treatment enclosures. However, DO measured at other UBR spawning locations in the spring across a wide range of water flows (0.1–0.9 m/s; Forsythe, unpublished) were within those reported for proper egg development in sturgeon (≤10 ppm; Brannon 1985) and likely did not have deleterious effects on eggs in this experiment. Water flow also plays an important role in regulating water chemistry in the microenvironment surrounding developing fish eggs (Finn 2007). Lower flow rates may have negatively influenced egg survival by allowing the accumulation of metabolic waste products including ammonia and CO$_2$ (Dhyebi et al. 2013).

Eggs that developmentally arrested during incubation eventually became covered with microbes (bacteria) and fungi (data not shown), something observed in many fishes (Rach et al. 1995; Kitancharoen et al. 1997) including sturgeon (Kempinger 1988; Parsley et al. 2002). Microbial infection could result from colonization after death or in eggs that were not fertilized. However, significant differences in rates of infection among treatments suggest microbial envelopment likely contributes to egg death, especially for eggs in a stressed physiological state or exposed to low water velocity. Differences in infection rates of eggs as a function of water temperature, egg density, and water velocity found in other fish species further support this conclusion (Côté and Gross 1993; Knoket and Orth 1998).

Several other factors that decrease probabilities of fertilization or negatively interact after fertilization takes place may also partly explain high levels of developmental arrest found in our study. Examples include nutritional (e.g., yolk volume) and genetic effects (Brooks et al. 1997), adult physiological condition leading to poor egg quality, the timing of spawning (degree of egg ripeness), toxins, or extreme fluctuation in water temperature (Parsley et al. 2002). Developmental arrest may also be attributed to polyspermy (too many sperm entering one egg; Gilkey 1981), prevalent in sturgeons and Paddlefish Polyodon spathula because of a large number of micropyles in the egg envelope (Dettlaff et al. 1993; Linhart and Kudo 1997). However, because mortality was low during the first 48 h of incubation and fertilization rates were apparently high, effects associated with maternal provisioning of eggs, atresia, or sperm quality would be expected to be similar across treatments and thus would not impact our ability to quantify differences among treatments.

**External Sources of Mortality**

Egg removal from mesh exclosure treatments accounted for 16% of total mortality. Significantly higher levels of removal were observed in mesh treatments of larger mesh size. Egg loss could be due to water currents that remove and translocate embryos to other stream habitats. Correlations between water velocity and probabilities of egg removal or scour and mortality rates of translocated eggs have been documented in other species (Ventling-Schwank and Livingstone 1994; Bunn et al. 2000; Lapointe et al. 2000). However, egg drift was not directly observed in this study. Further, our estimates of egg mortality that could be attributed to removal for two treatments under low-river flow conditions were larger (≥10%) than reported for other demersal spawning species (2% in Eurasian Dace Leuciscus leuciscus, Mills 1981; 1% in Bonneville Cisco Prosopium gennifer, Bouwes and Luecke 1997), as well as in other studies on Lake Sturgeon (Lahtay et al. 1992; Caroffino et al. 2010a). While we believe removal and mortality after translocation may be relatively minor (see below), physical disturbances have been shown to account for a higher percentage of egg mortality than other sources combined in some situations (Lake Trout Salvelinus namaycush; see Fitzsimons et al. 2007) and thus should not be completely dismissed.

The increasing magnitude of removal during incubation (Figure 3B) despite low and decreasing river water discharge and significantly higher levels of egg loss associated with large-mesh than smaller-mesh treatments suggest that most “removed” eggs were consumed by predators. Predation on fish embryos (and larvae) is an important contributor to early life history mortality in fish populations and was expected given the diversity of benthic predators (Bailley and Houde 1989; Bouwes and Luecke 1997; Dittman et al. 1998). Lab studies also show that predation on Lake Sturgeon eggs by a single species (e.g., rusty crayfish or Round Goby Neogobius melanostomus) can be extensive (Nichols et al. 2003). However, the small amount of predation relative to developmental arrest found here and in other field-based studies (18% on the Peshtigo River, Wisconsin; Caroffino et al. 2010b) conflicts with findings from laboratory studies. While it is clear that benthic predators pose a significant threat to Lake Sturgeon reproduction, predation rates may be highly dependent on the predator community and competing costs and benefits to predators associated with foraging. Risks of egg predation may be relatively low in some natural systems during times and in locations with low predator density (as was the case during this study) or large substrates with protective interstitial spaces (Forsythe 2010). Importantly, as shown by results from our experiments, because egg mortality can be attributed to multiple sources, estimates of total egg morality based solely on levels of predation likely represent underestimates.

**Total Egg Mortality**

We estimated Lake Sturgeon egg mortality averaged 91% over approximately 80% of the incubation period under natural conditions. Variation in total egg mortality (75–97%) was
documented among mesh treatments that simulated differences in water velocity and predator accessibility. In contrast, daily mortality for Lake Sturgeon eggs reared in a streamside hatchery on the UBR during this experiment never exceeded 9% for the first 4 d of incubation (Crossman 2008). Our average estimates from the field are generally concordant with those reported for sturgeons (83–99%; Nichols et al. 2003; Johnson et al. 2006; Caroffino et al. 2010a) and for other broadcast-spawning species with unprotected demersal eggs, including White Sucker (97%; Scott and Crossman, 1973), Bonneville Cisco (99%; Bouwes and Luecke 1997), Walleye (87%; Johnson 1961), and Rainbow Smelt Smolus mordax (99%; Rupp 1965). Egg mortality was higher than in species that construct nests (i.e., centrachids and salmonids) or display other parental behaviors that protect offspring (Clady 1975; reviewed in Dahlberg 1979). The significant treatment by time interaction observed in our study is particularly noteworthy because, although daily mortality rates attributed to different sources varied through incubation, total egg loss was not significantly different among treatments. Thus, mortality sources under our experimental conditions were compensatory.

Study Implications

Survival during early life history stages of Lake Sturgeon as a function of heterogeneous riverine spawning habitats are strong determinants of recruitment and thus have a role in overall long-term population growth. Despite the high egg mortality documented in this study, it is important to note that longevity and iteroparity greatly increase the probability that individuals will contribute to at least one spawning event over their life span (if the population is unexploited) that results in successful recruitment. High levels of mortality at the egg stage may also indicate that recruitment is unrelated to spawning adult abundance (Winemiller 2005). Relationships between mortality sources and environmental conditions identified in this study can be used to project rates of egg loss that can guide conservation or management activities. Further, in times of human-mediated change, managers should also be aware that increasing levels of egg morality due to “new” sources that degrade spawning habitat quality or increase the attractiveness of habitat relative to its quality (i.e., ecological traps; Schlaepfer et al. 2002) are likely to increase in importance, particularly given the philopatric tendencies of Lake Sturgeon and repeatability for spawning at the same time and place (Forsythe et al. 2012b). Knowledge of environmental complexity that is associated with mortality during the egg stage will be critical to sustainability of fish populations (Hilborn et al. 2003), including those of Lake Sturgeon.

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Bayesian Estimation of Age and Length at 50% Maturity
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Bayesian Estimation of Age and Length at 50% Maturity

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Abstract
Fish age and length at 50% maturity are used extensively in the management of exploited fish populations. These parameters are historically estimated using logistic regression models (e.g., frequentist inference) for individual year-classes and often fail to converge or result in insignificant results when a small sample size is used. The sample-size problem motivated us to evaluate whether a hierarchical logistic regression model fit using frequentist inference or Bayesian inference, could improve our ability to fit these models. Our objective was to compare Bayesian and frequentist inference for estimating age and length at 50% maturity to determine whether the models produced similar values. To make this evaluation, we used a long-term data set of Yellow Perch *Perca flavescens* from southern Lake Michigan. Frequentist inference of the year-class-specific models resulted in significant results when sample size was sufficiently large, a result that occurred in 76% of the models. The hierarchical model produces estimates of age (or length) at 50% maturity for all year-classes using both frequentist and Bayesian inference. However, Bayesian inference of the hierarchical model resulted in more precise parameter estimates and provided the complete posterior distribution in one seamless and easy approach, and the computation time was 78% to 83% faster. We suggest that a hierarchical model fit using Bayesian inference of age (or length) at 50% maturity is an improvement over frequentist inference methods by providing more information about the population of interest, particularly when sample sizes are limited.

Fish age and length at maturity are used extensively in the management of fish populations (Shephard and Jackson 2005; Wilberg et al. 2005; Schill et al. 2010; Stark 2012). These values are traditionally identified by estimating age or length at 50% maturity (Shephard and Jackson 2005; Stark 2012), but for the purposes of modeling population dynamics this value is often assumed constant and based on historical data collections (Jennings et al. 1999; Wilberg et al. 2005). Age (or length) at 50% maturity describes the point at which 50% of the population is mature.

The logistic regression model is commonly used to make these estimations (Cook et al. 1999), and maturity is expressed as a binary value of either 1 (mature) or 0 (immature). Parameters of the logistic regression model are traditionally estimated using maximum likelihood techniques that are common in most statistical packages (e.g., SAS: PROC LOGISTIC, R–glm(), and STATA–logit). However, the maximum likelihood estimates require a relatively large sample size for convergence (Peduzzi et al. 1996; Greenland et al. 2000). When the events per predictor variable are fewer than 10, regression coefficients are biased and confidence limits around the estimated parameters cannot be calculated (Peduzzi et al. 1996). Further, bias in the odds ratios from logistic regression has been detected with sample sizes as large as 100 (Nemes et al. 2009). Simulation studies evaluating bias of a frequentist hierarchical logistic regression suggested a minimum group size of 50 and 50 groups are needed for valid parameter estimates (Moineddin et al. 2007). This event and group-size threshold can be problematic with fish data sets that include year-classes with poor recruitment (O'Brien 1999; Wang et al. 2009) or limited sampling, resulting in incomplete descriptions of maturity.

The sample size problem associated with maximum likelihood estimates (e.g., frequentist inference) of the logistic regression model motivated us to evaluate the use of Bayesian
Bayesian estimation of age and length

Bayesian inference is a fundamentally different way to describe probability (Ellison 1996). Under the Bayesian framework, parameters are considered random and data are considered fixed; whereas, the frequentist inference approach considers the parameters as fixed unknowns and the data random. Bayesian inference results in posterior distributions of a parameter and makes a direct probability statement of the parameter of interest, while frequentist inference results in point estimates with 95% confidence intervals that are based on hypothetical replicates and do not make a direct statement about the true parameter.

The use of Bayesian inference has dramatically increased over the past 20 years, particularly in ecological studies (Reckhow 1990; McCarthy 2007; Royle and Dorazio 2008, Kéry 2010, Kéry and Schaub 2012). In fisheries management, Bayesian inference has been applied to stock assessments (Chen et al. 2003; Wilberg et al. 2005), estimates of sport fish abundance from stream depletion sampling (Mäntyniemi et al. 2005; Ruiz and Laplanche 2010), estimates of annual growth variation using the von Bertalanffy growth function (He and Bence 2007), and determination of Brook Trout Salvelinus fontinalis ontogical population structure from genotypic data (Rogers and Curry 2004). Bayesian methods are also discussed as an alternative to maximum likelihood estimates in advanced fisheries textbooks (e.g., Quinn and Deriso 1999; Brown and Guye 2011).

The foundation of Bayesian inference is based on Bayes’ theorem where the probability of a model parameter (θ) given the observed data (X) is estimated using the data, the prior belief about θ, and the evidence. Bayes’ theorem states the posterior distribution of the model parameters is calculated by

$$p(\theta|X) = \frac{p(X|\theta)p(\theta)}{\int d\theta p(X|\theta)p(\theta)}, \quad (1)$$

where \(p(\theta|X)\) denotes the posterior distribution of the parameter given the data, \(p(\theta|X)\) denotes the probability of the data given the parameter (i.e., the likelihood function), \(p(\theta)\) denotes the prior probability of the model parameter, and the denominator (the evidence) is a normalizing parameter calculated by summing across all possible parameter values weighted by the strength of their belief. For a thorough discussion on Bayesian inference see Gelman et al. (2004) and Kuschke (2011).

Bayesian inference predates frequentist inference methods (Bayes and Price 1763); however, until recently the computations required were too great for most computers. Beginning in the 1990s modern advances in computing speed, Markov chain Monte Carlo (MCMC) algorithms, and the BUGS language brought Bayesian methods within reach to many non-mathematicians (Gilks et al. 1996; Lunn et al. 2000). Bayesian inference can now be conducted using a variety of software that requires only pseudocode to represent the model (Lunn et al. 2000; Plummer 2003; Stan Development Team 2012).

The objective of this study was to evaluate estimation of age and length at 50% maturity from a long-term Yellow Perch Perca flavescens data set using frequentist inference of individual-level regressions, frequentist inference of a hierarchical model, and Bayesian inference of a hierarchical model. We hypothesize Bayesian inference will provide similar results to the frequentist inference model when a sufficient sample size is used. However, we also hypothesize when sample sizes are limited, Bayesian inference will provide usable results, in contrast to the frequentist inference models.

METHODS

Data.—The data set format consists of \(n_i\) individuals sampled from year-class \(j\). For each individual \(i\) the maturity state \(Y_i\) was recorded as a binary outcome of mature (1) or immature (0). We used a long-term monitoring data set of Yellow Perch from southern Lake Michigan (Lauer and Doll 2012) to evaluate the two methods of statistical inference. Yellow Perch were sampled in early and late June in southern Lake Michigan at up to three sites between 1984 and 2009, resulting in six samples per year. Multifilament gill nets were set at 10- and 15-m depths and fished for approximately 12 h. In addition, a semiballoon bottom trawl was towed at the 5-m depth contour at night for 1 h each sample date. From 1984 to 1988 only two sites were sampled resulting in a total gill-net effort of four net-nights per year and 4 h of trawling per year. From 1989 to 2009, three sites were sampled resulting in a total gill-net effort of six net-nights per year and 6 h of trawling per year. See Lauer and Doll (2012) for a detailed description of the sampling protocol.

At the conclusion of each sample, fish \(\geq\) age 1 collected in the trawl and gill nets were measured for TL, weight, sex, and maturity following Treasurer and Holliday (1981). Those more than 300 fish were captured, a subsample of 300 Yellow Perch was randomly selected for measurement. Individuals \(\geq\) age 1 were differentiated from age-0 fish by size.

Yellow Perch aging structures were removed from up to 10 individuals in each 10-mm length class each year. Scales from samples in 1984–1993 and opercular bones for samples from 1994 to 2009 were aged independently by two readers. Aging methods were changed in 1994 as opercular bones were shown to have a lower coefficient of variation when compared with scales (Baker and McComish 1998). Discrepancies were discussed by both readers until a consensus was reached. Only fish where the maturity status and age were known were used in this analysis. Males and females were analyzed separately due to known sexual dimorphism (Headley and Lauer 2008).

General maturity model description.—Maturity state is modeled using logistic regression where the probability of an individual being mature is assumed to follow the Bernoulli distribution,

$$Y_{ij} \approx \text{Bernoulli} (\pi_{ij}), \quad (2)$$

where \(\pi_{ij}\) is the probability of individual \(i\) of year-class \(j\) being mature. The Bernoulli parameter \(\pi_{ij}\) is then modeled as a...
linear function of covariate \( x_{ij} \) (e.g., age and length, modeled separately) with the logit link so that

\[
Y_{ij} | x_{ij}, \alpha_j, \beta_{1j} \sim \text{Bernoulli} \left[ \text{logistic} \left( \alpha_j + \beta_{1j} x_{ij} \right) \right],
\]

\[
\alpha_j \sim N \left( \theta, \sigma^2 \right), \quad \text{and}
\]

\[
\beta_{1j} \sim N \left( \theta_1, \sigma^2_1 \right),
\]

where \( \alpha_j \) is the intercept parameter of year-class \( j \) and assumed to follow a normal distribution with mean \( \theta \) and variance \( \sigma^2 \), \( \beta_{1j} \) is the log odds parameter of the logistic regression model and represents the effect of the age or length, \( x_{ij} \) on the logit of \( \pi_{ij} \), and is assumed to follow a normal distribution with mean \( \theta_1 \) and variance \( \sigma^2_1 \). Estimates of age and length at 50% maturity for year-class \( j \) (i.e., inflection point of the curve) are derived using the equation \(-\alpha_j/\beta_{1j}\). Estimates of age and length at 50% maturity were calculated for each year-class.

Frequentist inference.—Individual frequentist models were fit to each year-class and sex using the glm() function with the binomial distribution and logit link in R version 2.15.3. Bootstrap parameter estimates were used to derive 95% CIs for the maturity index using the boot package (Canty and Ripley 2012). For each cohort where \( n_j \) individuals were sampled, \( n_j \) individuals were selected at random with replacement. The resampled data set was used to derive age (or length) at 50% maturity as described above. The process was repeated to obtain 1,000 replicates and the resulting distribution of the estimated age (or length) at 50% maturity was used to derive the 95% CIs. An alpha level was set at 0.05 to determine statistical significance for frequentist results.

The hierarchical model was fit to all year-classes combined for each sex using the lmer() function with the binomial distribution and logit link in R version 2.15.3 (Appendix 1). Here, the intercept and slope are given a grouping variable, year-class, where both are allowed to vary. Thus, the frequentist hierarchical model is now a varying-intercept and varying-slope model with year-class as a random effects grouping variable (Gelman and Hill 2007). Bootstrap parameter estimates were used to derive 95% CIs for the year-class-specific maturity index using the boot package similar to the single level models (Appendix 2).

Bayesian inference.—Parameters were estimated using Bayesian inference through a hierarchical framework so that parameters for each year-class were randomly drawn from the same probability distribution. That is, the hyperpriors \( (\theta, \theta_1, \sigma^2, \sigma^2_1) \) represent the global distributions from which the year-specific mean and variance of the regression coefficients (\( \alpha \) and \( \beta_1 \)) are drawn. The hierarchical model allows year-classes with a small sample size to borrow strengths from data-rich years. We used MCMC simulations to estimate posterior probability intervals of model parameters using the JAGS version 3.3.0 software (Plummer 2003) implemented in R version 2.15.3 (R Development Core Team 2013). Within R, JAGS was called using the rjags package (Plummer 2012). We ran three MCMC chains for a total of 100,000 steps, sampling every step and discarding the first 10,000 steps as a burn-in period. The burn-in period is necessary to reduce the effect of the starting values on the MCMC results (Gelman et al. 2004). Parameters were given a noninformative prior distribution (Table 1). To determine whether the prior distributions specified for the model parameters were influencing the results more than were the data we ran each model a second time assuming a t-distribution rather than a normal distribution. The Student t-distribution allows for more extreme data points. Similar results from both models would suggest the data contain enough information to overcome information in the prior distribution. Bayesian parameter estimates were generated using the JAGS language; complete model specifications can be found in Appendix 3. Convergence of the MCMC algorithm was checked using the Brooks–Gelman–Rubin (BGR) scale-reduction factor (Brooks and Gelman 1998). The BGR factor is the ratio of between-chain variability to within-chain variability. When the chains have mixed well, there is not more variability between chains than within chains. Convergence is obtained when the upper limit of the BGR factor is close to 1.00.

Inference comparisons.—Inherent differences exist in the definition of probability between Bayesian posterior distributions and frequentist point estimates with 95% CIs. Therefore, we focused on their respective interpretation used in making management decisions for comparisons. Additionally, mean point estimates from the results of the hierarchical model fit with frequentist inference are compared with the median estimates of the posterior distribution from hierarchical model fit with Bayesian inference using root mean squared error (RMSE). The RMSE is calculated using the equation

\[
\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (FM_i - BM_i)^2},
\]

where \( n = \) number of year-classes, \( FM_i = \) frequentist estimate of age (or length) at 50% maturity, and \( BM_i = \) Bayesian estimate of age (or length) at 50% maturity. The RMSE is on the same scale as the original units; therefore, the value represents the number by which the estimates of age (years) and

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Prior distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \alpha_j )</td>
<td>Normal ( (\theta, \sigma^2) )</td>
</tr>
<tr>
<td>( \beta_{1j} )</td>
<td>Normal ( (\theta_1, \sigma^2_1) )</td>
</tr>
<tr>
<td>Global level: hyperpriors</td>
<td></td>
</tr>
<tr>
<td>( \theta )</td>
<td>Normal ( (0, 1000) )</td>
</tr>
<tr>
<td>( \theta_1 )</td>
<td>Normal ( (0, 1000) )</td>
</tr>
<tr>
<td>( \sigma^2 )</td>
<td>Uniform ( (0, 10) )</td>
</tr>
<tr>
<td>( \sigma^2_1 )</td>
<td>Uniform ( (0, 10) )</td>
</tr>
</tbody>
</table>

TABLE 1. Prior distributions used for the Bayesian hierarchical logistic regression model.
length (mm) differ. Parameter estimation time for bootstrap CIs from the hierarchical model fit with frequentist inference and Bayesian inference will also be used as a benchmark for evaluation. The time required for the individual \( \text{glm()} \) and \( \text{lmer()} \) functions to complete is minimal; thus, they are not included in the total time to analyze the data using frequentist methods. The computer used for this analysis was a Dell Precision model M 6700 (64-bit, 32 GB RAM, and Intel Core i7 2.70 GHz processor, Windows 7 Professional operating system).

RESULTS

A total of 5,465 Yellow Perch (3,321 females and 2,144 males) were included in the analysis (Table 2), and generally more mature fish than immature fish were collected for each year-class. Females consisted of 61% mature individuals and males consisted of 80% mature individuals. Four year-classes of females and five year-classes of males had fewer than 10 individuals in either the mature or immature category.

<table>
<thead>
<tr>
<th>Year-class</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mature</td>
<td>Immature</td>
</tr>
<tr>
<td>1984</td>
<td>92</td>
<td>51</td>
</tr>
<tr>
<td>1985</td>
<td>76</td>
<td>53</td>
</tr>
<tr>
<td>1986</td>
<td>77</td>
<td>28</td>
</tr>
<tr>
<td>1987</td>
<td>56</td>
<td>22</td>
</tr>
<tr>
<td>1988</td>
<td>117</td>
<td>85</td>
</tr>
<tr>
<td>1989</td>
<td>69</td>
<td>52</td>
</tr>
<tr>
<td>1990</td>
<td>61</td>
<td>59</td>
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<tr>
<td>1991</td>
<td>20</td>
<td>61</td>
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<td>1992</td>
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<td>1993</td>
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<td>1994</td>
<td>99</td>
<td>27</td>
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<td>1995</td>
<td>31</td>
<td>79</td>
</tr>
<tr>
<td>1996</td>
<td>71</td>
<td>17</td>
</tr>
<tr>
<td>1997</td>
<td>193</td>
<td>82</td>
</tr>
<tr>
<td>1998</td>
<td>454</td>
<td>161</td>
</tr>
<tr>
<td>1999</td>
<td>82</td>
<td>27</td>
</tr>
<tr>
<td>2000</td>
<td>86</td>
<td>21</td>
</tr>
<tr>
<td>2001</td>
<td>107</td>
<td>73</td>
</tr>
<tr>
<td>2002</td>
<td>61</td>
<td>136</td>
</tr>
<tr>
<td>2003</td>
<td>25</td>
<td>93</td>
</tr>
<tr>
<td>2004</td>
<td>16</td>
<td>37</td>
</tr>
<tr>
<td>2005</td>
<td>3</td>
<td>39</td>
</tr>
<tr>
<td>2006</td>
<td>0</td>
<td>43</td>
</tr>
<tr>
<td>2007</td>
<td>5</td>
<td>18</td>
</tr>
<tr>
<td>Total</td>
<td>2,012</td>
<td>1,309</td>
</tr>
</tbody>
</table>

Frequentist Inference

Frequentist estimates of the individual maturity models resulted in significant parameter estimates for 73 of the 96 models (76%; Table 3). Estimates of female age and length at 50% maturity ranged from 2.2 to 4.7 years and from 154 to 202 mm (Table 3). Male age and length at 50% maturity ranged from 1.1 to 2.3 years and from 90 to 129 mm (Table 3).

The hierarchical model estimated parameters for all year-classes; however, 95% CIs for all year-classes were large compared with parameters from Bayesian inference (Tables 4, 5). Estimates of female age and length at 50% maturity ranged from 1.0 to 5.8 years and from 157 to 201 mm (Figures 1A, 2A). Male age and length at 50% maturity ranged from 1.2 to 2.1 years and from 94 to 120 mm (Figures 1C, 2C).

Bayesian Inference

The Bayesian inference models converged after 100,000 iterations. The upper 95% CIs of the BGR factors for all model parameters was less than 1.15. Parameter estimates were nearly identical between noninformative normally distributed priors and noninformative \( t \)-distributed priors, suggesting the data contain enough information to overcome the prior distributions.

At the year-class level, maturity models showed that the variability in the effect of age was higher in females than males while there was no difference in variance in the effect of length. The median value of the hyperprior variance \( (\sigma^2) \) for female age was 0.917 (95% CI = 0.564–1.558) while that for males was 0.422 (95% CI = 0.204–0.801). The median value of the hyperprior variance \( (\sigma^1) \) for female length was 0.005 (95% CI = 0.001–0.009) while that for males was 0.007 (95% CI = 0.002–0.012). These results suggest there is a more consistent increase in the odds of a male being mature as age increases than there is for a female, while the effect of length is more consistent among year-classes. Precision as measured by 95% credible intervals were generally smaller than 95% CIs for all models (Tables 4, 5).

Posterior median estimates of female age and TL at 50% maturity ranged from 2.2 to 6.1 years and from 157 to 201 mm, respectively (Figures 1B, 2B). Posterior median estimates of male age and length at 50% maturity ranged from 1.2 to 2.2 years and from 92 to 122 mm, respectively (Figures 1D, 2D). Overall, the posterior median estimate of female age and length at 50% maturity was 3.3 years (95% CI = 2.6–4.3) and 178 mm, respectively (95% CI = 172–184). Posterior median male age and TL at 50% maturity was 1.6 years (95% CI = 1.4–1.8) and 105 mm (95% CI = 99–110), respectively.

Inference Comparisons

Mean estimates of the hierarchical model fit using frequentist inference were nearly identical to the median estimates of age and length at 50% maturity from Bayesian inference for most year-classes. The point estimates of age at 50% maturity differed at most by 2 years for females (RMSE = 0.41) and by 0.3 years
TABLE 3. Age (years) and length (TL, mm) at 50% maturity estimates of Yellow Perch from individual year-class logistic regression models using frequentist inference; upper and lower limit (±) of the 95% CI is in parentheses. Asterisk (*) indicates individual logistic regression models resulted in insignificant coefficients.

<table>
<thead>
<tr>
<th>Year-class</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Age</td>
<td>Length</td>
</tr>
<tr>
<td>1984</td>
<td>3.11 (±0.33)</td>
<td>154.41 (±6.61)</td>
</tr>
<tr>
<td>1985</td>
<td>3.71 (±0.41)</td>
<td>158.85 (±7.23)</td>
</tr>
<tr>
<td>1986</td>
<td>3.47 (±0.33)</td>
<td>164.94 (±11.45)</td>
</tr>
<tr>
<td>1987</td>
<td>3.15 (±0.42)</td>
<td>172.01 (±9.61)</td>
</tr>
<tr>
<td>1988</td>
<td>3.17 (±0.12)</td>
<td>167.43 (±5.23)</td>
</tr>
<tr>
<td>1989</td>
<td>3.01 (±0.32)</td>
<td>164.5 (±7.80)</td>
</tr>
<tr>
<td>1990</td>
<td>3.14 (±0.28)</td>
<td>177.48 (±7.71)</td>
</tr>
<tr>
<td>1991</td>
<td>*</td>
<td>185.59 (±7.22)</td>
</tr>
<tr>
<td>1992</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>1993</td>
<td>2.51 (±0.51)</td>
<td>194.07 (±10.71)</td>
</tr>
<tr>
<td>1994</td>
<td>2.19 (±0.21)</td>
<td>190.25 (±10.63)</td>
</tr>
<tr>
<td>1995</td>
<td>2.32 (±0.20)</td>
<td>192.17 (±5.10)</td>
</tr>
<tr>
<td>1996</td>
<td>2.64 (±0.43)</td>
<td>196.49 (±14.54)</td>
</tr>
<tr>
<td>1997</td>
<td>2.38 (±0.16)</td>
<td>201.55 (±6.53)</td>
</tr>
<tr>
<td>1998</td>
<td>3.02 (±0.18)</td>
<td>176.83 (±4.16)</td>
</tr>
<tr>
<td>1999</td>
<td>3.69 (±0.61)</td>
<td>165.09 (±13.00)</td>
</tr>
<tr>
<td>2000</td>
<td>3.68 (±0.60)</td>
<td>174.4 (±14.67)</td>
</tr>
<tr>
<td>2001</td>
<td>3.65 (±0.38)</td>
<td>189.19 (±6.36)</td>
</tr>
<tr>
<td>2002</td>
<td>4.74 (±0.47)</td>
<td>189.72 (±7.67)</td>
</tr>
<tr>
<td>2003</td>
<td>4.74 (±0.45)</td>
<td>177.37 (±7.09)</td>
</tr>
<tr>
<td>2004</td>
<td>4.26 (±0.68)</td>
<td>168.04 (±7.36)</td>
</tr>
<tr>
<td>2005</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2006</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>2007</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

The point estimates of TL at 50% maturity differed at most by 14 mm for females (RMSE = 8.14) and 4 mm for males (RMSE = 1.30). Additionally the range of 95% credible intervals and 95% CIs were similar for all models (Figures 1, 2).

The computation time to conduct the bootstrap CIs of age at 50% maturity for the hierarchical model fit with frequentist inference was 22.5 min for females and 18.1 min for males. Bootstrap parameter estimates for TL at 50% maturity took 50.6 min for females and 25.8 min for males. Bayesian inference of the hierarchical model describing age at maturity finished in 3.8 min for females and 3.3 min for males. Bayesian inference of the hierarchical model describing length at maturity finished in 8.5 min for females and 5.8 min for males. Overall the computation time of Bayesian inference was 78% to 83% less than bootstrap CIs.

DISCUSSION

This study compared the performance of two statistical inference paradigms in the analysis of age and length at maturity. First we showed that when using traditional methods of statistical inference, a hierarchical approach is preferred over single-level logistic regressions, particularly when sample size is small. Further, our results showed that when using a hierarchical model similar age and length at 50% maturity estimates are produced by both frequentist and Bayesian inference. However, Bayesian inference resulted in more precise estimates of uncertainty around the model parameters, required one step in the modeling process, and provided the complete posterior distribution in one seamless and easy approach. Frequentist inference required a second step to generate CIs for estimates of age (or length) at 50% maturity. Further, the large 95% CIs from frequentist inference of parameter estimates suggest bootstrap CIs of the derived parameters (age or length at 50% maturity) are misleading (i.e., the high precision is biased). Finally, Bayesian inference finished as much as 83% faster than bootstrap estimates of 95% CIs.

Bayesian inference of the maturity model explicitly provides more information about the model and data in the global parameters (e.g., θ1 and θ2); this is not easily gained through frequentist inference. These parameters represent the distribution of the parameters given the data and describe the most credible estimates...
<table>
<thead>
<tr>
<th>Year-class</th>
<th>Female age at maturity model</th>
<th>Frequentist</th>
<th>Intercept</th>
<th>Bayesian</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td></td>
<td>1.85</td>
<td>–0.040, 3.742</td>
<td>–5.78</td>
<td>–7.674, 3.886</td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td>1.65</td>
<td>–0.373, 3.678</td>
<td>–6.10</td>
<td>–8.131, –4.069</td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td>2.12</td>
<td>–0.466, 4.709</td>
<td>–7.29</td>
<td>–9.878, –7.022</td>
</tr>
<tr>
<td>1987</td>
<td></td>
<td>1.74</td>
<td>–0.729, 4.214</td>
<td>–5.57</td>
<td>–8.045, –5.095</td>
</tr>
<tr>
<td>1988</td>
<td></td>
<td>3.34</td>
<td>0.491, 3.185</td>
<td>–10.40</td>
<td>–13.323, –7.477</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td>2.03</td>
<td>–0.201, 4.262</td>
<td>–6.14</td>
<td>–8.375, –5.905</td>
</tr>
<tr>
<td>1990</td>
<td></td>
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<td>0.046, 5.151</td>
<td>–8.01</td>
<td>–10.605, –5.415</td>
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<tr>
<td>1993</td>
<td></td>
<td>2.66</td>
<td>–0.153, 5.423</td>
<td>–6.93</td>
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<td>1996</td>
<td></td>
<td>2.28</td>
<td>–0.909, 5.472</td>
<td>–6.23</td>
<td>–9.396, –3.324</td>
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<td>1997</td>
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<td>0.990, 4.757</td>
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<td>1998</td>
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<td>0.583, 2.332</td>
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<td>2000</td>
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<td>–0.702, 3.336</td>
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<td>–6.944, –2.916</td>
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<td>2001</td>
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<td>1.18</td>
<td>–0.105, 2.421</td>
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<td>2002</td>
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<td>–6.33</td>
<td>–8.124, –4.536</td>
</tr>
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<td>-16.93 (-19.01, -14.960)</td>
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FIGURE 1. Female and male Yellow Perch age at 50% maturity estimates from hierarchical model by year-class. Frequentist inference results of (A) females and (C) males display the mean estimated age at 50% maturity (black dots) and 95% bootstrap CIs (upper and lower vertical lines). Bayesian inference results for (B) females and (D) males display the median estimated age at 50% maturity (black dots) and 95% credible intervals (upper and lower vertical lines).
Figure 2. Female and male Yellow Perch length at 50% maturity estimates from hierarchical model by year-class. Frequentist analysis results of (A) females and (C) males display the mean estimated length at 50% maturity (black dots) and 95% bootstrap CIs (upper and lower vertical lines). Bayesian inference results of (B) females and (D) males display the median estimated length at 50% maturity (black dots) and 95% credible intervals (upper and lower vertical lines).
of age and length at 50% maturity. A analogous frequentist estimates require treating the estimated age and length at 50% maturity as fixed estimates with no variation and taking the average of bootstrap techniques, thus providing a biased estimate of uncertainty for the global maturity estimates. Additionally, bootstrap techniques require large data sets and few outliers, and assume no dependence structures (e.g., time series). In contrast, the Bayesian inference method provides a more direct measure of uncertainty. Further, if one chooses to conduct multiple post hoc comparisons among year-classes, P-values would have to be estimated for the frequentist approach and adjusted based on the number of comparisons the researcher intends to make. Bayesian inference does not suffer from this limitation and the posterior distribution of the parameters can be compared without penalizing for multiple comparisons (Kruschke 2010).

Variability of the parameters in the year-class level from Bayesian inference provided additional information that would be useful to managers while this information was lacking using frequentist inference. For example, knowing the variance in the log odds parameter of the age effect suggests the effect of age on female maturity is much more variable. Further, there were no differences in the variance of the effect of length suggesting factors that are influencing age rather than length at maturity have a greater impact on females than on males. Both parameters would be of great interest to managers to fully understand the life history of exploited fish. These parameters are not known using frequentist inference since the focus is on the point estimate of the log of the odds parameter rather than the distribution of credible values.

The model fit with Bayesian inference can easily be extended to assess a variety of hypotheses under one modeling framework. For example, adding group-level effects to the log odds parameter ($\beta_{\text{ij}}$) can test hypotheses regarding factors that best explain changes in the maturation rate. Two competing hypotheses have been proposed that can account for these changes (Law and Grey 1989; Law 2000; Heino et al. 2002). The first is a compensatory response hypothesis that predicts a phenotypic plastic response to a reduction in stock size. The reduced abundance results in higher growth rates, thus individuals more quickly attain the size required for maturation. This hypothesis could be tested for by including a group-level factor (i.e., year-class level) describing year-class strength. The second is an evolutionary response hypothesis that predicts individuals that have a late maturing phenotype are harvested, thus reducing the expected number of spawning for those individuals, resulting in generations that have the phenotype favoring maturation at earlier ages or smaller size. This hypothesis could be tested by including a group-level factor describing periods of increased harvest. Other possible extensions include modeling variability among year-classes as a function of covariates to test hypotheses regarding what factors are influencing the variation in the maturation rate among year-classes. Evaluating factors that influence how quickly fish mature or how variable the maturation rate is would be of great interest to fisheries managers.

Comparing frequentist and Bayesian inference is not new (Ghosh et al. 2006; Ismaila et al. 2007). Results of logistic regression using competing statistical paradigms have been evaluated in the pharmacology and clinical trial literature (Austin et al. 2001; Ambrose et al. 2012). However, to our knowledge this is the first study that compares results from a hierarchical logistic regression model fit using traditional frequentist and Bayesian inference in the fisheries literature.

Our results suggest that both inference methods are similar when fitting a hierarchical model; however, Bayesian inference provided more information about the data, was conducted in one seamless framework, and was completed in significantly less computational time. While concordant results were obtained, others have found discrepancies (Nielsen and Lewy 2002; Broomhall et al. 2010; Kruschke 2013). We suggest that Bayesian estimation of maturity indices using a hierarchical model is an improvement over frequentist methods by providing more information about the complete distribution of parameters and is not subject to secondary analysis to establish confidence intervals and P-values.

Two limiting factors to the widespread adoption of Bayesian inference have been computational time and familiarity with writing the necessary code. Both of these limitations are quickly eroding due to the continuous improvements in computer speed and emergence of programs that are easy to use. Computer memory is inexpensive and a standard personal computer with 4 GB of RAM and Microsoft Windows operating system can easily and quickly conduct Bayesian inference. While Bayesian inference using MCMC algorithms is usually considered slow, our results showed that the use of bootstrap techniques to generate CIs for frequentist inference can take significantly more time. Statistical packages such as R and SAS require the user to write code for their analysis. A user familiar with these two languages should have no difficulty picking up the BUGS language and the code can often be less complex, as in our case where bootstrapping was necessary (Appendices 1–3). Finally, there has been recent focus to include programming skills into the curriculum of environmental science programs (Valle and Berdanier 2012). As more environmental scientists become comfortable with programming, taking advantage of Bayesian approaches will become much more within reach.

While this study focused on one population statistic, we suggest the statistical properties of other life history parameters that are routinely estimated for fisheries management purposes be evaluated using the Bayesian framework. For example, mortality estimates from catch curves, growth rates estimated from von Bertalanffy models, stock recruitment models, and population abundance estimates from depletion experiments are all commonly used in fisheries management. Most of the above-listed parameters have published methods using Bayesian inference (Mántyniemi and Romakkaniemi 2002; Mántyniemi et al. 2005; He and Bence 2007; Su and Peterman 2012). However, few go beyond describing their methods and detail how Bayesian and frequentist inference results differ.
Although there are fundamental differences between frequentist and Bayesian methods, it is important that natural resource managers identify advantages and disadvantages of each. Frequentist CIs and Bayesian credible intervals describe two different measures of uncertainty about a parameter of interest. However, both describe precision and could similarly be used to direct management recommendations. While the advantages of Bayesian inference are widely known (Beaumont and Rannala 2004; Kruschke 2013; this study) a thorough review of how it compares with frequentist inference may further enable the use of Bayesian methods, bringing this paradigm to the main stream of statistical inference in fisheries science. Ultimately, these comparisons may assist managers and researchers to better understand the complexity of data describing our natural resources.

ACKNOWLEDGMENTS

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Lauer, T. E., and J. C. Doll. 2012. Final project report: dynamics and management of the Yellow Perch in Indiana waters of Lake Michigan and near-shore fish community characteristics. Report to Indiana Department of Natural Resources, Aquatic Biology and Fisheries Center, Ball State University, Muncie, Indiana.


Appendix 1: Frequentist Inference Code for Model 3

Frequentist inference code for the hierarchical logistic regression model of length at maturity (model 3). Models of age at maturity are identical except age is substituted for length.

```r
#load required packages
require(lme4)
require(arm)

#model statement with random effects for year-class.
mod1 <- lmer(formula=mature~length + (1 + length|yc),data=data.frame(slope
  name,family = binomial("logit"))
#extract slopes with 95%CI
ci <- coef(mod1)$yc
#extract y-intercept with 95%CI
yint <- coef(mod1)$yc[1]
#combine information
df1 <- rbind(df2,yint) #send to data frame
}
#extract y-intercept with 95%CI
df2 <- data.frame() #data frame to hold intercepts and 95% confidence intervals
for (i in 1:nrow(coef(mod1)$yc)){#oop to go through all year classes
  est <- coef(mod1)$yc[i,2] #extract slope
  ci <- coef(mod1)$yc[i,2] + c(-2,2)*se.ranef(mod1)$yc[i] #calculate 95% CI
  yci <- data.frame(slope=est,ci=ci[1],uci=ci[2]) #combine information
  df2 <- rbind(df2,yci) #send to data frame.
}
```

Appendix 2: Bootstrap Procedure for Estimating Confidence Interval

Bootstrap procedure for estimating 95% CIs for length at 50% maturity; model for age at maturity is identical except age is substituted for length.

```r
#load required packages
require(lme4)
require(arm)

#model statement with random effects for year-class.
mod1 <- lmer(formula=mature~length + (1 + length|yc),data=
  name,family = binomial("logit"))
#extract slopes with 95%CI
ci <- coef(mod1)$yc
#extract y-intercept with 95%CI
yint <- coef(mod1)$yc[1]
#combine information
df1 <- rbind(df2,yint) #send to data frame
}
#extract y-intercept with 95%CI
df2 <- data.frame() #data frame to hold intercepts and 95% confidence intervals
for (i in 1:nrow(coef(mod1)$yc)){#oop to go through all year classes
  est <- coef(mod1)$yc[i,1] #extract slope
  ci <- coef(mod1)$yc[i,1] + c(-2,2)*se.ranef(mod1)$yc[i] #calculate 95% CI
  yint <- data.frame(slope=est,ci=ci[1],uci=ci[2]) #combine information
  df2 <- rbind(df2,yint) #send to data frame.
}
```
matfuncL <- function(dat, indices) {
  # Function to pass through
  d <- dat[indices,]
  mod <- lmer(formula = mature ~ length + (1 + length|yc), data = d, family = binomial("logit"))
  coef <- coef(mod) # get coefficients
  alpha <- as.numeric(coef$yc[,1]) # intercept
  beta <- as.numeric(coef$yc[,2]) # logits
  lmat <- (-alpha / beta) # calculated length at 50% maturity
  rbind(lmat) # return 50% maturity
}

# bootstrap function
bootfuncL <- function(mod, dat) {
  # run bootstrap function on mixed model
  mat.boot <- boot(dat = dat, statistic = matfuncL, R = 50)
  # initialize data frame to hold confidence intervals
  ciop <- data.frame()
  params <- c()
  cis <- data.frame()
  # loop through bootstrap confidence intervals and combine data
  for (i in 1:ncol(mat.boot$t0)) {
    # for i = 1 to number of year classes
    matci <- boot.ci(mat.boot, type = "norm", index = i) # calculate 95% confidence intervals
    lci <- matci$normal[2] # extract lower confidence intervals
    uci <- matci$normal[3] # extract upper confidence intervals
    cis <- rbind(cis, lci, uci = uci) # organize 95% confidence intervals
    ciop <- rbind(ciop, cis) # combine 95% confidence intervals
  }
  mcoef <- coef(mod) # get coefficients for each year-class
  alpha <- as.numeric(mcoef$yc[,1]) # intercept
  beta <- as.numeric(mcoef$yc[,2]) # slope
  lmat <- alpha / beta # calculate length at maturity
  for (i in 1:ncol(mat.boot$t0)) {
    # loop through year classes and organize 50% maturity into a data frame
    params <- rbind(params, lmat[i])
  }
  ciop <- cbind(ciop, params) # combine everything
  return(ciop)
}

# length model
mod <- lmer(formula = mature ~ length + (1 + length|yc), data = data.male, family = binomial("logit"))

# start timer and run bootstrap analysis
Sys.time() -> start
bootfuncL(mod = mod1, dat = data.name)
print(Sys.time() - start)

### Appendix 3: JAGS Model Code

JAGS model code for the hierarchical logistic regression model.

model {
  # hyperpriors
  beta ~ dnorm(0, 0.0001) # mean = 0, precision = 1/1000
  sigma ~ dunif(0, 10)
  tau <- pow(sigma, -2)
  beta1 ~ dnorm(0, 0.0001) # mean = 0, precision = 1/1000
  sigma1 ~ dunif(0, 10)
  tau1 <- pow(sigma1, -2)

  # Priors
  for (j in 1:Y) {
    b0[j] ~ dnorm(beta, tau) # prior for year-class specific intercept parameter
    b1[j] ~ dnorm(beta1, tau1) # prior for year-class specific log-odds parameter
  }

  # likelihood
  for (i in 1:N) {
    mat[i] ~ dbern(mu[i]) # maturity follows a Bernoulli distribution
    logit(mu[i]) <- b0[yc[i]] + b1[yc[i]] * X[i] # logit link with linear function
  }

  # Derived parameter
  for (k in 1:Y) {
    Ffiftymat[k] <- (-b0[k]) / (b1[k]) # calculate age or length at 50% maturity from logistic regression parameters
  }
  avgFfiftymat <- (-beta + 0.0000001) / (beta1 + 0.0000001) # overall age or length at 50% maturity for entire data set - a small constant is added to the numerator and denominator to prevent division by 0.}
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Alligator Gar Movement and Macrohabitat Use in the Lower Trinity River, Texas

David L. Buckmeier,* Nathan G. Smith, and Daniel J. Daugherty
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Abstract
Using acoustic telemetry, we characterized movements and macrohabitat use of 46 Alligator Gars Atractosteus spatula in the lower 180 km of the Trinity River, Texas. Although several Alligator Gars used over 100 km of the river, 83% of the tagged fish had linear home ranges less than 60 km during the 22 months of study. As a result, home ranges of fish that were tagged in different parts of the study area rarely overlapped. Home range size varied by season, with the smallest home ranges occurring in winter. Greatest movements occurred during the spawn (May–June) and postspawn (July–October) seasons, and movements were correlated with increasing water temperatures based on detections of tagged fish at fixed receiver stations. Tagged Alligator Gars were most often associated with main-channel habitats when river stage was at base level and during small flood pulses (<3-m rise). When in the main channel, tagged Alligator Gars selected water that was deeper than the average within their home ranges. In contrast, during large flood pulses (≥3-m rise), tagged fish were found in tributaries and inundated floodplains, regardless of season. Use of tailwater and estuarine macrohabitats was seasonal and limited to fish that had been tagged near those areas. Limited home ranges and observed spatial segregation of fish tagged near the upper and lower boundaries of the 180-km study area suggest that the fish have access to critical habitats needed for reproduction, feeding, and migration within relatively small spatial scales. As such, Alligator Gars in the lower Trinity River do not appear to represent a single panmictic population, indicating that localized rather than regional management efforts would be appropriate.

Although management of the Alligator Gar Atractosteus spatula has historically focused on eradication (Burr 1931; Scarnecchia 1992), recent recognition that this species serves an important ecological function as a top predator and that it can support locally valuable sport and commercial fisheries has inspired new interest in its conservation and management. The historic range of the Alligator Gar has been dramatically reduced, and remaining populations appear to be vulnerable to habitat loss and overfishing (Jelks et al. 2008). Habitat loss primarily results from reduced access to spawning areas where flow regimes have been altered (Ferrara 2001; Brinkman 2008; Mendoza-Alfaro et al. 2008; Inebnit 2009; Kluender 2011). Recently, all states in the Alligator Gar’s historic U.S. range, with the exception of Louisiana, have either implemented harvest regulations or issued declarations of extirpation (A. Ferrara, Nicholls State University, personal communication).

Efforts to rebuild depleted populations and to manage recreational and commercial fisheries where healthy populations exist require knowledge of population structure, movements, and habitat use. To date, such studies of Alligator Gars have been rare. We are aware of only one published study (Sakaris et al. 2005) that examined movements of Alligator Gars. Additionally, two theses (Brinkman 2008; Kluender 2011) described movements of and habitat use by Alligator Gars, but small numbers of fish and problems with transmitter loss limited the inferences that could be made. Although these previous studies have provided much-needed insight regarding the behaviors of individual fish, more information is needed to develop testable hypotheses for populations in large river ecosystems.

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To be effective, conservation and management must occur at spatial scales that encompass all habitats needed to complete critical life stages. Alligator Gars are known to inhabit large rivers, tributaries, reservoirs, backwaters, and estuaries; however, the role served by each of these habitats is unclear. It is suspected that flooded tributaries provide important spawning habitats for Alligator Gars (Inebnit 2009; Kluender 2011) and that backwaters might be important for juvenile development (Robertson et al. 2008), but published data are limited. Alligator Gars may be similar to other long-lived, large-bodied species (e.g., Shortnose Sturgeon Acipenser breviscrostrum: Hall et al. 1991, Fernandes et al. 2010; Robust Redhorse Moxostoma robustum: Grabowski and Isely 2006; Striped Bass Morone saxatilis: Wingate and Secor 2007; and Paddlefish Polyodon spathula: Mettee et al. 2009) that require large home ranges (Minns 1995) because habitats used for reproduction, feeding, and migrations are widely dispersed. Alternatively, Alligator Gars may require smaller home ranges if critical habitats are available locally. For example, Flathead Catfish Pylodictis olivaris tend to have small home ranges and exhibits localized movements (Grace 1985; Jackson 1999; Travnichek 2004; Daugherty and Sutton 2005) because they do not require expansive stretches of river in order to complete critical life stages. Travnichek (2004) suggested that because Flathead Catfish tend to have relatively small home ranges, different reaches of the Missouri River could be managed locally for different fishery goals.

A lack of data currently precludes inferences about the habitats that are needed for critical life stages of the Alligator Gar; thus, the spatial scale that is necessary to conduct conservation and management is unknown. Previous work suggests that Alligator Gars have the potential for long-distance movements, yet linear home ranges tend to be relatively small (~20 km; Sakaris et al. 2005; Brinkman 2008). Studies have also suggested that individual Alligator Gars exhibit strong fidelity to spawning and overwintering sites (Brinkman 2008; Kluender 2011). Systemwide investigations of Alligator Gars are needed to characterize population structure and to describe the habitats used for reproduction, feeding, and overwintering. We used acoustic telemetry to characterize movement and to identify macrohabitats used by tagged Alligator Gars in the lower 180 km of the Trinity River, a large, coastal river–estuarine ecosystem in Texas. Where applicable, we used exploratory analyses to identify variables that were correlated with movement and habitat use.

**METHODS**

Study area.—The Trinity River flows 885 km through east Texas, passing through the cities of Dallas and Fort Worth and east of Houston. Lake Livingston, a 33,500-ha impoundment created by Lake Livingston Dam, serves as the upstream boundary of our study area, the lower Trinity River. The river flows from the dam for about 180 km before entering Trinity and Galveston bays. A lock-and-dam structure at Wallisville (about 3 km upstream of the confluence of Trinity Bay) serves as a saltwater barrier during low flows and constituted the lower boundary of our study area (Figure 1).

The lower Trinity River watershed is dominated by forest and agricultural lands, although industry (primarily petrochemical) is scattered throughout. The river is predominately low gradient (0.03–0.20 m/km), ranges from 70 to 120 m wide, and has a maximum depth of about 18 m, although much of the river is less than 2 m deep. A few rock shoals are present (primarily within 50 km of Lake Livingston Dam), but sand is the dominant substrate. Large woody debris is present throughout the river, particularly in pool habitats. Large woody debris is present throughout the river, particularly in pool habitats. The floodplain along the upper 50 km of the study area consists of agricultural and forested lands that are inundated when waters back up into small tributaries as the main channel rises. The floodplain along the middle 75 km of the study area is more densely forested, with numerous backwaters and oxbow lakes in addition to tributaries. In the lowest part of the study area, the floodplain transitions into tidally influenced freshwater marsh near Trinity Bay.

Fish collection and tagging.—Alligator Gars (800–2,130 mm TL) were collected from one or two large pools in each of four areas along the lower Trinity River (Figure 1) during September 2008 through August 2009. Fish were classified based on the river reach from which they were collected: group A (N = 21) at river kilometers (rkm) 6–12 downstream of Lake Livingston Dam (i.e., the dam = rkm 0); group B (N = 12) at rkm 30–32; group C (N = 4) at rkm 104–115; and group D (N = 14) at rkm 172–177. Collection areas were chosen (1) based on repeated observations of Alligator Gars at those sites and (2) to distribute tagged fish throughout the study area. Although Alligator Gars were frequently observed at each site, few group C fish were collected because boat access to this portion of the river was limited.

Alligator Gars were collected by using rod-and-reel, jug lines, and large-mesh (76–127-mm bar-length), multifilament gill nets. Upon capture, fish TL was recorded and a 14-month ultrasonic transmitter (Model CT-82-2-E; Sonotronics, Tucson, Arizona) was attached to the base of the dorsal fin by methods similar to those of Sakaris et al. (2005), Brinkman (2008), and Kluender (2011). A cordless drill and bit were used to make two holes (about 50 mm apart) through the scales and musculature at the base of the dorsal fin. A 12-gauge biopsy needle was inserted through each hole on the right side of the fish. A loop of 125-kg stainless-steel leader was threaded through holes on each end of the transmitter and then through the ends of the needles from the left side of the fish. The needles were removed, and two or three stainless-steel crimps were threaded through the tag ends of the leader material and crimped to secure the tag to the fish. Excess leader was removed, and Betadine was used to sterilize the affected area of the fish. Fish were released near their respective capture sites.

Telemetry.—Seasonal movement and macrohabitat use were examined by using a combination of fixed telemetry and mobile telemetry. Sonotronics submersible underwater receivers.
FIGURE 1. Map of the study area in the lower Trinity River, Texas, showing submersible ultrasonic receiver (SUR) locations (black shaded circles; FM = Farm to Market; RKM = river kilometer, with RKM 0 = Lake Livingston Dam) and Alligator Gar collection areas (rectangles).
TABLE 1. Number of Alligator Gars that were available for detection during each season in the Trinity River, Texas, after being tagged in one of four areas (see Figure 1; rkm = river kilometer, with rkm 0 = Lake Livingston Dam). Numbers of fish varied because of the prolonged tagging period, tag loss or failure, harvest, and suspected emigration.

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(SURs) were deployed at fixed locations throughout the lower Trinity River to log the dates and times of individual fish movements. During October 2008 through July 2010, we maintained eight SUR stations in the main channel (at rkm 1, 17, 51, 81, 123, 139, 165, and 177) and one off-channel station in the Old River downstream of the confluence with the Trinity River (at rkm 159; Figure 1). A digital SURs were deployed at other locations but could not be maintained because of flooding or vandalism. One SUR was deployed at each location except Wallisville (rkm 177), where up to three SURs were used to increase fish detections. Although the Wallisville SUR array did not provide 100% coverage at all flows (Casto-Yerty and Bettoli 2009), it generally acted as a series of gates and allowed us to detect large-scale movements by tagged Alligator Gars within the 180-km study area (similar to the study by Grothues et al. 2005).

Mobile tracking was used to evaluate macrohabitat use by tagged Alligator Gars. Tracking was conducted by traveling downstream (about 8 km/h) by boat, with a Sonotronics USR-96 tracking receiver and a TH-2 towed omnidirectional hydrophone. When a signal was detected, we circled until the tag code could be identified. Fish location was estimated and georeferenced. Occasionally, a Sonotronics DH-4 directional hydrophone was needed to separate multiple signals and identify individual fish locations. Mobile tracking of the entire study area occurred during six events: April 6–9, August 13–16, and November 2–4, 2009; and January 25–28, April 27–28, and July 6–8, 2010. Supplementary mobile tracking occurred opportunistically. Tributaries, inundated floodplains, and oxbows were also tracked when flooding allowed access from the main river channel.

Data processing.—Data from SURs were processed using SURsoftDPC (Sonotronics). Anomalous detections can be recorded by SURs from background noise or when tagged fish are close to the hydrophone (e.g., a fish tagged with a 70-kHz transmitter can be detected and misidentified at 68–72 kHz). An anomalous data resulting from background noise were omitted by removing single-fish detections unless a second detection was recorded within 5 min of the first. Recognition of anomalous data on adjacent frequencies required the database to be sorted by date, time, and ping interval; rare detections on adjacent frequencies with the same ping interval were removed. After we removed anomalous data, fish detections were limited to one per minute (by fish and SUR station). The number of fish available for detection varied (Table 1) because of the prolonged tagging period (September 2008–August 2009) and the loss of some fish due to tag failure, harvest, or suspected emigration. Tagged fish were included in analyses through the day prior to a full mobile tracking event (after its last detection) during which the fish was not detected in the study area.

Home range size and movement.—Linear home range size was calculated for each tagged fish and was compared across seasons. Linear home range was defined as the minimum linear distance (km) along the river channel between outermost relocations (from SURs and manual tracking) of each fish with a minimum of five relocations on different days (Sakaris et al. 2005). Differences in home range size across behavior-based seasons (defined by Kluender 2011: prespawn = February–April; spawn = May and June; postspawn = July–October; winter = November–January) were assessed using a repeated-measures approach because of the repeated observations of individual fish. Prior to analysis, home range data were normalized by using a log transformation. The MIXED procedure in the Statistical Analysis System (SAS; SAS 2008) was used to perform repeated-measures ANOVA with unstructured variance, and the df were calculated using the Kenward–Roger option. Pairwise comparisons of home range size among seasons were controlled for multiple comparisons by using a Tukey adjustment (α = 0.05; SAS 2008).

To identify variables that potentially influenced Alligator Gar movements, we explored the effects of water temperature, river stage, and time of day on detections of tagged fish at SUR stations. For these analyses, we used only shallow-water SUR stations where Alligator Gars were not typically observed; this was done to minimize possible detections of resting fish. We estimated the probability of detecting at least one tagged Alligator Gar in a given week based on average weekly water temperature, deviation from average river stage, and the interaction between
the two variables by using logistic regression (LOGISTIC procedure in SAS). Model fit was assessed with a Wald chi-square test in SAS. Average weekly water temperature and river stage data were collected at SUR 2 (rkm 17). Water temperature data were collected using an optic temperature logger (HOBO Pendant; Onset Computer Corp., Bourne, Massachusetts), and river stage data were obtained from the U.S. Geological Survey (USGS). Deviation from average river stage was estimated by subtracting the overall average river stage from the weekly average value. Diel patterns of fish movement were evaluated by plotting, for each hour of the day, the number of tagged Alligator Gars that were detected at each of the shallow-water SUR stations used in the above analyses. A two-sample t-test was used to identify differences in detection rates between daytime (0700–1900 hours) and nighttime (2000–0600 hours).

Macrohabitat use.—Through telemetry, we determined when Alligator Gars used main-channel, floodplain tributary, inundated floodplain, tailwater, and estuarine macrohabitats. Kuehner (2011) provided descriptions of most of these macrohabitats for Alligator Gars in the Fourche LaFave River, Arkansas, based on descriptions by Baker et al. (1991). Use of the main channel, floodplain tributaries, and inundated floodplain was evaluated by determining the percentage of relocations (from mobile telemetry) that occurred in each of these habitat categories at different river stages. River stage was classified as base level, a small flood pulse (0–3 m maximum rise), or a large flood pulse (>3 m maximum rise). At base level, only the main channel and the mouths of floodplain tributary habitats were available. During small flood pulses, fish access to floodplain tributary habitats greatly increased. A access to inundated floodplain habitats was only available during large flood pulses, when the river extended out of its banks. Manual relocations within 1 week of any previous relocation were excluded to allow sufficient time for tagged Alligator Gars to traverse the entire study area.

Alligator Gar use of main-channel macrohabitats was further characterized by evaluating the water depth at sites where fish were found. For each main-channel detection of a tagged fish, we divided the median water depth of that 0.1-km river segment by the average median depth across the overall home range of that individual fish (based on the bathymetric model described below). For this depth index, values greater than 1.0 indicated that the fish was in water deeper than the average within its home range, and values less than 1.0 indicated that the fish was in shallower water. A chi-square test was used to evaluate whether depth index values deviated from the expected values indicating selection of deeper or shallower water. Alligator Gars from group D were not included in these calculations because the lower 35 km of the study area are channelized, with relatively uniform water depth.

Water depth in the main channel was characterized by using a bathymetric model of the lower Trinity River; this model was constructed from water depth data collected during a large flood pulse in November 2009. We traversed the entire study area—along the left and right riverbanks and along the center of the channel—to gather georeferenced point-sample data depicting water depth. Water depth data were entered into ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California), and a triangulated irregular network was used to create a three-dimensional model of water depth. A relationship between river discharge and water depth (i.e., a rating curve) based on USGS gage station data was then used to calculate median depth for each 0.1-km river segment at base flow (~28 m3/s).

Use of tailwater and estuarine macrohabitats was evaluated graphically. We plotted the number of individual tagged Alligator Gars that were detected each day at SUR 1 and SUR 10 to determine when fish moved between the main channel and tailwater (SUR 1) or estuary (SUR 10) habitat. Daily river stage and water temperature data were also plotted to determine whether either of these variables coincided with the use of tailwater and estuarine habitats. River stage data were obtained from USGS gages at rkm 17 (for SUR 1) and rkm 177 (for SUR 10). Water temperature data were collected by using optic temperature loggers (HOBO Pendant; Onset Computer Corp.).

RESULTS

Of the 51 Alligator Gars that were tagged, 46 were relocated (N = 21 fish from group A; 12 from group B; 4 from group C; and 9 from group D) during the 22-month study; the fate of the other five fish is unknown. Individual fish were monitored for a period of 1–22 months (mean = 11.5 months; SD = 5.7). Five of the 46 relocated Alligator Gars had fewer than five daily relocations and were not included in home range calculations (N = 1 fish from group A; 2 from group B; 1 from group C; and 1 from group D) but were included in macrohabitat use analyses.

Home Range

Home range size varied substantially among individuals (1–176 km; Figure 2), with most (83%) of the tagged Alligator Gars having home ranges less than 60 km. Home range size was also variable among tagging groups (group A: mean = 49.5 km, SD = 46.5; group B: mean = 54.2 km, SD = 43.1; group C: mean = 27.2 km, SD = 1.5; group D: mean = 12.5 km, SD = 13.0). Furthermore, the spatial distribution of tagged Alligator Gars’ home ranges also differed and appeared to be related to tagging location (Figure 2). Fish from tagging groups A and B overlapped, with most fish residing in the upper 60 km of the study area. Home ranges of group C fish were confined between rkm 104 and rkm 114, and home ranges of group D fish were below rkm 139 (Figure 2); however, 78% of the group D fish periodically emigrated out of the study area and into Trinity Bay.

Alligator Gar home range sizes differed throughout the year (repeated-measures ANOVA: F = 4.78; df = 5, 17.3; P = 0.0063). Tests of seasonal differences in mean home range size were limited to fish from tagging groups A, B, and C (N = 33) because home range estimates for group D fish did not include movements in Trinity Bay. Pairwise comparisons of the six seasons (from the prespawn season in 2009 through the spawn
season in 2010) revealed that home ranges were smaller during the 2009 winter season than during the 2009 prespawn and 2010 spawn seasons. In addition to seasonal differences in home range size, overlap between tagging groups (other than groups A and B) were limited (5 of 41 fish) and only occurred during the 2009 spawn, 2009 postspawn, and 2010 spawn seasons. In each of these seasons, 1–2 fish from groups A and B moved downstream and overlapped with group C or D, generally for less than 14 d.

Only one fish from a tagging group other than group D was ever detected at Wallisville (SUR 10; rkm 177); one group A fish was detected at SUR 10 in August 2009 and remained below rkm 139 for at least 38 d.

**Variables Influencing Movement**

The probability of detecting movement of tagged Alligator Gars within a given week was influenced by water temperature, although the relationships differed slightly by SUR station (Figure 3). For SUR 1, a significant logistic regression model was identified, with water temperature, deviation from average river stage, and their interaction term ($\chi^2 = 17.4$, df = 3, $P = 0.0006$). Mean river stage influenced how Alligator Gars responded to water temperature (interaction term: $\chi^2 = 6.7$, df = 1, $P = 0.0095$; Figure 3). For example, at the 25th percentile of river stage (i.e., low water level), the 50% probability of detection ($P_{50}$) was not reached, whereas at average river stage the $P_{50}$ occurred at 20.0°C, and at the 75th percentile of river stage (i.e., high water level) the $P_{50}$ occurred at 17.5°C (Figure 3). Thus, higher river stage increased the probability of detection at lower water temperatures. For the other SURs, only water temperature (SUR 2: $\chi^2 = 12.8$, df = 1, $P = 0.0004$; SUR 3: $\chi^2 = 10.4$, df = 1, $P = 0.0013$) was related to detection probability, with $P_{50}$ values occurring at 22.5°C for SUR 2 and 28.0°C for SUR 3.

Time of day also influenced Alligator Gar movements: tagged fish were detected more often at night at all shallow-water SURs (SUR 1: $t = 3.9$, df = 18, $P = 0.0011$; SUR 2: $t = 4.5$, df = 14, $P = 0.0005$; SUR 3: $t = 4.8$, df = 11, $P = 0.0006$). Timing of peak movements varied slightly by SUR station but tended to be between 2000 and 0200 hours (Figure 4).

**Macrohabitat Use**

During mobile tracking, Alligator Gars were generally found in pools within the main channel of the lower Trinity River, except during large flood pulses. At base level, all mobile tracking
FIGURE 3. Logistic regression relationships between average weekly water temperature and the predicted probability of detecting a tagged Alligator Gar at submersible ultrasonic receiver (SUR) station 1 (top panel), SUR 2 (middle panel), and SUR 3 (bottom panel; for locations, see Figure 1) in the lower Trinity River. For SUR 1, the three curves represent how the probability of detection at a given water temperature was affected by river stage (solid line = relationship at average [Avg] river stage; dotted line = relationship at the 25th percentile [P25] of river stage [low water level]; dashed line = relationship at the 75th percentile [P75] of river stage [high water level]). The water temperature × river stage interaction terms were not significant for SURs 2 and 3. Solid dots represent the water temperature at which the 50% probability of detection was achieved.

FIGURE 4. Number of tagged Alligator Gars that were detected during each hour of the day at submersible ultrasonic receiver (SUR) stations in the Trinity River, Texas, during 2008–2010. Stations represented are SUR 1 (top panel), SUR 2 (middle panel), and SUR 3 (bottom panel; for locations, see Figure 1). Shaded areas represent nighttime hours.

detections of tagged fish occurred in the main channel, with fish selecting water depths greater than the average median depth within their individual home ranges ($\chi^2 = 26.1$, df = 1, $P < 0.0001$; Figure 5, top panel). Alligator Gars were also found
was seasonal (most usage occurred during the prespawn and postspawn seasons) and limited to groups that had been tagged nearby. Alligator Gars from tagging groups A and B migrated to the tailwater of Lake Livingston Dam in March–June 2009, September–November 2009, and April–June 2010 (Figure 6, top panel). Between March and June 2009, 89% (N = 17 fish) of group A Alligator Gars and 30% (N = 3) of group B Alligator Gars were detected in the tailwater habitat; 78% (N = 14) of group A fish were again detected in the tailwater between September and November 2009. Similar to 2009, Alligator Gars from groups A and B migrated to the tailwater between April and June 2010 (83% [N = 10] from group A; 33% [N = 3] from group B).

Seasonal use of Trinity Bay and the main channel of the Trinity River’s lower reach by group D fish was also evident based on detections at SUR 10 (rmk 177). Peak detections occurred in December 2008, July 2009, and August–September 2009, with 67% (N = 2 fish), 57% (N = 4), and 71% (N = 5), respectively, of available group D fish being detected by the SURs (Figure 6, bottom panel). Thus, movements between estuarine and main-channel habitats in the lower study reach occurred primarily during the postspawn and winter periods.

Periods of peak SUR detections at SUR 1 and SUR 10 sometimes corresponded with increased flows and water temperatures, but trends were not consistent (Figure 6). Detections at SUR 1 in April 2009 coincided with a large flood pulse, whereas peak detections in April 2010 followed a flood pulse. Both peaks corresponded to rising water temperature; peak detections observed on March 19, 2009, and April 12, 2010, each corresponded with a water temperature of 18°C. Detections at SUR 1 from September to November 2009 were not correlated with either river stage or water temperature. River stage and water temperature did not appear to be related to peak detections of Alligator Gars at SUR 10.

**DISCUSSION**

Although home ranges of tagged Alligator Gars in the lower Trinity River were generally less than 60 km, fish in our study had home ranges that were larger than those reported in previous studies (3–12 km: Sakaris et al. 2005; 5–17 km: Brinkman 2008). However, compared with other long-lived, large-bodied species such as Paddlefish and sturgeons (Hall et al. 1991; Mettee et al. 2009; Fernandes et al. 2010), Alligator Gars in the lower Trinity River had relatively small home ranges. This suggests that the habitats necessary to complete critical life stages were typically available within 60-km reaches. Only a few individual fish from tagging groups A and B had home ranges greater than 60 km, and their interactions with other tagging groups were generally rare, temporary, and brief. Alligator Gars tagged within 5 km of the lower boundary of the study area were not observed at sites more than 40 km upstream, and these fish (group D) were the only tagged fish that used Trinity Bay. Lack of movement into the...
river during the prespawn or spawn season by group D suggests that these fish may be spawning in estuarine habitats of Trinity Bay, similar to Alligator Gars that were observed spawning in Louisiana estuaries (A. Ferrara, personal communication). Although our study was limited to a relatively short period in the life cycle of this long-lived fish, these observations suggest that Alligator Gars in the lower Trinity River do not represent a single panmictic population. Further research is needed to determine whether the estuarine and riverine groups are discrete stocks or whether some limited exchange occurs among these groups.

Home range size of Alligator Gars varied across seasons, with movements being influenced by water temperature. During winter, the home ranges of tagged fish were typically short, and detections at SUR stations were rare. Home range size and SUR detections increased during prespawn periods, with detections becoming more frequent as water temperatures exceeded 15°C. Increased movements during prespawn periods may have been...
associated with staging and feeding in preparation for spawning. Kluender (2011) previously reported that during the prespawn season, Alligator Gars began to move away from overwintering sites. Observed use of the tailwater habitat by tagging groups A and B also supports this hypothesis. Peak use of the tailwater occurred during prespawn seasons at a water temperature of 18°C, with most fish dispersing by mid-May when water temperatures approached 25°C. During the prespawn season, large concentrations of clupeids, ictalurids, catostomids, moronids, and sciaenids occur in the tailwater (Texas Parks and Wildlife Department [TPWD], unpublished data), and these fishes are known to be important diet items for Alligator Gars (Bonham 1941; Seidensticker 1988). Similarly, use of the tailwater again in the fall may be related to foraging prior to the movement of fish into overwintering pools.

Movements of tagged Alligator Gars peaked during spawn and postspawn periods, when water temperatures were high. These movement patterns were similar to those observed by Kluender (2011) for Alligator Gars in the Fourche LaFave River, Arkansas, and by Snedden et al. (1999) for Spotted Gar Lepisosteus oculatus in the lower Atracostostus spatula river basin, Louisiana. Increased movements during these seasons were likely associated with (1) migrations to tributary backwaters for spawning (Inebnit 2009) and (2) subsequent dispersal to summer feeding areas in the main channel. Kluender (2011) also noted substantial movements during the postspawning season, with several fish emigrating from the study area and into the Arkansas River.

Main-channel pool macrohabitats were the dominant habitat type used by Alligator Gars, regardless of season. Similar to the results of Inebnit (2009) and Kluender (2011), we found that tagged Alligator Gars showed strong fidelity to specific pools. It is unclear why these pools were used while others were not. Some bias could have existed because fish were captured from many of these same pools; however, untagged Alligator Gars were rarely observed in other pools. Use of specific pool habitats was likely influenced by the adjacent habitats used for feeding or reproduction. Some evidence of nighttime use of adjacent shallow-water habitats was provided by nearby SURs. Increased nighttime detections by these SURs indicate (1) the occurrence of nighttime movements between main-channel pool habitats or (2) the use of these shallow areas, possibly in association with nighttime feeding (Snedden et al. 1999). Because manual tracking was limited to daylight hours, such hypotheses could not be evaluated. Future research should examine nocturnal movements of Alligator Gars to better understand their use of these main-channel habitats.

Relocations of tagged Alligator Gars in floodplain tributary and inundated floodplain habitats primarily occurred during large floods. Previous studies have documented the importance of these habitats for spawning (Brinkman 2008; Inebnit 2009; Kluender 2011) and have noted the use of these areas by juvenile Alligator Gars (Sakaris et al. 2005; Robertson et al. 2008; Inebnit 2009). We suspect that in the lower Trinity River, these areas were also used for spawning. During the May 2009 flood pulse, we collected gar eggs (species unknown) from several backwater and tributary areas. In addition to tagged individuals, untagged Alligator Gars were also seen in these areas, particularly at the mouths of tributaries where water had backed up from the main channel (as opposed to flowing into the main channel). Observations of Alligator Gars using tributaries and inundated floodplains during a large flood pulse in November 2009 suggest that these areas also provided refuge during high flows.

Relatively small home ranges, coupled with limited interactions among tagging groups (other than groups A and B), suggest that management and conservation of Alligator Gars at relatively small spatial scales may be appropriate. If vital rates (i.e., recruitment, mortality, and growth) vary among groups of Alligator Gars, then different harvest regulations (e.g., daily creel, quotas, and seasonal fishing closures) may be needed. Recruitment in particular is likely to vary among estuarine and riverine habitats because of the availability of potential spawning areas. Estuarine spawning likely occurs in shallow, vegetated areas of the tidally influenced river mouth and estuary. As a result, recruitment may be stable from year to year because the availability of these areas does not fluctuate annually. In contrast, tributary backwater habitats that are used for spawning by Alligator Gars in the river (Inebnit 2009) are only available during large flood pulses, which do not occur every year. To sustain existing Alligator Gar fisheries and to best meet management objectives for the Trinity River, future research should evaluate vital rates and assess environmental conditions that result in successful recruitment of fish in both riverine and estuarine habitats.

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Microsatellite Analysis of Population Structure in Alaska Eulachon with Application to Mixed-Stock Analysis

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Microsatellite Analysis of Population Structure in Alaska Eulachon with Application to Mixed-Stock Analysis

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Abstract

Estimation of genetic population structure, diversity, and effective population size ($N_e$) is important for defining meaningful conservation units and assessing genetic health. Recent conservation concerns in Alaska have highlighted the need for research on Eulachon Thaleichthys pacificus, a species about which relatively little is known. Therefore, genetic variation was assayed at 14 microsatellite loci to investigate the genetic population structure of Alaska Eulachon. This analysis revealed a low degree of genetic divergence ($G_{ST} = 0.005$) that is structured by broad-scale northern and southern geographic regions. Overall, there is a significant correlation between genetic and geographic distances, suggesting that gene flow is geographically restricted and follows an isolation-by-distance (IBD) model. However, closer analysis reveals an absence of IBD within regions and that gene flow is primarily restricted by the geographic distance between regions, a pattern that better approximates the hierarchical island model. Gene flow is likely restricted between regions by a biogeographical barrier (i.e., the Alexander Archipelago). Alaska Eulachon have high levels of genetic diversity and relatively large $N_e$ estimates of 3,535 and 2,823 for the northern and southern regions, respectively, although a large variance in reproductive success is likely responsible for a low $N_e/N$ ratio. The observed genetic divergence suggests that it would be advantageous to manage the two regions separately to maintain productivity and evolutionary potential for Eulachon. Mixed-stock analysis (MSA) of simulated and known-origin mixtures supports the feasibility of regional stock separation. The northern and southern regions had MSA accuracies that were near or greater than 90% when fish from a single region comprised the mixtures. Further population structure may be present within regions, but additional analyses of collections across sampling years are necessary to clarify the microevolutionary processes.

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Estimation of genetic population structure, diversity, and effective population size \((N_e)\) is important for defining meaningful conservation units and assessing genetic health. Physical or behavioral barriers can result in intraspecific reproductive isolation, allowing for the accumulation of genetic differences through genetic drift. The diverging effects of genetic drift are constrained by limited time of separation, large gene flow, and large \(N_e\). These factors may be significant for North Pacific marine species due to their potentially recent colonization following the Pleistocene glaciation, the absence of obvious barriers to dispersal, and large census sizes. Detecting genetic divergence in this situation can be difficult even when suggested by differences in life history, morphology, and parasites (Hauser and Carvalho 2008). Whereas morphology and life history differences may represent phenotypic plasticity and not local adaptation, the observation of genetic divergence suggests that there are distinct populations, which must be accounted for in fishery management (Hauser and Carvalho 2008). Long-term sustained yield, ultimately the goal of fishery management, can only be accomplished through conservation of genetic resources to maintain diversity and a population's adaptive potential in the face of a fluctuating environment (Altukhov 1987; Nelson and Soule 1987).

A bundant marine fish populations are often characterized by a low value of \(F_{ST}\) (a measure of genetic divergence) due to the previously stated reasons (DeWoody and Avise 2000; Cano et al. 2008). Hence, significant differences in \(F_{ST}\) among localities strongly indicate the existence of distinct populations (Conover et al. 2006). For example, Atlantic Cod Gadus morhua populations at the head and toe of a fjord exhibited a significant but low \(F_{ST}\) (0.0037; Knutsen et al. 2011), calling into question the biological significance of this value. However, mark-recapture showed that the two populations were completely isolated, demonstrating its relevance.

Management units should be established for populations that exhibit a level of genetic divergence that is consistent with demographic independence (Palsbøll et al. 2007). Demographic independence is inferred at rates of migration less than 10% (Hastings 1993). The level of genetic divergence required to make this inference can be determined from the Wright-Fisher island population model wherein \(F_{ST} = 1/(4N_em + 1)\), where \(m\) is the migration rate per generation (Palsbøll et al. 2007). Once management units are established, fisheries should be managed to ensure effective conservation by harvesting each population in proportion to its size and productivity (Allendorf et al. 1987). This can be difficult when dealing with a mixture of populations, but mixed-stock analysis (MSA) using genotypic frequencies is a proven method for estimating the population composition of fisheries (Cadrin et al. 2005).

Recent conservation concerns have sparked research on Eulachon Thaleichthys pacificus, which are also known as Candlefish due to a high oil content (Payne et al. 1999) that enables a dried fish to burn when lit. Eulachon are an anadromous forage fish from the family Osmeridae, with a geographic distribution from California to the Pribilof Islands in the Bering Sea. They are highly fecund and thought to be semelparous spawners (Moffitt 2002; Spangler et al. 2003). Females broadcast an average of 35,000 eggs, while males simultaneously release milt. Eggs are fertilized in the water column, attach to river substrate, and hatch in 20–40 d. Larvae are immediately flushed to sea where they are dispersed by estuarine and ocean currents. After 3–5 years in the ocean, Eulachon return to rivers to spawn, usually in the lower tidally influenced reaches. The extent to which Eulachon home to their natal spawning sites is unknown (Hay and McCarter 2000). In the Pacific Northwest, their spawning run strength and use of rivers for spawning are variable (Hay and McCarter 2000). This variability has been observed in Alaska as well. For instance, in Behm Canal, the strongest runs of fish have been reported to vary between the Eulachon, Unuk, and Klahini rivers (T. Tisler, U.S. Forest Service [USFS], personal communication). Varying runs of Eulachon are known to occur in adjacent rivers of the Copper River Delta (S. Moffitt, Alaska Department of Fish and Game [ADFG], personal communication), the Yakutat Forelands (D. Gillikin, USFS, personal communication), upper Lynn Canal (R. Bachman, ADFG, personal communication), and Berners Bay (K. Koski, National Oceanic and Atmospheric Administration, personal communication; USFS, unpublished data).

Eulachon have long been an important food resource for humans and other animals (Hay and Boutillier 1999). Historically, Native Americans prized the oil that they rendered from Eulachon, which remained a solid at room temperature. This fat was widely traded through a network of “grease trails” between coastal and inland tribes (Spangler et al. 2003). In the Pacific Northwest, Eulachon were once caught in vast quantities in both subsistence and commercial fisheries, with commercial hauls often exceeding 1,000 metric tons a year from the Columbia River (NOAA 2009). This occurred until the early 1990s when Eulachon abundance collapsed, leading to the listing of the southern distinct population segment (Pacific Northwest) of Eulachon as threatened under the U.S. Endangered Species Act (ESA; NOAA 2010). In Alaska, Eulachon have not been similarly exploited, though they constitute a popular subsistence and personal-use fishery (Spangler et al. 2003; Joyce et al. 2004), and the collapse of Eulachon in the Pacific Northwest has prompted interest in expanding the currently limited commercial fishery in Alaska (Moffitt 2002). An ESA ruling has not been proposed for A laska Eulachon, whose biomass has increased (Ormseth et al. 2008), but the collapse of the Behm Canal Eulachon run (Ormseth et al. 2008; USFS, unpublished data) illustrates that A laska Eulachon are not immune to local perturbations. Though the cause of the Behm Canal crash is not clear (Ormseth et al. 2008), it may be a cyclical pattern of habitat use by Eulachon and not reflective of a stock collapse.

The population structure for Eulachon within and among river systems in Alaska is unknown. Relatively little is known...
FIGURE 1. Sites at which collections of Eulachon were obtained (see Table 1). The northern region is comprised of Cook Inlet, Prince William Sound, and the Yakutat Forelands, the southern region of upper Lynn Canal, Berners Bay, the Stikine Strait, and Behm Canal.

about the life history of Eulachon. This lack of knowledge, combined with the variable spawning run strength and use of rivers for spawning, complicates fishery management. Studies of genetic variation in Rainbow Smelt Osmerus mordax, a closely related Atlantic osmerid, suggest that estuarine isolation is primarily responsible for population structure (Bernatchez and Martin 1996; Bradbury et al. 2008). Initial genetic studies of Eulachon from the Pacific Northwest found little population structure and suggested that Eulachon exist as large populations with low levels of genetic diversity (McLean et al. 1999; McLean and Taylor 2001). However, in a more thorough study from the Pacific Northwest, Beacham et al. (2005) observed that Eulachon exhibited much higher levels of genetic diversity than originally thought and that significant differences occurred among Eulachon from different rivers. These contradictory results raise questions as to whether Eulachon in Alaska are a panmictic population or structured by river or estuary and make it clear that an understanding of Eulachon genetic population structure in Alaska is necessary to identify appropriate management units for the maintenance of biodiversity and productivity. In this study, we investigated the genetic population structure and $N_e$ of Eulachon by assaying the variation at 14 microsatellite loci to evaluate the patterns of genetic diversity within and among 26 collections from seven geographic areas (estuaries) of Eulachon distributed throughout Alaska (Figure 1). We also evaluated the microsatellite variation for its utility with respect to mixed-stock analysis of identified management units. The general hypothesis that we tested is panmixia, or the homogeneity of allele frequencies among collections of Alaska Eulachon. In the absence of panmixia, we hypothesized that genetic variation is structured based on a geographic hierarchy, with gene flow conforming to the isolation-by-distance model (Wright 1943).

METHODS
Sample collection and laboratory analysis.—Tissue samples were collected from adult Eulachon at 26 spawning locations from seven geographic areas in south-central and southeastern Alaska (Table 1; Figure 1). Total genomic DNA was extracted from the tissue (~25 mg) using proteinase K with the Dneasy DNA isolation kit (Qiagen Inc., Valencia, California), quantified by fluorometry, and diluted to 30 ng/µL. Polymerase chain reaction (PCR) DNA amplification was used to assay the genetic variation at the following 14 microsatellite loci that were
TABLE 1. Geographic region of Alaska, area, collection, label, year collected, and number of samples (N) for the Alaska Eulachon in this study (see Figure 1).

<table>
<thead>
<tr>
<th>Region</th>
<th>Area</th>
<th>Collection</th>
<th>Label</th>
<th>Year</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>North</td>
<td>Cook Inlet (CI)</td>
<td>Kenai</td>
<td>1</td>
<td>2004</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Yetna</td>
<td>2</td>
<td>2004</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Susitna</td>
<td>3</td>
<td>2004</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Prince William</td>
<td>38 mile</td>
<td>4</td>
<td>2003</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>Sound (PWS)</td>
<td>Ibeck</td>
<td>5</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Alaganik</td>
<td>6</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Yakutat</td>
<td>Esker</td>
<td>7</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Forelands (YF)</td>
<td>Tawah</td>
<td>8</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lost</td>
<td>9</td>
<td>2003</td>
<td>14</td>
</tr>
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<td></td>
<td></td>
<td>Situk</td>
<td>10</td>
<td>2003</td>
<td>55</td>
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<td></td>
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<td>Seal</td>
<td>11</td>
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<td>55</td>
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<td></td>
<td></td>
<td>Aawkwe</td>
<td>12</td>
<td>2003</td>
<td>55</td>
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<tr>
<td>South</td>
<td>Upper Lynn</td>
<td>Chilkat</td>
<td>13</td>
<td>2003</td>
<td>51</td>
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<tr>
<td></td>
<td>Canal (ULC)</td>
<td>Chilkoot</td>
<td>14</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tiaya</td>
<td>15</td>
<td>2003</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Berners Bay</td>
<td>Skagway</td>
<td>16</td>
<td>2005</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>(BB)</td>
<td>Berners</td>
<td>17</td>
<td>2003</td>
<td>55</td>
</tr>
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<td></td>
<td></td>
<td>Lace</td>
<td>18</td>
<td>2003</td>
<td>55</td>
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<tr>
<td></td>
<td></td>
<td>Antler</td>
<td>19</td>
<td>2003</td>
<td>55</td>
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<tr>
<td></td>
<td>Stikine Strait</td>
<td>Stikine</td>
<td>20</td>
<td>2003</td>
<td>55</td>
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<td></td>
<td>Behm Canal</td>
<td>Eulachon</td>
<td>21</td>
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<td>55</td>
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<tr>
<td></td>
<td>(BC)</td>
<td>Unuk</td>
<td>22</td>
<td>2003</td>
<td>55</td>
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<tr>
<td></td>
<td></td>
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<td>23</td>
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<td>55</td>
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<td>24</td>
<td>2003</td>
<td>55</td>
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<td></td>
<td></td>
<td>Upper Landing</td>
<td>25</td>
<td>2003</td>
<td>55</td>
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<tr>
<td></td>
<td></td>
<td>Side Channel</td>
<td>26</td>
<td>2003</td>
<td>55</td>
</tr>
</tbody>
</table>

developed from Eulachon: Tpa103, Tpa104, Tpa111, Tpa112, Tpa113, Tpa114, Tpa115, Tpa117, Tpa118, Tpa119, Tpa121, Tpa122, Tpa127, and Tpa129 (Kaukinen et al. 2004). The PCR amplicons were electrophoresed and visualized with the Applied Biosystems 3730 Genetic Analyzer utilizing a polymer denaturing capillary system. The sizes of bands were estimated and scored by the computer program GENEMAPPER version 4.0. Applied Biosystems GeneScan-600 LIZ size standards (20–600 base pairs) were loaded with every PCR amplicon to ensure consistency of allele scores. All scores were verified manually. Alleles were scored by two independent researchers, with any discrepancies being resolved by rerunning the samples in question and repeating the double-scoring process until the scores matched. In addition, samples from one eight-well column from each DNA plate were analyzed a second time for the full suite of loci as a quality control measure.

Data analysis.—The collections from the seven geographic areas were also grouped into two regions (northern and southern) for hierarchical analyses, such as likelihood ratios, based on the population structure as depicted by neighbor-joining and principal components analyses. A sequential Bonferroni method was used to maintain the overall value of alpha at 0.05 for simultaneous tests (Rice 1989). Any duplicated genotypes were removed from the data set by the program MICROSEAT LITE TOOLKIT (Park 2001).

Hardy-Weinberg and gametic-phase equilibrium were assessed for the data using the programs FSTAT 2.9.3 (Goudet 1995) and GENETIX 4.05 (Belkhir et al. 2004). Significant tests of disequilibrium ($P < 0.05$) were compared with binomial expectations to determine whether chance alone explained the results (Apostal et al. 1996).

The genetic relationships among the collections were analyzed. A neighbor-joining dendrogram (Saitou and Nei 1987) was produced from chord distances (Cavalli-Sforza and Edwards 1967) calculated among all pairs of collections from allele frequencies using the program PHYLIP 3.57 (Felsenstein 1989), with support for the dendrogram being determined by bootstrapping over the loci 1,000 times. The genetic relationships were also investigated by principal components analysis (PCA) of allele frequencies using the computer program PCA-GEN (Goudet 1999). The significance of inertia for each axis was determined by randomizing genotypes 1,000 times.

To assess whether gene flow was geographically restricted and followed the isolation-by-distance model (IBD), collection pairwise matrices of genetic distance ($F_{ST}$) and geographic distance (km) were analyzed by standard linear regression. Geographic distance was measure along the coastline between collections in ArcGIS 9.2 (ESRI). The significance of the correlation between the two matrices was determined by the Mantel test (Mantel 1967) with 10,000 randomizations using FSTAT 2.9.3.

The homogeneity of allelic frequencies among the collections was analyzed. GENEPOP 4.1 (Raymond and Rousset 1995) was used to conduct tests of allelic frequency homogeneity among all pairs of collections. Hierarchical likelihood ratio tests were conducted to determine the homogeneity of allelic frequencies among collections within areas, among areas, and between regions ($G$-test; Sokal and Rohlf 1995). Alleles with expected overall counts of less than 3 were pooled with adjacent alleles to maintain asymptotic assumptions (Sokal and Rohlf 1995). The magnitude of divergence within and between regions was compared using an approximate $F$-statistic (Smouse and Ward 1978).

The genetic variation resulting from divergence among collections was partitioned hierarchically (Nei and Chesser 1983; Chakraborty and Leimar 1987). Coefficients of gene differentiation ($G_{ST}$ statistics) were calculated to examine the magnitude of divergence among the collections and hierarchical levels. The significance of the $G_{ST}$-statistics was inferred from likelihood ratio tests of allelic frequency homogeneity (Chakraborty and Leimar 1987). The effective number of migrants ($N_{m}$), a measure of gene flow, was estimated from the $G_{ST}$ statistics assuming a hierarchical island model at equilibrium with migration and genetic drift (Zhivotovsky et al. 1994). In addition, $N_{e}$ between regions was estimated using MIGRATE 3.0 (Beerli and Felsenstein 2001; Beerli 2006), as
mixed-stock analysis of simulated and known-origin mixtures was conducted for the regions to determine whether the observed genetic divergence was sufficient for apportioning fishery mixtures. The program ONCOR (Kalinowski et al. 2007) was used to conduct simulations with regional mixture proportions varying from 0% to 100% at 25% increments. The size of the simulated mixtures was set to 400 fish, and 1,000 simulations were performed for each mixture scenario. The stock compositions of the simulated mixtures were estimated by ONCOR using conditional maximum likelihood (CML).

For the known-origin mixture analysis, samples were randomly removed from the regions and used as a mixture independent of the baseline. The known-origin mixtures were assembled to range in regional proportions from 0% to 100% at 25% increments. The sample size for each known-origin mixture was 200. The stock compositions of the mixtures were estimated by Bayesian and CML mixture modeling using the programs cBAYES (Neaves et al. 2005) and SPAM 3.7b (Debevec et al. 2000). The variance of the Bayesian estimates was estimated from nine Markov chain–Monte Carlo simulations, which were iteratively sampled 30,000 times each. The variance for the CML estimates was estimated by bootstrapping the baseline and mixture 1,000 times.

The genetic diversity for the loci and collections was estimated by calculating allelic richness, percentage polymorphic loci (95%), observed and expected heterozygosity, and gene differentiation (GST) with FSTAT 2.9.3 and GENETIX 4.05. Estimates of the effective number of alleles (Hartl and Clark 1997) were made in Microsoft Excel. A Mann–Whitney test (Zar 1984) was used to test for significant differences (P < 0.05) in the observed levels of genetic diversity between regions. Significant genetic divergence was observed in 59 of the 325 collection pairwise tests of allelic frequency homogeneity. The pairwise FST estimates for the significant tests ranged from 0.004 to 0.017 (see Table A.1 in the appendix). Only one of the significant pairwise tests was within regions, namely, that between Skagway and upper Landing Slough. The hierarchical analysis of allelic frequency homogeneity revealed highly significant genetic divergence between regions, but genetic divergence within regions was limited (Table 2). No genetic divergence was observed among collections within areas or among areas within regions (Table 2). However, overall accumulative effects resulted in significant genetic divergence for the following hierarchical levels: within southern areas, the total northern region, and the total within regions (Table 2). The level of genetic divergence between regions was four times as great as that within regions (F_{18,432} = 4.2, P < 0.05). The northern and southern regions did not exhibit different levels of genetic divergence (F_{198,234} = 1.1, P > 0.05).

Partitioning the genetic variation into hierarchical components revealed that 99.5% of the genetic variation was present in each collection. Variation among collections accounted for 0.5% (GST = 0.005) of the total, which, though low, was significant (P < 0.05). Variation between regions was significant (P < 0.05) as well and accounted for 0.24% (GST = 0.0024) of the genetic variation among collections. However, variation among areas within regions and among collections within areas...
FIGURE 2. Neighbor-joining dendrogram of Cavalli-Sforza and Edwards (1967) chord distances calculated from the allele frequencies at 12 loci. Percent bootstrap values (1,000 iterations) are shown for nodes that clustered together at least 50% of the time. The northern and southern regions are delineated by the dashed line. The collections from Susitna, Yetna, and Kenai are from Cook Inlet.

FIGURE 3. Principal components analysis of allele frequencies at 12 microsatellite loci. See Table 1 for collection names. [Figure available online in color.]
TABLE 2. Hierarchical tests of homogeneity of allele frequencies for Alaska Eulachon based on 12 loci. Abbreviations for the areas within the regions are as follows: CI = Cook Inlet, PWS = Prince William Sound, YF = Yakutat Forelands, ULC = upper Lynn Canal, BB = Berners Bay, SS = Stikine Strait, and BC = Behm Canal (BC). Asterisks indicate significance at \( P < 0.05 \).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>G-test</th>
</tr>
</thead>
<tbody>
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<td>36</td>
<td>40.0</td>
</tr>
<tr>
<td>PWS</td>
<td>36</td>
<td>43.6</td>
</tr>
<tr>
<td>YF</td>
<td>90</td>
<td>117.7</td>
</tr>
<tr>
<td>Within northern areas</td>
<td>162</td>
<td>201.3</td>
</tr>
<tr>
<td>Among northern areas</td>
<td>36</td>
<td>61.5</td>
</tr>
<tr>
<td>Total northern region</td>
<td>198</td>
<td>262.8*</td>
</tr>
<tr>
<td>Southern region ULC</td>
<td>54</td>
<td>73.0</td>
</tr>
<tr>
<td>BB</td>
<td>36</td>
<td>41.3</td>
</tr>
<tr>
<td>SS</td>
<td>No test</td>
<td></td>
</tr>
<tr>
<td>BC</td>
<td>90</td>
<td>122.8</td>
</tr>
<tr>
<td>Within southern areas</td>
<td>180</td>
<td>237.0*</td>
</tr>
<tr>
<td>Among southern areas</td>
<td>54</td>
<td>49.4</td>
</tr>
<tr>
<td>Total southern region</td>
<td>234</td>
<td>286.5</td>
</tr>
<tr>
<td>Total within regions</td>
<td>432</td>
<td>549.2*</td>
</tr>
<tr>
<td>Between regions</td>
<td>18</td>
<td>97.0*</td>
</tr>
<tr>
<td>Total</td>
<td>450</td>
<td>646.2*</td>
</tr>
</tbody>
</table>

TABLE 3. Mixed-stock analysis of simulated mixtures using conditional maximum likelihood. Simulations were conducted for regional proportions varying from 0% to 100% of the mixture in 25% increments. The size of the simulated mixtures was set to 400 fish and the number of simulations to 1,000.

<table>
<thead>
<tr>
<th>Expected</th>
<th>North</th>
<th>South</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SD</td>
</tr>
<tr>
<td>0.00</td>
<td>0.09</td>
<td>0.02</td>
</tr>
<tr>
<td>0.25</td>
<td>0.30</td>
<td>0.04</td>
</tr>
<tr>
<td>0.50</td>
<td>0.48</td>
<td>0.03</td>
</tr>
<tr>
<td>0.75</td>
<td>0.68</td>
<td>0.03</td>
</tr>
<tr>
<td>1.00</td>
<td>0.88</td>
<td>0.02</td>
</tr>
</tbody>
</table>

TABLE 4. Known-origin mixture analysis using conditional maximum likelihood (SPAM) and Bayesian (cBAYES) mixture modeling.

<table>
<thead>
<tr>
<th>Expected</th>
<th>North (SPAM)</th>
<th>North (cBAYES)</th>
<th>South (SPAM)</th>
<th>South (cBAYES)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SD</td>
<td>Estimate</td>
<td>SD</td>
</tr>
<tr>
<td>0.00</td>
<td>0.10</td>
<td>0.05</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>0.25</td>
<td>0.26</td>
<td>0.05</td>
<td>0.21</td>
<td>0.06</td>
</tr>
<tr>
<td>0.50</td>
<td>0.43</td>
<td>0.05</td>
<td>0.43</td>
<td>0.06</td>
</tr>
<tr>
<td>0.75</td>
<td>0.72</td>
<td>0.05</td>
<td>0.81</td>
<td>0.06</td>
</tr>
<tr>
<td>1.00</td>
<td>0.85</td>
<td>0.05</td>
<td>0.98</td>
<td>0.03</td>
</tr>
</tbody>
</table>
heterozygosity, and 0.694–0.793 for observed heterozygosity (Table 6). All loci were polymorphic at the 95% criterion. Collections from the southern region had significantly higher levels of allelic richness and expected heterozygosity, but there were no significant differences between the regions for effective number of alleles and observed heterozygosity (Table 6).

Contemporary estimates of \( N_e \) were 3,525 (95% confidence interval, 2,578–5,498) for the northern region and 2,823 (2,392–3,427) for the southern region. The estimated values of \( \phi \) were 0.0983 for the northern region and 0.0984 for the southern region. Long-term estimates of \( N_e \) were 24.6, 245.8, and 2,457.5 for the northern region and 24.6, 246.0, and 2,460.0 for the southern region using probable mutation rates ranging from \( 10^{-6} \) to \( 10^{-3} \). The range in long-term \( N_e \) estimates reveals the sensitivity to the mutation rate, which is unknown, so these estimates should be treated with caution.

**DISCUSSION**

In Alaska, Eulachon exhibit a low degree (\( G_{ST} = 0.005 \)) of broad-scale, regionally based population structure. This structure is largely explained by two regional groups, with collections from the Yakutat Forelands, Prince William Sound, and Cook Inlet areas forming a northern region and collections from upper Lynn Canal, Berners Bay, the Stikine Strait, and Behm Canal areas forming a southern region. The lack of conformance to the IBD model over the entire geographic range indicates that gene flow is better explained by an alternative model. There is a barrier to gene flow between regions, but no known impediment exists within regions. This pattern of gene flow better approximates the hierarchical island model (Slatkin and Voelm 1991). The counterclockwise Alaska gyre may facilitate larval dispersal from the Yakutat Forelands toward Prince William Sound and Cook Inlet and therefore promote gene flow among these three areas. In contrast, the Alexander Archipelago likely shelters Southeast Alaska Eulachon from oceanic currents, restricting gene flow between regions and allowing for the development of regional genetic divergence.

Based on the estimates of \( N_e \), the \( F_{ST} \) threshold for a 10% migration rate is \( 3 \times 10^{-7} \), which is the point where populations are considered to be demographically isolated and constitute separate management units (Palsbøll et al. 2007). The estimates of \( F_{ST} \) (0.005) and \( F_{RT} \) (0.002) from this study are considerably larger than the threshold, which illustrates the regional distinctiveness. The estimates of \( N_{m} \) between regions (26–41 migrants per generation) would not replenish a depressed population on an ecological or manager’s time frame (Waples 1998). Although it is difficult to estimate migration (e.g., Whitlock and McCauley 1999), it may be advantageous to manage the two regions separately to prevent differential harvest and the subsequent erosion...
of genetic diversity and structure, which are required for long-term sustainability and productivity (Allendorf et al. 1987). The MSA of simulated and known-origin mixtures supports the feasibility of regional stock separation, as the estimates are close to expected values and the accuracies are near or exceed 90% for mixtures comprised of fish from a single region, an indication that the regions are identifiable in actual fishery mixtures (Seeb and Crane 1999).

These results agree and contrast with observations of genetic variation that are primarily from Pacific Northwest Eulachon (McLean et al. 1999; McLean and Taylor 2001; Beacham et al. 2005). The present and previous studies of genetic variation in Eulachon rejected the hypothesis of panmixia (McLean et al. 1999; McLean and Taylor 2001; Beacham et al. 2005). Regional structure was observed by Beacham et al. (2005) and in the present study, but only Beacham et al. (2005) observed fine-scale genetic population structure (e.g., divergence among collections within a river or among collections from geographically adjacent rivers). The observed genetic variation suggested that gene flow generally conformed to the IBD model (McLean et al. 1999; Beacham et al. 2005). However, closer inspection by the present study revealed that IBD was not realized over the full range of geographic distances for Alaska Eulachon. Moreover, while differing mutational rates of loci do not allow for direct comparisons of $F_{ST}$ or analogs (Olsen et al. 2004), the present study and Beacham et al. (2005) used the same suite of loci and derived identical estimates of $F_{ST}$ (0.005) for Eulachon from Alaska and the Pacific Northwest.

There are a number of possible reasons (which might act separately or in combination) for the observation of fine-scale population structure in Eulachon from the Pacific Northwest (Beacham et al. 2005) and the absence of such structure in Eulachon from Alaska. Eulachon likely survived Pleistocene glaciations in the Pacific refuge of which the Columbia River was the major freshwater habitat (McPhail and Lindsey 1970). Eulachon are not believed to have resided in the Bering Sea refuge due to their absence in Russia and the Far East (McPhail and Lindsey 1986). An mtDNA study supports the concept of a single Pacific refuge for Eulachon (McLean et al. 1999), and the shallow mtDNA genealogy indicates a recent age for the extant populations (Aman 2004). Following deglaciation, Eulachon likely underwent a northward range expansion, re-colonizing newly available freshwater habitat. The absence of a latitudinal trend in Eulachon genetic diversity suggests that founder effects were not experienced during this range expansion. A large $N_e$ may have prevented founder effects; only 30 founders are required to maintain 98% of heterozygosity and have a 95% likelihood of capturing alleles with a frequency of 0.05 or greater (Frankham et al. 2002). The potential similarity (depending on the mutation rate) of the long-term and contemporary estimates of $N_e$ further suggests that a bottleneck was not experienced at founding. Therefore, insufficient time of separation (vis-à-vis the older southern populations) may explain the lack of divergence among Alaska Eulachon collections within a region. This is suggested by the lack of migration-drift equilibrium within the regions, although the significant within-region G-tests and clustering of Cook Inlet collections may indicate emerging population structure. A burgeoning or perhaps primarily responsible for this dearth of divergence could be higher rates of gene flow. Longer pelagic larval durations, which would facilitate dispersal and gene flow, are noted for northern-latitude fish (Hauser and Carvalho 2008) and have been shown to decrease genetic divergence (Taylor 2004). Alternatively, non-random sampling due to reproductive variance (the sweepstakes effect) and statistical power may contribute to the perceived discrepancy. Allele frequencies can vary among cohort and location by random chance through the sweepstakes effect (Hedgecock 1994), resulting in genetic divergence that is not geographically influenced. With large sample sizes, even small deviations from random sampling can lead to significant results (Waples 1998). A lack of temporal stability was observed in the Beacham et al. (2005) study, which is supportive of a possible sweepstakes effect; however, regional divergence was three to six times greater than the divergence among sampling years, which is indicative of a stable regional structure. Lastly, the difference could simply be a matter of sample size. The two studies had the same estimate of $F_{ST}$, but Beacham et al. (2005) analyzed a larger sample for each collection, which would increase the statistical power of tests and ability to discriminate among populations. Clearly, further genetic analyses of collections across sampling years are required to vet the presence or absence of fine-scale population structure in Eulachon that is both temporally stable and geographically based.

In general, Eulachon appear to be less influenced by genetic drift than by gene flow. Such a relationship is not unexpected for a species whose larvae have a limited freshwater existence and inadequately developed nervous systems compared with those of Pacific salmon Oncorhynchus spp. (Hay and McCarter 2000). This implies that imprinting to their natal rivers is not strong and that homing is imprecise. Lack of freshwater imprinting has led to greater straying rates in Pink Salmon O. gorbuscha than in Sockeye Salmon O. nerka (Quinn 1984). Evidence of homing imprecision is seen in the great variability of Eulachon abundance and use of specific rivers for spawning.

Our analysis of Eulachon genetic variation in Alaska revealed that genetic diversity is high and similar among the collections and regions. Although the southern region has significantly higher levels of expected heterozygosity and allelic richness, the differences are slight and other measures of genetic diversity do not support a latitudinal trend, which agrees with the observations by McLean and Taylor (2001). The observed levels of genetic diversity are similar to those reported by Beacham et al. (2005) and further confirm that Eulachon are not depauperate in microsatellite genetic diversity, as suggested by McLean and Taylor (2001). Mutation rates can vary widely among loci (Olsen et al. 2003); therefore, the dearth of microsatellite genetic diversity observed by McLean and Taylor (2001) is likely specific to those loci (as
they postulate) and not indicative of the species, especially in light of the high levels of mtDNA genetic diversity observed in Eulachon (McLean et al. 1999). Because it is haploid and maternally inherited, mtDNA has an \( N_e \) that is one-fourth that of the nuclear genome, which makes it more vulnerable to loss of genetic diversity. The high levels of observed microsatellite genetic diversity from this study and Beacham et al. (2005) concur with mtDNA results from McLean et al. (1999), indicating that Eulachon harbor sufficient genetic diversity to maintain evolutionary potential (Frankham et al. 2002).

The genetic health of a population can also be measured by estimating \( N_e \), which is the population size that corresponds to the rate at which genetic diversity is lost and is usually much less than census size (\( N \)). Populations are considered at risk of short- and long-term loss of genetic diversity if their \( N_e \) is below 50 and 500, respectively (Hallerman 2003a). The northern and southern regions both exceed these critical \( N_e \) values for the loss of genetic diversity. However, the \( N_e \) estimates are not high compared with the theoretical (0.5; Nunney 1993) and empirical (0.11; Frankham 1995) expectations of \( N_e/N \) ratios. While there is little data on census size for Eulachon in Alaska, the abundance in the Copper River (which is based on total biomass and mean weight per fish) ranges from 43 million to 150 million fish (Moffitt et al. 2002). This number alone puts the \( N_e/N \) ratio at approximately 10−5, which is quite low, but a growing body of literature suggests that this value is comparable and not unusual for marine species that have high fecundity and high mortality (Hauser and Carvalho 2008).

Likely reasons for the low \( N_e/N \) ratio include fluctuating population size, hierarchical population structure, unequal sex ratio, and variance in reproductive success among individuals and locations (Nunney 1999; Hallerman 2003b). Fluctuating population size has a greater effect on long-term \( N_e \) (Hauser and Carvalho 2008) and therefore is an unlikely cause for the low \( N_e/N \) ratio, which is based on the contemporary estimate of \( N_e \). Furthermore, the recent population fluctuations that have occurred in Behm Canal Eulachon would only reduce \( N_e \) moderately (Aason 2004). Inbreeding due to hierarchical population structure can reduce \( N_e \), but an analysis of the \( G_{ST} \) values in an island-structured metapopulation model indicates that its effect is negligible (Nunney 1999). Unequal sex ratios may play a role; the mean annual percentage of Eulachon males was 67% from 1998 to 2002 in the Copper River and was significantly different from 1:1 in all 4 years (Moffitt et al. 2002). In another river from the northern region, sex ratios were also skewed toward males (2:1; Spangler et al. 2003), but this moderate inequality of sex ratios alone cannot explain the low \( N_e/N \) ratio (Hallerman 2003b). Thus, the driving influence may be a large variance in reproductive success among individuals and locations (Turner et al. 2002; Hallerman 2003b; Aason 2004). Eulachon must spawn at times that coincide with optimal river and ocean conditions for successful reproduction and recruitment. Variable environmental conditions are known to strongly affect recruitment in estuarine-dependent species, leading to large reproductive variances and low \( N_e/N \) ratios (Turner et al. 2002; Hallerman 2003b).

In summary, despite the indications of high gene flow, a degree of reproductive isolation for the two regions is supported by the observed genetic divergence. Thus, managing the two regions separately may be worth considering. Further population structure may be present within regions, but additional analyses of collections across sampling years are necessary to clarify the microevolutionary processes.

ACKNOWLEDGMENTS

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REFERENCES


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0.011 0.002 0.000
0.001 0.003 0.008 0.000

23

TABLE A.1. Collection pairwise F ST estimates for Alaska Eulachon. Estimates in bold italics are significantly different from zero (P < 0.05), as determined by tests of allele frequency homogeneity.
See Table 1 for collection names.

APPENDIX: PAIRWISE F ST ESTIMATES

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Site Fidelity and Movement of Etheostoma fonticola with Implications to Endangered Species Management

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PLEASE SCROLL DOWN FOR ARTICLE
Site Fidelity and Movement of *Etheostoma fonticola* with Implications to Endangered Species Management

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Abstract

We quantified site fidelity, directionality and magnitude of movement, and factors associated with movement of the endangered Fountain Darter *Etheostoma fonticola*, a narrowly distributed (<11 km of stream habitat) and small etheostomid, within a 200-m section of a spring-fed river on the Edwards Plateau of south-central Texas. *Etheostoma fonticola* exhibited high site fidelity, moving on average (± 1 SD) 10 ± 17 m during a 1-year period. Site fidelity was most notable in areas with low-growing aquatic vegetation (i.e., algae or *Ricca fluitans*). Movement was most often towards areas with low-growing aquatic vegetation (69%), more frequently in an upstream direction (81%), and among larger fish (> 30 mm TL). Maximum distance moved was 95 m within 26 d. Movement of *E. fonticola* was consistent with movement of narrowly distributed and slackwater etheostomids as well as widely distributed, swift-water etheostomids. As such, movement potential and maximum movement do not satisfactorily explain why some darters are more widely distributed than others. Collectively, etheostomids conform to the theory of restricted movements among resident stream fishes, but movement of large distances occurs and is probably necessary, even among species with high site fidelity.

Instream movement of small-bodied, freshwater fishes enables species persistence in lotic systems under a variety of environmental conditions (Meffe 1984), maintenance of genetic connectivity and life history requirements (Hall et al. 1991; Johnston 2000; Hutchings and Gerber 2002), and recolonization of areas after episodes of spates or dewatering (Labbe and Fausch 2000). However, under a range of average hydrological conditions, small-bodied fishes are relatively sedentary and move <50 m (Gerking 1953). The restricted-movement paradigm (Gerking 1959; Gowan et al. 1994) describes the general pattern of limited instream movement and is supported for several species, including cyprinids (Johnston 2000; Belica and

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Etheostoma (Page 1983), cottids (Brown and Downhower 1982; Knaepkens et al. 2004; Petty and Grossman 2004; Hudy and Shiflet 2009), centrarchids (Gerking 1953), and percids (Freeman 1995; Roberts and Angermeier 2007). Recent studies expand the restricted-movement paradigm to include heterogeneity in movement by small proportions of conspecifics within high site fidelity populations, and although it is not known whether these individuals are genetically predisposed to movement or stimulated by environmental triggers, they are probably essential to population persistence (Smithson and Johnston 1999; Skalski and Gilliam 2000; Roberts et al. 2008; Breen et al. 2009).

Restricted movement, small body sizes, and long-term environmental stability are interrelated with high rates of species diversification in North America, especially among the family Percidae (Smith 1981). In central and eastern North America, darter (genera Percina, Ammocrypta, and Etheostoma) richness is highest in unglaciated drainages of the Mississippi River drainage (N = 87), Gulf Slope drainages (N = 48), and Atlantic drainages (N = 28) (Page 1983). With small body sizes and restricted movements, percentages of darters endemic to a drainage range from 44% in the Gulf Slope drainages to 64% in the Atlantic drainages. Restricted movements and narrow distributional ranges make these taxa susceptible to anthropogenic alterations. Currently, 44% of percids are considered imperiled (Jelks et al. 2008). Therefore, greater understanding of the quantification of darter movement is needed not only to assess anthropogenic effects on populations (i.e., habitat degradation, instream flow alterations, instream barriers, and fragmentation) for conservation measures but also to support the premise that small body fishes, such as the darters, conform to the restricted-movement paradigm.

Etheostoma, the smallest in TL and the most derived genera of darters, inhabit small to large sloughs, creeks, and rivers in slackwater to swift-flowing mesohabitats (Ultsch et al. 1978). Site fidelity among etheostomids is high, with 80–97% of individuals remaining within the habitat patch of initial capture during a period of up to 1 year (Mundahl and Ingersoll 1983; Boschung and Nieland 1986; Labbe and Fauch 2000; Roberts and Angermeier 2007). Mean distance moved is <200 m (M undahl and Ingersoll 1983; Roberts and Angermeier 2007), and maximum distance traveled is up to 3 km (Boschung and Nieland 1986). Direction of movement is biased towards upstream (M undahl and Ingersoll 1983; Labbe and Fauch 2000; Roberts and Angermeier 2007) at times by older fish (Labbe and Fauch 2000) and other times by younger fish (Roberts and Angermeier 2007). Factors associated with movement are speculative, but instream movement generally occurs more often during nonreproductive periods (Scalet 1973; Mundahl and Ingersoll 1983), ontogenetic shifts in habitat associations (Labbe and Fauch 2000), and times of declining habitat quality (M undahl and Ingersoll 1983; Roberts and Angermeier 2007). A mong published studies, no discernible pattern in site fidelity or movement has been noted between narrowly distributed Etheostoma (E. boschungi, E. cragini, E. podostemone) and widely distributed Etheostoma (i.e., E. flabellare, E. nigrum) or between swift-water and riffle-associated species (E. flabellare, E. podostemone) and slackwater-associated species (E. boschungi, E. cragini, E. nigrum).

The Fountain Darter E. fonticola, a U.S. federally listed endangered species, is endemic to the Guadalupe River basin of central Texas and is currently restricted to two populations in a total of 11 km of stream habitat (Schenck and Whiteside 1976). Considered the smallest species of Etheostoma (Page 1983), E. fonticola persist in high-volume spring outflows and headwater reaches of the Comal River (1928–2011 daily discharge: mean, 8.8 m3/s; range, 0.2–620 m3/s; U.S. Geological Survey [USGS] station 08169000) and the San Marcos River (1994–2011 daily discharge: mean, 5.6 m3/s; range, 2.4–175 m3/s; USGS station 08170500). Instream habitat is fragmented by low-head dams or culverts. As it is the smallest darter and is a representative of the narrowly distributed Etheostoma genus, we predicted that E. fonticola would be highly sedentary with limited instream movement. Furthermore, we predicted that the E. fonticola would be sedentary year round, because it is one of the few North American fishes to spawn year round (Schenck and Whiteside 1977). When movement does occur, it is biased towards upstream. Specific objectives of this study were to assess level of site fidelity, quantify directionality and magnitude of movement, and correlate biotic and abiotic factors associated with movement of E. fonticola within a section of the Comal River. Implications of this study will inform various aspects of endangered species and habitat management within the Comal and San Marcos rivers, including assessing potential effects of instream recreation, dredging, instream barriers, and water quantity alterations on E. fonticola populations. In addition, site fidelity and movement information for a narrowly distributed Etheostoma will provide further opportunity to assess relationships between instream movement and distributional ranges of small-bodied Etheostoma.

METHODS

The headwaters of the Comal River are located in central Texas along the Balcones Fault Zone of the Edwards Plateau in a highly urbanized watershed. As with many Edwards Plateau rivers, base flow is supported by groundwater discharge from the Edwards Aquifer (Comal Springs) and has constant chemical and physical environmental conditions year round (Groeger et al. 1997). Instream damming regulates stream discharge and creates Landa Lake at the headwaters of the Comal River. Discharge from this impoundment enters either the old (former river channel) or new channel (constructed channel) through a head gate. The 2.5-km-old channel is the less anthropogenically altered section of the Comal River; stream width ranges from 10 to 15 m and maximum depth is 1.5 m. Site fidelity and movement were assessed in a 200-m reach of the old channel (29° 42' 39.66" W, 98° 07' 40.52" N) within a 1.5-km section of the old channel bounded on each end by road crossings with concrete culverts. Therefore, Fountain Darter movements are restricted to a 1.5-km section of stream.
The old channel reach of the Comal River was selected because the area supports little recreational activity and contains several vegetation types and a single geomorphic unit (run), which is typical of the E. fonticola habitat within the Comal and San Marcos rivers. Mark-recapture methods were used to evaluate site fidelity and movement. The 200-m reach was divided into three sections: a 100-m core section for marking and searching, and 50-m upper and lower sections for searching only. Dominant and subdominant aquatic vegetation were quantified in the area before the start of the study. A quatic vegetation types were Hygrophila polysperma and Ludwigia repens (combined as one vegetation type based on similar growth forms and referred to as H. polysperma herein), Riccia fluitans, and filamentous algae Rhizoclonium. Hygrophila polysperma is a rooted macrophyte that extends through the water column, whereas R. fluitans and filamentous algae growth extends only a few centimeters above the substrate.

When available, four replicates (20 m²) of each vegetation type (H. polysperma, R. fluitans, filamentous algae, and mixed stands [H. polysperma with R. fluitans]) were selected in the 100-m core reach for sampling, and two replicates of each vegetation type were selected and sampled in the 50-m upstream and downstream reaches. Replicates were randomly selected at the beginning of the study if more than four replicates were available. Nonvegetated areas were not selected as replicates, because E. fonticola infrequently occurs in habitats lacking vegetation (Schenck and Whiteside 1976; Linam 1993). The midpoint of each replicate was established through GIS methods using a Trimble GeoXT (Trimble, Sunnyvale, California) to maintain a permanent record of replicate locations and obtain distances between pairs of replicates. Replicates were subdivided into multiple 5-m² quadrats. Each quadrat was sampled once with a drop net (2-m² frame with 1-mm mesh extending throughout the water column) for a maximum of four drop nets (8 m²) sampled in a 20-m² replicate. Replicates were consistently placed in the study reach, whereas quadrats within a replicate were randomly selected during each sampling event. The area covered by drop net was repeatedly swept with dip nets until no additional darters were captured after three successive attempts. At each quadrat, depth (cm), instantaneous flow (cm/s), pH, water temperature (°C) and dissolved oxygen (mg/L) were measured.

From August 2008 to June 2009, nine field collections were made among three seasonal units (summer–fall: August–October, winter: December–February, spring–summer: April–June). During the final sampling event, a seine survey was completed within the remaining 1.5-km section of the old channel to document darters that might have dispersed outside of the 200-m reach. For all collections excluding the final sampling event, E. fonticola were anesthetized in a 60-mg/L solution of tricaine methanesulfonate (Finquel, Argent Chemical Laboratories, Redmond, Washington). Ethoestoma fonticola were sexed and TL (mm) was measured. Darters > 20 mm TL were marked with a unique batch mark to indicate time and location (replicate) of collection. Fish were marked with visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington) using a 0.3-cm³ insulin syringe with a 29-gauge needle. The VIE mark has high retention in this species and the method has no observed effects on survival and growth in a laboratory study (Phillips and Fries 2009). To reduce potential stress on individual fish, only experienced personnel were used to mark wild fish in the field. To uniquely identify each batch of darters, the VIE mark was placed according to a combination of location on the fish and VIE color. Two marks were injected into each fish into two of five body locations (proximal base of left and right anterior dorsal fin, left and right ventral muscle tissue, and caudal peduncle) and with one or two of four possible color combinations. Darters were held in fresh river water until they recovered from the anesthetic and then were released in the sampling replicate from where they were captured.

Movement was measured as the distance (in meters) between midpoints of replicates where the darter was initially captured and the replicate where the darter was later recaptured. Individuals recaptured in the same replicate as the initial capture were classified as nonmovers and assigned a movement distance of 0 m. To assess directional bias in movement, upstream movements were assigned positive values, whereas downstream movements were assigned negative values. Mean distance moved was calculated for all fish with respect to direction of movement with and without nonmovers. To assess site fidelity, mean distance moved by recaptured fish was determined as the absolute value of distance moved (1) for all fish, (2) only fish classified as movers, and (3) with respect to direction including nonmovers.

Fidelity to the site of initial capture was assessed by comparing the mean distance moved by recaptured fish with the mean observable distance. Mean observable distance was defined as the mean distance between all pairs of replicates in the core 100-m section. One criticism of mark–recapture studies is that bias is introduced to the analysis by a study design in which shorter movement distances are sampled with greater frequency than longer distances (Albanese et al. 2003). This was evident in this study where 23% of pairs of sampling replicates were <10 m distant, whereas only 3% were >90 m. Therefore, randomization tests were used to compare the mean of the distribution of observable movement distances with the mean of the distribution of distances moved by recaptured fish. By considering only the frequency of observable distances, the bias introduced through study design was compensated in the analysis (Roberts et al. 2008).

All statistical tests were analyzed with the program R (version 2.9.1; R Development Core Team 2005). Estimate of directional bias in movement was assessed through a t-test of a single mean (Turchin 1998). Chi-square goodness of fit was used to test for differences in effort among vegetation types, vegetation type of initial capture and recapture, and sex ratio.

Logistic regression and corresponding Z-tests were used to identify factors associated with movement. Independent variables season, sex, body size (TL), and time elapsed between marking and recapture were examined. The dependent variable

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for all models was the probability of an individual leaving the patch of initial capture. Models for comparison were built by combining the four independent variables and a null model for a total of 16 candidate models. A kaike’s information criterion corrected for small sample size (AICc) was used to evaluate models. Difference in AICc (ΔAICc) values was used as a measure of support for each model relative to the best model from the available data. Models with a ΔAICc < 2 are considered to have substantial support, whereas models with a ΔAICc > 7 are generally thought to have very little support and models have essentially no support when ΔAICc > 10 (Burnham and Anderson 2002). The model with the minimum AICc was interpreted for the influence of independent variables, which appeared in this model as the probability of an individual leaving the replicate of initial capture.

RESULTS

A total of 434 quadrats were sampled in the available habitats. Riccia fluitans and H. polysperma were the most commonly sampled (28% each), followed by mixed stands (24%), and algae (21%). Availability of each vegetation type varied by season (ranges: 25–31% for H. polysperma, 26–30% for R. fluitans, 22–28% for mixed stands, and 15–24% for algae) and less algae and R. fluitans were available in winter and spring–summer, but effort among vegetation types did not differ (across seasons: $\chi^2_3 = 7.0, P = 0.07$; within seasons: $\chi^2_{11} = 12.8, P = 0.31$). Variation in available habitat within the study reach was consistent with typical seasonal trends in vegetation. Water depth was 77 ± 28 cm (mean ± SD) among habitats and ranged from 51 ± 24 cm in algal habitats to 102 ± 20 cm in R. fluitans habitats. Current velocity was 7 ± 6 cm/s and ranged from 3 ± 2 cm/s in algal habitats to 12 ± 7 cm/s in H. polysperma habitats. Otherwise, abiotic conditions (i.e., dissolved oxygen, pH, and water temperature) varied little among habitats and through time. Water temperature was 23.5°C ± 1.3°C, pH was 7.2 ± 0.2, and dissolved oxygen content was 8.3 ± 1.8 mg/L.

A total of 1,103 E. fonticola were captured and released. An additional 150 fish (lengths not taken; no marked fish found) were captured with seines within the remaining 1.5-km section during the final sampling event. Among the 1,103 captured with drop nets, 56 fish were captured during the final sampling event, measured, and their sex determined, but they were not marked. Etheostoma fonticola ≤ 20 mm TL (N = 105) were released without marking: 68% were captured during spring–summer, 31% were captured in summer–fall, and 1% was captured in winter. Etheostoma fonticola > 20 mm in TL (N = 942) were captured, marked, and released from all vegetation types. Mortality due to anesthesia, handling, and marking prior to recovery was <1% (N = 7). Length of darters > 20 mm TL was 29 ± 3 mm (mean ± SD; N = 998). Sex ratio did not differ ($\chi^2_1 = 0.02, P = 0.49$) from 1:1. The highest percentages of E. fonticola marked were captured and released in R. fluitans (44%) and algae (39%), followed by mixed stands (13%), and H. polysperma (4%). Etheostoma fonticola density was 1.3 ± 0.9 fish/m² and ranged from 0.3 ± 0.1 fish/m² in H. polysperma to 2.2 ± 1.0 fish/m² in algae.

Among the 942 marked E. fonticola, 8.7% (N = 82) were recaptured with the highest percentages collected in algae (52%) and R. fluitans (32%), followed by mixed stands (15%), and H. polysperma (1%). Proportions of darters captured in each vegetation type differed between initial capture and recapture events when pooled across season ($\chi^2_3 = 11.7, P < 0.01$) but did not differ within season ($\chi^2_9 = 14.9, P = 0.09$). Among recaptured darters, 49% (N = 40) were nonmovers, all of which were initially captured and recaptured in algae or R. fluitans. Of all recaptured darters 51% (N = 42) moved from the site of initial capture. Ten individuals moved from algae or R. fluitans to another replicate of algae or R. fluitans. Thirty-two individuals moved into a vegetation type different from that where they were initially captured; 50% moved into algae, 34% into mixed stands, 13% moving into R. fluitans, and 3% into H. polysperma.

Distance of recaptured E. fonticola movement (N = 82), incorporating the direction of movement, was 6 ± 19 m (mean ± SD) upstream and 12 ± 25 m upstream when nonmovers were excluded. Movement was biased in an upstream direction (t = 2.90, df = 81, P < 0.01) with 81% of darters classified as movers directed upstream (Figure 1). Independent of direction, distance of E. fonticola movement was 10 ± 17 m for all recaptured fish or 20 ± 18 m when nonmovers were excluded. The maximum distance moved by an individual was 95 m over a 26-d interval. Distances of E. fonticola movement among all fish, movers only, and upstream or downstream movers were less than the mean observable movement. Observable movement distance, which is the mean distance between all pairs of replicates in the core 100-m section, was 35 ± 27 m and was greater than...
mean distance of *E. fonticola* movement of all recaptured fish (10 ± 17 m [mean ± SD], \( P < 0.01, N = 82 \)) and movers only (20 ± 18 m, \( P < 0.01, N = 42 \)), upstream movers and nonmovers (9 ± 16 m, \( P < 0.01, N = 74 \)), and downstream movers and nonmovers (4 ± 10 m, \( P < 0.01, N = 48 \); Figure 2).

Probability of *E. fonticola* movement was influenced by both season and TL (Figure 3; Table 1). The probability of an individual moving from the point of initial capture was 4.1 times greater in winter (\( Z = 2.5, \text{df} = 77, P = 0.01 \)) and 2.3 times greater in spring–summer (\( Z = 0.8, \text{df} = 77, P = 0.41 \)) as opposed to summer–fall (Table 2). The proportion of individuals classified as movers was 36% in summer–fall, 72% in winter, and 55% in spring–summer. Probability of a darter moving from the replicate of initial capture was 1.2 times greater with every increase of 1 mm in TL (\( Z = 1.9, \text{df} = 77, P = 0.06 \)), and smaller fish (<30 mm) were classified as movers (32%, \( N = 31 \)) less frequently than larger fish (≥30 mm; 64%, \( N = 50 \)).

**DISCUSSION**

*Etheostoma fonticola* exhibited high site fidelity, moving on average 10 ± 17 m (mean ± SD) throughout the year during a stable hydrological regime (mean daily discharge, 7.7 m³/s; range, 4.7–8.7 m³/s; USGS Station 08168913). Site fidelity
null 1

Sex 2

Time 2

Sex, time 3

Time, season 4

Length, sex 4

Sex, time, season 5

Length, sex, time

Length, season

Length, sex,

season

Sex, season

Length, sex, time

Season

Length, time

Length

Length, time,

season

Length, sex, time,

season

Sex, time, season

Sex, length

Length, sex,

time

Sex, time

Time

Sex

Null

TABLE 1. Candidate logistic regression models of E. fonticola movement: predictors (β), regression coefficients (estimate), SD of estimate, Z-value, and P-value.

<table>
<thead>
<tr>
<th>β</th>
<th>Estimate</th>
<th>SD</th>
<th>Z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−5.76</td>
<td>2.80</td>
<td>−2.06</td>
<td>0.04</td>
</tr>
<tr>
<td>TL</td>
<td>0.18</td>
<td>0.09</td>
<td>1.87</td>
<td>0.06</td>
</tr>
<tr>
<td>Spring</td>
<td>0.58</td>
<td>0.70</td>
<td>0.83</td>
<td>0.41</td>
</tr>
<tr>
<td>Winter</td>
<td>1.41</td>
<td>0.56</td>
<td>2.50</td>
<td>0.01</td>
</tr>
<tr>
<td>Null deviance</td>
<td>112.18</td>
<td>80 df</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Residual deviance: 97.52 on 77 df

was most notable in areas with low growing aquatic vegetation (i.e., algae or R. fluviatilis). Distance of movement was 20 ± 18 m among fish that moved from the initial area of capture (51%). Movement was most often towards areas with low growing aquatic vegetation (69%), more frequently in an upstream direction (81%), in winter and spring–summer seasons (>55%), and among larger fish (>30 mm TL). Etheostoma fonticola movement generally conformed to our initial predictions. As a small-bodied darter with preference for slackwater habitat and a narrow distribution, mean movement of the E. fonticola was considerably less than those reported for widely distributed and narrowly distributed, swift-water darters (122–181 m; Roberts and Angermeier 2007). As predicted, site fidelity was high, but E. fonticola moved more often (51%) from the initial area of capture than other slow-water darters, such as E. cragini (<20% moved from initial area of capture; Labbe and Fausch 2000) and E. nigrum (3%; Mundahl and Ingersoll 1983). The percentage of E. fonticola moving upstream was similar to those reported for both widely and narrowly distributed darters (73–86%; Roberts and Angermeier 2007).

Our prediction of high site fidelity during peak periods of reproduction (Scalet 1973; Mundahl and Ingersoll 1983) was not supported in this study. Etheostoma fonticola spawn year round but greater reproductive effort occurs during winter and summer (Schenck and Whiteside 1977). Movement among E. fonticola was highest among larger individuals and during their reported peak reproductive efforts, suggesting that movement increases and therefore site fidelity decreases during peak reproductive seasons as E. fonticola search for mates and suitable spawning areas. We attributed high site fidelity to the quality of available habitat that meets their year-round needs and as well as their needs during peak reproductive efforts. Site fidelity among benthic fishes is positively associated with habitat quality (Albanese et al. 2004; Roberts and Angermeier 2007; Breen et al. 2009) and decreases when habitat quality is altered (Gowan and Fausch 2002; Roberts and Angermeier 2007). Etheostoma fonticola are often associated with low-growing aquatic vegetation in the San Marcos and Comal rivers (Schenck and Whiteside 1976; Linam et al. 1993; Alexander and Phillips 2012). They opportunistically feed on drifting and pelagic
copper, and cladocerans, as well as benthic amphipods, dipterans, and ephemeropterans commonly found above and in attached vegetation (Bergin 1996), and lay adhesive eggs on vegetation or on bare substrates (Schenck and Whiteside 1977; Brandt et al. 1993; Phillips et al. 2011). Consequently, preference for low-growing aquatic vegetation, such as algae and R. fluitans, probably optimizes a balance among being a benthic invertevo laking a swim bladder, consuming drifting and benthic prey, and having a phytolithophil reproductive strategy while avoiding piscivorous predators.

Maximum distance moved was 95 m within 26 d, and 7% of E. fonticola moved farther than the mean observable distance (35 m). Maximum distance moved by E. fonticola is similar to those reported for widely distributed (100–500 m) and narrowly distributed darters (185–250 m; Mundahl and Ingersoll 1983; Roberts and Angermeier 2007), less than those reported for swift-water, riffle-associated darters (250–500 m), and similar to those reported for slackwater darters or darters observed in slackwater habitats (100–200 m), excluding migratory darters (E. boschungi) move up to 3 km (Boschung and Nieland 1986). Percentages of darters moving >33 m within a year range from 3% to 13% (Mundahl and Ingersoll 1983; Roberts and Angermeier 2007). The tendency for a small proportion of individuals moving greater distances than conspecifics is common among stream fishes, including centrarchids, cottids, cyprinids, and percids (Hill and Grossman 1987; Smithson and Johnston 1999; Roberts et al. 2008). Long-distance movement observed in some individuals is probably based on genetics (e.g., boldness: Fraser et al. 2001) and could be essential to dispersion and colonization abilities of a population (Turchin 1998). More mobile individuals disperse at faster rates (Skalski and Gilliam 2000) and are probably the first to reach newly available or defaunated habitats (Scheurer et al. 2003) and areas of refugia during periods of duress (Labbe and Fausch 2000). Potomac Sculpin Cottus girardi, a species with high site fidelity, repopulated experimentally defaunated areas rapidly, probably as a result of a small percentage of a large population making longer movements (Hudy and Shiflet 2009). Consequently, maintaining conduits for movement is not only important for migratory species (i.e., Mountain Mullet Agonostomus monticola, freshwater eels, numerous cyprinids: Lee 1980; McDowell 1988; Skov 2008) but also for fishes that exhibit high site fidelity (Roberts and Angermeier 2007; Breen et al. 2009).

The Comal and the upper San Marcos rivers are located within the third-most populated area of Texas (Austin–San Antonio corridor) and are identified as critical habitat for E. fonticola and several other federally listed taxa (USFWS 1980). Headwaters of both rivers emerge within urbanized watersheds and have undergone extensive instream modifications, including channelization, construction of low-head dams, dredging, and water quantity alterations (Sanborn 1944; Kimmel 2006). Currently, the rivers are popular summertime destinations for waders, swimmers, and for those engaging in other types of water recreational activities. Instream uses and modifications pose potential additional concerns for species with high site fidelity, such as the E. fonticola. A habitat conservation plan (Thornton 1993) recently was accepted by the U.S. Fish and Wildlife Service that will request the incidental take of federally listed species within the Comal River and San Marcos River systems while minimizing and mitigating effects of river use by local government entities. Local government entities propose a number of measures and presumably recovery efforts to mitigate and minimize effects of river use on listed species, including flow management of the old channel, non-native plant and animal removal, native aquatic plant reintroductions, management of public recreation use, and sediment removal. Quantification of Fountain Darter site fidelity and movement will inform mitigation and minimization efforts by providing predictions on how the Fountain Darter will respond to alterations of their current habitat (i.e., removal of non-native vegetation and sediment, water level fluctuations during flow management), disruption of habitats by recreational use, and recolonization expectations of native vegetation reintroductions. A further implication of the quantification of Fountain Darter movement is the effect that low-head dams and culverts have on fragmentation of the Fountain Darter population and the impediment of a few more mobile individuals on gene flow and genetic diversity. This issue is not addressed in the habitat conservation plan but is necessary given the results of this study. This study quantified E. fonticola site fidelity and movement during a base flow hydrological condition that was slightly less than average. Quantifying site fidelity, movement, and other related life history characteristics (e.g., reproductive success and feeding) under various hydrological regimes (e.g., subsistence flows, higher base flows, high flow pulses) and levels of recreational use will provide a better model of community responses to natural and anthropogenic environmental influences.

As a representative of the small-bodied and narrowly distributed ethostomids, the proportion of E. fonticola with high site fidelity and the maximum distance moved was not noticeably different from that of widely distributed ethostomids. As such, movement potential and maximum movement do not satisfactorily explain why some darters are more widely distributed than others. However, differences in the upper range of maximum distance moved differed between slackwater-associated (250 m) and swift-water-associated (500 m) darters. These differences may be sufficient to explain observed patterns in local-
2006). Understanding the role restricted movement plays on recolonization of suitable habitat in light of anthropogenic fragmentation of populations is one of the necessary next steps towards development of a conservation plan for this and other imperiled etheostomids.

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REFERENCES


Juvenile Coho Salmon in the Elwha River Estuary Prior to Dam Removal: Seasonal Occupancy, Size Distribution, and Comparison to Nearby Salt Creek

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NOTE

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Abstract

In addition to the downstream migration of smolts in spring, Coho Salmon Oncorhynchus kisutch also enter estuaries throughout the year but especially in the spring as fry and in the fall as parr. The removal of two large dams on the Elwha River, Washington, has increased the area accessible to salmon and is affecting many aspects of the system. For comparison with the postdam period, when the Elwha River estuary will likely expand in size and complexity, monthly sampling was conducted in the estuary during 2007–2011 to determine patterns of Coho Salmon presence and size prior to dam removal; Salt Creek, a nearby undammed stream, was also sampled to allow comparison of fish size and seasonal patterns. The spring smolt migration in the Elwha River included a large fraction of unmarked fish (primarily of natural origin) as well as marked fish from the Lower Elwha Kallam Tribe Fish Hatchery. Subyearlings entered both estuaries during much of the year, exhibiting a peak in September. Coho Salmon from the Elwha River (including wild and hatchery-origin fish) were larger and more heavily represented in the fall relative to the spring smolt migration compared to those from Salt Creek. Future patterns in the Elwha River may include reduced presmolts but improved estuarine habitat may make it more suitable for presmolts.

Pacific salmon Oncorhynchus spp. and trout populations are a vital component of commercial, recreational, ceremonial, and subsistence fisheries around the Pacific Rim (NRC 1996; Augerot 2005) and are keystone species in their ecosystems (Willson and Halupka 1995). However, overall abundance and population diversity of salmonids in the southern end of their distribution have declined for decades, and many populations are extinct or in jeopardy (Nehlsen et al. 1991; Gustafson et al. 2007). Impassable dams have contributed to these losses (Lichatowich 1999), and removal or modification of dams is increasingly viewed as an option for restoring salmonid populations and their ecosystems (Hart et al. 2002). Dams can block fish movements, but they also alter temperature and flow regimes and reduce transport of sediment and woody debris, thus affecting the habitat that is available to fishes and other biota (Bednarek 2001). The trajectory of fish recovery therefore...
depends on complex combinations of intraspecific and interspecific population dynamics in the context of changing habitat quantity and quality. Accordingly, documentation of alternative migration and life history patterns may be important in assessing the recovery process.

The removal of two large dams on the Elwha River in the Olympic Peninsula, Washington, provides exceptional opportunities for studying the processes of fish life history and ecology, as anadromous fishes can expand their ranges upstream and formerly landlocked populations can resume anadromy or interact with anadromous fishes (Duda et al. 2008; Pess et al. 2008). Since the construction of Lower Elwha Dam in 1910–1913, migratory fishes have been blocked and sediment transport and other physical and ecological processes have been altered. Removal of Lower Elwha Dam (at river kilometer 7.9) and Glines Canyon Dam (at river kilometer 21.6) began in September 2011. Surveys prior to dam removal indicated that the numerically dominant salmonid above the dams was the Rainbow Trout Oncorhynchus mykiss (Brenkman et al. 2012). Coho Salmon O. kisutch were restricted to the section below Lower Elwha Dam, and adult escapements were estimated at 2,900, of which 76% were hatchery produced (Pess et al. 2008). However, the density of juvenile Coho Salmon was roughly comparable to that of steelhead (anadromous Rainbow Trout) below the dam (Pess et al. 2012); based on habitat capacity, Coho Salmon abundance might expand 10-fold during the postdam period (Pess et al. 2008).

Coho Salmon typically spawn in streams during late fall and early winter; fry emerge in spring, reside in freshwater for a full year (or 2 years in environments that are less conducive to growth), and then migrate to the sea as smolts in spring (Sandercock 1991; Weitkamp et al. 1995; Quinn 2005). During the fall, when streamflows increase in coastal, rain-dominated systems, parr often move downstream and overwinter in wetlands, beaver ponds, and other off-channel habitats (Bustard and Narver 1975; Peterson 1982; Swales et al. 1988). However, the downstream movement of fry in the spring and parr in the fall can take them into marine waters as well (Hartman et al. 1982; Miller and Sadro 2003; Bennett et al. 2011); these fish can represent a substantial fraction of the total population (Bennett et al. 2011; Roni et al. 2012). The fall migrants, which are missed by typical spring smolt sampling operations, may be numerically important and also reflect important aspects of the species’ ecology in streams. Coho Salmon smolts tend to move through estuaries rapidly and then disperse, but the use of estuaries by fry and parr is less well known and might be important for the survival of individuals and for persistence of the population (Koski 2009).

The estuary of the Elwha River has been greatly reduced in size and complexity due to a series of processes, including (but not limited to) the retention of sediment behind the dams, diking, and channelization (Drault et al. 2008; Shaffer et al. 2008; Duda et al. 2011b), which have disrupted the fish’s use of nearshore habitat in the Elwha River (Shaffer et al. 2009, 2012). Future physical changes in the estuary from sediment and wood deposition, and perhaps beaver activity, are likely (Hood 2012), thus affecting riverine and estuarine communities. Here, we report the results of monthly beach seining conducted on the west side of the Elwha River estuary during March 2007 through September 2011, when removal of Lower Elwha Dam began. These pre-dam-removal data will allow for comparisons with future postremoval patterns in (1) the seasonal catch of Coho Salmon representing different life history stages (fry in spring, parr in fall, and smolts in spring) and (2) juvenile Coho Salmon body size. In addition, similar seining efforts were conducted in the estuary of nearby Salt Creek as a comparison. There are three scenarios for future use of the Elwha River estuary by Coho Salmon. First, body size and temporal patterns of estuarine occupancy may be similar to those observed in the period prior to dam removal (i.e., the null hypothesis). Second, the estuary may become more extensive and more complex, leading to increased occupancy (although in the short term, the patterns of sediment transport and deposition might also limit access to some habitats). Third, if the spawning distribution of Coho Salmon shifts farther upstream, fry and parr that move downstream may find suitable habitat in the river, and use of the estuary during fall will therefore decrease. A large fraction of the hatchery-produced Coho Salmon in the Elwha River were externally marked by removal of the adipose fin, allowing us to make some comparisons between natural- and hatchery-origin fish. This is important because full restoration of the ecosystem will require the expansion of natural production.

METHODS

The Elwha River on the Olympic Peninsula, Washington, flows north into the Strait of Juan de Fuca (Figure 1). The estuary’s total area is about 35–40 ha, with 25–28 ha on the eastern side and 10–12 ha on the western side, including a pond that is not accessible to salmon (Shaffer et al. 2009; Duda et al. 2011a). Sampling took place in two tidally influenced channels (maximum depth = 2 m) on the western side of the estuary (Shaffer et al. 2009, 2012); these channels were separated from the main channel during low tides. At the higher-elevation northern site, the substrate consisted of sand, flat beach rock (up to 12 cm in diameter), and aggregated woody debris. The southern site was bordered by a rock levee with fine silt substrate and vegetation on the margins, and this site was more closely connected to the river. Tidal amplitudes in this area can exceed 3 m. Between the estuary and Lower Elwha Dam, the river had some floodplain channels that were used by juvenile Coho Salmon, but most of the tributary habitat in the basin was inaccessible to them and to other anadromous fishes prior to dam removal.

Estuaries are challenging habitats in which to sample because they change on complex tidal and lunar time scales and in response to river flow fluctuations. Thus, the two sites in the Elwha River’s small estuary were selected for their convenience and consistent access; they were not intended to represent the estuary as a whole but rather to allow seasonal sampling of the fish. In addition, there is no “reference” against which the Elwha River estuary can be paired. A review of the
FIGURE 1. (A) Map of western Washington and vicinity, showing the locations of the Elwha River, Salt Creek, and other nearby rivers mentioned in the text; (B) orthophoto of the Elwha River estuary in 2011, showing locations of the sampling sites (X) on the west side; and (C) orthophoto of the Salt Creek estuary in 2011, depicting locations of the sampling sites (X).
FIGURE 1. Continued.
The dam removal evaluation process concluded that “... the most appropriate design for the Elwha River dam removal [is] a BA [before–after] study design” (Roni et al. 2008). The sampling reported here was intended to be used in that manner; however, the estuary of Salt Creek, located approximately 10 km west of the Elwha River, was also sampled at two sites by similar methods to allow comparison of fish size and seasonal timing patterns. The Salt Creek estuary consists of approximately 29 ha of salt marsh and includes the main channel and side channels of lower Salt Creek. The mouth of Salt Creek enters directly into the east end of the highly productive and stable Crescent Bay. The Salt Creek estuary is bisected by a century-old dike that divides the eastern and western portions, although fish are present on both sides as well as in the main channel. The main channel, where the sampling occurred, is shallow, broad, and low energy and has heavy tidal influence upstream from the mouth. Salt Creek has about 38 km that are accessible to salmon and has a basin area of 49 km². The Coho Salmon is the dominant salmonid species in Salt Creek (McHenry et al. 2004). The habitat has been degraded to some extent, and there are some fish passage barriers within the system as described by McHenry et al. (2004), but many of those barriers have been eliminated since that report was completed (Michael McHenry, Lower Elwha Klallam Tribe, personal communication). The flow regime of Salt Creek is dominated by winter rainfall, whereas the Elwha River shows a snowmelt peak in early summer and a rain-dominated peak in winter (Draut et al. 2011).

Sampling was conducted in mid- to late morning on a single day of each month during the first monthly neap tide; we used a 24.4-m-long × 1.8-m-deep beach seine with a cod end of 1.8 m³ and 5-mm knotless mesh. Sampling is ongoing; in this paper, we report only the sampling that occurred during the period when the dams were in place (i.e., March 2007–September 2011). The net was deployed at the 2-m water depth mark parallel to the beach by using a row boat and was brought in by hand. All fish were identified to species; FL was recorded for all Coho Salmon if the catch was small or for about 20 Coho Salmon as a subsample if the catch was very large; and all specimens were counted but not measured. Most of the hatchery-origin Coho Salmon were marked externally by removal of the adipose fin (Table 1), in addition to coded wire tagging of a fraction; in late March to early or mid-May of each year, these fish were released volitionally from the Lower Elwha Klallam Tribe Fish Hatchery, which is operated by the Lower Elwha Klallam Tribe. The average mass of 30 g for these hatchery fish (Regional Mark Information System, Pacific States Marine Fisheries Commission, http://www.rmpc.org/) indicated a FL of about 136 mm based on unpublished length–weight data for hatchery Coho Salmon (Organ Bond and Sean Hayes, National Oceanic and Atmospheric Administration [NOAA] Fisheries, Santa Cruz, California).

RESULTS

In total, 239 beach seine sets (127 in the Elwha River estuary and 112 in the Salt Creek estuary, with at least six sets in each

<table>
<thead>
<tr>
<th>Year</th>
<th>Number released</th>
<th>Fin clipped (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>410,866</td>
<td>80.2</td>
</tr>
<tr>
<td>2008</td>
<td>323,813</td>
<td>73.7</td>
</tr>
<tr>
<td>2009</td>
<td>444,514</td>
<td>64.4</td>
</tr>
<tr>
<td>2010</td>
<td>218,720</td>
<td>63.2</td>
</tr>
<tr>
<td>2011</td>
<td>506,402</td>
<td>84.2</td>
</tr>
<tr>
<td>Total</td>
<td>1,904,315</td>
<td>74.5</td>
</tr>
</tbody>
</table>
Table 2. Numbers of beach seine sets and average catch per unit effort (CPUE, fish/set; SD in parentheses) of juvenile Coho Salmon in the Elwha River estuary and the Salt Creek estuary during spring 2007 through fall 2011. The percentage of smolts (i.e., yearlings, as inferred from length frequency distributions) among fish captured at each site during each month is also reported.

<table>
<thead>
<tr>
<th>Month</th>
<th>Elwha River estuary</th>
<th>Salt Creek estuary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sets</td>
<td>Mean CPUE (SD)</td>
</tr>
<tr>
<td>Jan</td>
<td>6</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Feb</td>
<td>10</td>
<td>0.2 (0.4)</td>
</tr>
<tr>
<td>Mar</td>
<td>17</td>
<td>0.1 (0.3)</td>
</tr>
<tr>
<td>Apr</td>
<td>15</td>
<td>42.1 (63.0)</td>
</tr>
<tr>
<td>May</td>
<td>15</td>
<td>3.9 (4.8)</td>
</tr>
<tr>
<td>Jun</td>
<td>14</td>
<td>5.7 (15.1)</td>
</tr>
<tr>
<td>Jul</td>
<td>9</td>
<td>34.6 (94.6)</td>
</tr>
<tr>
<td>Aug</td>
<td>8</td>
<td>2.6 (7.4)</td>
</tr>
<tr>
<td>Sep</td>
<td>6</td>
<td>5.8 (13.8)</td>
</tr>
<tr>
<td>Oct</td>
<td>6</td>
<td>0.2 (0.4)</td>
</tr>
</tbody>
</table>

Month at each site) were performed, resulting in a total catch of 4,213 juvenile Coho Salmon (2,469 in the Elwha River estuary; 1,744 in the Salt Creek estuary). Fish were caught during all months of the year, but there were clear modes of CPUE (fish/set) during spring and fall (Table 2). However, the timing and relative magnitude of the modes differed between the two estuaries. In the Elwha River estuary, the spring mode (dominated by smolts; Table 2) was observed in April and to a lesser extent in May, whereas in the Salt Creek estuary the mode was observed in May and more fish were caught during June than during April. The mode of fall migrants relative to the spring smolt migration was greater for the Elwha River estuary than for the Salt Creek estuary. The CPUE of smolts in spring was similar between the two estuaries (Elwha River: 77.1 fish/set in April; Salt Creek: 71.6 fish/set in May), but the peak fall (September) CPUE was higher in the Elwha River estuary (34.6 fish/set) than in the Salt Creek estuary (10.7 fish/set).

Young-of-the-year fish from the Elwha River were larger than those from Salt Creek during spring through fall (Table 3). The Elwha River smolts were also much larger than Salt Creek smolts in April (Elwha River: mean ± SD = 135.3 ± 17.5 mm; Salt Creek: 98.6 ± 17.0 mm; t = 9.66, P < 0.001) and in May (Elwha River: 129.2 ± 15.61 mm; Salt Creek: 117.4 ± 17.5 mm; t = 4.96, P < 0.001) but not significantly so in June (Elwha River: 116.2 ± 12.9 mm; Salt Creek: 111.3 ± 14.7 mm; t = 1.32, P = 0.19). These size differences between streams were influenced by the mixture of hatchery- and naturally produced fish but did not seem to simply reflect larger, hatchery-produced fish in the Elwha River. In the Elwha River, the adipose fin-clippered (hatchery) smolts varied less in length than the unclippered (mix of hatchery and natural origin) smolts during April (clipped [N = 37]: variance = 140.5 mm; unclipped [N = 12]: 462.1 mm; F = 0.304, P = 0.003) and during May (clipped [N = 39]:

Table 3. Fork lengths (mm) of age-0 Coho Salmon sampled in the Elwha River estuary and the Salt Creek estuary from 2007 to 2011; n = number of fish measured. Samples with fewer than 10 fish were omitted.

<table>
<thead>
<tr>
<th>Month</th>
<th>Elwha River estuary</th>
<th>Salt Creek estuary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean FL</td>
</tr>
<tr>
<td>Apr</td>
<td>21</td>
<td>47.0</td>
</tr>
<tr>
<td>May</td>
<td>60</td>
<td>58.2</td>
</tr>
<tr>
<td>Jun</td>
<td>41</td>
<td>76.9</td>
</tr>
<tr>
<td>Jul</td>
<td>16</td>
<td>70.9</td>
</tr>
<tr>
<td>Aug</td>
<td>57</td>
<td>83.6</td>
</tr>
<tr>
<td>Sep</td>
<td>46</td>
<td>93.7</td>
</tr>
<tr>
<td>Oct</td>
<td>17</td>
<td>106.5</td>
</tr>
<tr>
<td>Nov</td>
<td>25</td>
<td>112.3</td>
</tr>
</tbody>
</table>
Our power to detect interannual patterns was reduced due to (1) the small number of years ($n = 5$) of data and (2) the fact that seine sets in some month × site × year combinations were missing. At both sites, a great deal of among-year variation was detected in CPUE for any given month. For example, catches of Coho Salmon parr in the Elwha River estuary during September (the mode for fall catches; Table 2) varied from 0 to 286 fish/set, and the corresponding catches in the Salt Creek estuary varied from 0 to 28.5 fish/set. In general, CPUEs in both estuaries were low during 2007 (all months combined; Elwha River: 7.17 fish/set; Salt Creek: 6.52 fish/set) and were high during 2010, especially for the Elwha River (51.27 fish/set; Salt Creek: 14.90 fish/set). The expectation that catches in spring would reflect the number of Coho Salmon released from Lower Elwha Klallam Tribe Fish Hatchery was not supported. Indeed, April catch rates of Coho Salmon of all sizes in the Elwha River estuary were negatively correlated with the number released ($r^2 = 0.77$, $P = 0.05$), and the relationship was improved when only the catch rates of smolts were considered ($r^2 = 0.83$, $P = 0.03$). No relationship was detected between the number of hatchery fish released and the catch rates in May.

**DISCUSSION**

The primary purpose of this study was to document the patterns of juvenile Coho Salmon size distribution and timing in the small, degraded estuary of the Elwha River during the years immediately prior to removal of the two large dams; secondarily, we sought to compare these patterns with those of juvenile Coho Salmon in the nearby Salt Creek estuary. The salient findings were the substantial numbers of presmolts Coho Salmon in the estuaries of both systems, including (1) fry in the spring, which overlapped with the conventional smolt migration in May and June, and (2) parr in the fall (Figure 2; Table 2). These migratory patterns have been documented in other nearby systems, such as the East Twin and West Twin rivers, which are situated along the Strait of Juan de Fuca west of Salt Creek (Bennett et al. 2011; Roni et al. 2012); such patterns have also been documented in British Columbia (Hartman et al. 1982) and Alaska (Koski 2009). The smaller members of the cohort in the East Twin and West Twin rivers were more likely to move downstream and enter estuarine waters during fall than were the larger members of the cohort (Roni et al. 2012), but the factors affecting this downstream movement (e.g., density and competition, high flows, and decreasing temperatures) remain uncertain (Roni et al. 2012). Prior to dam removal, Coho Salmon in the Elwha River were found primarily in the lower 4 km (Pess et al. 2008) compared to the broader range available in Salt Creek. Thus, many Elwha River juveniles may have encountered the estuary in the course of their normal downstream movement because they emerged only a short distance above the estuary and did not find suitable habitat prior to reaching the estuary. If so, an increased upstream distribution of Coho Salmon spawning after dam removal may decrease the proportion of the population that enters the estuary as fry and parr because suitable rearing habitat is present above the sites where the dams were located (Pess et al. 2008), at least until the carrying capacity is reached. The somewhat smaller fraction of the Salt Creek population that was caught during the fall may reflect the greater length of stream available for rearing habitat, although many other factors might affect the proportions of fall versus spring catches and presmolts versus smolt catches, including differences between the two rivers and their estuaries. One additional complication is that the estuaries contained some smolts from other river systems, as indicated by genetic analyses (Shaffer et al. 2012); this occurs because the Strait of Juan de Fuca is a migratory corridor and feeding area for salmon (Weitkamp and Neely 2002). Future changes in the Elwha River estuary’s configuration may make it more attractive to smolts from other systems, making comparisons even more difficult.

The Elwha River Coho Salmon presmolts were also larger than Salt Creek presmolts, but information on the size distribution of juveniles residing upstream in each system at the time of estuarine sampling was not available, thus limiting our ability to interpret the difference. Density depresses growth in Coho Salmon (Scrivener and Anderson 1984; Spalding et al. 1995), so the larger size of the Elwha River fish might reflect the lack of competition; however, thermal regimes and other ecological factors also affect size. It will be important to monitor body size in the future as the population expands spatially and numerically and reaches its carrying capacity.

The Lower Elwha Klallam Tribe Fish Hatchery produced an average of 380,863 smolts/year from 2007 to 2011 (Table 1), and these fish probably contributed to the earlier smolt migration in the Elwha River relative to Salt Creek (Table 2). The hatchery’s smolt production is probably far greater than would be possible from the few adults spawning naturally (Pess et al. 2008), so the vast majority of Elwha River Coho Salmon smolts were probably of hatchery origin. Indeed, it is likely that the approximately 80,000 unclipped Coho Salmon smolts that were released from the hatchery each year (Table 1) considerably outnumbered the wild smolts based on an estimate of smolt production as a function of stream length (Bradford et al. 1997). However, despite the numerical dominance of hatchery fish in overall production, three lines of evidence indicate that the presence of naturally spawned fish in the Elwha River estuary was disproportionate to their likely abundance. First, unclipped presmolts were caught during periods when hatchery fish would not be present. Second, the length distributions of clipped and unclipped smolts differed significantly. Third, at least half of the smolts sampled in the estuary were unclipped, even though approximately 75% of the hatchery fish were clipped. Thus, fish of natural origin were probably over-represented in estuarine sampling relative to their abundance. The hatchery fish may have moved through the river and into the Strait of Juan de Fuca more rapidly than the wild fish and therefore would have comprised a smaller fraction of the fish sampled in the Elwha River estuary relative to their overall abundance. This is consistent with
the tendency for large Coho Salmon smolts to migrate earlier than small smolts (Shapovalov and Taft 1954; Durkin 1982; Irvine and Ward 1989), the tendency for hatchery Coho Salmon smolts to migrate rapidly (Hayes et al. 2004), and the tendency for hatchery-produced Chinook Salmon O. tshawytscha to occupy northern Puget Sound for a shorter period than naturally produced fish (Rice et al. 2011). In addition, the inverse correlation between the number of smolts released from the hatchery and the catches in April but not in May of the same year suggests that there is some tendency for density to affect residence time; however, the limited number of years makes such a conclusion speculative.

The before–after study design has its advantages (Roni et al. 2008) but also has many limitations in this and other cases wherein the goal is to detect the beneficial or harmful effects of a large event. Interruption variation owing to spawner–recruit processes, climate, and other factors greatly complicates this approach (e.g., Holtby and Scrivener 1989). As many authors have pointed out, natural variation hinders the ability to detect changes in salmonid (and other) populations unless the effect is large or unless the period of record is long (e.g., Lichatowich and Cramer 1979; Bisson et al. 2008; Dauwalter et al. 2009). Consequently, the short period of record (5 years) in the present study will inevitably compromise our ability to conduct comparisons with post-dam-removal abundance, size, timing, and other aspects of salmon population biology. However, this information is still an advance over cases of natural or anthropogenic disasters for which the “before” data were even more limited, with serious consequences for the ability to detect change (e.g., the Exxon Valdez oil spill in Prince William Sound, Alaska; Paine et al. 1996).

Prior to dam removal, an assessment of salmon production in the region concluded that “Restoration of the Elwha River may represent one of the best opportunities to improve natural production of Coho [in the Strait of Juan de Fuca region]” (PSSSRG 1997). It remains to be seen whether this potential will be realized, but the information in the present study provides some basis for comparison as the population expands spatially and numerically towards its natural carrying capacity in the rapidly changing environment of the Elwha River system.

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Parental Influence on the Size and Age at Maturity of Bluegills

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Parental Influence on the Size and Age at Maturity of Bluegills

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Abstract
The Bluegill Lepomis macrochirus is one of the most ubiquitous fish species in North America and often exhibits a stunted population size structure. Although previous research has shown that the size and density of mature males have a significant influence on Bluegill size and age at maturity, little is known about the influence that mature females have on Bluegill life history. Offspring produced by four possible crosses of Bluegill males and females from stunted and nonstunted source populations were raised in a common-garden environment, and we compared size and age at maturity among these groups of offspring to determine whether the traits are maternally inherited. Growth, age at maturity, and energy investment into maturation did not differ between offspring of females from the two source populations, thus indicating that Bluegill size and age at maturity are not maternally inherited. Instead, the occurrence of stunting in Bluegills appears to be linked to previously identified in-situ environmental factors, such as male social structure and predator presence.

Size and age at maturity are two important life history attributes that are often correlated (Stearns 1976; Roff 1984). Inter- and intrapopulation variation in size and age at maturity can be influenced either by genetics or by environmental conditions (e.g., temperature, competition, and prey availability). For example, in Lake Trout Salvelinus namaycush (McDermid et al. 2007) and Montezuma Swordtails Xiphophorus montezumae (Kallman 1983), size and age at maturity are genetically inherited. In contrast, the size and age at maturity of many organisms, including Atlantic Salmon Salmo salar (Rowe and Thorpe 1990) and various anurans (Skelly and Werner 1990; Peacor and Werner 2000), have been shown to be plastic and influenced primarily by the environment. In many situations, however, genetic inheritance and the environment may interact to influence the age and size at maturity. Examples of such interactions occur in Sailfin Mollies Poecilia latipinna (Trexler and Travis 1990) and Coho Salmon Oncorhynchus kisutch (Silverstein and Hershberger 1992).

Parental effects are a special case in which genetics and environment interact to influence phenotype (Wolf and Wade 2009). These effects occur when the offspring’s phenotype is influenced by either the genotype or the phenotype of a parent or by the environmental conditions that the parent has experienced (Mousseau and Dingle 1991). These effects occur apart from the nuclear genes (Rossiter 1996). Because eggs contain nutrients that are essential to the hatch and early life history of fish, females frequently exert a greater parental effect than males (Kirkpatrick and Lande 1989). The most commonly reported

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maternal effects in oviparous fish are related to egg size. For example, larvae that hatch from larger eggs typically hatch at a larger size and have greater survival and growth than those hatching from smaller eggs (Heath and Blouw 1998). Egg size in oviparous fish has been associated with the length, age, and body condition of the female (Thorpe et al. 1984; Springate and Bromage 1985). Maternal influences have also been shown to vary among populations. For example, in Atlantic Tomcod Microgadus tomcod, larval yolk reserve quantity at hatch varied between the offspring of females from polluted estuaries and the offspring of females from nonpolluted estuaries (Green and Chambers 2007). The maternal environment has been shown to influence offspring growth (Reznick 1991; Reznick et al. 1996), disease resistance (Lombardi 1996), and larval hatch timing (Lin and Dunson 1995). Nevertheless, little is known about how maternal effects influence the size and age at maturity of most organisms, including fish. Most studies have compared maternal populations originating from habitats with contrasting environmental conditions. Little is known about maternal effects originating from populations that are characterized by differing size and age at maturity.

The Bluegill Lepomis macrochirus is a good model species for examining how size and age at maturity are influenced by parental effects, genetics, and differences in environmental conditions experienced by the source populations. Bluegills exhibit considerable variation in size and age at maturity, and the timing of maturation is important because stunted populations develop when a population consists primarily of smaller, earlier-maturing individuals. Because of their smaller adult body size, Bluegills in stunted populations (i.e., populations with a small adult size structure) are less desirable to anglers than those from nonstunted populations (Drake et al. 1997). Consequently, a considerable amount of research has been conducted to determine factors that influence the size structure of Bluegill populations. Recent studies have shown that the presence of large, mature males delays the maturation of younger males and causes them to mature at a larger size than they would in a population that lacks these larger mature males (Jennings et al. 1997; Aday et al. 2003b). However, the Bluegills used in these previous studies were born in their respective source environments, making it impossible to determine whether the observed differences in size and age at maturity were attributable to the treatments manipulated in these experiments or to genetic or environmental differences between source populations. Even though the influence of males on Bluegill life history is well established (e.g., Aday et al. 2003b), less is known about the influence that female Bluegills have on size and age at maturity. The parental care behavior exhibited by male Bluegills likely explains why they have a significant influence on life history (Aday et al. 2003b); in contrast, female Bluegills exhibit no parental care, and therefore it is probable that any maternal influence on progeny is inherited.

We hypothesized that size and age at maturity in Bluegills are inherited. We assessed whether size and age at maturity are passed from parent to progeny by transferring adult Bluegills from both stunted and nonstunted populations into experimental ponds and allowing them to spawn, thus creating four offspring crosses (stunted male × stunted female; stunted male × nonstunted female; nonstunted male × stunted female; and nonstunted male × nonstunted female). These offspring were born in a common-garden setting and were reared in this setting until maturation. We were able to test whether size and age at maturity were inherited genetically or were primarily influenced by differences in environmental conditions experienced by the parental source populations. We also assessed potential management strategies by comparing our findings with those of studies that have examined how environmental conditions influence Bluegill size and age at maturity.

**METHODS**

In spring 2005, we used a boat electrofishing unit (AC, 240 V, 6–9 A) to collect adult Bluegills from two established lake populations in southeastern Illinois: Pana Lake, which contains a historically stunted Bluegill population (mean TL ± SD for mature males: 141 ± 27 mm, n = 61; mature females: 117 ± 23 mm, n = 121); and Forbes Lake, which contains a historically nonstunted Bluegill population (mean TL ± SD for mature males: 180 ± 11 mm, n = 52; mature females: 135 ± 28 mm, n = 123). In addition to having a smaller adult body size distribution, Bluegills in Pana Lake mature earlier than those in Forbes Lake. Male Bluegills in Pana Lake generally mature at age 3, whereas males in Forbes Lake typically mature at age 4 (Diana et al. 2007). Pana Lake females typically mature at age 2, whereas Forbes Lake females mature at age 3 (Diana et al. 2007). Males in Forbes Lake also have a greater TL at a common age (age 3) than males in Pana Lake (Forbes Lake: 142.2 ± 6.3 mm; Pana Lake: 123.4 ± 6.3 mm; t115 = 5.3, P < 0.01), but length at age 2 does not differ between the two source populations (t115 = 0.03, P = 0.97). The Bluegill populations in these two lakes were selected from among a group of 54 surveyed populations and are representative of other stunted and nonstunted populations in Illinois (Diana et al. 2007). Routine samples collected from 1996 to 2005 indicated that there was little change in the size and age at maturity of Bluegills from the two populations over that time period.

Adult Bluegills were introduced into eight experimental ponds at the Illinois Natural History Survey’s Sam Parr Biological Station. The females that were added to the ponds were between 110 and 160 mm TL (<5% of females did not meet this criterion), and female mean size did not vary between source populations (t126 = 0.90, P = 0.36). Females from both source populations were added to every pond. All of the males were at least 120 mm TL, and males from the nonstunted population tended to be larger than those from the stunted population (t128 = 6.4, P < 0.01). Each pond received males from a single source population; four ponds were stocked with males from the stunted population, and the other four ponds were stocked with...
males from the nonstunted source. Due to limited pond availability, two pond surface areas were used: four ponds had a surface area of 0.14 ha, whereas the remaining four were 0.40 ha. The number of adults introduced into each pond varied depending on pond size. In the 0.14-ha ponds, four females from each source population were stocked along with five males, whereas the 0.40-ha ponds were stocked with 12 females from each source population along with 15 males. Two of the 0.14-ha ponds and two of the 0.40-ha ponds contained males from the stunted population, whereas the remaining two ponds of each size contained males from the nonstunted population. In the ponds containing stunted males, two different crosses (genotypes) of offspring were produced (stunted male × stunted female; stunted male × nonstunted female). Likewise, two different crosses were possible in the ponds that contained the nonstunted males. Although four offspring crosses were produced in the experiment, only two crosses were possible in each pond.

To identify the offspring of the possible crosses, the adult Bluegills from each source population were selected on the basis of their genotype at a neutral allozyme marker (sIDH-1*; Avise and Smith 1974). During the initial collection, adults were held temporarily in holding tanks at the Sam Parr Biological Station. Each fish was measured, and a caudal or pectoral fin clip was collected. The fin clips were immediately analyzed by using vertical starch protein electrophoresis to determine the genotype of each fish at the isocitrate dehydrogenase 1 (IDH-1) locus (Avise and Smith 1974). Bluegills have two sIDH-1* alleles, and thus there are three possible genotypes: *1/*1, *1/*2, and *2/*2. Electrophoresis was performed for each fish sample by macerating the fin clip in a tris-buffer solution (0.01-M tris, 0.001-M EDTA, 5 × 10^-3-M NADP, pH adjusted to 6.8; Avise and Smith 1974). The homogenate was then centrifuged and loaded onto a potato starch gel. A fter electrophoresis, the gel was stained via the methods described by Avise and Smith (1974). Only homozygous *1/*1 adults from the stunted population and homozygous *2/*2 adults from the nonstunted population were selected for use in stocking the ponds. A fter pond introduction, the adults were allowed to naturally spawn during 2005. To prevent multiple year-classes from co-occurring, the ponds were drained prior to the 2006 spawning season, and all of the adults were removed. The young were collected, stored temporarily in holding tanks, and placed back into the same pond from which they were removed. A t the time of pond restocking, the densities of young Bluegills were adjusted to ensure an equal density in each pond (i.e., 10,000 fish were introduced into each 0.4-ha pond, and 3,000 fish were stocked into each 0.14-ha pond). These densities were selected because they are typical for Bluegills in Midwestern lakes (Johnson et al. 1988; Diana et al. 2007).

The experiment was terminated when approximately half (40–60%) of the progeny born in 2005 had sexually matured (fish were collected periodically, and maturity was assessed as described below). When the experiment ended (July 2008), a random sample consisting of 250 progeny born in 2005 was collected from each pond. A sample of caudal fin tissue was removed from each fish and was subjected to genetic analysis, allowing us to determine the maternal and paternal source populations of the offspring. The remainder of each fish was frozen at −2°C and then returned to the laboratory, where it was later thawed to determine TL, weight, and gender (all fish were thawed and examined within 60 d of collection). The investment into gonadal development was assessed by weighing the gonads and calculating a gonadosomatic index (GSI; ratio of gonad weight to somatic weight) for each fish. A n established gonad scoring system (with scores ranging from 1 to 5) was also used to determine the maturity status of each fish (Aday et al. 2002). Fish with a score of 1 or 2 were immature, with small, undeveloped gonads that lacked vascularization or signs of egg or sperm development. Fish that received a score of 4 or 5 were mature and had larger gonads with well-developed vascularization; eggs were clearly visible in females with these scores. A score of 3 was assigned to fish that were in the process of maturing.

Although four offspring crosses (genotypes) were produced, only two of the genotypes could appear in any single pond. Progeny from both maternal sources (stunted and nonstunted) were present in each pond, whereas progeny from a given paternal source were present in only half of the ponds. The experimental design allowed us to analyze for both maternal and paternal source effects. Because both maternal sources were present in every pond, more replication and statistical power were available for detecting maternal source effects than for detecting paternal effects. The data were analyzed with ANOVA using the MIXED procedure in the Statistical Analysis System (SAS 1998). M aternal population source, paternal population source, and the maternal source × paternal source interaction were main effects in the statistical models. The effect of pond size was nested within paternal population source and was treated as a random block in the analysis. Fish TL and GSI and the percentage of fish that were sexually mature were evaluated as dependent variables in the analysis. There were eight available replicates (ponds) for testing the maternal main effect. Offspring that were produced by males from the stunted source population were present in four of the ponds, whereas the other four ponds contained offspring produced by males from the nonstunted source. A s a result, there were four replicates available to test the paternal effect. All differences in means were considered significant at P-values less than 0.05. Data for the analysis of percentage mature were normalized by using an arc sine transformation. The growth and GSI data met the assumptions of the analysis and were not transformed. Cuckolders (male Bluegills that mature at a considerably younger age and smaller size than other males in the population; Gross and Charnov 1980; Gross 1982) constituted less than 2% of the Bluegills collected in the ponds, and these individuals were not included in analyses.
RESULTS

At the time of adult Bluegill removal (spring 2006; prior to the second spawning season), the number of young Bluegills recovered did not differ between ponds that contained adult males from the stunted population and ponds that contained males from the nonstunted population (ANOVA blocked by pond size: $F_{1,4} = 0.67, P = 0.46$). On average, 14,000 ± 3,000 young Bluegills (mean ± SD) were recovered from the 0.4-ha ponds, and 5,000 ± 600 young were recovered from the 0.14-ha ponds. By the time the progeny reached age 3, about 50% of them had become sexually mature; at that time, the ponds were drained and the experiment was terminated. The number of recovered fish representing each pond × sex × maternal source combination (e.g., male progeny from stunted mothers, female progeny from nonstunted mothers, etc.) ranged from 24 to 68 individuals. Fish of both sexes tended to grow slightly larger in the 0.4-ha ponds than in the 0.14-ha ponds (mean difference in TL = 29 mm for male offspring and 23 mm for female offspring; Table 1). The TLs of the males and females that matured during the experiment did not vary in relation to maternal source (Table 1; Figure 1). Similarly, the GSI of males and females that matured did not vary with maternal source (Table 1; Figure 2). Neither the TL nor the GSI of mature male and female progeny varied with paternal source (all $P ≥ 0.06$).

The proportion of males and females that were sexually mature at the completion of the experiment did not vary with maternal source (Table 1; Figure 3). A higher proportion of male progeny matured in the ponds with the nonstunted paternal source (mean ± SE = 52.4 ± 1.4%; Table 1) than in ponds with the stunted paternal source (39.5 ± 6.7%). The proportion of female progeny that matured did not vary between the paternal source populations (Table 1). For immature fish, the TL and GSI did not vary with maternal source (all $P ≥ 0.28$). The growth and reproductive investment of immature fish also did not vary with paternal source (all $P ≥ 0.30$).

DISCUSSION

Growth and reproductive investment (GSI; percentage of fish that matured) did not vary among Bluegill offspring from crosses of parents representing stunted and nonstunted populations. Our common-garden experiment indicated that Bluegill size and age at maturity are not maternally influenced. However, differences in these life history traits are observed among natural Bluegill populations, suggesting that differences in environmental conditions among lakes and streams constitute the primary influence on the size and age at maturity of Bluegills. These observations are consistent with the results of other recent studies; for example, experiments have shown that juvenile Bluegills mature earlier when raised in the absence of large, mature males (Aday et al. 2003b). The social structure of the paternal source population had no influence on size at maturity. Similarly, the presence of predatory Largemouth Bass Micropterus salmoides had a stronger influence on Bluegill size and age at maturity than paternal population source (Oplinger

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**Table 1.** Results of ANOVA used to determine the effect of maternal and paternal population source (stunted or nonstunted) on the TL, gonadosomatic index (GSI), and percent maturation of 3-year-old male and female Bluegills in a common-garden environment (MS = mean square).

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Source</th>
<th>Effect</th>
<th>df</th>
<th>F</th>
<th>P</th>
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<td>9.00</td>
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<td>25.37</td>
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<td>0.03</td>
<td>1,117.44</td>
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<tr>
<td></td>
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<td>30.83</td>
<td>0.05</td>
<td>0.95</td>
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<tr>
<td></td>
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<td>341.70</td>
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<tr>
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<td>0.46</td>
<td>0.52</td>
<td>0.31</td>
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<td>1.55</td>
<td>4.73</td>
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<td>0.39</td>
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<td>0.42</td>
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<td></td>
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<tr>
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<tr>
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<td>&lt;0.01</td>
<td>0.05</td>
<td>0.83</td>
<td>&lt;0.01</td>
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<td>&lt;0.01</td>
<td>0.07</td>
<td>0.93</td>
<td>0.01</td>
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<tr>
<td></td>
<td>Error</td>
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<td>&lt;0.01</td>
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Both of these studies reported that juvenile Bluegills from a stunted population matured earlier and had a greater GSI than those from a nonstunted population. Therefore, both environmental conditions and source population influenced Bluegill size and age at maturity; however, a greater amount of variation in GSI was explained by social structure than by source population or the presence of predators (Aday et al. 2003b; Oplinger et al. 2011). These prior studies used juvenile fish that were collected from their respective source populations, so the observed effects may have been a “carryover” caused by environmental differences between source populations. In the current study, individuals were born in and spent their entire lives in a common-garden environment. Thus, individuals from all genotypes experienced the same environmental conditions throughout their lives, and any differences in growth or age at maturity could be solely attributed to parental effects or differences in genetics. However, we observed no differences in growth or age at maturity among the Bluegill crosses. Therefore,
FIGURE 2. Gonadosomatic index (mean + SE) of male (top panels) and female (bottom panels) Bluegills that were produced by crosses between parents from nonstunted and stunted source populations (four possible crosses). Offspring were spawned and reared in ponds as part of a common-garden experiment. Left panels show the results for mature offspring, whereas right panels show the results for immature offspring. The x-axis indicates the cross used to produce each offspring group; allozyme analysis was used to determine the paternal and maternal source populations.

Differences in growth and age at maturity between stunted and nonstunted Bluegill populations can most likely be attributed to differences in environmental conditions among lakes. Despite the fact that we did not observe differences in Bluegill size and age at maturity between maternal source populations, it is still possible that parental effects influenced the growth and size at maturity of the Bluegills in our experiment. For example, larger, older, or better-conditioned mothers—regardless of population source—may have produced faster-growing, earlier-maturing offspring. Such maternal effects could influence short-term (i.e., prior to age 1) survival and growth and could have a pronounced influence on survival and life history. The most widely cited individual-level maternal effects are related to female length (Rossiter 1996). The TLs of female Bluegills used in our study, however, were similar between source populations. At the individual level, age and condition of female Bluegills could also influence the size and age at maturity of their offspring. Unfortunately, it would have been logistically impossible to
BLUEGILL SIZE AND AGE AT MATURITY

FIGURE 3. Proportion (mean + SE) of Bluegills that were mature at the end of the experiment among males (top panel) and females (bottom panel) that were produced by crosses between parents from nonstunted and stunted source populations (four possible crosses). Offspring were spawned and reared in ponds as part of a common-garden experiment. The x-axis indicates the cross used to produce each offspring group; allozyme analysis was used to determine the paternal and maternal source populations.

simultaneously control for size, age, and condition differences between source populations.

The Bluegills in our ponds matured at a smaller size than is commonly observed in the wild, but their age at maturity was similar to that of wild fish. Length at maturity of Bluegills is not inherited; rather, environmental conditions must cause this small size at maturation. Water temperature, chemistry, and food availability in the ponds were typical of waters in Illinois (Diana et al. 2007). The small size at maturation was likely caused by the lack of mature males in our ponds. There was little competition for nesting sites and mates in the ponds; as a result, males were able to mature at a small size. These observations are supported by other pond experiments demonstrating that the presence of larger, mature male Bluegills forces smaller, immature males to delay maturation (Aday et al. 2003b). Our findings and those of Aday et al. (2003b) suggest that new populations should not be established solely by using young, immature Bluegills, as such populations are likely to develop a stunted size structure. Some larger, mature individuals should be added to delay the maturation of the immature fish.

Our findings help to reduce the list of potential factors that influence Bluegill size and age at maturity and should aid in the management of this species. We did not detect a genetic effect, and it appears that stunting in Bluegills is caused by differences in the environmental conditions experienced by populations. Thus, transplanting individuals from nonstunted populations into stunted populations is unlikely to improve population size structure (through “improved” genetics). Instead, it appears that other environmental factors may have a greater influence on adult size. Previous research suggests that protecting large, mature males through minimum length regulations could delay the maturation of immature males and cause them to mature at a larger size, thereby improving population size structure (Aday et al. 2003b). Minimum length regulations may have the added benefit of preventing overharvest (Goedde and Coble 1981; Coble 1988). Other studies suggest that predator manipulations may bolster Bluegill growth (Oplinger et al. 2011) and that management actions to reduce Gizzard Shad Dorosoma cepedianum densities may help to improve Bluegill population size structure (Aday et al. 2003a; R. W. Oplinger, M. J. Diana, and D. H. Wahl, Illinois Natural History Survey, unpublished data).

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Genetic Population Structure of Muskellunge in the Great Lakes

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ARTICLE

Genetic Population Structure of Muskellunge in the Great Lakes

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Abstract

We quantified genetic relationships among Muskellunge Esox masquinongy from 15 locations in the Great Lakes to determine the extent and distribution of measurable population structure and to identify appropriate spatial scales for fishery management and genetic conservation. We hypothesized that Muskellunge from each area represented genetically distinct populations, which would be evident from analyses of genotype data. A total of 691 Muskellunge were sampled (n = 10–127/site) and genetic data were collected at 13 microsatellite loci. Results from a suite of analyses (including pairwise genetic differentiation, Bayesian admixture prediction, analysis of molecular variance, and tests of isolation by distance) indicated the presence of nine distinct genetic groups, including two that were approximately 50 km apart. Geographic proximity and low habitat complexity seemed to facilitate genetic similarity among areas, whereas Muskellunge from areas of greater habitat heterogeneity exhibited high differentiation. Muskellunge from most areas contained private alleles, and mean within-area genetic variation was similar to that reported for other freshwater fishes. Management programs aimed at conserving the broader diversity and long-term sustainability of Muskellunge could benefit by considering the genetically distinct groups as independent fisheries, and individual spawning and nursery habitats could subsequently be protected to conserve the evolutionary potential of Muskellunge.

Conservation of global biodiversity requires the preservation of ecosystems, species, and their genes (IUCN 2011), so information on within-species genetic diversity and spatial structure is essential to conservation practitioners. The Esocidae, which are fishes native to the freshwaters of Asia, Europe, and North America, have been considered to contain lower levels of within-population diversity than other freshwater fishes based on studies of Northern Pike Esox lucius (Hansen et al. 1999; Senanan and Kapuscinski 2000; Miller and Senanan 2003). The genetic diversity and structure of the Muskellunge E. masquinongy, the largest member of Esocidae, has not been described across its native range. The Muskellunge is a long-lived species (up to 30 years; Casselman et al. 1999) with overlapping generations (Scott and Crossman 1998) and is the apex aquatic predator throughout its native range in eastern North America, which includes nearshore habitats of the Great Lakes. Unfortunately, the Muskellunge has suffered significant population declines and local extinctions due in part to overexploitation and the
ongoing degradation and loss of spawning and nursery habitats (Wihllans 1979; Trautman 1982; Farrell et al. 2007; Kapuscinski et al. 2007). Despite these population declines, Muskegullung are still economically important as sport fish (Menz and Wilton 1983; New York Power Authority 2005; Simonson 2008) and are managed by multiple environmental agencies in Canada and the USA.

Contemporary Muskegullung populations typically occur at low densities and are difficult to sample, so substantial information on Muskegullung reproductive biology, genetic diversity, and stock structure are lacking. The Muskegullung is a spring spawner that broadcasts eggs near shore (<1.5-m depth) among submerged aquatic vegetation and provides no parental care (Farrell et al. 1996; Scott and Crossman 1998; Zorn et al. 1998; Farrell 2001). A dult Muskegullung implanted with radio transmitters have been shown to move up to 98 km away from spawning sites postspawn (LaPan et al. 1996), and several researchers have captured tagged Muskegullung at the same spawning location in multiple years (Crossman 1990; Farrell et al. 2007; Jennings et al. 2011). Natality philopatry is assumed to be the mechanism that maintains genetic spatial structure of other vagile fishes in the Great Lakes such as the Lake Sturgeon Acipenser fulvescens (DeHaan et al. 2006) and Walleye Sander vitreus (Stepien et al. 2009), but it is unknown if spawning-site fidelity by Muskegullung is natal philopatry that influences genetic spatial structure. Although many advances in molecular techniques have recently been made, only a single published study has attempted to examine genetic diversity among several Muskegullung populations from a wide geographic range (Koppelman and Philipp 1986). Koppelman and Philipp (1986) assessed genetic diversity of Muskegullung from nine potential populations (five wild and four hatchery populations) using 10 polymorphic isozyme loci. While their study was limited by small sample sizes (n = 2–26 per potential population) and the use of isozyme loci that have largely been replaced by microsatellite loci in studies of genetic population structure, Koppelman and Philipp (1986) were able to demonstrate the existence of genetic variation among populations. However, they considered their study preliminary because of these aforementioned limitations and called for a more extensive genetic analysis that has not yet been conducted. As a consequence of the lack of information on the genetic structure of Muskegullung, fish have been stocked across drainage boundaries and Muskegullung in large bodies of water are typically managed as single stocks, even where demographic evidence for intrasystem stock structure exists (Haas 1978; Mooradian et al. 1986; Strand 1986; Bryant and Smith 1988; Crossman 1990; Farrell et al. 2007).

Stocking Muskegullung has been a common management action in many areas of the Great Lakes to supplement or reintroduce populations. For example, the upper Niagara River was stocked with 408,000 Muskegullung fry during 1941–1955 that were progeny of Chautauqua Lake (New York) Muskegullung and 18,425 fingerlings during 1960–1974 that were progeny of Stony Lake (Ontario) Muskegullung (M. Wilkinson, New York State Department of Environmental Conservation, personal communication). A total of 553,800 Muskegullung fry (<50 mm), 682,081 fingerlings (50–270 mm), and 195 juveniles (<270 mm) also were stocked in Lac des Deux Montagnes and the Montreal region of the St. Lawrence River during 1950–1997; fish of known origin were progeny of Chautauqua Lake (New York) Muskegullung (Y. de Lafontaine, Environment Canada, personal communication). In addition, 119,000 Muskegullung fry (mean length = 24 mm) and 763 fingerlings (mean length = 76 mm) that were progeny of locally caught, wild fish were stocked into a total of 10 sites on the St. Lawrence River during 1990–1992, 1994, and 1996 for an experiment (Farrell and Werner 1999). Finally, the Fox River (a tributary to Green Bay, Lake Michigan) was stocked with progeny of Muskegullung captured from the Indian River Spreads (northcentral Michigan) and Lake St. Clair in most years since 1989 as part of a reintroduction program (Kapuscinski et al. 2007). Although stocking has been widespread, effects on the integrity of the Muskegullung genome have not been quantified. A assessment of the spatial genetic structure of Muskegullung populations is an important first step toward genetic conservation and understanding what effects, if any, stocking has had on the genome (Koppelman and Philipp 1986).

Losses of genetically distinct Muskegullung populations, whether caused by introgression with stocked fish or failures to protect populations and their critical habitats, could ultimately reduce the species’ ability to adapt to environmental changes. Therefore, sound management plans for Muskegullung could usefully consider genetic issues such as differentiation among spawning groups, conservation of rare alleles, and inbreeding depression. The objective of our study was to determine if interpopulation diversity and genetic spatial structure exists among the putative Muskegullung populations in the Great Lakes and to quantify this diversity and structure to inform management plans that will be effective at conserving the species’ evolutionary potential. In addition, we discuss how patterns in genetic structure relate to the results of Muskegullung movement studies that indicated reproductive homing and how within-population diversity of Muskegullung compares to other freshwater fishes. The genetic variation of potential Muskegullung populations was compared at 13 microsatellite loci; microsatellite loci were chosen because (1) they are highly polymorphic and therefore ideal for analyses of genetic variation among small potential populations (Allendorf and Luikart 2007), (2) they allowed for nonlethal sampling, and (3) developed markers being used in multiple locations across the Muskegullung native range were available (Sloss et al. 2008a). It was our aim that the results of this study would benefit resource managers by identifying appropriate scales for fishery management and protection of spawning and nursery habitats and by determining population boundaries, across which stocking could risk disrupting potential locally adapted gene complexes.
**METHODS**

Sampling locations.—Muskellunge were collected from 15 areas throughout the Great Lakes drainage, including (1) the Fox River, a tributary to Green Bay, Lake Michigan; (2) Pointe Au Baril, Georgian Bay, Lake Huron; (3) Moom River, Georgian Bay, Lake Huron; (4) Severn Sound, Georgian Bay, Lake Huron; (5) Lake St. Clair; (6) Buffalo Harbor, Lake Erie; (7) the upper Niagara River; (8) the lower Niagara River; (9) the Thousand Islands region of the St. Lawrence River; (10) Blind Bay, a known spawning location in the eastern Thousand Islands region of the St. Lawrence River; (11) Garlock Bay, a known spawning location at the eastern edge of the Thousand Islands region of the St. Lawrence River; (12) the St. Lawrence River below the dam at Massena, New York (hereafter M assena); (13) the Grasse River, a tributary to the St. Lawrence River; (14) Lac des Deux Montagnes, Quebec; and (15) the St. Lawrence River near Montreal, Quebec (Table 1; Figure 1). The geographic area of sampling localities ranged from point locations (e.g., trap nets or immediately placed in vials containing nondenatured 100% ethanol. Attempts were made to collect ≥50 Muskellunge from each area, but low capture numbers often made this impractical. Therefore, sample sizes ranged from 10 (M assena) to 127 (Lake St. Clair) individuals.

DNA extraction and microsatellite genotyping.—All DNA extractions and microsatellite genotyping were conducted by the Molecular Conservation Genetics Laboratory, College of Natural Resources, University of Wisconsin–Stevens Point. Genomic DNA from individual tissue samples was extracted using the Promega Wizard Genomic DNA purification kit (Promega, Madison, Wisconsin) modified for 96-well extractions with rehydration of the DNA in 100 μl of tris-low-EDTA buffer solution (TLE; 10mM NaCl, 0.1 mM EDTA, pH 8.0). Extracted DNA was quantified using a Nanodrop ND-1000 spectrophotometer (Nanodrop Technologies, Wilmington, Delaware). All DNA samples were normalized to a final concentration of 20 ng/μL prior to genotyping. Thirteen of the 14 microsatellite loci described by Sloss et al. (2008a) were used to genotype individual

**TABLE 1. Summary of genetic diversity measures calculated from 13 microsatellite loci of Muskellunge sampled from 15 potential populations including sample size N, expected heterozygosity H_e and standard deviation H_e SD, observed heterozygosity H_o and standard deviation H_o SD, mean number of observed alleles per locus A and standard deviation A SD, mean allelic richness per locus after rarefaction A_r, observed number of private alleles PA, and mean number of private alleles per locus after rarefaction PA_r.**

<table>
<thead>
<tr>
<th>Population</th>
<th>Latitude</th>
<th>Longitude</th>
<th>N</th>
<th>H_e</th>
<th>H_e SD</th>
<th>H_o</th>
<th>H_o SD</th>
<th>A</th>
<th>A SD</th>
<th>A_r</th>
<th>PA</th>
<th>PA_r</th>
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<td>Fox River (Lake Michigan)</td>
<td>44°28′36.07″N</td>
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<td>0.5242</td>
<td>0.0865</td>
<td>0.5114</td>
<td>0.0135</td>
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<td>0.44</td>
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<td>27</td>
<td>0.4900</td>
<td>0.0727</td>
<td>0.4843</td>
<td>0.0267</td>
<td>4.23</td>
<td>3.11</td>
<td>3.46</td>
<td>1</td>
<td>0.08</td>
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<td>0.0240</td>
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<td>0.5656</td>
<td>0.0785</td>
<td>0.5240</td>
<td>0.0346</td>
<td>5.15</td>
<td>3.69</td>
<td>4.49</td>
<td>4</td>
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<td>82°27′43.03″W</td>
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<td>0.5422</td>
<td>0.0775</td>
<td>0.5253</td>
<td>0.0126</td>
<td>7.31</td>
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<td>0.5198</td>
<td>0.0618</td>
<td>0.4530</td>
<td>0.0325</td>
<td>5.00</td>
<td>3.16</td>
<td>4.06</td>
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<td>78°56′12.77″W</td>
<td>113</td>
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<td>0.0643</td>
<td>0.4498</td>
<td>0.0130</td>
<td>5.77</td>
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<td>79°03′17.78″W</td>
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<td>76°00′57.42″W</td>
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<td>0.5226</td>
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<td>0.0389</td>
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<td>2.90</td>
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<tr>
<td>Garlock Bay (St. Lawrence River)</td>
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<td>75°56′43.88″W</td>
<td>16</td>
<td>0.5029</td>
<td>0.0715</td>
<td>0.4924</td>
<td>0.0356</td>
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<td>3.03</td>
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<td>74°47′40.85″W</td>
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<td>0.0691</td>
<td>0.5154</td>
<td>0.0438</td>
<td>4.38</td>
<td>2.96</td>
<td>4.38</td>
<td>0</td>
<td>0.11</td>
</tr>
<tr>
<td>Grasse River (St. Lawrence River tributary)</td>
<td>44°44′53.01″N</td>
<td>75°07′47.18″W</td>
<td>15</td>
<td>0.5034</td>
<td>0.0593</td>
<td>0.4769</td>
<td>0.0358</td>
<td>3.46</td>
<td>1.66</td>
<td>3.25</td>
<td>0</td>
<td>0.09</td>
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<tr>
<td>Lac des Deux Montagnes</td>
<td>45°30′03.72″N</td>
<td>73°56′17.06″W</td>
<td>37</td>
<td>0.6103</td>
<td>0.0578</td>
<td>0.6119</td>
<td>0.0226</td>
<td>5.85</td>
<td>4.45</td>
<td>4.45</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td>St. Lawrence River, near Montreal</td>
<td>45°30′08.63″N</td>
<td>73°32′03.72″W</td>
<td>64</td>
<td>0.5974</td>
<td>0.0595</td>
<td>0.6072</td>
<td>0.0172</td>
<td>6.77</td>
<td>5.53</td>
<td>4.62</td>
<td>0</td>
<td>0.04</td>
</tr>
</tbody>
</table>
Muskellunge and determine genetic variation among the 15 potential populations; locus EmAD12a failed in a subset of samples and was therefore removed from all records prior to analysis. Five multiplex PCR reactions were used for each sample to amplify individual loci with fluorescently labeled primers (Sloss et al. 2008a). Microsatellite variation was visualized on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, California). An in-lane standard (GeneFlo 625; Chimerx, Milwaukee, Wisconsin) was included with all samples and GeneMapper 4.0 genetic analysis software (Applied Biosystems) identified individual genotypes that were visually verified and entered into a master database.

Data analysis.—Population (sample) conformance to Hardy-Weinberg equilibrium (HWE) expectations was tested using the chi-square test implemented in GENALEX 6.3 (Peakall and Smouse 2006). Because of known biases with highly polymorphic loci and HWE tests, all locus and population comparisons with statistically significant chi-square tests were retested for deviations from HWE after rare genotypes (expected frequency < 1; Hedrick 2000) were pooled into one expected and one observed frequency value. A sequential Bonferroni correction (initial $\alpha = 0.05$ for all tests herein; Rice 1989) was applied.

Next, gametic disequilibrium between each locus pair was tested to determine if loci were linked or independently assorted. Fisher’s exact tests for each locus pair were performed in GENEPOP 4.0 (Raymond and Rousset 1995a, 1995b) using a Markov chain method (10,000 dememorization steps, 100 batches, and 5,000 iterations/batch; Guo and Thompson 1992), and a sequential Bonferroni correction was applied to the resulting $P$-values.

The genetic variation of populations was compared using the following measures: (1) expected heterozygosity $H_e$,
used iterative STRUCTURE analysis to determine if further hierarchical structure (multiple spawning groups) existed within the populations. Following the suggestions of Pritchard et al. (2000), we based on a minimum sample size of 10 individuals (20 genes).

Genetic differentiation among potential populations was quantified with pairwise comparisons of (1) Weir and Cockerham’s (1984) $\theta$, an analog of Wright’s (1931) $F_{ST}$, that uses a weighted analysis of variance (ANOVA) to quantify the amount of allelic variation in the entire sample that is attributable to differences among potential populations, and (2) harmonic means (across all loci) of Jost’s $D$ (Jost 2008), which provides the proportion of each potential population’s alleles that are unique to that group. Tests of $\theta$ and significant deviations from zero were conducted in ARLEQUIN 3.5.1.2 (1,000 permutations; Excoffier and Lischer 2010), and harmonic means of $D$ were calculated in SMGD 1.2.5 (1,000 bootstrap replicates; Crawford 2010). We then used the values of $\theta$ and $D$ from each potential population pair to generate two similarity matrices (similarity $= 1 - \theta$ and $1 - D$), and created a nonmetric multidimensional scaling model (NMDS; SAS 9.2, SAS Institute, Cary, North Carolina) based on each to visually examine the genetic similarity among populations.

We further examined the spatial genetic structure of Muskellunge populations with the Bayesian algorithm implemented in the program STRUCTURE 2.3.3 (Pritchard et al. 2000), using the following hierarchical approach. First, we excluded the Fox River population because it was introduced, and then evaluated the remaining data set (583 Muskellunge from 14 populations) for $K = 1$–12 potential discrete groups (five runs per $K$ value) with the following conditions: (1) 500,000 replicate burn-ins followed by 500,000 replicates, (2) the admixture model with a uniform prior on the degree of admixture $\alpha$ (initial value $= 1$, maximum $= 10$, SD $= 0.025$), and (3) allele frequencies were considered correlated among populations (prior mean $= 0.01$, prior SD $= 0.05$, $\lambda = 1$). The best estimate of $K$ groups was chosen following the methods of Evanno et al. (2005), using STRUCTURE HARVESTER 0.56.4 (Earl 2010). Each group was then evaluated for $K = n + 2$ (where $n$ is the number of populations within a group) potential discrete subgroups using the conditions outlined above to determine whether spatial genetic structure (multiple spawning groups) existed within the group. Following the suggestions of Pritchard et al. (2000), we used iterative STRUCTURE analysis to determine if further hierarchical structure existed in the data. After $K$ was determined as described above, each population sample was categorically put into discrete subgroups for testing based on its majority Q-value score. The composite subgroups were then tested using STRUCTURE as described.

Next, we performed a hierarchical analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010) to compare the molecular variance within and between population groups. The population groups tested were those suggested during three main steps of the STRUCTURE analysis ($K = 2$, 5, and 8). Significance levels for each AM OVA were calculated using 50,175 permutations of the data (Excoffier et al. 1992), and the three different grouping strategies were evaluated based on which maximized molecular variance among groups and minimized molecular variance among populations within groups.

Finally, tests of isolation by distance (IBD) were conducted using the ISOLATION BY DISTANCE WEB SERVICE 3.21 (Jensen et al. 2005) to determine if migration between populations influenced spatial genetic structure. The IBD tests consisted of a reduced major axis regression of pairwise $\theta$ and $D$ values against pairwise geographical distance measurements (distance in kilometers between each population pair measured across water), followed by a Mantel test (Mantel 1967) with 999 randomizations to determine the statistical significance of the relation between genetic and geographic distance measures. In initial IBD tests, the relations of $\theta$ versus geographic distance and $D$ versus geographic distance were nonlinear, with an inflection at Niagara Falls. Therefore, prior to the final IBD tests reported here, the $\theta$ versus geographic distance and $D$ versus geographic distance matrices were each divided into two matrices based on whether potential populations were located upstream or downstream of Niagara Falls. The Fox River population was excluded from IBD tests because it was established by stocking, with one of the sources having been the Lake St. Clair population.

RESULTS
A total of 691 individual Muskellunge samples remained for analyses after duplicates (e.g., recaptured Muskellunge) were removed and records with genotype data missing from five or more loci were excluded. The number of alleles per locus (across all populations) ranged from 2 to 12 and averaged 10.4. All populations were considered to conform to HWE expectations for subsequent analyses because only one of 184 (0.5%) exact tests deviated from HWE following sequential Bonferroni correction (locus EmaA11 for the FOX population). Linkage analysis, excluding the FOX population because it resulted from a small number of founding events, showed 12 significant locus-by-locus comparisons following sequential Bonferroni correction within populations (66 comparisons per population); the maximum number of significant locus pair comparisons was three. Given a total of 924 locus pair comparisons, we concluded the data conformed to overall linkage equilibrium expectations with the 12 significant comparisons being the result of genetic drift within select populations.

Each locus was polymorphic for each population, with the following exceptions: (1) locus Ema-A10 was monomorphic for the Moon River population, (2) Ema-D4 was monomorphic for the Blind Bay and Garlock Bay populations, and (3) Ema-A104 was monomorphic for the Fox River, Pointe Au Baril, Severn Sound, Lake St. Clair, Buffalo Harbor, the upper
SLR populations) to 5 (Fox River), averaged 1.5, and was positively
from 3.25 (Grasse River) to 4.62 (Montreal) and averaged 4.06. Where the mean allelic richness following rarefaction ranged
3.46 (Grasse River) to 7.31 (Lake St. Clair), with a mean of 5.20,
of 0.5067. The mean number of alleles per locus ranged from
Observed heterozygosity values ranged from 0.4498 (upper Ni-
expected heterozygosity values ranged from
0.4564 (upper Niagara River) to 0.6103 (Lac des Deux Montagnes, and MON = St.
Whereas the mean allelic richness following rarefaction ranged
from 0.01 (Garlock Bay) to 0.27 (Fox River–Grasse River pair) and averaged 0.1428 across all
additional seven population pairs had D values < 0.05. Values of θ ranged from -0.0025 (effectively zero; Thousand Islands
region of the St. Lawrence River–Garlock Bay pair) to 0.2510 (Fox River–Grasse River pair) and averaged 0.1428 across all
population pairs. Values of D ranged from 1.3 × 10^{-7} (up-
upper Niagara River–lower Niagara River pair) to 0.2712 (Fox River–Grasse River pair) and averaged 0.11 across all
population pairs. Genetic similarities among populations (1–θ and
1–D), as illustrated with N M D S models, were consistent with the expectation that populations in close geographic proximity
would be more similar than distant population pairs. For example, Buffalo Harbor, the upper Niagara River, and the lower
Niagara River populations, which are geographically adjacent to
one another (centers of sampling areas about 12–60 km apart),
showed a high level of genetic similarity (Figure 2), whereas
g eographically distant pairs of native populations (e.g., the Pointe Au Baril–Grasse River pair; separated by about 1,330 km)
showed the greatest genetic differentiation. Additionally, the six
St. Lawrence River populations were clustered close to one an-
other in the N M D S models, indicating that they were genetically
more similar to each other than to more geographically distant

Niagara River, the lower Niagara River, and the Grasse
River populations. Expected heterozygosity values ranged from
0.4564 (upper Niagara River) to 0.6103 (Lac des Deux Montagnes, with a mean across all populations of 0.5274 (Table 1).
Observed heterozygosity values ranged from 0.4498 (upper Ni-
agara River) to 0.6119 (Lac des Deux Montagnes), with a mean of 0.5067. The mean number of alleles per locus ranged from
3.46 (Grasse River) to 7.31 (Lake St. Clair), with a mean of 5.20,
whereas the mean allelic richness following rarefaction ranged
from 3.25 (Grasse River) to 4.62 (Montreal) and averaged 4.06. The number of private alleles per population ranged from 0 (six populations) to 5 (Fox River), averaged 1.5, and was positively
related to sample size (Pearson’s correlation coefficient = 0.524,
= 0.022 for a one-tailed test). The mean number of private alleles per locus following rarefaction ranged from 0.01 (Garlock Bay) to 0.44 (Fox River) and averaged 0.12.

Patterns of genetic differentiation among pairs of potential
populations were consistent whether calculated by θ or D. All
but nine population pairs were significantly different according to
timates of θ, and each of these nine pairs had D values
< 0.05 (i.e., <5% allelic difference between pairs; Table 2); an

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<th>PAB</th>
<th>MOR</th>
<th>SEV</th>
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<th>LNR</th>
<th>SLR</th>
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Values in parentheses; an asterisk indicates
= 0.0001) calculated across 13 microsatellite loci for 15 potential populations of Muskellunge in the Great Lakes. Population abbreviations are as follows: FOX = Fox River, PAB = Pointe Au Baril, MOR = Montreal River, SEV = Severn Sound, LSC = Lake St. Clair, BUH = Buffalo Harbor, UNR = upper Niagara River, LNR = lower Niagara River, SLR = St. Lawrence River, BLB = Blind Bay, GAR = Garlock Bay, MAS = Massena, GRA = Grasse River, LDM = Lac des Deux Montagnes, and MON = St. Lawrence River near Montreal.
populations. The Grasse River population was positioned closer to the St. Lawrence River populations than others, consistent with its connectivity to the St. Lawrence River.

The Bayesian clustering algorithm of the program STRUCTURE (Pritchard et al. 2000) identified two likely grouping scenarios (K = 2 and K = 5) for M uskellunge sampled from the 14 potential populations (Figure 3). The hierarchical approach further parsed the K = 5 groups into eight total groups (Figure 3). Percent assignment of M uskellunge from each potential population to the most likely group averaged 89% (range 83–94%) for K = 2, 78% (range 55–89%) for K = 5, and 82% (range 55–95%) for K = 8 (Table 3).

In the three subsequent AMOVA analyses, 82.42–87.04% of molecular variance was attributed to differences among individual M uskellunge (Table 4). Of the three grouping scenarios tested (Table 3; Figure 3), the eight-group AMOVA maximized the amount of molecular variance among groups and minimized the amount of molecular variance among populations within groups. The assignment of 14 populations into eight groups, as suggested by the program STRUCTURE and supported by AMOVA, is consistent with patterns observed from the genetic differentiation measures \( \theta \) and D. No pair of populations within a group had D values >0.05, and only the Lac des Deux Montagnes–Montreal pair \( (\theta = 0.02, P = 0.0020) \) and Blind Bay–M ussassa pair \( (\theta = 0.0416, P = 0.0147) \) had significant \( \theta \) values.

M uskellunge in the Great Lakes exhibited a strong pattern of IBD that was statistically significant whether based on \( \theta \) (linear regression, \( P < 0.001, r^2 = 0.678 \) above Niagara Falls; \( P < 0.001, r^2 = 0.392 \) below Niagara Falls; Figure 4) or D (linear regression, \( P < 0.001, r^2 = 0.704 \) above Niagara Falls; \( P < 0.001, r^2 = 0.460 \) below Niagara Falls; Figure 5). This pattern was consistent with results from the program STRUCTURE, which only assigned geographically proximate populations into common groups.

### DISCUSSION

Significant spatial structuring of M uskellunge genetic resources in the Great Lakes was evident from multiple methods of examination, including NMDS models of genetic similarity (1–\( \theta \) and 1–D), results of the Bayesian clustering algorithm generated with the program STRUCTURE, AMOVA, tests of isolation by distance, and the presence of private alleles in 9 of the 15 potential populations sampled. Most populations examined were geographically distant enough to prevent reproductive mixing at rates high enough to cause genetic homogenization. For example, M uskellunge populations from three areas in Georgian Bay that are about 50–100 km apart had significant pairwise \( \theta \) values ranging from 0.0404 to 0.1030, mean pairwise D values ranging from 4% to 8%, and contained private alleles. While Koppel- man and Philipp’s (1986) results from isozyme loci supported the hypothesis that genetically distinct stocks of M uskellunge likely existed, our work clearly shows spatial genetic structure of M uskellunge populations across the Great Lakes basin and describes how genetic resources are partitioned in the Great Lakes.

These findings are also evidence that stocking of M uskellunge in the Great Lakes basin has not eradicated underlying genetic structure and likely signify locally adapted groups with genetic resources critical for conservation of Great Lakes M uskellunge. M uskellunge sampled from Buffalo Harbor, the upper Niagara River, and the lower Niagara River, which are separated by about 10–60 km, were genetically very similar but collectively very different from all other populations. The small sample sizes from Buffalo Harbor \( (n = 18) \) and the lower Niagara River \( (n = 12) \) make conclusive statements about genetic differentiation among these areas tenuous. However, the significant amount of habitat destruction that has occurred in this region could have eliminated areas that once supported distinct spawning groups of M uskellunge and forced reproductive mixing (genetic homogenization) in the remaining suitable habitats. For example, about 60% of the upper Niagara River shoreline is armored with bulkhead, riprap, or other materials (Wooster and M atthies 2008), and more than 75% of wetlands are thought to have been destroyed (Whillans 1982; NY SDEC 1994). Furthermore, M uskellunge stocked in the Niagara River that were progeny of fish from Chautauqua Lake (New York) and Stony Lake (Ontario) may have introgressed with native M uskellunge of Buffalo Harbor and the Niagara River, contributing to the genetic similarity within these waters and dissimilarity with other populations (see Management Implications and Research Needs, below). In addition to the genetic homogenization that may have resulted from habitat destruction and stocking, downstream migration probably contributes to the genetic similarity of M uskellunge in Buffalo Harbor and the Niagara River. Recapture data from M uskellunge tagged by anglers and in agency surveys shows downstream migration among Buffalo Harbor, the upper Niagara River, and the lower Niagara River areas, whereas no upstream movement has been observed (Niagara M usky Association and K. L. Kapuscinski, unpublished data). Of the 10 recaptures of M uskellunge tagged in Buffalo Harbor with complete tag–recapture records, eight occurred in Buffalo Harbor and two occurred downstream in the upper Niagara River. Similarly, of the 51 recaptures of M uskellunge tagged in the upper Niagara River, 50 occurred in that same stretch of river and 1 occurred in the lower river, confirming downstream passage of Niagara Falls occurs.

The observed genetic structure of M uskellunge in the Great Lakes and the presence of IBD are consistent with results of tag–recapture studies on the species. L aPan et al. (1996), who implanted St. Lawrence River M uskellunge with radio transmitters during the spawning season, tracked their postspawning movements, and recaptured them the following spawning season, concluded that M uskellunge returned to the same spawning area in successive years despite migrating about 30–80 km away after spawning. In addition, all 33 M uskellunge tagged and recaptured during the spawning season over many years in the Thousands Islands region of the St. Lawrence River were
FIGURE 2. First two dimensions for NMDS analysis of genetic similarity quantified as 1-θ (top panel) and 1-D (bottom panel) for 15 potential populations of Great Lakes Muskellunge. Note: solid lines connect population pairs with θ values that did not differ (top) or D values < 0.05 (bottom), dashed ovals indicate populations assigned to common groups by the program STRUCTURE, and population abbreviations are as follows: FOX = Fox River, PAB = Pointe A u Baril, MOR = Moon River, SEV = Severn Sound, LSC = Lake St. Clair, BUH = Buffalo Harbor, UNR = upper Niagara River, LNR = lower Niagara River, SLR = St. Lawrence River, BLB = Blind Bay, GAR = Garlock Bay, MAS = Massena, GRA = Grasse River, LDM = Lac des Deux Montagnes, and MON = St. Lawrence River near Montreal.
MUSKELLUNGE GENETICS

FIGURE 3. Plot of mean $Q$-values for all sampled individuals for $K = 5$. The two-colored bar under the plot shows the majority distribution for $K = 2$ (see A in Table 3). Results of iterative STRUCTURE analysis are presented below the plot for each of the five predicted groups. Plots of mean $Q$-values for all sampled individuals for PAB–MOR–SEV (see B in Table 3) and GRA–LDM–MON (see C in Table 3) are below each group. Population abbreviations are as follows: FOX = Fox River, PAB = Pointe au Baril, MOR = Moon River, SEV = Severn Sound, LSC = Lake St. Clair, BUH = Buffalo Harbor, UNR = upper Niagara River, LNR = lower Niagara River, SLR = St. Lawrence River, BLB = Blind Bay, GAR = Garlock Bay, MAS = Massena, GRA = Grasse River, LDM = Lac des Deux Montagnes, and MON = St. Lawrence River near Montreal. [Figure available online in color.]

Recaptured at the original tagging location despite having more than 100 known spawning-nursery sites in the region (Farrell et al. 2007), providing further evidence of philopatry. Muskellunge in Stony Lake, Ontario (Crossman 1990), and four Wisconsin lakes (Jennings et al. 2011) also made postspawning movements away from spawning sites and exhibited reproductive philopatry in subsequent years. Reproductive philopatry by Muskellunge and the considerable geographic separation of Great Lakes populations has likely facilitated the creation and further strengthening of the spatial genetic structure described above. Researchers using tag-recapture and genetic data found evidence of spawning-site and natal-site fidelity by the congeneric Northern Pike in the upper Niagara River (Harrison and Hadley 1978), the St. Lawrence River (Bosworth and Farrell 2006), and the relatively large (>10,000 ha) Abetogama Lake (Miller et al. 2001). Isolation by distance also was considered important in shaping the genetic structure of Northern Pike in the Baltic Sea (Laikre et al. 2005), and distinct spawning groups have been identified that either reproduce in fresh or brackish waters, but not both (Westin and Limburg 2002).

Esocids have typically been considered to contain low within-population genetic variation, but results from recent studies suggest this is not the case. Early studies of Northern Pike, although broad in geographic scope, found low levels of within-population genetic variation. For example, mean $H_e = 0.14$ at eight microsatellite loci for 20 populations throughout the global range of Northern Pike (Senanan and Kas榃sinski 2000) and mean $H_e = 0.24$ at 13 loci for two Danish populations (Hansen et al. 1999). These findings led Miller and Senanan (2003) to conclude that Northern Pike contained lower genetic variation than many other fishes, including sympatric Walleye and Yellow Perch Perca flavescens; no comparable data were available for the congeneric Muskellunge at the time. Subsequent studies of Northern Pike found relatively high levels of within-population genetic variation. Laikre et al. (2005), using five of the eight loci used by Senanan and Kas雅黑ski (2000), found mean $H_e = 0.54$ for Northern Pike from nine sites in the Baltic Sea. Bosworth and Farrell (2006), who used the six most polymorphic loci from an initial suite of 14, found mean $H_e = 0.66$ for Northern Pike from four sites in the upper St. Lawrence River.

The use of different suites of loci in these studies makes direct comparisons difficult and highlights the need for the use of standardized suites of loci. Our study used 13 of the 14 loci identified by Sloss et al. (2008a) that also were used in two other recent studies of Muskellunge, so comparisons can be made regarding within-population genetic variation across a large portion of the range of Muskellunge. The mean $H_e = 0.53$ for Muskellunge from 15 areas of the Great Lakes was similar to that observed for Muskellunge from 43 water bodies in northern Wisconsin ($H_e = 0.56$; Spude 2010), both much greater than the genetic variation of Muskellunge from Shoepack Lake in northern Minnesota ($H_e = 0.25$; Miller et al. 2009). For the 55 total Muskellunge populations sampled to date, $H_e$
TABLE 3. Mean population-specific Q-value of each predicted genetic unit for (A) \( K = 2 \) and \( K = 5 \), the two most likely number of genetic units according to the Evanno et al. (2005) method (Figure 3), (B) all individual Muskellunge sampled from PAB–MOR–SEV, and (C) all individual Muskellunge sampled from GRA–LDM–MON. Colors below group designations are from Figure 3, and population abbreviations are as follows: FOX = Fox River, PAB = Pointe Au Baril, MOR = Moon River, SEV = Severn Sound, LSC = Lake St. Clair, BUH = Buffalo Harbor, UNR = upper Niagara River, LNR = lower Niagara River, SLR = St. Lawrence River, BLB = Blind Bay, GAR = Garlock Bay, MAS = Massena, GRA = Grasse River, LDM = Lac des Deux Montagnes, and MON = St. Lawrence River near Montreal.

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TABLE 4. Analysis of molecular variance (AMOVA), including sum of squares SS, percent variance, and fixation index (F) explained by source for three grouping strategies of Muskellunge sampled from 14 potential populations in the Great Lakes. The P-values for each variance component were < 0.003. Population abbreviations are as follows: FOX = Fox River, PAB = Pointe Au Baril, MOR = Moon River, SEV = Severn Sound, LSC = Lake St. Clair, BUH = Buffalo Harbor, UNR = upper Niagara River, LNR = lower Niagara River, SLR = St. Lawrence River, BLB = Blind Bay, GAR = Garlock Bay, MAS = Massena, GRA = Grasse River, LDM = Lac des Deux Montagnes, and MON = St. Lawrence River near Montreal.

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FIGURE 4. Pairwise θ (top panel) and D (bottom panel) calculated across 13 microsatellite loci for potential populations of Muskellunge in the Great Lakes upstream of Niagara Falls versus geographic distance (km) between potential populations. Note: the lines, equations, and $r^2$ values resulted from reduced major axis regressions, $P_M$ denotes the $P$-values of Mantel tests with 999 permutations, and $r$ denotes the correlation coefficients from the Mantel tests.
FIGURE 5. Pairwise θ (top panel) and D (bottom panel) calculated across 13 microsatellite loci for potential populations of Muskellunge in the Great Lakes downstream of Niagara Falls versus geographic distance (km) between potential populations. Note: the lines, equations, and $r^2$ values resulted from reduced major axis regressions, $P_M$ denotes the P-values of Mantel tests with 999 permutations, and $r$ denotes the correlation coefficients from the Mantel tests.
ranged from 0.25 (Shoepack Lake; Miller et al. 2009) to 0.61 (Lac des Deux Montagnes, this study; Grindstone Lake, Spude 2010) and averaged 0.54. This mean level of within-population variation is essentially equivalent to that reported for Yellow Perch in Lake Michigan \((H_e = 0.54;\) Miller 2003) and Brook Trout Salvelinus fontinalis in Lake Superior \((H_e = 0.55;\) Sloss et al. 2008b), but less than that reported for Lake Sturgeon in the upper Great Lakes \((H_e = 0.63;\) DeHaan et al. 2006), Walleyes in the Great Lakes \((H_e = 0.78;\) Stepnie et al. 2009), and Lake Whitefish Coregonus clupeaformis in Lake Michigan \((H_e = 0.64;\) VanDeHey et al. 2009). On average, the within-population variation exhibited by \(M\) uskellunge is equal to that reported by DeWoody and Avise (2000) for 13 freshwater fish species \((H_e = 0.54);\) so \(M\) uskellunge, and perhaps the Esocidae more generally, should not be considered to have low levels of genetic variation.

**Management Implications and Research Needs**

Management plans for \(M\) uskellunge could focus on conserving individual populations, even those in close geographic proximity to each other within larger water bodies (e.g., Lake Michigan and Severn Sound populations in Georgian Bay, Lake Huron), and protecting individual spawning and nursery habitats. The significant spatial structuring of \(M\) uskellunge genetic resources in the Great Lakes, presence of private alleles in most populations, and evidence of reproductive philopatry by esocids suggest that robust \(M\) uskellunge populations and individual spawning and nursery habitats could be maintained as part of an effort to preserve the evolutionary potential of the species. Knowing whether the reproductive philopatry exhibited by \(M\) uskellunge is actually natal or site fidelity following adulthood would help further refine management plans for \(M\) uskellunge and their habitat, as suggested by Farrell et al. (2003). A thorough evidence suggestive of natal philopatry is mounting, this hypothesis has not been adequately tested, so the appropriate spatial scales for management of spawning and nursery habitat remain unidentified.

Research focused on obtaining movement data and genetic samples from multiple geographically proximate spawning groups (e.g., within Georgian Bay or the Thousand Islands region of the St. Lawrence River) should be able to provide this critical information, although obtaining adequate sample sizes will be a challenge. Until such a study is conducted, an approach that individually manages populations and fisheries and preserves all spawning and nursery habitats could be adopted to avoid losses of genetic resources.

Our study identified three additional areas of research that could enhance the management of \(M\) uskellunge in the Great Lakes and our understanding of the historical distribution of this species. First, a more extensive genetic analysis of \(M\) uskellunge from Buffalo Harbor and the upper and lower Niagara River (with larger sample sizes) is needed to determine if \(M\) uskellunge from these three areas are truly genetically similar or if the small sample sizes used in this study failed to detect more than one genetic unit. Second, an assessment is needed to determine if stocking \(M\) uskellunge across population boundaries has affected contemporary gene pools. For example, two brood sources (Indian River Spreads, north-central Michigan, and Lake St. Clair) were initially used for stocking Green Bay and its tributaries, but the effective contributions of each source to current populations are mostly unknown. Our results show genetic dissimilarity between the Fox River and Lake St. Clair populations, suggesting that most \(M\) uskellunge sampled from the Fox River were progeny of broodstock captured from the Indian River Spreads (not sampled in this study), rather than Lake St. Clair. A n in-depth analysis of source populations could adequately address this issue and rule out the unlikely possibility that remnant native \(M\) uskellunge persist—this is especially important because the majority of \(M\) uskellunge stocked into Green Bay since the program began in 1989 are progeny of recaptured stocked fish. Research is also needed to determine if the progeny of Chautauqua Lake (New York) and Stony Lake (Ontario) \(M\) uskellunge that were stocked into the Niagara and St. Lawrence rivers, which contained naturally reproducing populations of native fish, successfully reproduced and contributed to contemporary populations. The Niagara River was stocked with 408,000 fry during 1941–1955 that were progeny of Chautauqua Lake (New York) \(M\) uskellunge and 18,425 fingerlings during 1960–1974 that were progeny of Stony Lake (Ontario) \(M\) uskellunge (M. Wilkinson, New York State Department of Environmental Conservation, personal communication). A total of 1,236,076 \(M\) uskellunge from three size-classes \((<50\) mm, \(n = 553,800; 50–270\) mm, \(n = 682,081; >270\) mm, \(n = 195)\) were stocked into Quebec waters of the St. Lawrence River and its tributaries during 1950–1997 (Y. de Lafortune, Environment Canada, personal communication). Most of these stocked \(M\) uskellunge appear to have been progeny of Chautauqua Lake (New York) \(M\) uskellunge, but information on the origin of stocked fish is incomplete. Information on the presence and extent of introgression between stocked and native \(M\) uskellunge is needed so managers can mitigate negative consequences (e.g., see Miller et al. 2009) and avoid propagating nonnative \(M\) uskellunge within the Great Lakes. Finally, more extensive sampling of \(M\) uskellunge from throughout the Great Lakes and other drainages (i.e., the Ohio River, Mississippi River, Hudson Bay, and Atlantic drainages) could elucidate which areas served as glacial refugia and recolonization pathways. Understanding the historical distribution and contemporary genetic spatial structure of \(M\) uskellunge will help resource managers conserve the genetic resources of this important species.

Kopperman and Philipp (1986) stated that stocking \(M\) uskellunge into an established population may reduce fitness by irreversibly disrupting locally adapted gene complexes. This warning is repeatedly echoed in the fisheries literature (Crossman 1984; Reisenbichler and Rubin 1999; Miller and Kapschinski 2003; Jennings et al. 2010). If one assumes that observations of neutral (microsatellite) genetic diversity and spatial structure are indicative of adaptive variation in the genome, even at a remedial level, then our results strongly support these warnings.
Stocking Muskellunge across population boundaries into areas containing native Muskellunge increases the risk of disrupting adaptive genetic diversity.

ACKNOWLEDGMENTS

Many employees of the Thousand Islands Biological Station and the New York State Department of Environmental Conservation assisted with tissue sample collection. Paul Mckeown and Michael Wilkison (New York State Department of Environmental Conservation) provided extensive logistical support and help in the field. In addition, Arunas Liskauskas (Ontario Ministry of Natural Resources), David Rowe (Wisconsin Department of Natural Resources), Michael Thomas (Michigan Department of Natural Resources and Environment), and Simon Despatie and Yves de Lafontaine (Environment Canada) collected or coordinated the collection of Muskellunge tissue samples. Numerous anglers, including members of the Niagara Muskusky Association and Muskies Canada Gananoque and Thousand Islands Chapter, voluntarily submitted Muskellunge tissue samples; Rich Clarke, Scott Kitchen, Josh Ketry, Greg Reynolds, John Kennedy, J-P Cloutier, Mike Lazarus, Rocky Gauthier, and Jim Hutchings made especially significant contributions. Ryan Franchowiak and Brandon Spude coordinated and conducted genotyping of Muskellunge tissue samples. This work was funded by Federal Aid in Sport Fish Restoration Grants (most recently F-61-R) administered by the New York State Department of Environmental Conservation and a grant from the Niagara River Greenway Ecological Fund Standing Committee. This is a contribution of the Thousand Islands Biological Station. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Use of Ultrasonic Telemetry to Estimate Natural and Fishing Mortality of Red Snapper

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Use of Ultrasonic Telemetry to Estimate Natural and Fishing Mortality of Red Snapper

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Abstract
An accurate estimate of natural mortality is critical for the management of any fishery but is typically difficult to directly measure. Mortality rates for Red Snapper Lutjanus campechanus (n = 87) were estimated by telemetry from December 2005 to June 2009 in the northeastern Gulf of Mexico. At five separate sites an array of five receivers was deployed with one receiver at the center (reef) and four receivers placed 1,100 m (or 420 m) north, south, east, and west of center. These arrays enabled the direct estimation of fishing mortality, natural mortality, and emigration of acoustically tagged Red Snapper. Out of the 70 fish that remained after the 6-d recovery period, 19 were caught, 10 died naturally, and 27 emigrated from the 2-km-radius study sites. The Kaplan–Meier staggered-entry method was used to estimate survival from different mortality events, and survival was converted to instantaneous mortality rates. For all years combined, total mortality (95% confidence interval) was 0.39 (0.19–0.64), fishing mortality (F) was 0.27 (0.11–0.54), and natural mortality (M) was 0.11 (0.06–0.20). Each year estimated annual M increased, M = 0 in 2006, M = 0.19 (0.07–0.48) in 2007, and M = 0.21 (0.09–0.44) in 2008, while annual F rates decreased, F = 0.61 (0.16–1.67) in 2006, F = 0.22 (0.09–0.51) in 2007, and F = 0.14 (0.05–0.35) in 2008. Thus, in more recent years (2007–2008) M estimates were higher, while F estimates were lower than past estimates used in stock assessments (M = 0.1; F = 0.35). These decreasing rates of F over 2006–2008 suggests that in recent years restrictive management efforts have succeeded in reducing fishing mortality, and although M has increased it may have leveled off near M = 0.2 such that populations will continue to increase.

Historically, Red Snapper Lutjanus campechanus have supported important commercial and recreational fisheries in the Gulf of Mexico and are found over both natural and artificial reef habitats (Camber 1955; Mosley 1966; Beaumariage 1969; Bradley and Bryan 1975; Fable 1980; Stanley and Wilson 1989; Szedlmayer and Shipp 1994; Szedlmayer and Shipp 1994; Szedlmaier and Shipp 1994; Wattersen et al. 1998; Patterson et al. 2001; Szedlmayer and Schroepfer 2005; Westmeyer et al. 2007; Gallaway et al. 2009). Although approximately 14,000 of these artificial habitats have been built in the northern Gulf of Mexico, possibly enhancing available habitat for this reef-oriented species (Minton and Heath 1998; Gallaway et al. 2009), a recent assessment showed that the Red Snapper fishery was overfished (SEDAR 2009). To rebuild Red Snapper stocks, managers set an objective of rebuilding stock biomass to a maximum sustainable yield (MSY = 25.4 million pounds) by 2032, which may be accomplished with an instantaneous fishing mortality rate (F) of F msy = F spr 26% (F at 26% spawning potential ratio; SEDAR 2005; NOAA 2006; SEDAR 2009). This objective was based on a conservative assumption of instantaneous natural mortality (M) equal to 0.10/year; however, if M was actually higher, the goal of MSY may be achieved in a shorter period of time (Goodyear 1995; Schirripa and Legault 1999; Slipke and Maceina 2005). Therefore, to allow for an appropriate fishing level for Red Snapper in the northern Gulf of Mexico, it is important to obtain an accurate estimate of M.

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The Red Snapper fishery has continued for well over a century, and like most exploited fish stocks, the level of M for Red Snapper in the Gulf is not well defined (Camber 1955; Schirripa and Legault 1999). Total mortality (Z) has been obtained for Red Snapper from fishery-independent catch curve analysis (Gitschlag et al. 2003; Szedlmayer 2007); however, the separation of Z into its components of M and F has been difficult. Estimates of M for Red Snapper have been primarily derived from life history parameter equations based on maximum age, Von Bertalanffy growth coefficient K, and water temperature, with estimates of M for Red Snapper ranging from 0.02 to 0.40, with 95% confidence intervals of 0.02 to 1.0 (A1verson and Carney 1975; Pauly 1980; Nelson and M anouch 1982; Hoenig 1983; Goodyear 1995; Schirripa and Legault 1999). The presently applied value of M (0.10) is based on maximum ages of Red Snapper around 40–50 years (Hoenig 1983; Szedlmayer and Shipp 1994; Schirripa and Legault 1999; Wilson and Nieland 2001; SEDAR R 2005). This value of M (0.10) is conservative when compared with estimates of M based on other life history parameters. This uncertainty in M has led to cautious management practices and severe reductions in fishery quotas (Hood et al. 2007). Despite its critical importance in population assessment, direct estimates of natural mortality for Red Snapper have not been reported in the literature.

Recent advances in telemetry systems, such as continuous automated monitoring, long-life transmitters, and long-distance detection, have allowed researchers to directly estimate natural and fishing mortality in both fresh and saltwater environments (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pine et al. 2003; Pollock et al. 2004; Young and Isely 2004; Starr et al. 2005). With these advances in technology, estimates of mortality are possible for species like Red Snapper that inhabit large open water systems. In this study, strategic placement of remote telemetry receivers allowed separation of total declines in tagged fish into its component parts of emigration, natural mortality, and fishing mortality.

METHODS

Study Area

The study sites were located 20–30 km south of Mobile Bay, Alabama, an area that includes numerous artificial habitats (>10,000) and a few natural rock-reef habitats (Scroeder et al. 1988; Minton and Heath 1998). Red Snapper were tagged on one natural and four artificial habitats. Artificial habitats included a pipeline covered with a concrete mat (A1), a 15-m sunken barge (A2), a 6.9-m³ steel metal cage (A3), and an M-60 army tank (A4). The natural habitat site (N1) was composed of a 20-m long drowned riverbed (~1 m high, ~5 m apart), with undercut banks lined with tree stumps (Figure 1). Depths of the sites ranged from 20 to 30 m. These sites were a mix of public (published latitude, longitude) and private locations (Figure 1).

Fish Tagging

Red Snapper (>500 mm TL) were captured at the sites via hook and line and tagged with ultrasonic transmitters (Szedlmayer and Schroepper 2005). Fish were placed in a 70-L container of seawater containing M S-222 (tricaine methanesulfonate; 150 mg M S-222/L seawater) and quickly anesthetized (level 4; Summerfelt and Smith 1990). Fish were weighed and measured, and an ultrasonic transmitter was implanted through a small (18 mm) vertical incision into the peritoneal cavity with a number 11 scalpel slightly above the ventral midline and then sutured with plain gut suture (Ethicon, number 2, 3.5 metric). An internal anchor tag (Flgy) was also inserted into the incision before it was sutured. Sterile surgical methods and betadine were used throughout the procedure. The fish were released after being held at the surface for a short (~1 min) recovery period (when strong fin and gill movements were observed). Fish were released at the capture site by lowering fish to the bottom with weighted line with an inverted barbless hook that was attached to the fish’s lower jaw. Retrieval of the weighted line released the fish at the bottom near the reef.

Two types of transmitters were used for this study. Individually coded Vemco transmitters (V16-6 L-R64K; code intervals: 20–69 s, 16 × 94 mm, battery life: 6 years) were used at sites with Vemco V R2 receivers, and Sonotronics transmitters (CT-05-48; continuous, 16 × 79 mm, battery life: 4 years) were used at site A 4 with Sonotronics SUR-1 receivers. The effects of the transmitter implantation on the behavior or health of the Red Snapper were assumed to be negligible after a 6-d recovery period, because transmitter weights were <2% of the total body weight of the fish (Winter 1983; Adams et al. 1998; Brown et al. 1999). Maximum detection ranges were 1,600 m (Szedlmayer and Schroepper 2005; effective detection range ~800 m) for Vemco and 600 m for Sonotronics transmitters; however, detection ranges in the study area can vary due to various environmental conditions (Topping and Szedlmayer 2011a). In the present study, a stationary transmitter (same as implanted within fish) was deployed at each site to monitor changes in detection ranges and detection rates throughout the study and was used to help determine the fates of each fish at each site (Topping and Szedlmayer 2011a).

Continuous Remote Monitoring

An underwater acoustic receiver array was deployed at each site, which included five separate omni-directional receivers (Vemco VR2 or Sonotronics SUR) moored ~5 m above the bottom. For each array, one receiver was located at the release site (center) and the other four were placed at 1,100 m (VR2) or 420 m (SUR) to the north, south, east, and west of the center (Figure 2). Receivers placed at 1,100 m (or 420 m) away from the center receiver were predicted to result in complete detection of the fish within a ~2 km (VR2) or 1 km (SUR) radius of the release sites (Szedlmayer and Schroepper 2005). Receivers were coated with copper-based antifouling paint to prevent possible signal occlusion due to biofouling (Heupel et al. 2008).
Detection patterns of fish by these arrays identified if a fish was caught (fishing mortality), died (natural mortality), or emigrated. Fishing mortality was also estimated from tag returns by fishers. For example, a fishing mortality was identified by a detection pattern that would show consistent, continuous detections at the center site, followed by a sudden loss of detections at time of capture. Emigration was shown as a decrease in detections of a fish at the center site followed by an increase in detections at a surrounding receiver prior to complete detection loss. A natural mortality was identified when a fish stopped being detected at any outside receiver but was still detected by the center receiver (Figure 3). This natural mortality detection pattern resulted from a lack of fish movement and decrease in detection range from a transmitter that was lying on the bottom. Each site was periodically surveyed with scuba divers, aided with a hand-held receiver, to visually identify live fish with external tags and transmitters and search for stationary transmitters laying on the substrate from fish mortalities. A stationary control transmitter was placed 400 m (VR2) or 150 m (SUR) south of the center location at each site to estimate changes in detection range throughout the study and enabled contrasts between movements and mortality (Topping and Szedlmayer 2011a). To increase the probability of tag returns by fishers, a tag return reward of US$50 to $150 was advertised via internet fishing forums, posters distributed at local tackle stores and marinas, and newspaper coverage of the project.

Estimates of Survival and Mortality

Staggered-entry Kaplan–Meier method.—Mortality rates were calculated from the survival function, $S(t)$, estimated from the product limit method (Kaplan and Meier 1958; Pollock et al. 1989), which gives the probabilities ($S$) of surviving a specified event (i.e., fishing, natural, or total mortality) over a given time ($t$). This method allows for removal (right-censor) of fish that were not subject to the particular mortality under analysis. For example, when estimating survival from natural mortality events, fish caught and fish that emigrate from the site are censored from the analysis at the time when that event occurred and were not at risk of a natural mortality event. The Kaplan–Meier (K–M) method was applied using the survival function:

$$\hat{S}(t) = \prod_{t_j \leq t}(1 - d_j/r_j);$$

the probability of surviving to $t$, where $t$ is the time interval over which survival is estimated from the product of the conditional probabilities of survival at each event point $j$, and where $d_j$ represents the number of individuals experiencing an event and $r_j$ represents the number of individuals at risk of an event at time
FIGURE 2. Receiver array design for each site, with one receiver at the reef and four others surrounding the reef 1.1 km (0.4 km at site A4) away to the north, south, east, and west. Circles represent the detection range of 0.8 km (50% of the maximum detection range). A stationary control transmitter was placed 400 m south of the reef (150 m at A4).

interval \( t_j \) (Kaplan and Meier 1958; Pollock et al. 1989; Allison 1995; Schroepfer and Szedlmayer 2006).

The staggered-entry method is a modification of the K–M survival function method and has been applied to telemetry data (Pollock et al. 1989; Heupel and Simpfendorfer 2002). The staggered-entry method is modified to allow individuals to enter at any time during the study. Individuals that emigrated or did not experience the specified mortality event over the given time interval were right censored (e.g., a fish emigrating 200 d after release was known to survive for at least 200 d and was then censored because its final fate could no longer be determined). In the staggered-entry method, the number of fish at risk could fluctuate from period to period depending on the number of fish present, new releases (additions), and removals from the sites (fishing mortality, natural mortality, and emigrations) in the previous period. The survival function was estimated by taking the product of the conditional survival probabilities calculated for weekly time intervals over the 1,295-d study period (i.e., 185 weekly time periods). The mortality rate equations were adjusted to estimate an overall annual survival \( S(52) \) from the survival probabilities at the end of the study \( S(185) \) weeks by applying an exponent of 52/185 (e.g., \( F, M, \) or \( Z = -\log_e[S(185)\]^{52/185}]\); Starr et al. 2005). When survival estimates were calculated for each separate year (i.e., \( S(52) \) 2006, 2007, 2008), fish remaining (at risk) from the previous year were started from day 0 (January 1st) so that the survival probability was recalculated for each year. This assumed that surviving the previous year had no bias toward survival in subsequent time periods.

Survival functions were estimated separately for \( M, F, \) and \( Z. \) For example, for survival from fishing mortality (event), fish that emigrated and died naturally were right censored from the fish at risk. In this method, individuals censored are assumed to have the same probability of survival as individuals remaining at the study site, so only known fates experienced by individuals remaining at the study site continued to factor into survival probabilities. Since survival estimates are derived by only considering the specified mortality event, instantaneous annual (52 weeks) mortality rates were calculated using the following equations:

\[
F = -\log_e[S_F(52)],
\]

where survival is based on the probability of surviving fishing mortality over a year;

\[
M = -\log_e[S_M(52)],
\]

where survival is based on the probability of surviving natural mortality over a year; and

\[
Z = -\log_e[S(52)],
\]
where survival is based on the probability of surviving any mortality over a year (Ricker 1975). We used the "MARK" program (http://www.phidot.org/software/mark/docs/book) to estimate conditional survivals, total survivals, SE, and CI. Estimates were based on the maximum likelihood binomial (MLE; Edwards 1992):

$$L(\theta|n_i, y_i) = \prod_{i=1}^{t} S_i^{y_i} (1 - S_i)^{(n_i - y_i)}$$

where $\theta$ is the survival model for the time intervals, $n_i$ is the number of individuals alive (at risk) during each interval, $y_i$ is the number surviving each interval, and $S_i$ is the MLE of survival during each interval. Confidence intervals for instantaneous mortality rates were calculated from the 95% confidence intervals estimated from the MLE of the survival functions at 1 year (52 weeks; Klein and Moeschberger 2003).

RESULTS

Red Snapper ($n = 87$) were continuously monitored at five different sites (A1–A4, N1; Figure 1) for up to 185 weeks (December 2005 to June 2009). Total length of tagged Red Snapper ranged from 501 to 860 mm, with a mean of 639 mm (SD, 84 mm). These 87 fish remained present at the site, emigrated, died, or were removed by fishers, as determined by detections from the five receivers at each site and by fisher returns (Figure 4; Table 1). Residence time (or minimum residence time if still present at end of study) ranged from 0 to 1,020 d (Figure 4; Table 1). Of the 87 tagged fish, 17 either left the site or died within the first 6 d after release (14 emigrated, 2 died, and 1 unknown). These events within the first 6 d postrelease were considered tagging artifacts, and no fish that left within 6 d were detected again or returned by fishers. Thus, the 70 remaining fish were used for mortality rate estimations, and data were analyzed through June 2009. Also, based on the low postrelease mortality detected at the sites (2 of 87 fish) even after transmitter implantation, it was assumed that postrelease mortality caused by an angler catching or releasing a fish out of season was negligible at these sites (depths <30 m).

There were 14 fish still present at the various sites at the end of the study (Table 1). Additional emigrations were detected ($n = 27$) after the 6-d postrelease period, with 2 fish in 2006, 9 fish in 2007, 14 fish in 2008, and 2 fish in 2009 leaving the site from...
28 to 758 d after release. Six fish from the 27 emigrations were last detected at a site when one of the four outer array receivers was not functioning but were assumed to have emigrated based on the detections from other receivers at that site (unknowns; Table 1). No natural mortalities were detected in 2006, but there were five in 2007, five in 2008, and none in 2009 (up to June 2009). There were 19 fishing mortalities at four sites (A1–A4), while \( F = 0 \) at N1, with 17 fish returned by fishers and 2 estimated from telemetry detection data (i.e., 11% nonreporting). However, total fishing mortality was estimated from telemetry patterns (19 fish) independent of fisher returns (Figure 3). Nine fish were caught in 2006, five in 2007, and five in 2008. Of the nine fish caught in 2006, all were caught at site A1 in April, May, and June, and six were captured by one fisher. This fisher admittedly targeted this site. Overall, site A1 had the highest fishing mortality (13 fish out of 20 released). Targeting of this study site by a single fisher (four fish recaptures in 1 day) may have biased estimated fishing mortalities as few fish were at risk during the early part of this study (10 fish in April, 5 in May, and 6 in June). The staggered-entry model was sensitive to low sample sizes in the beginning of the study and resulted in unrealistic estimates (negative \( M \) values), and \( F \) values greater than 1.0. Based on this suspected bias from this particular fisher, these captures were right censored in the staggered-entry analysis and not included in the fishing mortality estimates for this study.

After removal of the captures from the biased fisher, annual survival from fishing mortality events based on the entire study period (185 weeks; i.e., \( S(185) = 0.52 \) and \( S(185) = 0.185 \)) was \( S_F \) (95% confidence intervals) = 0.76 (0.58–0.90) and \( F = 0.27 \) (0.11–0.54) (Table 2; Figure 5). While no natural deaths were detected in 2006 (probably due to low sample size), natural deaths were spread out relatively evenly in subsequent years. Annual survival from natural mortality events over all years using the \( K-M \) staggered entry was \( S_M = 0.90 \) (0.82–0.94) and \( M = 0.11 \) (0.06–0.20) (Figure 6); annual survival from all mortality was \( S_Z = 0.68 \) (0.53–0.82) and \( Z = 0.39 \) (0.19–0.64) (Table 2; Figure 7). Mortality rate estimates based on the staggered-entry method varied by year: in 2006, \( F = 0.62 \) (0.16–1.67) and \( M = 0.0 \); in 2007, \( F = 0.22 \) (0.09–0.51) and \( M = 0.19 \) (0.07–0.48); and in 2008, \( F = 0.14 \) (0.05–0.35) and \( M = 0.21 \) (0.09–0.44) (Table 2; Figure 8).

**DISCUSSION**

Ultrasonic telemetry allowed continuous, long-term (43 months) monitoring of tagged Red Snapper at the study sites. The arrangement of receivers enabled the estimation of emigration, natural mortality, and fishing mortality at various structured habitats. An important advancement in the present study was the use of stationary control transmitters at each site that allowed monitoring detection range changes due to environmental factors throughout the study (Topping and Szedlmayer 2011a). Knowledge of detection range and comparisons between detection patterns of stationary (dead fish) and moving (live fish) transmitters were necessary for identifying emigration and mortality events (Topping and Szedlmayer 2011a). Most studies

<table>
<thead>
<tr>
<th>Data</th>
<th>Fish</th>
<th>Z</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>All years</td>
<td>70</td>
<td>0.39 (0.19–0.64)</td>
<td>0.27 (0.11–0.54)</td>
</tr>
<tr>
<td>2006</td>
<td>26</td>
<td>0.62 (0.16–1.67)</td>
<td>0.62 (0.16–1.67)</td>
</tr>
<tr>
<td>2007</td>
<td>51</td>
<td>0.41 (0.20–0.77)</td>
<td>0.22 (0.09–0.51)</td>
</tr>
<tr>
<td>2008</td>
<td>41</td>
<td>0.35 (0.18–0.62)</td>
<td>0.14 (0.05–0.35)</td>
</tr>
</tbody>
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that employed telemetry techniques to estimate mortality of relatively mobile species (e.g., Striped Bass Morone saxatilis, Blacktip Shark Carcharhinus limbatus) have been successful in semiclosed systems and generally have estimated natural mortalities based on lack of movement (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Young and Isely 2004). For example, Heupel and Simpfendorfer (2002) were able to directly detect fishing and natural mortality of juvenile Blacktip Sharks in Terra Ceia Bay, Florida, by using a large number of VR2...
receivers to continuously monitor movement, lack of movement (mortality), sudden disappearance (capture), and emigration of individuals from the mouth of the bay (survival). More difficulty is encountered when attempting to estimate mortality with telemetry in open ocean systems than closed systems and has been limited to fish that show moderate residence (Starr et al. 2005). In the present study, high site fidelity of Red Snapper to reef sites (Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; Topping and Szedlmayer 2011a, 2011b) provided an opportunity to directly estimate mortality rates and emigration of Red Snapper in a large open water system (i.e., northern continental shelf of the Gulf of Mexico).

It is important to define the limits of the study area. Heupel and Simpfendorfer (2002) were able to monitor Blacktip Sharks (known fate) that remained in the semienclosed bay and estimate mortality while the sharks remained in their “study area.” Once fish left the bay, in less than 6 months their fates were unknown. In open systems known-fate models are still possible, but boundaries are not defined physically but rather by the limits of the telemetry system. Natural mortalities could only be detected for fish staying within the array. In the present study, it was assumed that fish within the array experienced the same probability of mortality outside the array (i.e., mortality rates were made based on the “known fates” of fish within the array). More importantly, Red Snapper showed behaviors (high residency to a particular reef site within an array, up to 36 months in this study) that allowed for long-term monitoring and fate determination within ~2 km of the artificial reef site (Topping and Szedlmayer 2011a, 2011b). Mobile species would probably not be detected long enough to make inferences on the fates of individuals.

Values of $F$ for some stock assessments are dependent on $M$ (i.e., $F = Z - M$), in which $M$ is determined indirectly from the life history parameter equations, with $F$ only as accurate as $M$ (Manooch et al. 1998). Estimates of $M$ derived indirectly from life history parameters for Red Snapper from the northern Gulf of Mexico (Table 3; e.g., maximum age, maximum weight, $K$, water temperature) can range from 0.08 to 0.36 (Pauly 1980; Hoenig 1983; Peterson and Wrobleski 1984; Chen and Watanabe 1989; Jensen 1996; Quinn and Deriso 1999; Wilson and Nieland 2001; Slipke and Macena 2005; Szedlmayer 2007). Life history parameters ($K$, maximum weight, $t_0$, $t_{max}$) used to calculate indirect estimates for comparison to telemetry-estimated values (Table 3) were primarily based on surveys from the northern Gulf of Mexico (Szedlmayer and Ship 1994; Schirripa and Legault 1999; Wilson and Nieland 2001; SEDAR 2005; Szedlmayer 2007; SEDAR 2009). A recent Red Snapper fishery assessment used a conservative $M$ of 0.10, which was lowered from the 0.20 used in an earlier assessment (Goodyear 1995; Schirripa and Legault 1999; SEDAR 2005; SEDAR 2009). The predicted $M$ was lowered due to evidence of older fish (up to 52 years) in the stock (Szedlmayer and Ship 1994; Schirripa and Legault 1999; Wilson and Nieland 2001). Over all years combined the direct estimates of $M$ from telemetry methods in this study (0.11 [0.06–0.20]; Table 2) were near the lower estimates derived from the indirect methods (0.08–0.36; Table 3), and the present 95% confidence limits encompass the estimate of $M$ used in the recent assessment (0.10). However when estimates were based on separate years, estimates of $M$ for 2007 and 2008 were about twice the recent assessment value. The present study provides the only empirically derived estimates of $M$ for Red Snapper, but such estimates will undoubtedly change from year to year depending on environmental conditions or from possible increases in density-dependent mortality associated with population increase during the Red Snapper stock rebuilding phase (Rose et al. 2001; Young and Isely 2004; Gaze et al. 2008).

There were no natural deaths detected in 2006 probably due to the combination of low sample size and the high number of released fish caught by fishers early in the study, and clearly $M = 0$ is incorrect. In 2007 and 2008, $M$ was higher based on the staggered-entry method (Table 2); however, uncertainty in $M$
was greater when estimates were based on data from individual years than data from all years. Even with this increased variance, we suggest that these later estimates of \( M \) (0.19 and 0.21) are probably better estimates of actual Red Snapper natural mortality rates because of an increase in sample size and number of study sites, and they may reflect reduced fishing mortality with the shorter recreational fishing seasons.

The use of \( M = 0.10 \) in the Red Snapper stock assessments is at the lower end when compared with the estimated 95% confidence intervals for 2007 and 2008 based on the present telemetry study and may be considered on the conservative side of management scenarios. A change back to the use of higher \( M = 0.20 \) in assessments based on present telemetry estimates would have substantial effects on total allowable catch limits and management decisions. However, we caution the use of higher \( M \) values in stock assessments based on telemetry estimates due to low sample sizes in the present study. Clearly, estimates of \( M \) should be reevaluated as these stocks continue to rebuild and telemetry-based methods would be ideally suited for such studies.

Over all years combined, the direct estimates of \( F \) in this study (0.27) were lower than \( F = 0.35 \) for Red Snapper from the 2005 stock assessment (SEDAR 2005) and \( F = 0.29–0.47 \) from the 1999 stock assessment (Schirripa and Legault 1999). However, \( F \) showed substantial annual variation during this study. Fishing mortality (\( F \)) was 0.62 in 2006 (95% CI, 0.16–1.67), 0.22 in 2007 (0.09–0.51), and 0.14 in 2008 (0.05–0.35). The higher rates in 2006 for the present study may be from lower sample sizes inflating exploitation but also may reflect changes in fishing regulations among years. Total allowable catch (TAC) quotas were decreased from 9.1 million pounds (MP) in 2006, to 6.5 MP in 2007, and to 5.0 MP in 2008. These reductions in TAC resulted in more restrictive seasonal and bag limits. For example, in 2006 federal waters were open to recreational Red Snapper fishing for 7 months (April to October 2006) with a four fish bag limit (407 mm TL minimum size), in 2007 a two fish bag limit was instituted, and in 2008 the fishing season was limited to 2 months (June and July 2008). Though it is difficult to compare the first year of the study due to low sample size, the decreasing pattern of fishing mortality from 2006 to 2008 in the present telemetry study appeared to reflect the changes in fishery management regulations. Despite an increase in fish available to be caught (at risk), the numbers of fish caught decreased in each subsequent year.

The detection of fishing mortality events was based on telemetry detection data (detection pattern: fish detected consistently before suddenly disappearing from the center receiver) and was validated by fisher returns (\( n = 17 \) fisher returns out of 19 telemetry detected fishing mortalities). In fact this was one of the greatest advantages of telemetry-based estimates, i.e., estimates of \( F \) were totally independent of fish captures. Confidence in the accuracy of detection of \( M \) was \( < F \) since we were not able to retrieve all of the transmitters from dead fish. However, all telemetry-calculated values were within the expected range of values obtained through indirect methods based on life history parameters, which increases confidence in the accuracy of \( M \). Total mortality (\( Z \)) estimates from the present study (0.39) were lower than the \( Z = 0.54 \) obtained by both Gitschlag et al. (2003) and Szedlmayer (2007) from catch curves of completely separate fishery-independent surveys. The lower \( Z \) values from the present study may represent a reduction in fishing mortality, compared with previous estimates that were based on catch curves prior to 2000 with greater TAC.

The present study has provided fishery-independent estimates of different mortalities. An important aspect of such telemetry methods is the independent estimation of \( F \) and \( M \). Another great advantage of these telemetry-based estimates is the independence of \( F \) estimation from fisher-reported recaptures. Overall it appears that present telemetry-based estimates reflect management restrictions and as such validate both telemetry-derived estimates and the effectiveness of management actions. For example, the present study suggests that natural mortality is higher than past estimates and may have actually increased to twice the past rates used in stock assessments during the Red Snapper rebuilding period under restrictive management. This higher level of \( M \), coupled with the decreasing rates of \( F \) in 2007 (0.22) and 2008 (0.14), suggests that management restrictions are helping in stock rebuilding efforts, and continued efforts at estimating mortalities from telemetry-based methods are recommended.

ACKNOWLEDGMENTS

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REFERENCES


Modeling the Influence of Parr Predation by Walleyes and Brown Trout on the Long-Term Population Dynamics of Chinook Salmon in Lake Michigan: A Stage Matrix Approach

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PLEASE SCROLL DOWN FOR ARTICLE
Modeling the Influence of Parr Predation by Walleyes and Brown Trout on the Long-Term Population Dynamics of Chinook Salmon in Lake Michigan: A Stage Matrix Approach

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Abstract
Predation events during ontogeny may have long-term consequences for fish population abundance and variability. We used a stage-based matrix model to evaluate Walleye Sander vitreus and Brown Trout Salmo trutta predation on Chinook Salmon Oncorhynchus tshawytscha parr of the Muskegon River stock and the relative influence of parr predation on the long-term population dynamics and recruitment of Chinook Salmon in Lake Michigan. The model predicted the number of Chinook Salmon individuals in each stage (fry, smolts, and lake age 0 [recruits] through lake age 4) and forecasted population trajectories based on demographic data (e.g., survival, growth, and fecundity). The relative influence of parr predation was compared with influences of environmental stochasticity in the egg stage and Alewife Alosa pseudoharengus abundance (prey for lake-stage salmon) on Chinook Salmon fecundity, recruitment, and population growth. To simulate environmental stochasticity and the influence of Alewife abundance, we varied Chinook Salmon stage-specific survival rates, growth rates, maturity schedule, and carrying capacity. Relative to a baseline recruitment scenario, removal of stocked Brown Trout resulted in a significant increase in parr survival and long-term Chinook Salmon abundance. Walleye predation on parr had little apparent influence on Chinook Salmon population dynamics. Predation on parr during out-migration was positively correlated with variation in Chinook Salmon population stability and was negatively correlated with population growth, suggesting that Brown Trout have a significant negative effect on Chinook Salmon recruitment and long-term population stability. The negative effects of variation in egg survival rates and Alewife abundance on Chinook Salmon recruitment and population growth rates were similar to the negative effects from parr predation scenarios. Our study suggests that management decisions to promote Great Lakes Chinook Salmon populations may require evaluation of trout stocking practices in nursery habitats.

Migratory fishes that utilize different habitats during their life history experience abiotic and biotic conditions that affect variability in population size and growth (Goodyear et al. 1985; Kraus and Secor 2004, 2005; Savoy and Crecco 2004). Relative to abiotic factors, predation mortality during ontogeny may have long-term consequences for fish population abundance and variability (Forney 1974, 1977; Bailey and Houde 1989). For example, predation by recovering U.S. Atlantic coast stocks of Striped Bass Morone saxatilis has been implicated in recent population declines of American Shad Alosa sapidissima (Savoy and Crecco 2004) and Atlantic Menhaden Brevoortia tyrannus (Uphoff 2003) and is suspected to affect management and recovery of Atlantic Salmon Salmo salar populations (Grout 2006). Population variability of anadromous Pacific salmonids is influenced by abiotic and biotic factors experienced in natal tributaries (Hilborn and Walters 1992; Shively et al. 1996; Jager et al. 1997; Johnson et al. 2007), estuaries, and ocean or Great Lakes environments (Kope and Botsford 1990; Warner et al. 1992; Kope and Botsford 1990; Warner et al. 2003).
While survival of Pacific salmonids in ocean environments may be affected by local ocean conditions after the out-migration of smolts from freshwater to marine areas (Ward 2000; Greene and Beechie 2004; Sharma et al. 2013), survival in stream environments can be heavily influenced by anthropogenic factors, including logging, hydropower dams, agriculture, and the stocking of nonnative predators (NRC 1996). Some of these factors can be manipulated by resource managers toward the goal of increasing recruitment of resident salmonids. For example, in many Great Lakes tributaries, variability in salmonid recruitment (number of individuals entering the lake or ocean; Jager and Rose 2003) can be mediated through reductions in the stocking of piscivores that may prey heavily on salmonid parr; predation can lead to high mortality rates in juvenile stages (e.g., Rieman et al. 1991; Johnson et al. 2007; Krueger et al. 2011).

The Chinook Salmon Oncorhynchus tshawytscha is a top piscivore in the Laurentian Great Lakes and helps to support recreational fisheries valued at $7 billion per year (Dettmers et al. 2012). Chinook Salmon were first introduced into Lake Michigan in 1967 and now reproduce successfully, with natural recruitment being equal to hatchery introductions of 4 million smolts/year (Carl 1982; Claramunt et al. 2006; Warner et al. 2008). Previous empirical work by Krueger et al. (2011) explored the potential for management actions to modify the survival of Chinook Salmon parr (henceforth, “parr”) over four field seasons in the Muskegon River (Michigan), a large tributary to Lake Michigan. We (Krueger et al. 2011) found that recruitment of Chinook Salmon may be affected by piscivory from Walleyes Sander vitreus and Brown Trout Salmo trutta. Walleyes and Brown Trout will generally feed upon hatchery-reared salmonids and invertebrates, respectively, but will consume parr when available. Walleyes are not gape limited and can consume parr for the duration of parr residence in the nursery (~3 months: April–June). However, alternate prey for Walleyes, such as hatchery-reared Rainbow Trout O. mykiss, can provide a significant buffer against Walleye predation on parr; other interactions between Rainbow Trout and parr appear to be minimal (Krueger 2010). Brown Trout appear to be gape limited and only prey upon the smallest parr (TL < 40 mm); predation by Brown Trout begins when they are first stocked and ends in mid-May, when parr are too large for Brown Trout to consume. Thus, predation on parr in the Muskegon River nursery area may have a large effect on Chinook Salmon recruitment and population abundance in Lake Michigan, as the Muskegon River produces more wild Chinook Salmon smolts than any other Lake Michigan tributary (Carl 1984; O’Neal et al. 1997).

Variable abundances of stocked predators can influence Chinook Salmon survival, recruitment, and population size, but the relative effect of this predation mortality in comparison with mortality at the egg or ocean (lake) life stages is poorly known. The goal of this study was to compare the relative influence of stream and lake factors on Chinook Salmon recruitment and population growth in the Great Lakes. This work builds upon our short-term (4-year) empirical study (Krueger et al. 2011), in which we quantified predation mortality on parr and the survival and recruitment of parr under variable predator regimes throughout the lower Muskegon River. We hypothesized that predation on parr in the relatively small nursery area of the Muskegon River over a short temporal scale (1–2 months) significantly influences Chinook Salmon recruitment and population growth relative to abiotic factors that affect egg survival or the biomass of prey for lake-stage Chinook Salmon. To test this hypothesis, we used a stage-based matrix model to simulate the effects of environmental stochasticity in Chinook Salmon egg survival, variability in prey biomass for lake-stage Chinook Salmon, and variable parr predation rates on the long-term (50-year) population dynamics of Chinook Salmon in Lake Michigan. Matrix models are widely used in fisheries research applications (e.g., Kareiva et al. 2000; Peters and armour 2001; Green and Beechie 2004; Savereide and Quinn 2004; Sable and Rose 2008), are easily constructed, and make use of readily available demographic information on survival, growth, and reproduction (Sable and Rose 2008). We parameterized the model to simulate the dynamics of the Chinook Salmon stock inhabiting the Muskegon River and Lake Michigan.

METHODS

Modeled Ecosystem

Our model incorporated all life stages of Chinook Salmon, so we considered influential processes in three major habitats: the Muskegon River (mean daily discharge ~ 88 m$^3$/s), Muskegon Lake, and Lake Michigan (Figure 1). In our simulations, we...
only considered those Chinook Salmon that were naturally produced from the Muskegon River. The other sport fish populations in the Muskegon River are supported by the stocking of predators, including Walleyes, Brown Trout, and insectivorous Rainbow Trout; the two trout stocks are entirely dependent on stocked individuals (O’Neal 1997), whereas Walleyes are mostly supported by stocking, with some contribution from natural spawning (Ivan et al. 2010). The spawning of Chinook Salmon and Walleyes and the stocking of Brown Trout (TL ~ 164 mm) and Rainbow Trout (TL ~ 174 mm) take place in the Muskegon River’s nursery section, which encompasses approximately 22.5 km of river from Croton Dam to Newaygo, Michigan (Figure 1; Godby et al. 2007; Krueger et al. 2011). Muskegon Lake, a 1,680-ha drowned river mouth of the Muskegon River, connects to southeastern Lake Michigan via a navigation channel (Muskegon Channel). Muskegon Lake is relatively shallow and mesotrophic and provides a temporary residence in which parr will begin smoltification during their first year before completing their out-migration into Lake Michigan. Lake Michigan is the second-largest Laurentian Great Lake (58,016 km²) and provides important habitat and prey for growing juvenile and adult Chinook Salmon.

**Modeling Approach**

We used Risk Analysis and Management Alternatives Software (RAMAS) Stage (Ferson 1993) to evaluate alternative predator management strategies affecting the early life history stages of Muskegon River Chinook Salmon and how those strategies might affect population dynamics. The RAMAS Stage program is a matrix modeling package that was developed for understanding the population dynamics of species with complex life histories. This program tracks the number of individuals in each stage (e.g., Caswell 2001) and provides a forecast of population trajectories based on minimal demographic data, such as survival, growth, and fecundity (e.g., Brook et al. 1999; Sable and Rose 2008). Model simulations can also include environmental drivers (e.g., water temperature and river discharge) that may affect survival and growth of life stages and hence the population dynamics of Chinook Salmon.

We configured RAMAS Stage to simulate seven finite stages of Muskegon River Chinook Salmon: fry and smolts in the Muskegon River and ages 0–4 in Lake Michigan. Model simulations began with an initial abundance of Chinook Salmon at each age or stage. Individuals that survived one stage moved into the next stage based on field-derived transition probabilities. We assumed that potential emigration (straying) by Chinook Salmon from the Muskegon River to other rivers was equal to immigration. This is an appropriate assumption based on tagging studies of Chinook Salmon movement in Lakes Huron and Michigan (Aderstein et al. 2007, 2008) and in Pacific coast tributaries (Quinn 2005).

**Parameter Estimation**

We parameterized the RAMAS Stage model by using stage-specific abundances, survival rates, and fecundities of Muskegon River Chinook Salmon. Initial survival rate from the fry stage to the smolt stage was based on estimates of predation mortality derived from 4 years of intense empirical observations of Walleye and Brown Trout diets and abundances in the Muskegon River (Table 1; Krueger et al. 2011). Survival of parr in the Muskegon River was varied based on the particular management scenario being simulated. Survival values for lake stages (i.e., ages 0–4 in Lake Michigan) were held constant and were based on analyses of Chinook Salmon density and age composition in biological surveys and creel data compiled for catch-at-age models that predict fishery yield as a function of stocking (CONNECT; Rutherford 1997; Benjamin and Bence 2003). The survival values in the catch-at-age models represent survival after losses from fishing, natural mortality, and bacterial kidney disease and provided reasonable correspondence among Chinook Salmon harvests and age distributions in Lake Michigan and age distributions of Chinook Salmon on spawning grounds given known numbers of stocked and wild smolts. Natural mortality rates (including spawner mortality) of lake-phase Chinook Salmon ranged from 27% at age 1 to 53% at age 4.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Fry</th>
<th>Smolt</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>River fry</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.026</td>
<td>0.601</td>
<td>8.336</td>
<td>15.939</td>
</tr>
<tr>
<td>River smolt</td>
<td>0.51</td>
<td>0</td>
<td>0</td>
<td>0.750</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lake age 0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lake age 1</td>
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<td>0</td>
<td>0.705</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lake age 2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.705</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0.350</td>
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<td>Lake age 4</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0.259</td>
<td>0</td>
</tr>
</tbody>
</table>

**TABLE 1.** Stage matrix used in the baseline simulation. Off-diagonal values represent stage-specific survival rates of Chinook Salmon, while top-row elements represent stage-specific fecundity values (number of river fry individuals per female). All values are representative of the entire population, although fecundity values are halved to account for the 1:1 male : female ratio. "Lake age x" represents Chinook Salmon in Lake Michigan in their xth year.
4 and were estimated by using Pauly’s (1980) equation relating natural mortality rate to growth, mean temperature, and maximum size (Rutherford 1997). Creel estimates from the 1980s and 1990s show that 20,000–40,000 spawners were harvested annually from the Muskegon River (Michigan Department of Natural Resources [MDNR], unpublished data); carcass count estimates (L. Ivan [University of Michigan] and E. S. Rutherford, unpublished data) indicated that spawner densities near the peak and end of the spawning season were twofold higher, or approximately 60,000 spawners. It is unknown how many “harvested” Chinook Salmon in creel surveys were actually removed from the river. Many of the female carcasses we saw in the Muskegon River lacked eggs, as anglers tend to harvest females before fungus sets in and to keep salmon eggs for spawn bags. We assumed that (1) half of the total number of Chinook Salmon carcasses we saw in the river (30,000) were harvested for their eggs and (2) half the number of harvested individuals (15,000) were removed from the river before spawning; this leaves a combined total of approximately 45,000 spawners. Thus, for all simulations, we implemented a 50% angler harvest rate for spawners of ages 1–4.

Because Chinook Salmon are no longer stocked into the Muskegon River, we used estimates of the mean abundances of natural fry (540,000) produced from 2004 to 2007 (Kruenger et al. 2011) as the initial fry abundance. Initial abundance of smolts was estimated from our empirical estimates of parr abundance (obtained by electrofishing; Kruenger et al. 2011) and from the estimated abundance of smolts caught in smolt traps (E. S. Rutherford, unpublished data). A ge-0 Chinook Salmon abundance in Lake Michigan was calculated by multiplying smolt abundance by the rate of survival (S) from smolt to lake age 0 (S = 0.75). Although the rate of smolt survival to Lake Michigan is unknown, we chose a value of S that would result in recruit numbers similar to those observed in the entire Lake Michigan population (Rutherford 1997). Johnson et al. (2007) compared relative return rates of hatchery smolts released in a tributary to nearshore Lake Huron with the return rates of hatchery smolts released at a nearby beach; those authors found that smolt survival depended on the presence of alewives Alosa pseudoharengus to buffer predation on smolts by various predators. In years when Alewives were present, return rates of smolts released into the tributary equalled the return rates of smolts released into Lake Huron, whereas during years in which Alewife abundance was low, return rates of smolts released into the tributary were 67% of the return rates observed for smolts released into Lake Huron (Johnson et al. 2007). Age-specific abundances of lake stages (adults) were based on age composition data from agency surveys in Lake Michigan (Table 2; CONNECT; Rutherford 1997; Benjamin and Bence 2003).

Chinook Salmon can reach reproductive maturity as early as age 1. Fecundity, defined as the number of river fry produced per adult, was estimated by first calculating egg deposition using a length-specific relationship averaged for 10 spawning populations of Chinook Salmon in the Pacific Northwest (Healey and Heard 1984):  

$$F = 0.00195 \times L^{2.234},$$  \hspace{1cm} (1)

where F is the number of eggs deposited by each female and L is TL (mm). Next, we estimated the number of spawning females by using spawning mortality estimates (CONNECT; Rutherford 1997; Benjamin and Bence 2003) and a maturity schedule (percent mature in each age-class; Table 3), and we assumed a 1:1 sex ratio (Richard O’Neal, MDNR, personal communication) and a 50% harvest rate:

$$\text{female}_i = P_f \times \text{Mature}_i \times A_i \sum_{i=1}^{4} PE_i,$$  \hspace{1cm} (2)

where female_i is the abundance of female Chinook Salmon spawners in stage i that actually spawned, P_f is the product

<table>
<thead>
<tr>
<th>Stage</th>
<th>Initial abundance</th>
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<tbody>
<tr>
<td>River fry</td>
<td>540,000</td>
</tr>
<tr>
<td>River smolt</td>
<td>275,400</td>
</tr>
<tr>
<td>Lake age 0</td>
<td>206,550</td>
</tr>
<tr>
<td>Lake age 1</td>
<td>145,618</td>
</tr>
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<td>Lake age 2</td>
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<td>Lake age 3</td>
<td>35,931</td>
</tr>
<tr>
<td>Lake age 4</td>
<td>9,306</td>
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<table>
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<th>Stage</th>
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<td></td>
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</tr>
<tr>
<td>Lake age 1</td>
<td>3.6</td>
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<tr>
<td>Lake age 2</td>
<td>20.4</td>
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<td>54.8</td>
</tr>
<tr>
<td>Lake age 4</td>
<td>20.9</td>
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<table>
<thead>
<tr>
<th>Stage</th>
<th>Percent of total spawner abundance</th>
<th>Lake survival</th>
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<tbody>
<tr>
<td></td>
<td>LOW</td>
<td>Alevin abundance</td>
</tr>
<tr>
<td>Lake age 0</td>
<td>na</td>
<td>na</td>
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<td>Lake age 1</td>
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<td>0.0</td>
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<td>Lake age 2</td>
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<td>5.7</td>
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<td>60.0</td>
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<tr>
<td>Lake age 4</td>
<td>20.9</td>
<td>31.4</td>
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</tbody>
</table>
of the sex ratio (females : males) and the harvest rate (0.5 × 0.5 = 0.25), Mature, is the proportion of stage-i spawners relative to the total spawner abundance observed on the spawning grounds, A, is the proportion of Chinook Salmon in lake stage i that migrated to spawn, and PE, is the initial abundance of lake-stage i Chinook Salmon (CONNECT; Rutherford 1997; Benjamin and Bence 2003). To determine stage-specific egg production, we multiplied stage-specific female spawner abundance by individual female egg production and divided that value by the summation of all eggs produced by all stages:

\[ \text{Egg}_i = \frac{F \times \text{female}_i \times \text{Fecundity}_i \times \#\text{Fry}_i}{\sum_{i=1}^{4} (F \times \text{female}_i)} \]

where Egg\(_i\) is the proportional contribution of stage i to the total egg production. Finally, we calculated stage-specific fecundity of all individuals by assessing the contribution of all Chinook Salmon in each stage to the total production of river fry (Fry):

\[ \text{Fecundity}_i = \frac{\text{Egg}_i \times \text{Fry}}{\text{PE}_i} \]

where Fecundity\(_i\) is the number of river fry individuals per adult Chinook Salmon of stage i.

Alevines, the primary prey of adult Chinook Salmon in Lake Michigan (Kitchell and Crowder 1986), influence the growth rate (Stewart and Ibarra 1991), maturity schedule (Quinn 2005), and survival of lake-stage Chinook Salmon (Rutherford 1997; Benjamin and Bence 2003; Warner et al. 2008). Furthermore, variation in Chinook Salmon body size changes population fecundity since fecundity is a nonlinear function of TL (equation 1). A length-at-age relationship for adult Chinook Salmon in Lake Michigan was estimated by using creel survey data (T. Kolb, MDNR, unpublished data) and an age and growth study (Wesley 1996) for years of LOW (1.0 kg/ha), intermediate (2.0 kg/ha), and HIGH (3.0 kg/ha) Alevine abundances (Table 4) as estimated by U.S. Geological Survey bottom trawl surveys (Bunnell et al. 2006). Chinook Salmon length at age for each Alevine abundance category (Table 4) was then used to calculate fecundity for each Chinook Salmon age-class (Table 5). We used survival rates of lake-stage Chinook Salmon from the early 1990s (CONNECT; Rutherford 1997; Benjamin and Bence 2003) for the simulation with LOW Alevine abundance in Lake Michigan (Table 3). Survival of lake-stage Chinook Salmon was not different between years with intermediate and HIGH Alevine abundances. Chinook Salmon may reach age 5 in Lake Michigan; however, age-5 fish represent a minimal component of harvest (Johnson et al. 2005) and thus were not considered in this exercise.

The effects of environmental factors (water temperature and discharge) on Chinook Salmon survival (Carl 1982), fecundity, and population dynamics (i.e., recruitment, population growth, and stability) were modeled implicitly in RAMAS Stage. Water temperature and discharge are key determinants of Chinook Salmon spawning success and nursery habitat quality (e.g., Zafft 1992; Jager et al. 1997; Quinn 2005; Yates et al. 2008).

Water temperature is positively correlated with development and metabolic rates of embryonic and juvenile Chinook Salmon (Jager et al. 1997; Quinn 2005). Discharge is generally positively correlated with out-migration abundance (Seelbach 1985; Zafft 1992; Quinn 2005) to a point; however, abnormally high discharge can lead to redd scouring, which negatively affects recruitment. To account for such environmental effects, we selected a vital rate (survival or fecundity) as a random variable from a normal distribution with a mean that was specified in the stage matrix and with an SD that was taken from the SD matrix. The range of settings for environmental variation was taken as the lowest and highest lengths at age from 1983 to 1993 as reported by Rutherford (1997; Table 1.6). Length-at-age equations (where yTL and x = age) and r\(^2\) values are also listed for each Alevine abundance category. "Lake age x" represents Chinook Salmon in Lake Michigan in their xth year.

<table>
<thead>
<tr>
<th>Stage</th>
<th>LOW</th>
<th>Baseline</th>
<th>HIGH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake age 1</td>
<td>370</td>
<td>393</td>
<td>416</td>
</tr>
<tr>
<td>Lake age 2</td>
<td>609</td>
<td>636</td>
<td>662</td>
</tr>
<tr>
<td>Lake age 3</td>
<td>765</td>
<td>828</td>
<td>891</td>
</tr>
<tr>
<td>Lake age 4</td>
<td>815</td>
<td>931</td>
<td>1,047</td>
</tr>
</tbody>
</table>

**Table 4.** Mean size (mm TL) of spawning Chinook Salmon under scenarios of baseline, LOW, and HIGH Alevine abundances. Changes in size at age were taken as the lowest and highest lengths at age from 1983 to 1993 as reported by Rutherford (1997; Table 1.6). Length-at-age equations (where yTL and x = age) and r\(^2\) values are also listed for each Alevine abundance category. "Lake age x" represents Chinook Salmon in Lake Michigan in their xth year.

<table>
<thead>
<tr>
<th>Stage</th>
<th>25% of egg S</th>
<th>50% of egg S</th>
<th>LOW Alevine abundance</th>
<th>HIGH Alevine abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake age 1</td>
<td>0.007</td>
<td>0.013</td>
<td>0.026</td>
<td>0.0</td>
</tr>
<tr>
<td>Lake age 2</td>
<td>0.150</td>
<td>0.301</td>
<td>0.601</td>
<td>0.172</td>
</tr>
<tr>
<td>Lake age 3</td>
<td>2.084</td>
<td>4.168</td>
<td>8.336</td>
<td>8.609</td>
</tr>
<tr>
<td>Lake age 4</td>
<td>3.985</td>
<td>7.969</td>
<td>15.939</td>
<td>20.022</td>
</tr>
</tbody>
</table>

**Table 5.** Variation in Chinook Salmon fecundity values (number of river fry individuals produced per female spawner) due to changes in egg-to-hatch survival (egg S) and Alevine abundance (Alevine; prey for lake-stage Chinook Salmon) in Lake Michigan, modeled as changes in the size of adult Chinook Salmon. "Lake age x" represents Chinook Salmon in Lake Michigan in their xth year. Carrying capacity of Chinook Salmon was assumed to be 1.0 million for the LOW Alevine abundance scenario and 3.0 million for the HIGH Alevine abundance scenario. Maximum population growth rate of Chinook Salmon was assumed to be 1.05 for the LOW Alevine abundance scenario and 1.10 for the HIGH Alevine abundance scenario.
was derived from relationships between river discharge and observed smolt production in four Michigan tributaries to Lake Michigan: the Muskegon, Manistee, Pere Marquette, and Little Manistee rivers (E.S. Rutherford, unpublished data). We assumed a LOW level of environmental variation by including a constant rate of 1 SD around fecundity and survival values; 1 SD is equal to 10% of mean values in the stage matrix. We assumed the MODEST level of environmental variability to be 20% of mean values in the stage matrix and the HIGH level to be 50% of mean values. The MODEST levels of variability in environmental characteristics is similar to the annual variability in Muskegon River spring discharge from March 15 through June 30, when parr are usually present before out-migrating to Lake Michigan. The mean spring flow from 1979 and 1998-2007 (the period of record for smolt monitoring in the Muskegon River) was about 230 m$^3$/s, while the SD in flow was 23% of the mean value. The SD in smolt abundance for that period of record was 52% of the mean value (i.e., HIGH environmental variability; Carl 1982; E.S. Rutherford, unpublished data).

Population dynamics and recruitment of Chinook Salmon are influenced by density-dependent mechanisms in early life stages (Ricker 1954, 1975; Jager et al. 1997). For Muskegon River Chinook Salmon, we assumed a Ricker-type density dependence function, which has been used to describe population dynamics for several salmonines, including Chinook Salmon (e.g., Ricker 1975; Quinn 2005). In RAMAS, the discrete form of the function used to model density-dependent recruitment given the parent stock is

$$N_t = N_{t+1} R_{max} \left(1 - \frac{N_t}{K}\right), \quad (5)$$

where $N_{t+1}$ equals recruitment of river fry, $N_t$ is the parent stock, $K$ is carrying capacity, and $R_{max}$ is maximum population growth rate at low population densities (i.e., density-independent growth rate; Akçakaya et al. 1999). The total abundance of all life stages equals the population size. In RAMAS, the population growth rate ($R$) is modified by adjusting all elements (fecundities and survival rates) of the stage matrix proportionately to (1) increase $R$ to greater than 1.0 if population size is less than $K$, or (2) decrease $R$ to less than 1.0 if population size is greater than $K$. If the total abundance of all stages is equal to $K$, then $R$ is set to 1.0. At each time step of a simulation, the vital rates in the stage matrix are modified to keep the population growth rate (i.e., eigenvalue) equal to the growth rate given by the Ricker equation for the current abundance (Ferson 1993). We assumed a maximal population growth rate of 10% ($R_{max} = 1.1$) per time step at low population densities in the absence of density-dependent effects.

We also tested the robustness of our baseline simulations in relation to Beverton-Holt recruitment function and ceiling (hockey-stick) forms of density dependence (Barrowman and Myers 2000; Bradford et al. 2000). The ceiling function is similar to but simpler than Ricker-type density dependence; the population grows exponentially until it reaches the ceiling (i.e., $K$). If abundance increases above $K$, it is set to the ceiling value (i.e., maximum). A population that reaches $K$ will remain at that abundance until the population declines through random fluctuation (i.e., demographic stochasticity or environmental stochasticity). A further difference is that the ceiling does not assume that a population will recover from low densities (e.g., Sabo et al. 2004). Whether the population grows or declines at any time step is entirely dependent on the mean values of vital rates in the stage matrix and the variability surrounding these rates (found in the SD matrix).

For all scenarios except LOW and HIGH Alewife biomass, we specified a $K$ of 2 million individuals to accommodate the initial abundance of Muskegon River Chinook Salmon (670,000 lake-stage individuals; 1.7 million individuals in all stages combined) and to allow for potential population growth. By comparison, the total estimated population of Chinook Salmon in Lake Michigan at its peak was 7–10 million individuals from all tributary sources (excluding river fry and smolt stages; Rutherford 1997; Benjamin and Bence 2003), with approximately 20–40% of these fish being wild and less than 10% of wild smolts recruiting from the Muskegon River (Carl 1982; Hesse 1994). For simulations of Alewife biomass, in addition to the changes in lake survival and fecundity described above, we also decreased or increased $K$ by 50% from the baseline value of 2 million Chinook Salmon; for the LOW Alewife biomass scenario, we decreased $R_{max}$ from 1.1 to 1.05.

**Model Scenarios**

*Baseline scenario.*—The baseline scenario used mean conditions to provide a baseline value of Chinook Salmon recruitment (number surviving to lake age 0), adult abundance, and risk of population decline for comparison with alternative management scenarios. Mean from the fry stage to the smolt stage was set at 0.51 for mean Walleye biomass (3,000) and Brown Trout (24,000) abundances estimated from 2005 to 2007 (Krueger et al. 2011). The abundance of predators used in modeling scenarios reflects the number of predators that actually consumed parr, which is lower than the abundance of spawning Walleyes (~38,000; Hanchin et al. 2007) or the abundance of stocked Brown Trout (~86,000; www.michigandnr.com/FISHSTOCK/). The baseline scenario also incorporates mean values of fecundity and sizes at age of adult Chinook Salmon. In addition, we assumed a LOW level of environmental stochasticity by placing a 1-SD boundary around all model parameters.

*Predator management scenarios.*—Because Walleye and Brown Trout abundances are largely dependent on stocking rates, predator management scenarios can be evaluated by varying the stocking rates (here, we assume an immediate response from both species). We first characterized the potential effects of variable predator abundance (LOW, MEAN, or HIGH) on Chinook Salmon population dynamics by varying the rate of survival from the fry stage to the smolt stage (parr survival; Table 6).
TABLE 6. Experimental design for matrix model simulations. Numeric values represent survival of Chinook Salmon parr (i.e., fry-smolt stage) predicted from a functional response model (Krueger 2010) for each simulation (RBT = Rainbow Trout). Baseline recruitment was achieved by using MEAN abundances of Walleye (WA E) and Brown Trout (BRT), LOW environmental stochasticity (1 SD around parameter values), MEAN Alewife abundance, and 60% egg-to-hatch survival (of total egg production; e.g., Quinn 2005).

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Chinook Salmon parr survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAE = ABSENT</td>
<td>1.00</td>
</tr>
<tr>
<td>BRT = ABSENT</td>
<td>0.85</td>
</tr>
<tr>
<td>BRT = LOW</td>
<td>0.64</td>
</tr>
<tr>
<td>BRT = MEAN</td>
<td>0.24</td>
</tr>
</tbody>
</table>

| WAE = LOW | 0.99 |
| BRT = ABSENT | 0.85 |
| BRT = LOW | 0.58 |
| BRT = MEAN | 0.23 |

| WAE = MEAN | 0.91 |
| BRT = ABSENT | 0.64 |
| BRT = LOW | 0.77 |
| BRT = MEAN | 0.51 |
| BRT = HIGH | 0.15 |

| WAE = HIGH | 0.80 |
| BRT = ABSENT | 0.68 |
| BRT = LOW | 0.41 |
| BRT = MEAN | 0.06 |

| WAE = MEAN; BRT = MEAN | 0.51 |
| Alewife abundance = LOW | 0.51 |
| Alewife abundance = HIGH | 0.51 |
| Environmental stochasticity = MODEST | 0.51 |
| Environmental stochasticity = HIGH | 0.51 |

| WAE = HIGH; BRT = HIGH | 0.06 |
| Environmental stochasticity = MODEST | 0.06 |
| Environmental stochasticity = HIGH | 1.00 |

No predation:
| Environmental stochasticity = MODEST | 1.00 |
| Environmental stochasticity = HIGH | 1.00 |

Chinook Salmon parr survival rates were based on predation mortality rates estimated for each piscivore species at a given population abundance (see Krueger et al. 2011). This was possible because the abundance of each predator was variable within and among study years (2004–2007). We did not, however, have the ability to determine parr survival at all combinations of predator abundance, so we had to make the assumption that predation mortality was additive. In our previous study (Krueger et al. 2011), Walleyes consumed Rainbow Trout more than any other prey type. Hence, we also estimated predation rates for other prey type. Hence, we also estimated predation rates for

We evaluated additional scenarios to determine the potential for environmental stochasticity to influence Chinook Salmon recruitment rates. The riverine-dependent stages of the Chinook Salmon life cycle are more likely to be influenced by environmental variation since survival from egg to hatch is almost entirely dependent on environmental conditions (Quinn 2005; Honea et al. 2009; Jensen et al. 2009). Furthermore, riverine conditions fluctuate more widely than conditions in Lake Michigan. Therefore, we only imposed the increased levels of environmental variation on riverine (i.e., fry and parr) survival and adult fecundity (as the environment affects egg-to-hatch survival). We increased environmental stochasticity by increasing variation around fecundity and parr survival estimates from 1 SD of mean values to 2 SDs (stochasticity = MODEST) or 5 SDs (stochasticity = HIGH) of mean values (in the SD matrix). The influence of environmental stochasticity was simulated in combination with LOW (0.06), MEAN (0.51), and HIGH (1.0) parr survival rates. Finally, we examined the effects of Alewife abundance on survival, body size, age at maturity, and population dynamics of Chinook Salmon by varying Chinook Salmon fecundity and K as a function of altered adult growth rates and maturity schedules and the lake-stage survival and R_{max} at LOW Alewife biomass (Table 5).

Model output.—All simulations were replicated (N = 100) and run for 50-year time spans. For each scenario, we report final stage distribution estimates of recruitment (abundance of Chinook Salmon at lake age 0) and the probability that the population would fall below one-third of initial abundance (~576,000);

TABLE 7. Predator abundances at ABSENT, LOW, MEAN, and HIGH designations in the Muskegon River nursery area (see Krueger et al. 2011). We assumed that 100% of these predators consumed Chinook Salmon parr as prey. All predators are stocked; Walleyes vary in age, while Brown Trout represent single cohorts.

<table>
<thead>
<tr>
<th>Predator</th>
<th>ABSENT</th>
<th>LOW</th>
<th>MEAN</th>
<th>HIGH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walleye</td>
<td>0</td>
<td>1,000</td>
<td>3,000</td>
<td>7,000</td>
</tr>
<tr>
<td>Brown Trout</td>
<td>0</td>
<td>11,000</td>
<td>24,000</td>
<td>56,000</td>
</tr>
</tbody>
</table>

Walleyes during times when the abundance of alternate prey varied; the presence/absence of alternative prey species (Brown Trout or Rainbow Trout), especially Rainbow Trout, appears to influence piscivory on juvenile Chinook Salmon (Krueger et al. 2011). We ran absence and presence scenarios for Walleyes and Brown Trout, singly and in combination (ABSENT, LOW, MEAN, or HIGH; Table 7), given relative abundances of alternate prey species for Walleyes (Table 6). For prey of Walleyes, we added a scenario that excluded Rainbow Trout but included the remaining prey species (Brown Trout; Table 6). We ran a scenario representing no predation (Walleyes and Brown Trout were both ABSENT) to yield theoretical maximum recruitment and population growth rates.

We evaluated additional scenarios to determine the potential for environmental stochasticity to influence Chinook Salmon recruitment rates. The riverine-dependent stages of the Chinook Salmon life cycle are more likely to be influenced by environmental variation since survival from egg to hatch is almost entirely dependent on environmental conditions (Quinn 2005; Honea et al. 2009; Jensen et al. 2009). Furthermore, riverine conditions fluctuate more widely than conditions in Lake Michigan. Therefore, we only imposed the increased levels of environmental variation on riverine (i.e., fry and parr) survival and adult fecundity (as the environment affects egg-to-hatch survival). We increased environmental stochasticity by increasing variation around fecundity and parr survival estimates from 1 SD of mean values to 2 SDs (stochasticity = MODEST) or 5 SDs (stochasticity = HIGH) of mean values (in the SD matrix). The influence of environmental stochasticity was simulated in combination with LOW (0.06), MEAN (0.51), and HIGH (1.0) parr survival rates. Finally, we examined the effects of Alewife abundance on survival, body size, age at maturity, and population dynamics of Chinook Salmon by varying Chinook Salmon fecundity and K as a function of altered adult growth rates and maturity schedules and the lake-stage survival and R_{max} at LOW Alewife biomass (Table 5).

Model output.—All simulations were replicated (N = 100) and run for 50-year time spans. For each scenario, we report final stage distribution estimates of recruitment (abundance of Chinook Salmon at lake age 0) and the probability that the population would fall below one-third of initial abundance (~576,000);
Jager and Rose (2003) suggested that a recovering Chinook Salmon population should be considered “healthy” when its abundance returns to one-third of its historical levels. Results from all model simulations are reported as percentage mean deviation from baseline conditions along with 95% confidence intervals (CIs; at $\alpha = 0.05$, df = 99). Differences between scenario results and baseline conditions were considered significant if their 95% CIs did not overlap. We report CVs (calculated as $100 \times [\text{SD/mean}]$) for recruitment and population abundance to quantify variability in each simulation. Finally, a particular scenario was defined as resulting in a population “crash” if the total population abundance fell below 1,000 individuals (of all age-classes) at any point during the simulation, and we noted the time period (in years) for which the population persisted.

**RESULTS**

**Baseline Scenario**

Mean abundance of all stages of Chinook Salmon remained relatively stable over the 50-year baseline simulation. The mean abundance ($\pm 95\%$ CI) of lake age-0 Chinook Salmon recruits after 50 years was $285,000 \pm 39,000$, and the total population abundance for the final 10 years was stable at $1,730,000 \pm 35,000$. The final age distribution indicated that most Chinook Salmon in the lake were ages 0–2, with relatively few individuals in subsequent stages. Chinook Salmon recruitment and abundance estimated under the assumption of Ricker-type density dependence were similar to values predicted by assuming a Beverton–Holt form of density dependence (recruitment = $255,000 \pm 35,000$ [mean $\pm 95\%$ CI]; total population = $1,700,000 \pm 218,000$) but were higher and less variable than values predicted by assuming a ceiling-type density dependence (recruitment = $83,000 \pm 20,000$; total population = $533,000 \pm 121,000$).

**Management Scenarios**

Relative recruitment success of Chinook Salmon was generally higher under Walleye-only regimes than under Brown Trout-only regimes. In the absence of Brown Trout, recruitment to lake age 0 increased significantly relative to baseline conditions (intermediate Walleye and Brown Trout abundances) but only when Walleye abundance was LOW. In the absence of Brown Trout and Rainbow Trout, Chinook Salmon recruitment to lake age 0 was not significantly different from that occurring under baseline conditions (Figure 2a). In contrast, relative recruitment of Chinook Salmon varied inversely with the relative abundance of Brown Trout in the absence of Walleyes. Relative recruitment of Chinook Salmon was higher than baseline at the LOW Brown Trout abundance, was unchanged at MEAN Brown Trout abundance, and decreased significantly below baseline at the HIGH Brown Trout abundance (Figure 2b).

When both Walleyes and Brown Trout were present, relative recruitment of Chinook Salmon was highly variable depending on predator abundances. Chinook Salmon relative recruitment did not increase or decrease beyond baseline when Brown Trout were at the LOW or MEAN abundance, regardless of Walleye abundance. Relative recruitment was significantly lower than baseline in all instances of HIGH Brown Trout abundance (Figure 3). A lack of predation mortality from Brown Trout and Walleyes did not result in a significant difference in Chinook Salmon recruitment relative to the baseline. The same was true for simulated removal of Brown Trout and Rainbow Trout (Figure 3).
Simulated changes in Alewife abundance and environmental stochasticity affected Chinook Salmon recruitment rates. Variable Alewife abundance (i.e., reduced Chinook Salmon survival, growth, and fecundity for reproductively mature adults) significantly influenced the long-term relative recruitment rates and the likelihood of population crash in the Muskegon River Chinook Salmon population (Figure 4). When Alewife abundance was LOW, Chinook Salmon recruitment decreased by 31% and the probability of the population declining below one-third of initial abundance increased to 0.91 (Table 8). Conversely, when Alewife abundance was HIGH, Chinook Salmon recruitment increased by 24% above baseline. Increases in environmental stochasticity to MODEST levels significantly reduced Chinook

### Table 8: Coefficients of variation (CV = 100 × [SD/mean]) for mean recruitment values and the probability of population decline for Chinook Salmon in all model simulations (see Table 6 for definition of abbreviations). The CV describes the stability of the Chinook Salmon population during each 50-year simulation. "Crash" indicates that population abundance fell below 1,000 total individuals (all age-classes); the number in parentheses is the number of years for which the population persisted. The probability of decline represents the likelihood that a given scenario will result in a Chinook Salmon population that is less than or equal to one-third of the baseline abundance (~576,000).

<table>
<thead>
<tr>
<th>Simulation</th>
<th>CV</th>
<th>Probability of decline</th>
</tr>
</thead>
<tbody>
<tr>
<td>WA E = ABSENT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRT = ABSENT</td>
<td>51.4</td>
<td>0.10</td>
</tr>
<tr>
<td>BRT = LOW</td>
<td>50.8</td>
<td>0.11</td>
</tr>
<tr>
<td>BRT = MEAN</td>
<td>42.9</td>
<td>0.09</td>
</tr>
<tr>
<td>BRT = HIGH</td>
<td>52.2</td>
<td>0.18</td>
</tr>
<tr>
<td>WA E = LOW</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRT = ABSENT</td>
<td>49.6</td>
<td>0.07</td>
</tr>
<tr>
<td>BRT = LOW</td>
<td>50.8</td>
<td>0.11</td>
</tr>
<tr>
<td>BRT = MEAN</td>
<td>45.1</td>
<td>0.06</td>
</tr>
<tr>
<td>BRT = HIGH</td>
<td>53.8</td>
<td>0.13</td>
</tr>
<tr>
<td>WA E = MEAN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRT = ABSENT</td>
<td>57.7</td>
<td>0.12</td>
</tr>
<tr>
<td>BRT = ABSENT; NO RBT</td>
<td></td>
<td>46.5</td>
</tr>
<tr>
<td>BRT = LOW</td>
<td>42.2</td>
<td>0.07</td>
</tr>
<tr>
<td>BRT = MEAN</td>
<td>49.0</td>
<td>0.14</td>
</tr>
<tr>
<td>BRT = HIGH</td>
<td>75.5</td>
<td>0.47</td>
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<tr>
<td>WA E = HIGH</td>
<td></td>
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</tr>
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<td>BRT = ABSENT</td>
<td>50.7</td>
<td>0.10</td>
</tr>
<tr>
<td>BRT = LOW</td>
<td>52.3</td>
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</tr>
<tr>
<td>BRT = MEAN</td>
<td>52.2</td>
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</tr>
<tr>
<td>BRT = HIGH</td>
<td>52.2</td>
<td>0.18</td>
</tr>
<tr>
<td>WA E = MEAN; BRT = MEAN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alewife abundance = LOW</td>
<td>93.1</td>
<td>0.91</td>
</tr>
<tr>
<td>Alewife abundance = HIGH</td>
<td>40.1</td>
<td>0.04</td>
</tr>
<tr>
<td>Environmental stochasticity = MODEST</td>
<td>76.0</td>
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<td>217</td>
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<tr>
<td>Environmental stochasticity = MODERATE</td>
<td>272, Crash</td>
<td>(32)</td>
</tr>
<tr>
<td>No predation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environmental stochasticity = MODEST</td>
<td>77.2</td>
<td>0.37</td>
</tr>
<tr>
<td>Environmental stochasticity = MODEST</td>
<td>84.2</td>
<td>0.37</td>
</tr>
</tbody>
</table>
Salmon recruitment below baseline at LOW and MEAN parr survival but increased recruitment significantly above baseline levels at HIGH parr survival (Figure 4). The trend was similar when environmental stochasticity was again elevated to HIGH levels, although recruitment under the scenario of MEAN parr survival was not significantly different from the baseline.

Simulated changes in predator abundance (hence, parr survival) appeared to greatly influence the probability that the Chinook Salmon population would decline to below one-third of its initial abundance. At ABSENT and LOW Walleye abundances, the probability of decline was low (≤0.18) at any Brown Trout abundance level. When Walleye abundance was MEAN or HIGH and Brown Trout abundance was HIGH, the probability of population decline was 0.18 or greater (Table 8). The probability of decline also was very high (0.48–1.0) when the level of environmental stochasticity was increased to MODEST or HIGH, but the probability of decline was lower (0.37) if predators were absent (Table 8).

Variability in Chinook Salmon recruitment increased with (1) increasing levels of predation mortality on parr, (2) increasing variation around survival and fecundity rates, and (3) increasing Alewife abundance. Increased environmental stochasticity generally yielded the highest variability in recruitment rates (Table 8; Figure 4). Removal of Brown Trout yielded the highest improvements in recruitment for individual predation scenarios (Table 8; Figure 3).

**DISCUSSION**

Past research has shown that variability in fish recruitment is influenced by changes in abundance of potential prey and predators of pre-recruits (e.g., Pepin 1990; Houde 2008). Our study shows that the effects of predation during the early life history stages (i.e., pre-recruit) of Chinook Salmon in riverine habitats can have a significant adverse effect on long-term Chinook Salmon recruitment and population stability. In comparison with Walleyes, Brown Trout may have a greater impact on parr survival because parr habitats overlap more with trout habitats than with Walleye habitats (Kruenger 2010). In fact, predation—especially by Brown Trout—in the nursery sections of the Muskegon River has important consequences for the long-term persistence of Muskegon River Chinook Salmon in Lake Michigan. Our results extend the implications of our previous 4-year empirical study (Kruenger et al. 2011) by indicating that Brown Trout predation can affect long-term recruitment and population dynamics of Muskegon River Chinook Salmon as much as abiotic factors that affect egg survival or forage conditions in open-lake environments.

Other studies suggest that predation rates during early life can negatively affect the population size and growth rate of salmonids and other fish species. A dream (2012) used bioenergetics models to estimate Caspian tern Hidroprogne caspia predation on out-migrating Chinook Salmon smolts in the San Francisco Bay area. Although the numbers of smolts consumed were large (167,000–205,000), consumption by Caspian terns represented a relatively minor (<1%) component of predation on smolts. Halsing and M oore (2008) used a matrix model approach to estimate the impact of eliminating Caspian tern predation on the endangered Snake River Chinook Salmon population in the Columbia River (quantified by Roby et al. 2003). Halsing and M oore (2008) estimated that eliminating Caspian tern predation would account for a minor (<2%) increase in the Chinook Salmon population growth rate. Studies of Striped Bass predation on juvenile stages of fishes indicate that Striped Bass may pose a significant bottleneck to the recovery of American Shad (Savoy and Crecco 2004), Atlantic Menhaden (Uphoff 2003), Atlantic Salmon, and Atlantic Cod Gadus morhua (Grout 2006). Swartzman et al. (2002) found that recruitment variability of Bering Sea Walleye Pollock Theragra chalcogramma was largely dependent upon predator and competitor distribution and abundance within the Pribilof Island nursery area.

Our simulation analysis suggests that the effects of environmental variability on Chinook Salmon recruitment may be as important as sustained predation from Brown Trout and Walleyes over long time periods. Although many of our scenarios suggested that increased predation (compared to a baseline scenario) resulted in significant changes, environmental stochastic events produced increased variability in recruitment. This result is consistent with time series of recruitment estimates from other Lake Michigan tributaries (Seelbach 1985; Zaft 1992; Murry et al. 2010). These studies indicate that Chinook Salmon recruitment in Great Lakes tributaries is much more variable when environmental influences are considered (~10-fold) than when only predation mortality is considered as the main driver (~fourfold; as observed in the Muskegon River by Kruenger et al. 2011). Environmental stochasticity may also be more influential in marine environments than we have modeled here (e.g., Jager and Rose 2003; Siegel et al. 2008; Simon et al. 2012).

Our model results also suggested that effects on Chinook Salmon recruitment from variability in Alewife prey biomass were similar to the effects created by predators of parr. The influence of Alewife biomass is consistent with trends observed since 2003 in the Lake Huron Chinook Salmon population, which exhibited visible signs of distress only 2 years after a sharp decline in Alewife abundance; one-fourth of all spawning-age adult Chinook Salmon were in critically low physical condition (Johnson et al. 2007). Trends in recruitment and population size of Pacific coast salmonid populations also indicate that survival is dependent on ocean conditions favoring growth during the postsmolt period (Kareiva et al. 2000; Friedland et al. 2009; Sharma et al. 2013).

Several assumptions were necessary for our application of RAMAS Stage to represent the fish community and interspecific interactions in the Muskegon River. Previous estimates of predation mortality (Kruenger et al. 2011) were likely conservative, as there may have been additional predation mortality in...
areas we did not quantify. Further, we only used our original estimates of predation mortality to calculate survival of Chinook Salmon for our simulations. Chinook Salmon likely experience additional mortality due to predation from other abundant predators in the Muskegon River (e.g., Northern Pike Esox lucius and Smallmouth Bass Micropterus dolomieu) and due to disease (Fitzsimons et al. 2007), which implies that actual mortality rates may be higher yet. We used length–fecundity estimates for Pacific coast populations of Chinook Salmon to estimate the fecundity of Chinook Salmon in Lake Michigan. The fecundity estimates for our stage matrix model of Muskegon River Chinook Salmon were similar to fecundities of ocean populations of Columbia River Chinook Salmon (Kareiva et al. 2000), as Chinook Salmon in Lake Michigan were originally cultured from eggs collected from the Green River, Washington. A typical fecundity of Lake Michigan Chinook Salmon may be higher or lower than that of Pacific coast populations. Collection of Lake Michigan population-specific fecundity data will facilitate more accurate parameterization in future efforts. Finally, we used Ricker-type density dependence in our simulations, which allows salmon populations to rebound more easily from low population densities than other types of density dependence, such as symmetric (Bradford et al. 2000) or compensatory (Beverton–Holt). When we imposed the ceiling type of density dependence, Chinook Salmon recruitment was more negatively influenced by Brown Trout predation and low Alewife biomass, and population abundance was more likely to crash.

Management Implications

This simple model describing the effect of species interactions in the Muskegon River could serve as a tool for fishery managers to develop and evaluate stocking scenarios (e.g., Cox and Walters 2002) for sport fisheries in the Great Lakes and coastal ocean tributaries that contain important salmonid nursery habitats. By manipulating the abundance of an important predator, we have shown that these management actions can significantly improve long-term recruitment and reduce recruitment variability of Chinook Salmon in productive tributary habitats. Based on our simulations, removal (i.e., cessation of stocking) of Walleyes from the Muskegon River does not appear to be warranted; this is good news for managers since Walleyes are highly sought after by anglers in this system (Krueger et al. 2011). Manipulating the abundance of alternative prey for Walleyes also can influence long-term recruitment and variability of Chinook Salmon populations. When Brown Trout (predator and alternative Walleye prey) and Rainbow Trout (alternative prey) were both removed, there was a 5% decrease in long-term Chinook Salmon recruitment. Thus, it seems that alternative prey species, especially Rainbow Trout in this case, are likely to be important for the long-term persistence of Chinook Salmon in natal tributaries. Our modeling scenarios, in combination with prior research, demonstrate that the removal of any predator or prey species without knowledge of the overall impact is not warranted. Our results also raise an interesting dilemma for fisheries managers: if the Chinook Salmon fishery is valued more than the fisheries for Walleyes or Brown Trout, then perhaps Walleye and Brown Trout stocking should be reduced during years of low Alewife abundance to increase Chinook Salmon abundance and harvest.

The Muskegon River was an ideal system for this analysis, as fishery managers essentially had near-total control of predator abundance (Krueger et al. 2011). Hence, the synergistic effects of Walleye and Brown Trout predation on Parr were controlled through stocking efforts. Similar assertions have been made in other studies to promote persistence of Great Lakes piscivores (e.g., Kitchell and Crowder 1986; Kitchell et al. 2000). Although Chinook Salmon are naturalized, they are nonetheless a nonnative species and managing for their persistence may not be a priority in some systems. Nevertheless, managers could apply this model to other systems in an exploratory manner to determine the population consequences of variable stream piscivory on the long-term reproductive success of Chinook Salmon. Although our modeling effort was simplistic, it is the first such analysis of a Great Lakes tributary and may provide the first step toward implementing such actions in the Great Lakes and beyond.

ACKNOWLEDGMENTS

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Do Beaver Dams Impede the Movement of Trout?

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Do Beaver Dams Impede the Movement of Trout?

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Abstract

Dams created by North American beavers Castor canadensis (hereafter, “beavers”) have numerous effects on stream habitat use by trout. Many of these changes to the stream are seen as positive, and many stream restoration projects seek to either reintroduce beavers or to mimic the habitat that they create. The extent to which beaver dams act as movement barriers to salmonids and whether successful dam passage differs among species is a topic of frequent speculation and warrant further research. We investigated beaver dam passage by three trout species in two northern Utah streams. We captured 1,375 trout above and below 21 beaver dams and fitted them with PIT tags to establish whether fish passed the dams and to identify downstream and upstream passage; 187 individual trout were observed to make 481 passes of the 21 beaver dams. Native Bonneville Cutthroat Trout Oncorhynchus clarkii utah passed dams more frequently than nonnative Brown Trout Salmo trutta and nonnative Brook Trout Salvelinus fontinalis. We determined that spawn timing affected seasonal changes in dam passage for each species. Physical characteristics of dams, such as height and upstream location, affected the passage of each species. Movement behaviors of each trout species were also evaluated to help explain the observed patterns of dam passage. Our results suggest that beaver dams are not acting as movement barriers for Bonneville Cutthroat Trout or Brook Trout but may be impeding the movements of invasive Brown Trout.

Before settlement by Europeans, North American beavers Castor canadensis (hereafter, “beavers”) played a significant role in shaping the habitats of North American fishes (Naiman et al. 1988). The extensive removal of beavers beginning in the 17th century affected native fish, such as Brook Trout Salvelinus fontinalis in the east and Cutthroat Trout Oncorhynchus clarkii in the west. With the recent recovery of beavers in some western streams (Naiman et al. 1988), the reintroduction of beavers into other streams, and restoration projects that seek to mimic the effects of beavers on stream processes (DeVries et al. 2012; Pollock et al. 2011), a better understanding of the interactions between beavers and native fish is needed. This understanding would permit improved choices and prioritization in how and where these types of restoration activities are used, especially in the presence of declining native populations of Cutthroat Trout (Budy et al. 2012) and Brook Trout (Marschall and Crowder 1996; Fausch 2008).

It has been suggested that the increased habitat complexity found in reaches (especially lower-stream-order reaches) with beaver dams benefits salmonid species in western North America (Neff 1957; Gard 1961; Collen and Gibson 2001; Kemp et al. 2012) and provides vital habitats for threatened or imperiled fish species. Deeper water with low velocities and high wood abundances provides important rearing habitat for Endangered Species Act (ESA)-listed Coho Salmon O. kisutch (Pollock et al. 2004). White and Rahel (2008) showed that complementation of different habitat types, including beaver ponds, supported the needs of multiple life stages of imperiled Bonneville Cutthroat
Trout *O. clarkii utah* and increased their recruitment. Beaver ponds provide vital overwinter habitat in streams that otherwise may freeze throughout their entire depth (Cunjak 1996; Lindstrom and Hubert 2004). Collen and Gibson (2001) identified other benefits to fish dwelling within the beaver pond, such as cover created by the beaver lodge and food cache; stabilization of streamflows; increased sediment storage in the pond, thus creating spawning habitats below the dam; and an increase in lentic invertebrates. These benefits may also be exploited by numerous pool-dwelling, ESA-listed Pacific salmon (Murphy et al. 1989). We postulate that native fish are more likely to benefit from the habitat heterogeneity created by beavers if they are adept at passing beaver dams to access those different habitats.

Even in small streams, beaver dams can be up to 2.5 m tall, and it is logical that such dams might act as barriers to the upstream migration of fish (Kemp et al. 2012). However, the diversity of flow paths over, through, under, and around (e.g., side channels that act as fish ladders) such dams provides a number of plausible pathways for upstream movement (Schlosser 1995). Moreover, these flow paths change regularly with beaver maintenance and construction activities and with fluctuations in discharge.

Whether beaver dams act as barriers to fish and the extent to which they impede the movement of different species are questions in need of clarification. Kemp et al. (2012) reviewed 108 studies evaluating the effects of beaver dams on fish and fish habitat; beaver dams were cited as “barriers to fish movement” in 43% of the papers, and this was the most common adverse effect discussed. However, the putative negative effect of beaver dams as barriers was speculative in that 78% of the studies did not support this claim with data (Kemp et al. 2012).

The objective of our study was to evaluate whether trout can pass beaver dams. The Logan River, Utah, serves as an ideal study area, as it contains native Bonneville Cutthroat Trout that compete with two nonnative species—the Brook Trout and Brown Trout *Salmo trutta*—in beaver-altered habitats. Differences in passage behaviors among the three trout species may provide information that is crucial to the future conservation of Bonneville Cutthroat Trout. Knowledge of dam passage by trout may also have implications for fisheries and land managers in streams where beaver dams exist or where beaver dam surrogate structures are being implemented as a means of stream restoration (Pollock et al. 2011; DeVries et al. 2012).

**STUDY SITE**

Temple Fork (watershed area = 41.5 km²) is a third-order tributary to the Logan River, and Spawn Creek (14.6 km²) is a second-order tributary to Temple Fork (Figure 1). The Temple Fork watershed is a good analog for lower-order, montane trout streams in the intermountain west. The annual hydrograph consists of peak flows that are dominated by spring snowmelt and base flow (0.28–1.39 m³/s) that is supported by spring flow (Seidel 2009). Peak streamflows usually occur in May to June and are approximately five times base flow (de la Hoz Franco and Budy 2005; Seidel 2009). At base flow, wetted widths in reaches without beaver dams are approximately 5.0 m in Temple Fork above Spawn Creek and 2.5 m in Spawn Creek.

From 2008 to 2011, beavers maintained 27 dams along Temple Fork and Spawn Creek (Figures 2, 3). It is worth noting that just upstream of our study site boundary on Temple Fork, beavers built 12 new dams within a 200-m reach during 2012. Of the 21 beaver dams that were evaluated in this study, three were constructed during the study period and four others were breached or blown out during the 2011 spring runoff floods (Table 1). Of the four dams that were impacted by the 2011 floods, all were on Temple Fork: two dams (T3 and T9) were completely blown out and have not been repaired, while the other two (T4 and T8) had only minor breaches and have not been repaired. Many of the ponds in the upper portion of Spawn Creek are part of a major beaver dam complex that has been...
FIGURE 2. Locations of beaver dams in Temple Fork. Dams are numbered in the upstream direction; side channels are indicated (A, B, and C locations in the upper right panel correspond to panels A–C). Brown Trout were not observed above dam T4, and Brook Trout were not present in Temple Fork. [Figure available online in color.]

present for over 30 years (Bernard and Israelsen 1982). By contrast, the valley bottom road up Temple Fork, which was not removed until the mid-1990s, minimized development of beaver ponds in this area until recently. The uppermost dams on Spawn Creek and Temple Fork were not included in this study because they were above the area where fish were marked and they were not consistently scanned for fish presence.

METHODS

Between 2008 and 2011, we captured 1,375 trout in Spawn Creek and Temple Fork and fitted them with PIT tags, which permitted us to track unique fish (Moore 1992). Some fish that were originally tagged in the Logan River were also detected in the study streams, and these individuals were included in our study. Fish were captured during summer months by electrofishing and angling. Upon initial capture of a trout, a Biomark full-duplex, 12-mm PIT tag was placed subcutaneously behind the dorsal fin. The capture location was recorded with a handheld GPS unit. The numbers of tagged fish varied within and among streams (Table 2). In addition to their use in evaluating beaver dam passage by trout, these PIT-tagged fish were part of a larger study to evaluate trout movement, growth, and habitat use within these streams.
FIGURE 3. Locations of beaver dams in Spawn Creek. Dams are numbered in the upstream direction; side channels are indicated (A and B locations in the upper right panel correspond to panels A, B). Dams S4 and S7 have left and right components. Brown Trout did not pass S7. [Figure available online in color.]
To determine whether the fish passed beaver dams, we used a variety of spatially explicit data collected for individual fish. The GPS coordinates of fish locations were taken from capture locations, stationary antennas, and mobile antennas. Stationary PIT tag antennas were located (1) in Temple Fork just upstream from its confluence with the Logan River, (2) in Temple Fork just upstream from its junction with Spawn Creek, and (3) in Spawn Creek just upstream from its junction with Temple Fork (Figure 1). The Temple Fork–Spawn Creek antenna array began operation in May 2009 and identified fish that moved into or out of the area with beaver ponds. Active scanning upstream of the stationary antennas in both creeks by using a mobile antenna commenced on a monthly basis in May 2009. Mobile efforts entailed one or two observers moving upstream with PIT tag receivers attached to a wand that detected fish in the stream. Detection of individual fish in this small stream system was aided by the use of two observers with mobile antennas to actively search all available habitat (Randall 2012). During mobile scanning, locations of tagged fish were determined by synchronizing the location of a handheld GPS unit when each fish was recorded by the PIT tag receiver.

Initial and resight locations of trout were plotted by snapping the GPS point to the nearest location on a stream layer that was digitized from 1-m aerial imagery using ArcGIS version 10.0. A fish was designated as having passed a beaver dam if we recorded that fish at locations both above and below a given dam. Each pass was summarized by pass direction, dam, and species. Statistical differences in beaver dam passes among the
trout species were determined by comparing the number of dam passes made by each species against the expected number of dam passes based on the proportional representation of each species among the tagged fish. We used a chi-square test to determine whether passage differed among the species. The null hypothesis was that the number of passes for a given species reflected the proportion of tagged fish of that species. The expected number of passes for a given species was calculated by multiplying the total number of passes (i.e., for fish of all species) by that species’ proportion among the tagged fish. This was done for both streams (overall) as well as for each stream. Additionally, we evaluated whether fish passage at a beaver dam was equally likely to occur in upstream and downstream directions.

Movement direction (upstream or downstream) was determined based on the locations and dates of the observations. The date of fish passage at a beaver dam was estimated by assigning the month representing the midpoint between two successive observations. For situations in which the period between the two observations exceeded 6 months, we disregarded those data in our evaluation of fish movement timing. The null hypothesis for fish movement was that movement was independent of month.

To determine whether dam passage was affected by differences in the propensity of each trout species to move, we summed the absolute values of minimum observed distances traveled by each individual fish over all observations. These sums provide information on minimum travel distances because we only recorded movement between two observations and not actual fish movement during unobserved periods. The total movement distances of each fish were used to determine the median of total movement distance for each species.

To determine the size of fish that passed beaver dams, fish length on the predicted date of dam passage was estimated. Growth in length (TL; mm/d) was based on all fish that had been captured multiple times and was calculated by dividing the observed growth by the time period between captures. Daily growth rates were calculated for each species. Average growth rates were applied to the length of time between the most recent capture event and the estimated date of beaver dam passage to determine the length of each fish at the time of passage. To reduce error with these predictions, we used size-class distributions consisting of 50-mm bins (<150, 151–200, 210–250, 251–300, and >300 mm). The size-classes for the tagged population of each species and the size-classes of fish that passed dams were compared by using a chi-square test.

The physical characteristics of the beaver dams within both streams were determined during spring 2011. Attributes that were recorded included dam height (from the streambed on the downstream side), maximum pond depth, and whether side channels were present (Figure 4). In addition, side channels and dam crests were mapped as polylines, and the upstream backwater of the pond from the dam was mapped as a point with a Juniper Archer map-grade GPS unit and ArcPad. Spawn
Creek dam 4 (S4) represented a set of three dams built on two channels (Figure 3). These dams were grouped for the analysis to avoid ambiguities arising from the fact that fish located above and below this complex could have passed the dams in either channel. A similar situation occurred at Spawn Creek dam 7 (S7). For each group of dams, the dam with the shortest height was used in the analysis of dam height.

We used linear regression to determine which beaver dam characteristics affected fish passage at the dams. We assumed that dam height, stream (Spawn Creek or Temple Fork), and side channels (present or absent) would be the primary dam characteristics governing fish passage. As such, we considered six models explaining passage by each trout species: (1) passage was affected by dam height; (2) passage was affected by the presence of a side channel around the dam; (3) passage was affected by dam number, which reflected dam position in the stream (i.e., higher numbers, such as T7 or S9, represented dams that were located further upstream); (4) passage was affected by dam height, with separate intercepts for each stream; (5) passage was affected by the presence of a side channel, with separate intercepts for each stream; and (6) passage was affected by dam number, with different intercepts for each stream. We used these models to evaluate all passes as well as only upstream passes. Because five of the dams (T3, T9, S1, S2, and S8) were not in place for the entire time frame of the study, the number of fish that would have passed each of those dams was estimated by expanding the number of fish detected as passing a dam to the 3.5-year study period. The best model for each species was chosen by using Akaike’s information criterion corrected for small sample size (AIC_c; package MuMIn in R software; Barton 2012). The best model was averaged across all models for which AIC_c values differed by less than 2.0 (Burnham and Anderson 2002). An attribute with a model weight of 1.0 meant that it was included in all competing models. The closer a model weight was to 0.0, the less evidence that inclusion of the attribute improved the understanding of the data. We present adjusted $R^2$ values for the best model to reflect the explained variation in the data.

RESULTS

We recorded 481 individual passage events by trout at beaver dams. Of those passes, 53 were single passes by unique individuals, whereas the remaining 428 passes were from fish that passed multiple dams (Figure 5). Overall, passage at beaver dams differed significantly among the three species ($P < 0.001$; Table 3). Relative to each species’ proportional representation among the tagged fish, Bonneville Cutthroat Trout were more likely to pass beaver dams, while Brown Trout were less likely to pass dams. Brook Trout passed dams as often as expected given the number of tagged fish.

Among the fish that were tagged in Temple Fork and Spawn Creek, at least 15.9% of the Bonneville Cutthroat Trout, 4.5% of the Brown Trout, and 18.7% of the Brook Trout passed at least one dam. These values represent minimum estimates because (1) not all tagged fish were relocated and (2) some fish could have moved over a dam and back to their previous location between detections and thus would not have been recorded as passing the dam. Of the fish that passed at least one dam, the majority were detected as exhibiting passage events at two or more dams (Figure 5).

<table>
<thead>
<tr>
<th>Location</th>
<th>Bonneville Cutthroat Trout (Exp)</th>
<th>Brown Trout (Exp)</th>
<th>Brook Trout (Exp)</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall</td>
<td>394 (312)</td>
<td>29 (107)</td>
<td>58 (55)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temple Fork</td>
<td>251 (197)</td>
<td>8 (62)</td>
<td>NA</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Spawn Creek</td>
<td>143 (112)</td>
<td>21 (45)</td>
<td>58 (55)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

TABLE 3. Beaver dam passage by the three trout species in Temple Fork, in Spawn Creek, and overall (both streams). The total number of passes in both upstream and downstream directions is shown, along with the number expected (Exp; in parentheses) based on the number of tagged fish. The $P$-values are the results of chi-square tests.
Every evaluated dam was passed by trout, and each dam was associated with both upstream and downstream passage events (Figure 6). We found that Bonneville Cutthroat Trout and Brook Trout were significantly ($P < 0.001$) more likely to move downstream over dams than to move upstream. The few Brown Trout that we detected as moving past dams seemed to have an equal likelihood of moving upstream and moving downstream.

Timing of fish movement differed among the trout species (Figure 7). Bonneville Cutthroat Trout passed beaver dams more often than expected from May to September and less often than expected during the remaining months ($P < 0.001$). Brown Trout passed dams more often than expected in January, September, and October and less often than expected during the remaining months ($P = 0.053$). Brook Trout passed dams more often than expected in June and July and less often than expected in other months ($P < 0.001$).

Dam passage could be partially explained by the difference in movement proclivities among species. The median movement distance of fish tagged within the study area was 227 m for Bonneville Cutthroat Trout, 48 m for Brown Trout, and 8 m for Brook Trout. The high median movement distance of Bonneville Cutthroat Trout and the extended tail of their movement distribution (Figure 8) corresponded to the more frequent dam passage of this species. The lower median movement distance and narrower movement distribution for Brown Trout could partially explain their lower frequency of beaver dam passage. The very limited distance traveled by Brook Trout did not correspond well with their dam passage counts in Spawn Creek. The combination of a low movement distance with a relatively high frequency of dam passage indicates the redistribution of Brook Trout within a dam complex rather than passage at multiple dams related to longer migratory movements.

The sizes of fish that passed beaver dams (upstream and downstream passes combined) differed by species. Our results indicate that for Bonneville Cutthroat Trout, fewer fish smaller than 200 mm and more fish greater than 300 mm passed dams than would be expected based on the size-class distribution of this population (chi-square test: $P \leq 0.001$). The size of Brown Trout that passed dams was different than expected based on the population’s size-class distribution ($P = 0.011$). The number of Brown Trout larger than 300 mm that passed dams was lower than expected. In contrast, Brown Trout in the 201–250-mm size-class passed dams nearly 2.5 times more often than expected. Size was not related to dam passage for Brook Trout ($P = 0.70$).

Physical attributes of individual beaver dams differed slightly between the two evaluated streams (Table 1). Beaver ponds in Temple Fork were taller on average than those in Spawn Creek (111 cm versus 89 cm). The depths of pools formed by beaver
ponds were greater in Temple Fork (83 cm) than in Spawn Creek (53 cm). Almost every beaver pond in both streams could be circumnavigated by a side channel; in Temple Fork, 89% of beaver ponds had side channels, whereas in Spawn Creek 75% of beaver ponds had side channels.

All of the study dams were passed by Bonneville Cutthroat Trout, regardless of the physical characteristics of the dam. Even the dams exceeding 2 m in height (T2 and T9) had 5 and 2 upstream passes, respectively, and 18 and 4 downstream passes, respectively.

The best model for total dam passage by Bonneville Cutthroat Trout included a single significant \( (P = 0.03; \text{adjusted } R^2 = 0.22) \) slope for dam number (model weight = 1.0; Figure 9). The further upstream a dam was in each river (i.e., as reflected by the dam number), the fewer fish passed that dam. The best model had the same negative slope for both streams. When only upstream passes were assessed for Bonneville Cutthroat Trout, three attributes were present in the best model \( (R^2 = 0.21) \): dam height (model weight = 0.44), dam number (model weight = 0.39), and side channel presence (model weight = 0.17). All of these predictors had a negative slope, indicating that dam passage decreased (1) as dam height increased, (2) as dam number increased, and (3) if side channels were present. Even though these predictors were included in the best model using AICc, the slope for each predictor was not significant \( (P > 0.10) \).

The best model for Brown Trout included dam number (model weight = 0.48) as well as dam height (model weight = 0.33) and side channel presence (model weight = 0.19). Passage at dams decreased as dam number increased and as dam height increased; passage increased at dams when side channels were absent. However, the best model did a poor job in explaining the data \( (P > 0.10; \text{adjusted } R^2 = 0.06) \). When only upstream passes of Brown Trout were considered, the same three attributes were present in the best model \( (R^2 = 0.15) \): dam height (model weight = 0.41), dam number (model weight = 0.33), and side channel presence (model weight = 0.26). Again, these predictors were not significant \( (P > 0.10) \).

We found that the best model for Brook Trout included stream (model weight = 1.0), dam number (model weight = 0.37), side channel presence (model weight = 0.37), and dam height (model weight = 0.26). The large weight due to stream was attributable to the absence of Brook Trout in Temple Fork. For Spawn Creek, the best model indicated that (1) dams higher in the system (i.e., higher dam number) were more likely to be passed; (2) the presence of side channels resulted in more Brook Trout passage events; and (3) as dam height increased, dam passage by Brook Trout decreased. This model was significant \( (P = 0.02; R^2 = 0.35) \), but this was mainly due to the lack of Brook Trout in Temple Fork. When only upstream passes were evaluated for Brook Trout, stream was identified as the most important predictor (model weight = 1.0) and the same three dam attributes were present in the best model \( (R^2 = 0.29) \): dam height (model weight = 0.30), dam number (model weight = 0.39), and side channel presence (model weight = 0.31). The slopes of dam number and side channel presence were both positive, indicating that dams with side channels and dams located further upstream were more likely to be passed by Brook Trout.

**DISCUSSION**

All three species of trout evaluated in our study passed beaver dams. Our observations show that Bonneville Cutthroat Trout
and Brook Trout passed beaver dams more than expected. Brown Trout passed dams less than expected, and the majority of passes observed were at smaller dams where Brown Trout concentrations were relatively high. Our results indicate that Bonneville Cutthroat Trout and Brook Trout are readily capable of negotiating large beaver dams. Brown Trout movements are more restricted, as shown by a lack of passage at larger dams. It appears that beaver dams benefit Bonneville Cutthroat Trout in the presence of Brown Trout by impeding the movements and migrations of Brown Trout and by keeping these nonnative fish out of upstream reaches. Still, questions remain regarding dam passage timing, movement behavior, specific mechanisms of dam passage, and restoration implications. We discuss each of these below.

**Dam Passage Timing**

We found that peak passage at beaver dams coincided with spawning migrations for Bonneville Cutthroat Trout and Brown Trout but not for Brook Trout. Bonneville Cutthroat Trout passed beaver dams at high frequencies during their spawning season in May to July (Seidel 2009), but their passage was also high in the months after spawning. Movement during these months spanned the breadth of streamflow conditions, ranging from peak flows to base flows. Movement in the upstream and downstream directions was approximately equal during May–August (54 upstream passes, 58 downstream passes), but movement was decidedly greater in the upstream direction during September (17 upstream passes, 8 downstream passes). Such movement patterns suggest that Bonneville Cutthroat Trout are seeking areas in which to recover after spawning. Movement during late summer indicates that these fish can pass beaver dams in both directions during times of the year with low base flows.

Elevated dam passage by Brown Trout coincided with spawning; the highest passage rate occurred just prior to their late-fall and early winter spawning season (Wood and Buddy 2009). The number of dam passes made by Brown Trout in September and October was low (4 upstream passes, 5 downstream passes) because 95.5% of the Brown Trout tagged for this study were never detected as passing a beaver dam. Observed passage by Brown Trout during fall low-streamflow periods suggests that they are able to pass dams at that time. The low passage rate provides some support to the assertion that passage by Brown Trout at beaver dams is hindered by low flows (Schlosser and Kallemeyn 2000; Rosell et al. 2005; Taylor et al. 2010). However, our sample size of Brown Trout passing beaver dams was limited, so further research is needed to test whether Brown Trout are able to pass dams at low flows.

Brook Trout passed beaver dams in June, when streamflows were high and when Bonneville Cutthroat Trout were spawning. Movement during this time of year would be facilitated by side channels with sufficient flow and by increased flows passing over and through dams. Brook Trout movement in June may correspond to Bonneville Cutthroat Trout spawning; Brook Trout could be relocating to benefit from foraging on Bonneville Cutthroat Trout eggs and on insects that are displaced during spawning by the native trout. Although Brook Trout passage was not related to their fall spawning season, it could reflect an adaptive history of Brook Trout to redistribute during times of high flow (Peterson and Fausch 2003). Within the Brook Trout’s native range, movement in relation to changing flows in small streams is likely related to rainfall events that are less predictable than the snowmelt-dominated runoff found in the Spawn Creek watershed (Scuton et al. 2003). Since this system has predictable snowmelt-mediated high-flow events, higher passage rates during these periods provide evidence that Brook Trout are being aided in dam passage by flashy, higher-peaked, rain-dominated flow events.

**Dam-Influenced Movement Behaviors**

Understanding beaver dam passage as it relates to movement patterns for each species is complicated. Behaviors inherent to each of these trout species could affect beaver dam passage, but the dams could be modifying these behaviors. Based on movement distances, Bonneville Cutthroat Trout encountered dams more frequently than Brook Trout or Brown Trout, yet approximately the same percentage of tagged Brook Trout passed at least one dam even though this species demonstrated the most restricted movement. All three species appeared to be adept at passing multiple dams (Figure 5). However, only 14 individual Brown Trout passed any dam at all. The majority of Brown Trout that passed more than one beaver dam did so in the upper Spawn Creek dam complex, where dams are closely spaced. This pattern of passing multiple dams is the same for Brook Trout in upper Spawn Creek. A higher number of individual Bonneville Cutthroat Trout (n = 145) passed at least one beaver dam, and a larger proportion of these fish passed more than two dams (Figure 5). Future research is needed to determine whether beaver dams restrict fish movement or whether fish exhibiting a higher propensity to migrate will pass multiple dams simply because they encounter more dams.

Beaver dams in downstream locations have the potential to restrict the movements of Brown Trout. In the Temple Fork area where Brown Trout are the dominant species, there are two large dams (T2 and T3) that were passed only seven times. We have yet to document a Brown Trout that has successfully passed T2 while moving in an upstream direction. This same pattern was seen in Spawn Creek at S1 and S2 (which were only in place during the last year of our study period), where we have yet to document any passage of Brown Trout. The lack of upstream passes by Brown Trout over these recently built beaver dams indicates that the dams have so far impeded the upstream movements of Brown Trout. Therefore, large dams in the downstream areas of these streams may slow the movement of Brown Trout into habitats that are occupied by Bonneville Cutthroat Trout.

The size-class distributions of fish that passed beaver dams differed among the three species. Brook Trout appeared to have the ability to pass dams regardless of fish size. In contrast, we
observed only one large (>300-mm) Brown Trout passing a beaver dam in the downstream direction. The high number of 201–250-mm Brown Trout passing dams in both directions (4 upstream passes, 6 downstream passes) may be the result of an increase in spawning-related movement as the fish reached sexual maturity. This observation suggests that younger Brown Trout would be more able to invade stream systems with beaver ponds. The higher-than-expected passage by large sizes of Bonneville Cutthroat Trout supports the idea that size does not affect the passage of this species at beaver dams. The largest size-class of Bonneville Cutthroat Trout (>350 mm) passed dams in both directions (4 upstream passes, 2 downstream passes) over three times more often than expected based on their frequency in the tagged population.

The high level of passage by Bonneville Cutthroat Trout at S1 and S2 is remarkable considering the height of these dams and the relatively short duration for which they were in place. Bonneville Cutthroat Trout passed S1 14 times and passed S2 17 times, even though the two dams were in place only for the final 16 months of the study period. High passage frequency at S1 and S2 is necessary since most of the spawning locations within Spawn Creek are upstream of these dams. Recently, spawning activity by Bonneville Cutthroat Trout has increased within the 75 m above the pool of S2 (Brett B. Roper, unpublished data).

**Dam Passage Mechanisms**

To fully understand the mechanisms of beaver dam passage, broader samples of streams and beaver ponds are needed. Measuring the geometry of scour pools at the base of dams could contribute to an understanding of whether it is possible for a fish to leap over a dam. We need a better understanding of how and when fish pass beaver dams as well as the characteristics of dam passage attempts that are unsuccessful. Placement of stationary antennas along the face of the dam and in side channels could be configured to provide a more direct measurement of whether some fish are attempting to pass dams and whether they are successful. The evaluation of trout passage at beaver dams is complicated by the dynamic nature of these dams. Beavers frequently reengineer their habitat. Over the course of this study, beavers constructed two new dams (S1 and S2), and two dams failed (T3 and T9). Two dams (T2 and S9) increased in height and length, and their ponds increased in depth. For a number of dams, flow patterns around (side channels) and through (over the dam to under the dam) the dams also changed during the study period. These physical changes can alter whether and how fish movement is facilitated on a daily to annual basis. The dramatic and subtle changes we observed in beaver dam configuration suggest that dam characteristics must be examined more closely over time rather than measuring them at a single point in time (i.e., as was done in this study).

**Restoration and Conservation Implications**

Our findings of the apparent ease with which Bonneville Cutthroat Trout and Brook Trout passed beaver dams are of fundamental importance to restoration and conservation efforts aimed at restoring native trout populations. Our results refute the largely speculative concerns about beaver dams acting as migration barriers. This is timely in light of an increasing number of examples in which dam-building beavers are used to reconnect floodplains and restore fish habitat (e.g., Pollock et al. 2011) or in which beaver activity is mimicked to bring about desired changes in stream habitat (DeVries et al. 2012). Our results also have positive implications for the management and conservation of declining native Brook Trout in eastern North America (Petry et al. 2005). Reintroducing beavers or promoting the beaver as a conservation species—instead of treating them as a nuisance—may provide a means to conserve and restore Brook Trout populations. If nonnative Brown Trout movement is indeed constrained by the presence of beaver dams, then beaver reintroduction may have the added advantage of shifting the competitive advantage back to native trout species.

**ACKNOWLEDGMENTS**

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**REFERENCES**


Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia

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Prey Selectivity of Fraser River Sockeye Salmon during Early Marine Migration in British Columbia

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Abstract
Mortality of salmon during early marine life has long been thought to be a critical factor in limiting overall abundance. One of the key hypotheses proposed to explain the long-term productivity decline of Canada’s iconic Fraser River Sockeye Salmon Oncorhynchus nerka, is deficient habitat conditions experienced during early marine life. Our study is a first step towards testing this hypothesis, with an aim of understanding food availability and prey choice of juvenile salmon early in their coastal migration. We investigated zooplankton density, diet composition, and foraging selectivity of juvenile Fraser Sockeye Salmon during the 2009 and 2010 migrations and determined whether the timing of their migration was related to feeding success. Sockeye Salmon diets showed high prey diversity and a preference for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey. Calanoid copepods, the most abundant available prey, were not strongly selected in either year. Zooplankton densities were highest in the tidally mixed Discovery Passage–Johnstone Strait area. The fish appeared to have an adequate prey resource pool during their early marine migration, and in the 2 years of our study we observed similar feeding success throughout the migration period. Importantly, we found no evidence of food limitations that might indicate that juveniles suffered food deprivation. Further research is needed to test the generality of these findings, including the potential impacts of warming ocean temperatures on the timing and availability of prey during migration.

Mortality of salmon during their early marine migration has long been thought to be an important factor limiting their overall abundance (Ricker 1976; Peterman 1982; Beamish et al. 2004). Marine survival of juveniles depends on their early marine growth (Farley et al. 2007; Duffy and Beauchamp 2011), and mortality is hypothesized to occur through interactions between ocean conditions, food, and predation (Beamish and Mahnken 2001; Beamish et al. 2004).

Sockeye Salmon Oncorhynchus nerka, is an economically and culturally important species in the northeast Pacific. Populations of Sockeye Salmon inhabiting southern portions of their range are in decline (IUCN 2009), and those returning...
to Canada’s iconic Fraser River in particular may be experiencing multiple interacting stressors. The 2009 return of Sockeye Salmon to the Fraser River was the lowest in 50 years, prompting the Canadian government to launch a Can$26 million Judicial Inquiry to investigate the cause of the decline and identify imminent threats to the survival of Sockeye Salmon (Cohen Commission 2012). Despite a substantial rebound by one year-class in 2010, there has been an overall decrease in productivity of most Fraser River Sockeye Salmon populations since the early 1990s (Peterman and Dorner 2012). Poor habitat conditions experienced during their early marine migration from the Fraser River is one of four hypotheses proposed to explain their recent decline (Peterman et al. 2010; Connors et al. 2012).

The Strait of Georgia, between British Columbia’s Vancouver Island and mainland coast, is the primary migration corridor for Sockeye Salmon leaving the Fraser River (Groot and Cooke 1987; Welch et al. 2009, 2011; Price et al. 2011). This coastal sea receives emissions and waste discharge from the activities of several million people (Ross 2006). Aquatic species are exposed to the cumulative effects of pollution, fishing, habitat destruction, invasive species, and climate change (Johannessen and Macdonald 2009). Secondary production in the Strait of Georgia has been declining since 2001, and a change in the zooplankton assemblage may be underway (Johannessen and Macdonald 2009). Importantly, knowledge of the feeding habits and prey abundance for Fraser River Sockeye Salmon during their early migration is incomplete and antiquated, the most recent study having occurred during 1990–1993 (Haegele 1997), the beginning of the modern productivity decline for Fraser Sockeye Salmon.

A panel of expert scientists recently recommended an ecological investigation of the Strait of Georgia to advance our knowledge of the state of Fraser Sockeye Salmon productivity (Peterman et al. 2010). Our study, a first step towards this goal, aimed to understand foraging behavior by juvenile Sockeye Salmon early in their migration at sea. We examined the prey assemblage, diet composition, and foraging selectivity of juvenile sockeye salmon. Furthermore, we investigated whether the timing of migration through the northern Strait of Georgia and southern Johnstone Strait is related to their feeding success and whether food limitations can be detected. More generally, our research attempted to shed light on a relatively unknown phase of salmon life histories, which may be related to productivity of populations.

METHODS

We collected 163 juvenile Sockeye Salmon from inland marine waters of northern Strait of Georgia and southern Johnstone Strait from May 24 to July 7, 2009, and 186 juveniles from May 14 to June 21, 2010 (Figure 1), as part of a broader ecological investigation (see Price et al. 2010, 2011). Each capture location was sampled weekly, and up to 10 juveniles per location per week were retained for diet analysis when the number of fish caught at a site exceeded 50; we did not catch fish at some locations each week (Table 1). The northern Strait of Georgia and southern Johnstone Strait region hosts the largest juvenile Sockeye Salmon migrations on Canada’s west coast (Groot and Cooke 1987), and our samples were collected throughout the main migration period of fish that originated from the Fraser River watershed (Welch et al. 2009, 2011; Price et al. 2011). Differences in sampling dates between years reflect differences in migration timing. Given the northbound migration of Sockeye Salmon through the study region, we did not catch fish at the most northern sites during the first 2 weeks, when fish were concentrated in the south, nor did we catch fish at the most southern sites during the final 2 weeks, once fish had migrated north. All fish collections occurred during daylight and crepuscular hours, which is reported to be the primary feeding time of juvenile salmon for this latitude and time of the year (Healey 1991; Landingham et al. 1998). We used a modified purse seine (70 m long, 10 m deep, 6 mm mesh) to capture the fish; after pursing the net, the catch was concentrated in the bunt of the seine, and fish were dip-netted out, euthanized by a swift
TABLE 1. Number of Sockeye Salmon stomachs collected during each sampling month in 2009 and 2010 by location (see Figure 1) and summary statistics (mean and SD in parentheses) for fish and oceanic variables.

<table>
<thead>
<tr>
<th>Location or measure</th>
<th>2009</th>
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<td>10</td>
</tr>
<tr>
<td>16</td>
<td>0</td>
<td>10</td>
</tr>
</tbody>
</table>

| Fork-length (cm)\(^a\) | 10.8 (1.8) | 10.4 (1.2) | 10.6 (1.5) | 10.2 (1.1) | 11.6 (1.3) |
| Mass (g)\(^b\)         | 14.3 (9.0) | 12.1 (4.2) | 13.1 (5.9) | 13.0 (3.0) | 15.2 (5.2) |
| Temperature (°C)\(^b\) | 14.0 (1.0) | 11.2 (1.0) | 10.6 (0.6) | 11.2 (0.9) | 11.1 (1.7) |
| Salinity (%o)\(^b\)    | 28.3 (0.8) | 29.3 (1.2) | 29.2 (0.6) | 28.4 (1.0) | 28.4 (1.9) |

\(^a\)Sample size equaled the number of stomachs sampled in 2009 and was 93 in 2010.

\(^b\)Sample size was 12 in 2009 and 18 in 2010.

blow to the head, and placed immediately in 1-L bottles containing a solution of 7% formalin in seawater. In the laboratory, individual fish were weighed and measured (fork length) prior to removing stomachs. Sea surface temperature and salinity were recorded during each sampling event via a YSI-30 SCT meter.

Stomach contents were examined using a Wild M-7 dissecting microscope, weighed to the nearest 0.01 g (wet weight), and divided into taxonomic categories. The percentages per taxonomic category for major components of each stomach were estimated visually. We used a feeding index (\(I_F\)) as a measure of foraging success, expressed as the percentage of body weight consisting of food items, which standardizes for differences in body size:

\[
I_F = \frac{M_{sc}}{M} \times 100,
\]

where \(M_{sc}\) is the mass of the stomach contents (g), and \(M\) is fish mass (g; Farley et al. 2007).

We used relative abundance (\(A\)) as the primary metric to rank prey taxa, expressed as percent contents:

\[
A = \left( \sum_{i=1}^{f} A_{i,f} \right)^{-1} \times 100,
\]

where \(A_{i,f}\) is the total of prey category \(i\) in the \(f\)th Sockeye Salmon stomach sampled for diet analysis (Farley et al. 2007).

We also calculated the frequency of occurrence of each major prey group (\(F\)), expressed as a percent, and calculated as:

\[
F = \frac{O}{S} \times 100,
\]

where \(O\) is the occurrence of a prey item (in numbers), and \(S\) is the number of samples examined (fish stomachs or zooplankton). Finally, we examined prey selectivity by juvenile Sockeye Salmon using the electivity index (\(E_i\)):

\[
E_i = \frac{r_i - p_i}{r_i + p_i},
\]

where \(r_i\) is the numerical proportion of the \(i\)th taxon in the stomachs; and \(p_i\) is the proportion of the same taxon in the environment (Ivlev 1961; see below). The electivity values provide a species-specific measure of prey selection by allowing a comparison of stomach contents to available prey. Values for \(E_i\) range from \(-1\) to \(+1\), where \(+1\) indicates the highest selectivity (i.e., present in the diet, but never in the zooplankton samples), and \(-1\) indicates lowest selectivity (i.e., never in the diet, but present in the zooplankton samples).

We also collected 16 zooplankton samples at Sockeye Salmon locations in 2009 and 20 in 2010 using a plankton...
net (1 m diameter, 125-µm mesh) towed vertically from a depth of 20 m. This should encompass the main depths where juveniles feed. For example, Landingham et al. (1998) showed that juvenile Sockeye Salmon more often select prey from surface waters than at a depth of 50 m. Zooplankton samples from each location were placed in 1-L bottles containing a 10% formalin–seawater solution. In the laboratory, plankton samples were decanted into a sieve stack of 1 mm, 500 µm, and 150 µm and rinsed with water to remove formalin. The filtrate was rinsed with ethanol and concentrated in a centrifuge. Subsamples of the concentrated zooplankton were examined with a counting slide under a compound microscope to determine the relative abundance of zooplankton taxa. Zooplankton density \( D_Z \) was calculated for 2010 only, using the formula \( D_Z = A_t/V \), where \( A_t \) is the total abundance of zooplankton per sample and \( V \) is the corresponding volume to pass through the plankton net, \( V = \pi r^2 d \), \( r \) being the radius of the plankton net, \( d \) is the distance of the tow measured with a RIGO flowmeter. Density was not calculated for zooplankton collected at the most southerly site in our study area (location 1, Figure 1), nor for any collections in 2009, because we lacked flowmeter data.

We tested whether zooplankton density in 2010 depended on latitudinal distance and sampling date via multiple regression. Distance was set to zero (0) for the southernmost collection site with density data (location 2, Figure 1), and all other sites were measured (km) from this reference location using the shortest linear distance by sea. Sampling day was set to 1 for the first collection of zooplankton in 2010, and all other subsequent days were counted sequentially. We also tested via linear regression whether foraging success depended on migration timing in each year (2009 and 2010), where migration day was set to 1 for the first collection of stomachs in a given sampling year and all other subsequent days were counted sequentially. Because the number of stomachs collected and examined at each sampling location over time was not equal, we averaged the feeding index for each sampling event. We transformed feeding index data using an arcsine square-root function to correct for unequal variances and nonnormality, and we performed all analyses in R version 2.15.0 (R Development Core Team 2012) using the lm package.

**RESULTS**

Juvenile Sockeye Salmon were significantly larger on average in fork length \( (t = 5.96, df = 193, P < 0.001) \) and mass \( (t = 4.06, df = 178, P < 0.001) \) in 2010 than in 2009 (Table 1). Calanoid copepods were the most abundant group in plankton samples both years (66.4% in 2009 and 71.0% in 2010), followed by barnacle larvae (12.2% in 2009 and 17.1% in 2010); frequency of occurrence for both groups

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<tr>
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<tr>
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<td>0.4</td>
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<tr>
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<td>0.4</td>
<td>77.8</td>
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<tr>
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<tr>
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<tr>
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</tbody>
</table>
FIGURE 2. Distribution of zooplankton density (zooplankters/m³) in relation to distance 0 (site location 2 on Figure 1), during May to June 2010, where squares are sites 2–4, circles are sites 5–11, and triangles are sites 12–16.

was 100% (Table 2). Remaining zooplankton were much less abundant in each year. The combined group, “other” in 2009 included several fish larvae and the marine ectoparasite *Caligus clemensi*. Multiple regression analysis showed that distance north ($\beta = 6.750, P = 0.035$; Figure 2) significantly predicted zooplankton density, but sampling day did not ($\beta = -6.225, P = 0.116$; the overall model fit was $R^2 = 0.202$).

Juvenile Sockeye Salmon ate a high diversity of prey across the study area (Table 2). Of 67,246 food items identified, calanoid copepods were the most common item in both abundance and frequency of occurrence for 2009 and 2010; euphausiids were the second most consumed prey in both years (in numerical terms). An adult female sea louse, *C. clemensi*, was found in a Sockeye Salmon stomach in 2010. Despite the large prey diversity, juvenile Sockeye Salmon in both years consistently and strongly selected for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey ($E > 0.75$); they routinely selected against brachyuran and cladoceran prey (Figure 3). Calanoid copepods, the most abundant available prey, were not strongly selected for in either year. Although foraging success did not differ between migration years ($t = 0.947, df = 240, P = 0.345$), the percentage of empty stomachs was higher in 2009 (3.1%) than in 2010 (0.0%); foraging success remained relatively constant over the migration period, both in 2009 ($R^2 = -0.043, df = 15, P = 0.568$) and 2010 ($R^2 = -0.027, df = 20, P = 0.514$; Figure 4).

DISCUSSION

Our study contributes novel insight into some important biotic conditions faced by Canada’s Fraser River Sockeye Salmon during an assumed critical period of marine migration. Prey were more plentiful in the north, and although juvenile Sockeye Salmon consumed a high diversity of zooplankton, they showed strong preferences for particular prey. Importantly, their foraging success was high in both years and consistent throughout the migration period.

Our finding that zooplankton are predominated by copepods confirms previous observations in this region (Legare 1957; Harrison et al. 1983) and further north in British
Columbia and Alaska (Landingham et al. 1998). Zooplankton abundance was not spatially uniform, however. For example, zooplankton density at southern locations 2–4 (Figure 1) averaged 111 zooplankters/m², and increased to an average of 223 zooplankters/m² in the northern tidally mixed Discovery Passage and Johnstone Strait region (locations 5–16), where there was also more variability among sites. Although there have been few studies of zooplankton in our study area (i.e., northern Strait of Georgia and southern Johnstone Strait), phytoplankton densities during spring in the Strait of Georgia are highest at both the mouth of the Fraser River (south of where we sampled) and at the approach of Johnstone Strait. These are areas where the most complete mixing of freshwater and seawater occurs (Hutchinson and Lucas 1931; Stockner et al. 1979; Parsons et al. 1981; Harrison et al. 1983). Mixing of waters may promote the up-welling of nutrients and increase productivity. Therefore, rather than indicating a trend of increasing zooplankton abundance along the entire Vancouver Island migration route, the spatial variation we observed in zooplankton density may best reflect differences in oceanographic properties and productivity between the stable two-layer Strait of Georgia and the tidally mixed Discovery Passage–Johnstone Strait area. It may also partly explain the rapid migration of juvenile Sockeye Salmon through the Strait of Georgia (i.e., 26 km/d; Welch et al. 2009, 2011).

Juvenile Sockeye Salmon migrating through the Strait of Georgia and Johnstone Strait consumed zooplankton almost exclusively, as opposed to fish or eggs, which we also recorded in small numbers. Prey diversity was high, consisting of more than 12 higher taxa in both years, which matches previous studies in the Strait of Georgia and other regions of the northeast Pacific (Healey 1980, 1991; Brodeur and Peary 1990; Landingham et al. 1998). Despite the large numbers of species consumed, our results show evidence of selectivity for particular prey. Sockeye Salmon routinely selected for euphausiid, amphipod, decapod, terrestrial insect, fish, egg, and cumacean prey, and avoided abundant brachyuran and cladoceran prey. Calanoid copepods, the most abundant and consumed prey, were not selected out of proportion to their availability in either year. Calanoid copepods have been described as a major diet item for juvenile salmon generally but are not considered preferred prey (Peary 1992), and Sockeye Salmon have been shown to avoid numerically predominant copepods elsewhere (Landingham et al. 1998).

Reasons for the selectivity of prey by juvenile Sockeye Salmon observed in our study are not clear. Salmonids are considered opportunistic drift feeders (Everest and Chapman 1972; Filbert and Hawkins 1995) that will consume visually obvious prey within a certain size range (Brodeur et al. 2003). But even within a particular size range, preferences are evident. For example, juvenile Sockeye Salmon migrating along British Columbia’s north coast consumed a disproportionately number of large prey; small copepods were ignored relative to their abundance (Healey 1991; Landingham et al. 1998). Large prey should be easier to detect and more profitable than small prey. This could explain the high selectivity shown in our study for amphipods: large, but limited prey, with relatively high gross energy (as per prey energy estimates in Tanasuchuck and Routledge 2011). The small size and low gross energy of brachyura may also explain why Sockeye Salmon in our study consistently selected against them, despite their high abundance. Confusing this rather simplistic interpretation, however, is the strong selectivity in 2010 for oikopleura, which are small and have the lowest estimated energy content of prey available to juvenile Sockeye Salmon (Tanasuchuck and Routledge 2011). Thus, the diet of Sockeye Salmon is undoubtedly a combination of prey abundance and preference, and we agree with Healey (1991) that, "The complex of factors underlying a particular diet cannot be fully sorted out in a descriptive study such as this."

This is the first report of Sockeye Salmon preying on C. clemensi. This is a common external parasite of Atlantic Salmon Salmo salar, in open-net salmon farms in the region, and on wild juvenile Sockeye Salmon (Korman 2011; Price et al. 2011). Our finding of adult C. clemensi in a Sockeye Salmon stomach and at sea suggests either a dispersal mechanism that may involve adult transfer between hosts (see Connors et al. 2008; Costello 2009) or simply the dislodgement of abundant lice in the study region from hosts and subsequent opportunistic capture.

Predictions of climate warming effects on Fraser River Sockeye Salmon include changes in the abundance and distribution of prey in the Strait of Georgia, which could result in a timing mismatch between nearshore productivity and migrating juvenile salmon (Healey 2011). In a recent study involving the northern Strait of Georgia region in 2009, zooplankton abundance was highest between mid-May and June and peaked during the first week of June (Chittenden et al. 2010). Juvenile Coho Salmon O. kisutch, which entered the marine environment of this region during the peak bloom period, had significantly higher survival rates than fish that began marine migration before or after this period (Chittenden et al. 2010). Our observations since 2007 suggest that the peak migration timing of Fraser River Sockeye Salmon through northern Strait of Georgia–southern Johnstone Strait is during the first 2 weeks in June. Prey were abundant during this time, and foraging success remained relatively unchanged, which suggests that fish may not be experiencing a trophic mismatch during their early marine migration, at least during the 2 years of our study. Importantly, the question remains as to whether this apparent resource abundance for juveniles relates to improved marine survival and consistent adult returns in subsequent years, as was shown for Coho Salmon out-migrating in 2009. Preliminary estimates suggest that productivity (recruits per spawner) for the 2009 and 2010 out-migration of Fraser River Sockeye Salmon smolts was above average compared to the modern low productivity era post-1993, but equal to and slightly below the long-term average (1956–2010), respectively (M. Lapointe, Pacific Salmon Commission, personal communication).

Juvenile Sockeye Salmon did not experience severe food limitations during the years of our study. Despite significantly
larger fish in 2010 than in 2009, foraging success was similar between years and averaged 1.9% for the 2 years of our study. These are the highest recorded for Sockeye Salmon during their first summer at sea and comparable with other juvenile salmon for this region and elsewhere. Juvenile Sockeye Salmon examined along British Columbia’s north coast showed an average feeding index between 0.3% (July 1986) and 0.5% (July 1987); levels considered at the time to indicate food limitations (Healey 1991). Concomitantly, averages for Chum Salmon O. keta, Chinook Salmon O. tshawytscha, and Coho Salmon in the Strait of Georgia (0.73–1.15%; Healey 1980), and Coho Salmon in Oregon and Washington (1.2–2.7%; Fisher and Peary 1988) were reported as evidence for an adequate food supply (Healey 1991).

The low percentage of juveniles with empty stomachs (3.1% in 2009, and 0.0% in 2010) further suggests that food limitation (if present during the years of this study) was not widespread. Haegele (1997) showed that on average 32% of juvenile Sockeye Salmon had empty stomachs during 1990–1993 in the Strait of Georgia (a high of 75% in 1993), which was the beginning of reduced returns of Sockeye Salmon to the Fraser River (Connors et al. 2012). Beamish et al. (2012) reported that about 40% of juvenile Sockeye Salmon in the Strait of Georgia had empty stomachs in 2007 and speculated that subsequent marine survival was affected, although this was based on a sample size of 65 fish. That same study, however, showed that about 40% of Sockeye Salmon in 2004 had empty stomachs, as did about 20% in 2009; yet no link was made with these years to food limitations. One plausible explanation for the lower empty stomach rates that we report for 2009 compared to those reported by Beamish et al. (2012) is that the Sockeye Salmon we examined were captured further north, whereas Beamish et al. (2012) may have captured fish as far south as the mouth of the Fraser River. Alternatively, perhaps we were just sampling the survivors of food-deprived fish that may have been preying upon. This is an inherent difficulty in interpreting any study. The principal unanswered questions for future work are: (1) whether juveniles grow fast enough to minimize size-related predation mortality, (2) whether or not there is a critical period in the early life history, and (3) whether or not it occurs in the Strait of Georgia.

In conclusion, juvenile Fraser River Sockeye Salmon appeared to have an abundant prey resource pool while migrating through south-coast British Columbia during the 2 years of this study. This was matched by consistently high foraging success in both years. Ocean conditions vary widely from year to year; hence, we cannot say anything about the 2007 cohort, which returned in exceptionally low numbers 2 years later. We also cannot say anything about future migrations and subsequent survival. Rather, further progress in linking oceanic conditions to survival of salmon will require comprehensive annual monitoring of both the fish and their prey during this assumed critical phase of their life cycle.

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Direct Field and Laboratory Evidence that a Combination of Egg and Larval Predation Controls Recruitment of Invasive Common Carp in Many Lakes of the Upper Mississippi River Basin

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ARTICLE

Direct Field and Laboratory Evidence that a Combination of Egg and Larval Predation Controls Recruitment of Invasive Common Carp in Many Lakes of the Upper Mississippi River Basin

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Abstract

Field and laboratory experiments tested the hypothesis that recruitment of the invasive Common Carp Cyprinus carpio is often controlled by the feeding activity of egg and larval predators in interconnected lakes of the upper Mississippi River basin. The survival of naturally spawned carp eggs was monitored in a seemingly typical lake by sampling the abundance of such eggs in spawning areas and in the diets of fish caught at these locations. Over 95% of the carp eggs found attached to spawning substrate disappeared within 4 d of spawning, at the same time that large numbers of eggs were found in the stomachs of Bluegills Lepomis macrochirus. Egg predation closely paralleled but lagged egg disappearance. Concurrent laboratory studies showed that carp eggs hatched after 4.75 d at lake temperatures, demonstrating that most (but perhaps not all) of the eggs had been eaten by egg predators prior to hatching. A second laboratory experiment found that Bluegills readily find and consume carp larvae while Black Bullheads Ameiurus melas do not, suggesting that predation on larvae contributes to carp recruitment. These data, together with previous studies of the survival of carp eggs placed into lakes and the distribution of young carp relative to various species of native fish, add strong support to the hypothesis that the recruitment of carp in interconnected lakes of the upper Mississippi River basin is often controlled by native fish predators.

The Common Carp Cyprinus carpio (hereafter “carp”) is a large, benthivorous minnow from the Ponto-Caspian area of Eurasia that is highly abundant and invasive in temperate regions of North America, Australia, and South America (Balon 1995). Its invasiveness is often attributed to its extremely high fecundity (females produce over a million eggs a year) and physiological resilience (Koehn 2004; Weber and Brown 2009; Sorensen and Bajer 2010), but these characteristics alone cannot always explain its invasiveness because the carp is not invasive in its native habitat. Nevertheless, in regions where it is highly abundant and invasive, adult carp cause dramatic declines in submerged vegetation which cause reductions in water clarity and quality (Bajer et al. 2009; Weber and Brown 2009; Kloskowski 2011). This phenomenon has made carp a target of numerous control programs that typically focus on adult removal using poisons, barriers, and water drawdowns but which usually prove ineffective because of the species’ high recruitment rates (Lubinski et al. 1986; Brown and Walker 2004; Sorensen and Bajer 2011). The factors that determine the recruitment of carp (here defined as survival to the juvenile stage) are poorly understood (Koehn et al. 2000; Weber and Brown 2009).

Recent studies of carp in the upper Mississippi River basin suggest that the high abundance of carp in the many watersheds of this region is linked to a lack of native egg predators in locations where winter hypoxia kills native fish (Bajer and Sorensen 2010). Particular lakes within chains of interconnected lakes appear to act as sources for adult carp for entire watersheds (Bajer and Sorensen 2010). The evidence for this hypothesis

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takess several forms. First, the age structure of adult carp in interconnected lakes suggests that recruitment is sporadic and coincides with years that follow a winterkill in at least one lake (Bajer and Sorensen 2010). Second, many adult carp have been found to aggressively move between interconnected lakes and into recently winterkilled wetlands and shallow lakes to spawn each spring when predator abundance is low (Bajer and Sorensen 2010). Third, detailed surveys of nearly two dozen lakes in the upper Mississippi River basin have found that high densities of young-of-the-year carp are only found in shallow interconnected lakes that have recently experienced winterkill and lack native fishes, Bluegills Lepomis macrochirus in particular (Bajer et al. 2012). Fourth, when carp eggs have been placed into lakes with large numbers of native fishes, they have been found to disappear within a few days and seemingly before hatching (Bajer et al. 2012). However, while the latter results are compelling, they did not fully mimic natural scenarios as carp naturally spawn their sticky eggs onto extremely dense mats of floating vegetation in very shallow (<0.5-m) water where they presumably are not readily susceptible to predation (Swee and McCrimmon 1966; Crivelli 1980; P. W. Sorensen and P. G. Bajer, University of Minnesota, unpublished data). Further, estimates of hatching have been based on disappearance alone because there have not been any systematic studies of the incubation times of carp eggs (Billard 1999). Finally, the possibility that predation pressure on larvae also plays a role in recruitment has not yet been addressed.

The objectives of the present study were (1) to determine the hatching success of naturally spawned carp eggs in a representative lake in the upper Mississippi River basin by simultaneously monitoring egg abundance and egg predation while determining hatching rate in the laboratory, and (2) to determine whether native fish also consume carp larvae in significant numbers.

METHODS

Study area.—This study took place in Keller Lake (45°00’N, 93°04’W), the fifth lake in a chain of interconnected lakes near St. Paul, Minnesota (Figure 1). This lake is representative of many lakes in the upper Mississippi River basin and one of the two dozen lakes whose carp populations and ecology we have been tracking since 2006 (Bajer et al. 2010, 2012). It has a surface area of 27.3 ha, an average depth of 2.1 m, and no history of winter hypoxia. At the time of this study (2009), approximately half of its littoral zone was covered by submergent vegetation, which included dense beds of curly leaf pondweed Potamogeton crispus, Eurasian water milfoil Myriophyllum spicatum, and coontail Ceratophyllum demersum. The native fish community in Keller Lake was large and diverse and included (in order of approximate abundance) Bluegills, Yellow Perch Perca flavescens, Largemouth Bass Micropterus salmoides, Pumpkinseeds Lepomis gibbosus, Black Bullheads Ameiurus melas, Black Crappies Pomoxis nigromaculatus, Walleyes Sander vitreus, Common Carp, and Northern Pike Esox lucius (Bajer et al. 2012). A mark–recapture survey for carp showed that Keller Lake contained approximately 1,275 ± 200 (95% CI around the mean) adult Common Carp at the time of this study but few, if any, juvenile carp (Bajer et al. 2012).

Experiment 1: Examining whether predation by fish determines the survival of naturally spawned carp eggs.—A two-part experiment was performed. First, we monitored the spawning of adult carp, the presence of their eggs, the diets of fishes, and water temperatures in Keller Lake. Next, we determined the hatching rate of carp eggs across the range of temperatures encountered in the lake to estimate the dates after which egg disappearance could be attributed to hatching versus other factors (e.g., egg consumption). The experiment started a few weeks prior to the start of the carp spawning season in April 2009 when temperature loggers (Onset Computer, Pocasset, Massachusetts; HOBO Pendant UA-002-08) were placed into Keller Lake and two other nearby lakes. A pair of observers then started surveying the lake each morning (0600 hours) for spawning adult carp, which were recognized by splashing in floating, shallow vegetation where they oviposit. When carp were observed, the number of spawning events (splashes) was quantified over a 5-min interval after which the edges of each spawning area were mapped from a small boat using a handheld GPS unit (Garmin Legend H, Olathe, Kansas). A fish mapping, the observers returned to sample these areas for fish and carp eggs. Fish were sampled first (often during spawning) because we were concerned that they might move. We conducted a single straight-line transect through the spawning area using a pulsed-DC electrofishing boat to collect fish. All fish encountered were collected, identified, and measured, along with having their stomach contents examined by means of gastric lavage and a 600-µm sieve before being released (Harthleb and Morris 1995). A few days after, we returned to each spawning area to sample for eggs at seven evenly spaced locations. Vegetation was collected using a garden rake which we lowered to a depth of 0.5 m (below the depth at which carp deposit their eggs on vegetation) and twisted to collect samples. Plants were weighed, placed in a tub, and examined in order to count the number of attached carp eggs (carp eggs are about 2 mm in diameter and adhere to plants). We revisited each spawning area once a day until eggs were no longer encountered. For analysis, we calculated the average number of eggs seen per 100 g of vegetation across time for each location in which eggs had been encountered. The average number of eggs found in fish stomachs was also calculated and tabulated. In August, we sampled Keller Lake for young-of-the-year carp using both electrofishing and five trap nets (13-mm mesh, five 0.8-m hoops) following established protocols (Bajer et al. 2012).

The second part of this experiment was conducted to determine the incubation time of carp eggs at the water temperatures encountered in Keller Lake during our experiment. Male and female carp were captured in Keller Lake in the spring of 2010, injected with a gonadotropin-releasing hormone analog–dopamine antagonist (0.5 mg/kg of Ovaprim; Western Chemical, Inc., Ferndale, Washington) to induce ovulation and
spermiation (Brzuska and Adamek 1999), and then placed in 1,000-L tanks with flowing 18°C well water. Twelve hours later, sperm and eggs were stripped into a 6-L bowl and mixed for 10 min using a spatula, after which 50 mL of well water was added to stimulate water hardening. Two hundred eggs were then placed onto 30-cm pieces of artificial vegetation (i.e., yarn; see Bajer et al. 2012) and placed into individual 10-L aquaria. Each aquarium was supplied with flowing well water and maintained at a different fixed temperature between 14.5°C and 30.3°C using submersible heaters (Hydor, Sacramento, California; Hydor Theo). Eggs were examined at 12-h intervals by removing the strands of yarn, counting the eggs and noting their appearance (clear [alive] or opaque [dead]), and looking for larvae in the aquaria. Time until hatching was defined as the time taken for the majority of the clear (live) eggs to disappear at each temperature.

The data were evaluated through a degree-day approach to estimate the lower developmental threshold (LDT, i.e., the minimum temperature at which development occurs) and the sum of effective temperatures (SET, the number of degree-days above LDT necessary for development; Kocourek et al. 1994; Hamel et al. 1997a). In order to calculate this, the inverse of time to hatch (hatch rate) was plotted against temperature. A general linear model was used to estimate the LDT (the y-intercept)
and the SET (the inverse of the slope). These values were then used to estimate the time to hatch of carp eggs in Keller Lake during the field experiments using water temperature data collected from our temperature loggers. A value was calculated for each of the spawning sites by summing the degree-days at 3-h intervals after spawning was first observed. An average time to hatch was then calculated for all sites.

Experiment 2: Determining whether native fish also consume carp larvae.—Experiment 1 suggested that a few carp eggs survived to hatching in Keller Lake, so we tested whether these larvae might have been subject to predation. We tested both Bluegills and Black Bullheads as potential larval predators in a relatively simple proof-of-concept laboratory study. Bluegills were tested both because they are abundant in Lake Keller (which was later found to lack young carp [experiment 1]) and because their presence is strongly and inversely correlated with the presence of young-of-the-year carp in our region (Bajer et al. 2012). Black bullheads were tested both because we wanted a contrast and because while they are abundant in most lakes of the upper Mississippi River basin, their abundance does not correlate with that of young-of-the-year carp (Bajer et al. 2012). To obtain carp larvae, carp eggs were collected and fertilized as described for experiment 1 except that they were treated to remove adhesiveness (Schoonbee and Brandt 1982) and raised to hatching in Zoug jars (Billard 1999). During this time, Bluegills and Black Bullheads were collected from Keller Lake, placed in 500-L flow-through tanks and fed fish flakes.

Once larvae had hatched, 1,500-L flow-through tanks (23°C) were stocked with natural vegetation (curly leaf pondweed and coontail) and maintained on a natural photoperiod. Groups of five Bluegills, five Black Bullheads, or no fish (control) were then introduced in these mesocosms at 1200 hours. Twelve hours later (i.e., in darkness), 1,000 larvae (SD = 74) were added to each tank (we estimated that this would have been the density in Keller Lake if all eggs had hatched). Larvae were sampled every 12 h using a dip net (35 cm × 25 cm; 350-µm mesh) at 16 evenly spaced locations in each tank. The dip net was placed parallel to the surface of the water and swept in a U-shape that touched the bottom to sample the entire water column. Captured larvae were counted and released back into the tank at the same place at which they were captured. Data were analyzed using a generalized linear model (R 2.13.0).

RESULTS

Spawning was observed on 12 occasions in Keller Lake between May 21 and June 24, 2009. Spawning was never observed in the same area for more than 1 d. The average size of the areas used for spawning was 5,654 m² (SD = 4,200 m²). The most intense spawning event that we noted had 352 spawning events during the 5-min interval. On 4 other occasions (locations), we observed 10–100 spawning events per 5-min interval, while on the remaining 7 occasions we observed spawning events with a frequency of less than 10 per 5-min interval. Carp eggs had a density of more than 10 eggs per 100 g of vegetation at the 5 locations which had more than 10 spawning events per 5-min interval, at a density of less than 0.1 eggs per 100 g of vegetation at 3 locations, and at a density of 0 at the other locations. At the five locations where carp eggs were found in abundance, an average of 21.3 eggs (SD = 17.8) were found per 100 g of vegetation on the first morning of spawning (Figure 2). This value increased on day 1 but then dropped dramatically each day thereafter until only 1.3 eggs (SD = 1.2), or 1.2% of the peak number, were present on day 4. A similar number (1.6 eggs, SD = 1.3) were found on day 5. Eggs were not relocated on the day after spawning at any of the locations where fewer than 0.1 eggs were found per 100 g of vegetation.

Eight species of fish were caught in the five primary carp spawning areas (Table 1). Lake temperatures varied between 15.6°C and 25.8°C, averaging 21.2°C. Bluegills comprised nearly half of all fish captured, and over a third of them (39%) were found to have consumed carp eggs at these sites. Although a few Black Bullheads and Pumpkinseeds were also found with eggs, their total consumption was less than 10% of the total number consumed by Bluegills. The average number of eggs found in Bluegill stomachs at these sites was highest on the first day of sampling and decreased in a quasilinear fashion from an average of over 100 to 0 by day 5, slightly lagging but paralleling the rate of egg disappearance (Figure 2). At no other location or time were more than four eggs found in a fish’s stomach. Notably, both trap-netting and electrofishing at summer’s end found no young-of-the-year carp in Keller Lake, although 30 were captured in the headwaters of the chain (Casey Lake).

An average of 56% (SD = 13%) of eggs raised in the laboratory were viable (i.e., clear after 2 d and hatched). Eggs hatched much sooner at warmer temperatures (approximately 2 d at 30°C) than at cooler temperatures (approximately 6 d at 15°C; Figure 3, upper panel). This relationship was described by a nonlinear regression (y = 38.906e−0.107x; r² = 0.93; P < 0.01).
TABLE 1. Mean number of fish caught per transect on which carp eggs were encountered, mean length of the fish caught, mean number of fish with carp eggs in their stomachs, and mean number of carp eggs found in stomachs of those fish. Standard deviations are given in parentheses.

<table>
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<tr>
<th>Species</th>
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<th>Length (mm)</th>
<th>Fish consuming eggs</th>
<th>Eggs/fish</th>
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<td>289 (19.9)</td>
<td>0.4 (0.9)</td>
<td>28.0 (na)</td>
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<td>Black Crappie</td>
<td>0.6 (0.5)</td>
<td>94 (12.1)</td>
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</tr>
<tr>
<td>Bluegill</td>
<td>23.2 (15.3)</td>
<td>134 (5.2)</td>
<td>9.2 (4.3)</td>
<td>25.9 (10.2)</td>
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<td>16.0 (6.9)</td>
<td>634 (12.8)</td>
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<tr>
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</tbody>
</table>

There was greater variation in time to hatch at lower temperatures (nearly 2 d at 15°C) than at high temperatures (less than 12 h at 30°C). The regression of hatching rate on temperature \( y = 0.0311x - 0.3837; r^2 = 0.90; P < 0.01; \) Figure 3, lower panel) estimated the LDT to be 12.3°C and the SET to be 32.2 degree-days. Carp eggs were estimated to hatch after an average of 4.75 d (SD = 0.91 d) after fertilization in Keller Lake during the 2009 spawning season.

FIGURE 3. Relationships between (1) the time taken for carp eggs to hatch and temperature (upper panel) and (2) the hatching rate (the inverse of the time to hatch) and temperature (lower panel).

Larval predation experiments in the laboratory showed that while all carp larvae had disappeared from those tanks with Bluegills within 12 h, half were still present after 2.5 d with Black Bullheads and almost all remained in tanks which lacked fish (Figure 4). All fish and larvae appeared to be healthy.

DISCUSSION

The results of this study support our hypothesis that the recruitment of young Common Carp in interconnected lakes of the upper Mississippi River basin is often controlled by native fish, especially Bluegills, which prey heavily on carp eggs (Bajer et al. 2010, 2012). While previous studies have shown that unprotected eggs placed into lakes with Bluegills disappear within 4 d, we demonstrated that Bluegills are largely responsible for this phenomenon by showing that the number of carp eggs in spawning vegetation drops almost to zero by the time the eggs hatch and the abundance of carp eggs in Bluegill diets parallels this trend. New data are also presented which show that while a few carp eggs may escape predation, predation by Bluegills on larvae is likely intense. Indeed, no young-of-the-year carp were

FIGURE 4. Mean number of carp larvae sampled per dip-net sweep in large laboratory tanks with vegetation and either no fish predators, five Bluegills, or five Black Bullheads. The error bars show standard deviations (n = 4).
found at year’s end in Keller Lake in spite of the fact that an estimated 500 million eggs were spawned in this system. These results appear capable of explaining the effect of native fish densities on carp recruitment in many lakes of the upper Mississippi River basin (Bajer et al. 2012). Nevertheless, the relevance of predatory fish needs to be confirmed in other locations with other types of fish communities.

The main strength of this study is that it directly tracked the fate of naturally spawned carp eggs in the field for the first time. The exceptionally tight correlation between the abundance of eggs in spawning habitat and the number of eggs in fish stomachs, and the fact that both trends downward sharply within the first 4 d after oviposition and prior to any hatching, strongly suggests that the survival of carp eggs is largely determined by native fishes. This conclusion is strengthened by our previous study which tracked the fate of carp eggs placed in mesh bags in several lakes (including Keller Lake) and found no indication that carp eggs die from disease, falling off, or unknown small organisms (Bajer et al. 2012). Further, because both of our studies have found large numbers of fish eggs in the stomachs of Bluegills, and our laboratory work shows that bluegills can eat up to 200 carp eggs a day (Silvernagel 2011), we believe that this ubiquitous species plays a key role in controlling carp recruitment in many lakes of the upper Mississippi River and adjoining areas. It is reasonable that we found a slightly higher survival rate for carp eggs in dense patches of vegetation (1–2%) than had been found in small clumps of yarn (0.8%; Bajer et al. 2012) because Bluegills rely heavily on their well-developed sense of sight and their foraging success is known to be reduced in complex habitat (Mittelbach 1981; Crowder and Cooper 1982). Other native fish, including Black Bullheads, Pumpkinseeds, and Yellow Perch, also appear capable of eating carp eggs (this study; Bajer et al. 2012) and presumably a larval role in carp recruitment success in systems where they are more common; however, this possibility needs to be tested.

Our study provides new evidence that certain species of fish, particularly Bluegills, also function as important predators on larval carp in carp-infested lakes. Although our studies were limited to the laboratory, it was striking that a few Bluegills could consume as many as 1,000 larvae at night in heavily vegetated tanks. Because wild carp larvae are free-swimming for about 2 weeks (Smallwood and Smallwood 1931; Billard 1999) and Bluegills are renowned for being adept visual predators on tiny organisms (Crowder and Cooper 1982), it seems reasonable that they could control carp recruitment even if significant numbers of eggs were to hatch. It is notable that Black Bullheads, which are abundant in many shallow regions where carp recruitment is observed but which lack Bluegills (Bajer et al. 2012), consume carp larvae at a rate less than a tenth of that of the latter species even under ideal laboratory conditions; these differences in larval predation may play a role in carp recruitment within watersheds. Of course, predation on yearling carp by larger predators such as Northern Pike may also play a role in recruitment processes (Mauck and Coble 1971), although this may often be limited by the extremely rapid growth rate of carp. A comprehensive study of fish predation on larval and juvenile carp across entire watersheds is needed to test these ideas.

Our study also appears to be the first to describe the precise relationship between temperature and incubation time for carp eggs. The fact that carp eggs take at least twice as long to hatch at 15°C (5–8 d) than at 25°C (2.5 d) may be significant because it would affect how long eggs are vulnerable to predators. These factors may be especially important in temperate regions, where springtime temperatures fluctuate and the persistence of eggs (and their susceptibility to predation) may change several fold. Notably, carp reproductive activity peaks when temperatures rise above 18°C (Crivelli 1981; P. W. Sorensen, unpublished results) and is synchronized (a pheromone appears to be involved [Sorensen and Stacey 2004]), suggesting that carp evolved to minimize egg and larval predation by predator swamping. The role of egg and larval predators in the carp’s native habitat in the Ponto-Caspian region would certainly be interesting to study. Synchronization of spawning and larval development at specific optimal temperatures has also been suggested to drive recruitment of the White Sucker Catostomus commersoni, which also can be invasive (Hamel et al. 1997b).

Although it is presently not possible to extend the specific details of our findings to other interconnected lakes, we believe it is reasonable to hypothesize that carp recruitment in similar systems is also driven by egg and larval predators. Keller Lake and its fish population are not atypical among the 2–3 dozen lakes that we have studied for the past 5 years (Bajer et al. 2011, 2012). Aditionally, other fishes in locations which do not suffer from environmental degradation, overfishing, hypoxia, and other environmental instabilities may be equally adept predators of carp eggs and larvae. It is interesting to speculate that even small, occasional differences in fish community structure and the timing of carp spawning and hatching rates (as driven by variations in springtime temperature) could have important ramifications on predation and recruitment and thus invasiveness. Carp are long lived (50 + years) and only need to successfully reproduce and recruit occasionally to reach enormous densities (Sorensen and Bajer 2011).

In conclusion, the present study demonstrates that egg predation, likely coupled with larval predation, plays an important and direct role in controlling the recruitment and invasiveness of carp in at least one relatively typical lake of the upper Mississippi River basin. Highly sporadic recruitment of carp has also been observed in other regions (see Phelps et al. 2008), and while climatic factors have been linked to this phenomenon the exact causes have not been assigned; significantly, predation has not yet been examined as a cause. It is conceivable that other factors, such as the suitability and stability of spawning substrate and the abundance of food for larval carp also play roles in carp recruitment processes, especially in locations where the abundance of egg and larval predators is low. Nevertheless, the
precise significance of predation on carp eggs, larvae, and young carp now warrants careful attention in systems with different fish communities both because of its implications to the life history of this fascinating species and because of its potential implications for carp management.

ACKNOWLEDGMENTS
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Impacts of Exotic Rainbow Trout on Habitat Use by Native Juvenile Salmonid Species at an Early Invasive Stage

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Impacts of Exotic Rainbow Trout on Habitat Use by Native Juvenile Salmonid Species at an Early Invasive Stage

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Abstract
The detrimental impact of introduced Rainbow Trout Oncorhynchus mykiss on native communities has been well documented around the world. Previous studies have focused on streams where the invasion has been successful and the species is fully established. In eastern Quebec, the invasion of Rainbow Trout is an ongoing process and, for now, there are few established populations. The presence of two native salmonids in these rivers, Atlantic Salmon Salmo salar and Brook Trout Salvelinus fontinalis, implies a risk of competition for habitat, despite the relatively low density of the Rainbow Trout populations, as all three species are known to use similar resources. In order to evaluate the strength of the interaction between the invading fish and the native species, we sampled nine rivers (five with Rainbow Trout and four free of Rainbow Trout) and characterized the habitat used by the three salmonids at the juvenile stage. River-scale analysis revealed that in invaded rivers, Rainbow Trout were associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover. Estimates of habitat niche overlap integrating depth, water velocity, and substrate size revealed that niche overlap between Brook Trout and Atlantic Salmon significantly increased in the presence of Rainbow Trout. Furthermore, the two indigenous species preferred full cover in the absence of Rainbow Trout but in the presence of Rainbow Trout, which also preferred full cover, the indigenous species moved to more open habitats. Rainbow Trout showed a high growth rate, despite a size disadvantage at the beginning of the growing season, as compared with Atlantic Salmon and Brook Trout. It thus appears that even at an early stage of invasion, when its density is still low, Rainbow Trout significantly impact native salmonids.
Welcomme 1984; Larson and Moore 1985; Fausch 1988; Kueger and May 1991; Crowl et al. 1992; Cambray 2003 and references therein; Hitt et al. 2003; Hasegawa and Maekawa 2006; Baxter et al. 2007. In many cases, Rainbow Trout invasions result in the displacement, reduction, or even extinction of native fish species, especially native salmonids. Rainbow Trout is considered among the 100 most harmful invasive exotic species (Lowe et al. 2007).

In Quebec, Rainbow Trout were introduced at the end of the 19th century for angling purposes and subsequently intensively stocked in the southwestern part of the province. Since the beginning of the 1980s, several decades following the first introduction, a few small established populations were documented in eastern Quebec, well outside the stocking area (Thibault et al. 2009; Thibault 2010). Reproduction was first documented in two rivers of the Charlevoix region (Malbaie and Du Gouffre) in 1982–1984. No other self-sustaining populations in eastern Quebec were observed before 2006, when the present study documented the presence of juveniles in five rivers. It is probable that Rainbow Trout were established in these rivers several years earlier, but their low abundance and the restricted area of reproduction impeded detection.

In 2007 and 2008, electrofishing surveys of five established populations in eastern Quebec revealed that the invader is mainly restricted to tributaries, where its density remains lower than 0.05 fish/m² (Thibault 2010). Questions have been raised about the potential impact of the exotic species on two native salmonids, Atlantic Salmon Salmo salar and Brook Trout Salvelinus fontinalis, that are abundant and almost ubiquitous (∼0.10 fish/m²; Thibault 2010) in the rivers of eastern Quebec. Several authors have demonstrated that the habitat requirements of Rainbow Trout are similar to that of Atlantic Salmon (Gibson 1981; Hearn and Kynard 1986; Fausch 1988) and Brook Trout (Larson and Moore 1985; Rose 1986; Magoullick and Wilzbach 1998; Blanchet et al. 2007).

The most serious impacts of introduced Rainbow Trout on native fish involve other salmonid species (Crowl et al. 1992). Whereas previous studies have demonstrated the negative impacts of introduced Rainbow Trout on indigenous salmonids once the invader is fully established (when abundant and widely distributed), questions remain concerning if—and to what extent—Rainbow Trout can impact native conspecifics at an early stage of the invasion process or at low population densities. The aim of this study was thus to obtain evidence of potentially detrimental interactions between low-density Rainbow Trout populations and native salmonids in eastern Quebec rivers.

Native salmonid species that inhabit the rivers recently colonized by Rainbow Trout are known to be territorial; Atlantic Salmon being aggressive and well adapted to exploiting riffles, whereas the early emergence of Brook Trout can provide a size advantage over Rainbow Trout of the same cohort during the first year of life (Gibson 1981; Rodriguez 1995 and references therein). In this context, sympatric native salmonids might compete successfully with Rainbow Trout at the juvenile stage as long as population densities of the salmonid invader are low, thus delaying or impeding its progression and impacts and increasing the capacity of managers to restrict or eliminate the newly established populations. On the other hand, Rainbow Trout are known to demonstrate strong competitive capacities (Hearn and Kynard 1986; Volpe et al. 2001; Hasegawa et al. 2004; Blanchet et al. 2007; Seiler and Keeley 2007a; Seiler and Keeley 2007b), and young of the year have a high growth rate related to their aggressive behavior in foraging and territorial defense (Gibson 1981; Whitworth and Strange 1983; Rose 1986). We thus predicted that the invader may negatively interact with native fish to such an extent that it could force them into less preferred habitats. To test this prediction, we evaluated habitat niche overlap among species and habitat preferences and growth rates of each species.

METHODS

The approach we adopted here does not allow us to directly demonstrate the presence or intensity of interspecific competition. To do so, species presence and densities must be manipulated (Fausch 1988), involving an unacceptable level of intervention into protected Atlantic Salmon habitat. Rather, a sampling plan was designed to exploit rivers characterized by natural variations in species composition and fish densities, allowing us to demonstrate interspecific interactions suggestive of true competition.

Study area.—A total of nine rivers, distributed in eastern Quebec on both shores of the St. Lawrence Estuary (Figure 1), were sampled during the summers of 2007 and 2008. Five rivers supported self-sustaining Rainbow Trout populations (designated as “invaded rivers”: Malbaie, Du Gouffre, Matane, M echins, Tortue rivers), and the four remaining rivers were free of the invader (designated as “noninvaded rivers”: Calway, Petit-Saguenay, Trois-Pistoles, Sud-Ouest rivers). All rivers supported Brook Trout populations, but Atlantic Salmon was present in only five, including three invaded rivers (Malbaie, Du Gouffre, Matane, Petit-Saguenay, Sud-Ouest rivers). In general, mean densities of native fish were approximately double that of Rainbow Trout (Thibault 2010). Since sampling took place exclusively during the summer season, we assumed minimal temporal variations in water temperature and in fish distribution and habitat preferences (e.g., Vondracek and Longanecker 1993; Sotiropoulos et al. 2006). Data obtained from thermographs installed by the Ministère des Ressources Naturelles et de la Faune (MRNF) in three rivers and water temperature obtained by extrapolating air temperature from nearby meteorological stations for the six other rivers (Environment Canada), showed that temperature ranges during sampling periods were not significantly different among rivers (data not shown).
River-scale surveys.—Sampling took place between mid-June and the end of August 2007. Between 9 and 24 sites of 100 m² were sampled at intervals of 1 km, in each river and some of their tributaries. Fishing was done during the daytime using portable electrofishers. Sites \( n_{\text{tot}} = 117 \) were sampled twice, with a pause of 10–15 min between passes. At each site, we noted the following: salmonid density, velocity (qualitatively), mean depth \( \pm 1 \text{ cm} \), from three measurements), slope (%), flow type (channel, riffle, run), site’s position (stream’s center or near the shores), and substrate composition (%) estimated using the following key: sand \(<5 \text{ mm}\), gravel \(5–40 \text{ mm}\), pebble \(40–80 \text{ mm}\), cobble \(80–250 \text{ mm}\), block \(>250 \text{ mm}\), bed rock.

Proportions of each category were thereafter multiplied by the median size of their own category and summed to obtain one relative substrate size per site. We also assessed shoreline cover (total, partial, no cover). Riparian vegetation, canopy, prominent rocks on the shore or structures overhanging the river are examples of shoreline cover. A “total” cover means that the position of the sampling site was 80% or more covered. No cover means there was little or no shelter at the fish location (with the exception of riverbed substrate). A “partial” cover means an intermediate situation between the total cover and no-cover situations.

Sampling and habitat characterization.—Based on the abundance and composition in salmonid species observed during river-scale surveys, three sites per river (two in Trois-Pistoles River) were selected for further sampling (Table 1). Depending on river width, two or three transects of \( 2 \text{ m} \times 30 \text{ m} \) per site were sampled parallel to the stream banks in habitats that appeared suitable for salmonids, both near the shores and in the middle of the rivers. Each transect was separated into 15 units of \( 2 \text{ m} \times 2 \text{ m} \) (hereafter referred to as 4-m² units). Two electrofishing passes, spaced approximately 0.5 m apart, were performed in each unit, from side to side. Positions of each salmonid (first sighting point) observed during each pass were identified with a weighted, color-coded flag for each species. To minimize disturbances and maximize success of capture, fishers progressed upstream, always staying just behind the anode. Although some imprecision of fish position relative to habitat characteristics may result from the disturbance of the fish by the fishers, the restricted sampling area insured that fish positions were flagged within at most 0.5 m of their original position. Beyond this, fish could not have been sampled as they would have moved out of the sampling area.

For each 4-m² unit, we noted shoreline cover (total, partial, no cover), mean depth \( \pm 1 \text{ cm} \), from three measurements), mean water velocity \( \text{m/s} \), and substrate size using a \( d_{50} \) index (Guay et al. 2003). To calculate the index, we measured the intermediate axis \( \beta, \pm 0.5 \text{ cm} \) of 30 particles haphazardly.
TABLE 1. Features of the nine rivers sampled in 2007 and 2008 in eastern Quebec. “Invaded” rivers supported a Rainbow Trout population, whereas no Rainbow Trout were captured in “noninvaded” rivers. For the Tortue River, density values were not determined (nd) since the area sampled was not available.

<table>
<thead>
<tr>
<th>River</th>
<th>Sampling starting date</th>
<th>Type</th>
<th>Mean density ± SE (fish/m²)⁰</th>
<th>Sampling design</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Rainbow Trout</td>
<td>Atlantic Salmon</td>
</tr>
<tr>
<td>Calway</td>
<td>Jun 18, 2007</td>
<td>Noninvaded</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Tortue</td>
<td>Aug 7, 2008</td>
<td>Invaded</td>
<td>nd</td>
<td>0.00</td>
</tr>
<tr>
<td>Du Gouffre</td>
<td>Jul 2, 2007</td>
<td>Invaded</td>
<td>0.019 ± 0.006</td>
<td>0.089 ± 0.025</td>
</tr>
<tr>
<td>M albaie</td>
<td>Jul 9, 2007</td>
<td>Invaded</td>
<td>0.046 ± 0.023</td>
<td>0.061 ± 0.028</td>
</tr>
<tr>
<td>Petit-Saguenay</td>
<td>Jul 16, 2007</td>
<td>Noninvaded</td>
<td>0.00</td>
<td>0.183 ± 0.054</td>
</tr>
<tr>
<td>Trois-Pistoles</td>
<td>Jul 23, 2007</td>
<td>Noninvaded</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Sud-Ouest</td>
<td>Jul 30, 2007</td>
<td>Noninvaded</td>
<td>0.00</td>
<td>0.020 ± 0.010</td>
</tr>
<tr>
<td>M atane</td>
<td>Aug 11, 2007</td>
<td>Invaded</td>
<td>0.026 ± 0.016</td>
<td>0.101 ± 0.024</td>
</tr>
<tr>
<td>M chéhins</td>
<td>Aug 6, 2007</td>
<td>Invaded</td>
<td>0.083 ± 0.070</td>
<td>0.00</td>
</tr>
</tbody>
</table>

⁰In sites where the species was present, based on a preliminary sampling.

¹In one site, we sampled a single transect of 39 units. In a second site, we sampled only two transects.

²Resampling was done by the MRNF and no site area was available, impeding density calculation.

³Only two transects by site.

⁴One site was abandoned since very few salmonids were captured in that river.

Data analysis.—To evaluate the distribution of sampling sites relative to habitat heterogeneity within and among rivers, a principal component analysis (PCA; princomp procedure with varimax transformation [SAS 2001]) was performed using the seven habitat variables (distance from the shore, depth, flow type, velocity, slope, shoreline cover, substrate size) measured during river-scale surveys in eight rivers. Since there is no P-value associated with the varimax transformation, variables significantly related to the PCA axis were identified according to the magnitude of loadings: (1) between the two axes for a given variable and (2) between all the variables for a given axis. In the present analysis, a variable was considered significantly related to the PCA axis when its loading after varimax rotation was ≥0.6.

The Tortue River could not be included in this analysis as the large-scale sampling was conducted by the MRNF and their measured habitat variables were not the same as those measured in the other eight rivers. To evaluate the success of assigning sampling sites to their river of origin (and hence the distinctiveness of rivers), we conducted a discriminant analysis (DA; discrim procedure) performed on the eigenvalues of PC 1 and 2, using rivers as categories. To evaluate if the occurrence of Rainbow Trout in invaded rivers (M atane, M chéhins, Du Gouffre and M albaie) was associated with particular combinations of habitat variables, logistic regression analyses (proc logistic, binary logit model, Fisher’s scoring) were conducted to relate the presence of Rainbow Trout at sampling sites quantified according to their PC1 and PC2 scores.

Estimates of habitat niche overlap, integrating three quantitative variables (depth, water velocity, and substrate size) were calculated using data obtained in the 4-m² units within the 60-m² transects. Estimates of weighted average (w) niche overlap (NO) were calculated based on a nonparametric index developed by M ouillot et al. (2005), NO_Kwt, that estimates the superposition strength of nonparametric kernel (K) density functions for several variables (t) between two species. A detailed description of the formula is presented in M ouillot et al. (2005). Niche overlap indices were compared (1) two by two between each pair of species (Rainbow Trout and Brook Trout, Rainbow Trout and Atlantic Salmon, and Brook Trout and Atlantic Salmon) based on samplings done in invaded rivers and (2) for native species only (Rainbow Trout and Atlantic Salmon), according to different levels of Rainbow Trout presence (Rainbow Trout present in the sample site versus Rainbow Trout absent from the sample site but present in the invaded river versus in noninvaded rivers). Nonparametric confidence intervals (CI95%) were generated for each niche overlap using the bootstrap resampling method (1,000 replicates) and the relationship between Rainbow Trout presence and the niche superposition of native fish was analyzed using a chi-square test, followed by a Z-test in R (Venables and Smith 2009).
Habitat preference, that is habitat use according to habitat availability (values measured in 4-m² units), was calculated using the method of Blanchet et al. (2007), which is based on the preference index developed by Beecher et al. (1993). The following formula was used:

$$M_i = \left( \frac{(n_i/n_1)(p_1/p_i)}{[(n_i/n_1)/(p_1/p_i)]_{\text{max}}} \right) - 0.5 \times 2. \quad (1)$$

where $M_i$ is the normalized habitat index for category $i$, $n_i$ is the number of samples (among all transects or sites) with fish in the considered category, $n_1$ is the total number of specimens, $p_i$ is the number of samples belonging to the category $i$, and $p_1$ is the total number of samples. Positive values indicate preference for a habitat category, whereas negative values indicate avoidance of a given category. The three quantitative variables (depth, substrate size, and velocity) were each subdivided in five categories (Table 2).

We considered that the presence of Rainbow Trout modified the habitat preferences of native species if, for a given habitat variable, preferred habitat categories ($M_i > 0.8$ to $1.0$) of Rainbow Trout and Atlantic Salmon or Brook Trout (in absence of the invader) were the same and if, in the presence of Rainbow Trout, preferred habitat categories of native fish were either actively avoided ($M_i < -1.0$ to $-0.8$) or simply occupied proportional to their availability ($M_i > -0.25$ to $+0.25$).

Growth rate was evaluated for age-0 fish captured during the entire sampling season, the most abundant year-class sampled for all species (Brook Trout: $n = 357$; Atlantic Salmon: $n = 674$; Rainbow Trout: $n = 303$). Slopes of the regressions of fish length on date of capture (35 sampling dates over a period of 66 d) were compared two-by-two using a 2-factor analysis of covariance (ANCOVA) (date, species, date*species) in SAS (SAS 2001).

**RESULTS**

**Habitat Heterogeneity and the Occurrence of Rainbow Trout**

The first principal component of the PCA conducted in eight study rivers explained 28% of the total variance in the seven habitat variables and was mainly related to the proximity of the shore and the presence of shoreline cover (Figures 2, 3A). The second principal component explained another 21% of the variation and was mainly related to flow type, water velocity, and substrate size (Figures 2, 3B). Habitat heterogeneity within rivers was so great that less than 30% of the 117 sites were correctly reassigned to their river of origin in the discriminant analysis (total rate of error count estimates for river: 0.712). Sites were considered as independent samples in further analyses as rivers could not be considered distinct based on the habitat characteristics considered here.

Sites where Rainbow Trout were present tended to cluster towards the positive end of PC1 and the negative end of PC2 (Figure 2), suggesting that well-covered habitats located near the river shore with a slower and more laminar flow were preferred by Rainbow Trout. Using only the sites located in invaded rivers (Matane, Méchins, Du Gouffre, and Malbaie), logistic regression analysis revealed that increasing scores on PC1 significantly predicted the presence of Rainbow Trout ($Wald = 5.56$; $DDL = 1$; $P = 0.018$) but not so on PC2 ($Wald = 2.93$; $DDL = 1$; $P = 0.087$). Rainbow Trout was thus significantly and positively associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover.

**Niche Overlap**

Niche overlap for substrate, water velocity, and depth between native salmonids and Rainbow Trout was higher than 0.80, and tended to surpass that of the two indigenous species (Figure 4). Niche overlap between Brook Trout and Rainbow Trout was greater than that of Atlantic Salmon and Rainbow Trout. In sites where Rainbow Trout was present, native species shared approximately 80% of the habitat based on the three measured variables (Figure 4). However, in sites and rivers free of Rainbow Trout, the niche overlap between the two indigenous species decreased significantly ($\chi^2_{obs} = 4.58$, $Z = 2.11$, $P = 0.03$).

**Habitat Preferences**

Among variables analyzed for habitat preferences, we observed a major modification in the habitat selection of native species for shoreline cover in response to the presence of Rainbow Trout. In the absence of Rainbow Trout, Atlantic Salmon and Brook Trout showed a clear preference for highly covered habitats ("total" cover scored at 1), but in sympathy with Rainbow Trout, which also preferred total cover, they shifted towards more open habitats ("partial" cover scored at 1) (Figure 5).

For all the other variables tested (distance from the shore, depth, flow type, velocity, slope, and substrate size; results not shown), no clear modification of habitat selection was observed in the presence of Rainbow Trout: either native species did not show a preference for any particular habitat category, or the selection pattern did not change in the presence of Rainbow Trout, or a habitat change was observed but could not be associated with the presence of Rainbow Trout.
Growth Rates
During their first year of life \((0^+)\), growth rate was similar \((F = 1.21, DDF = 1, P = 0.27)\) for Atlantic Salmon \((0.29 \text{ mm/d} [95\% \text{ CI}: 0.29-0.30 \text{ mm/d}])\) and Brook Trout \((0.26 \text{ mm/d} [95\% \text{ CI}: 0.24-0.29 \text{ mm/d}])\) but was significantly greater for Rainbow Trout \((0.46 \text{ mm/d} [95\% \text{ CI}: 0.44-0.47 \text{ mm/d}])\). Atlantic Salmon: \(F = 27.34, DDF = 1\); Brook Trout: \(F = 15.40, DDF = 1; P < 0.01\). Despite a later emergence date, and assuming constant growth rates until the end of the growing season, Rainbow Trout would have almost caught up in size with both native species.

DISCUSSION
Introduced Rainbow Trout has been shown to outcompete native salmonids where populations are well established and in designed experiments (Seiler and Keeley 2007a; Seiler and Keeley 2007b). But at an early stage of establishment and dispersal, when Rainbow Trout densities are low, interaction with indigenous species might not systematically favor Rainbow Trout. In eastern Quebec, the Rainbow Trout invasion is an ongoing process, and recently established populations are still at low densities. Since two native salmonids co-occurred in the colonized rivers, these provided an ideal system to evaluate the potential impact of the exotic species at a relatively early stage of the invasion.

Impact of Rainbow Trout on Native Species
In invaded rivers, Rainbow Trout were positively associated with habitats characterized by closer proximity to the shoreline and by increasing shoreline cover. Accordingly, when considering the species’ preference for three categories of shoreline cover (no cover, partial, and total), we found that preference changed for both native species according to Rainbow Trout occurrence. In the absence of Rainbow Trout, the two indigenous species preferred full cover, but in the presence of Rainbow Trout, which also preferred full cover, Atlantic Salmon and...
Brook Trout switched preference to partially covered habitats. Shoreline cover has been identified as an important habitat variable for salmonids, especially for Rainbow Trout (Platts 1976; Gibson 1978; Gatz et al. 1987 and references therein), and exclusion of native fish from the more shaded areas indicates that native salmonids are unable to resist displacement by the invading Rainbow Trout.

The increase in habitat niche overlap between the two indigenous salmonids in the presence of Rainbow Trout, in comparison to sites or rivers where the exotic species was not found, also suggests that Rainbow Trout is impacting native fish. Usually, in the absence of Rainbow Trout, sympatric Atlantic Salmon and Brook Trout segregate spatially, with Atlantic Salmon displacing Brook Trout to less optimal habitats (Rodríguez 1995). It appears that the presence of the invader changed the habitat uses of both species, forcing them to share more similar resources.

**FIGURE 3.** Loadings (after varimax rotation) on (A) PC1 and (B) PC2 of the principal component analysis. Significant loadings (≥0.6) are shown by black bars.

**FIGURE 4.** Nonparametric niche overlap indices (NO_{kwi} ± SE) for three quantitative habitat variables (substrate, depth, and velocity) between Rainbow Trout (RT), Atlantic Salmon (AS) and Brook Trout (BT), according to variable levels of Rainbow Trout presence. Eighty percent of habitat overlap is indicated by the horizontal dashed line.

**FIGURE 5.** Preference of Rainbow Trout, Atlantic Salmon, and Brook Trout for shoreline cover in (A) sites (three transects) and (B) transects (60 m²) in the presence and absence of Rainbow Trout. Riparian vegetation, canopy, prominent rocks on the shore, and bridges or other structures overhanging the river constitute examples of cover. A “total” cover means that the position of fish was more than 80% covered. A “null” cover means there was no shelter at the fish location (except the riverbed substrate). A “partial” cover means an intermediate situation between the total cover and the null cover emplacement. A value near 1 indicates an active selection for a cover category, a value near –1 indicates an active avoidance of a cover category, and a value near 0 indicates that habitat use is proportional to habitat availability.
The possibility that observed modifications in the habitat uses of Atlantic Salmon and Brook Trout is the result of ontogenetic habitat shifts cannot be totally discarded. Hasegawa et al. (2012) effectively demonstrated that the invasion of Brown Trout Salmo trutta in streams supporting native Masu Salmon Oncorhynchus masou—expected to be a greater competitor due to its size superiority related to an earlier emergence time—was facilitated by the ontogenetic niche shift of Masu Salmon, which reduced niche overlap between the two species. This phenomenon may very well contribute in part to explaining our observations. However, in the present study, habitat and niche overlap changes were revealed by comparing—almost simultaneously—sites and rivers with and without the invader. Thus, modifications in habitat use of native fish that were observed in the presence of Rainbow Trout were not observed for Atlantic Salmon and Brook Trout at the same ontogenetic development stage in noninvaded sites and rivers. This supports the contention that habitat changes were not only caused by an ontogenetic habitat switch.

Growth of Rainbow Trout

As demonstrated by the length-at-age relationships, the growth of Rainbow Trout during its first year of life was superior to that of the two native species, regardless of the delay caused by a later emergence date, which is consistent with other studies (Whitworth and Strange 1983). It appears that the foraging abilities of age-0 Rainbow Trout and their ability to displace indigenous salmonids from preferred habitat results in rapid growth despite the presence of two competitors at higher density. Rainbow Trout possessed a growth rate (0.46 mm/d) similar to that observed in long-time naturalized populations in the Great Lakes (0.32–0.42 mm/d; Johnson 1980; Rose 1986).

Management Implications

The invasion of Rainbow Trout in eastern Quebec is still ongoing; known established populations are rare and often at low density. Therefore, an absence of Rainbow Trout impact on native salmonids could have been expected. However, we found that juvenile Rainbow Trout showed a higher growth rate than its two sister species, revealing its ability to effectively exploit resources. Furthermore, this study demonstrated that introduced Rainbow Trout in eastern Quebec, despite the low densities, interact with indigenous salmonid species to such an extent that Atlantic Salmon and Brook Trout modified their habitat use. The increase in native fish niche overlap at small spatial scales is an indirect effect of the introduced salmonid, whereas the shift in preferred habitat categories of native species demonstrates a direct impact of the interactions with the invader (Hasegawa and Aekawa 2006). These results increase our concerns about the future impacts of the invader on native fish. They are consistent with the findings of Baxer et al. (2007), who demonstrated in a field experiment that the biomass of native Dolly Varden Salvelinus malma in the presence of the introduced Rainbow Trout, even at low density (0.2 fish/m²), was 75% lower than at sites without Rainbow Trout. Based on a comparative experimental study, this might have been in great part caused by a usurpation of terrestrial prey subsidy by Rainbow Trout that would have forced the native fish to shift their diet. In the near future, since the interaction between native and exotic salmonids in eastern Quebec is expected to continue and even increase, it will be primordial to determine how the modification in habitat use impacts the diet composition and consumption rate of native salmonids and to what extent it affects their growth and survival.

Observations of the displacement of Brook Trout by Rainbow Trout are more numerous than for Atlantic Salmon (e.g., Larson and Moore 1985; Moore et al. 1990; McEwan 1990; Pausch 1991; Pausch 1998). However, some authors have suggested that the decline of Brook Trout populations after the introduction of Rainbow Trout was probably more the consequence of the pre-existing weakened state of the native species (Clark and Rose 1997) in combination with the impact of the invader, rather than to the Rainbow Trout invasion itself. A similar tendency has also been observed following the introduction of Brown Trout (Waters 1983). Thus, intrinsic problems in native species’ populations (overexploitation, habitat degradation, etc.) may permit Rainbow Trout invasion to have a greater impact on indigenous communities. Both Brook Trout and Atlantic Salmon populations are declining in eastern Quebec because of habitat degradation and overfishing of the former (M. A. Rivais, personal communication) and a high marine mortality rate and various impediments to upstream movements for the latter (Friedland et al. 1993; Hansen and Quinn 1998; Hansen and Windsor 2006; ICES 2008). Both species may thus be less able to resist the encroachment of Rainbow Trout in their habitats.

It is often thought by anglers, and unfortunately by some wildlife managers too, that as long as an invader is not abundant and minimally dispersed, its impact on the ecosystem may be negligible, and thus management actions to eliminate or limit the potential threat are not called for. This perception is particularly true for species like Rainbow Trout, which are socially acceptable and desirable and support economic activities (such as aquaculture, angling, and tourism). However, the advantage of reacting quickly when biological invasions are discovered early in the invasion process is twofold: (1) mitigation measures are often only truly efficient when the invader is not yet abundant and is confined to a restricted area (Moore et al. 1986; M. Eyer et al. 2006; Peterson et al. 2008) and (2) as we demonstrated in this study for Rainbow Trout, impact on native fauna can be real and important from the start of the invasion, even when densities are low.

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A Review of “Historical Biogeography of Neotropical Freshwater Fishes”

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The neotropics have long been recognized as a center of remarkable biological diversity, with the freshwater fish fauna of the region being particularly noteworthy for the range of morphological types as well as the sheer number of species. An earlier estimate of over 6,000 species (Reis et al. 2003) seems increasingly too low, perhaps to a pronounced degree, in light of the accelerating rate of description of previously unknown species with no indication that this stream of newly recognized forms is abating. This flood of new species is a function, on the one hand, of ichthyological explorations in areas and habitats not sampled (or at best undersampled) until recently and, on the other hand, of in-depth revisionary studies that have revealed that collections in museums and universities across the Americas and Europe housed hundreds of species not previously recognized by science. Adding to the appreciation of this species richness is increased information on the phylogenetic history of many of the groups of fishes living in neotropical freshwaters. Information on the phylogenetic relationships among the major groups of such fishes (Mabababa et al. 1998) has been complemented by publications based on morphological and molecular techniques. Despite these major strides in our knowledge, publications dealing with the historical biogeography and diversity of neotropical fauna and their underlying causes rarely delve below the water's surface. When rivers are considered, they are most often treated as barriers to the dispersal of terrestrial vertebrates, with little or no discussion of the diversity in these aquatic systems or the historical factors that affected them. Clearly, the time was ripe for a thorough analysis of the temporal and spatial factors that have contributed to the remarkable diversity of fish fauna in the rivers and lakes of South and Central America.

Historical Biogeography of Neotropical Freshwater Fishes is organized around two major themes—continental and regional analyses—that are examined over the course of 18 chapters. The continental analysis section starts with a thorough introduction to neotropical freshwaters by J. S. Albert and R. E. Reis (Chapter 1) discussing the major river basins of South America, the large-scale geological events that contributed to the landforms of the continent (and presumably served as the catalyst for the species diversity), and the sea-level changes and climate shifts that have impacted the fish fauna. In Chapter 2, J. S. Albert, P. Petry, and R. E. Reis discuss the major biogeographic and phylogenetic patterns and analyze the fish fauna in multiple contexts, including species-area relationships, alternative modes of species richness, patterns of density, endemic species, and Amazonia versus the other regions of the continent. These discussions serve as the foundation for overviews of the broad phylogenetic patterns and some of the possible factors accounting for the diversity. F. P. Wesselin and C. Hoorn (Chapter 3) provide a comprehensive overview of the geological development of the Amazon and Orinoco River basins from the separation of South America from Africa to the recent era. This summary of the two major drainage systems in the northern part of the continent is complemented by M. Brea and A. F. Zucol in Chapter 4, which provides an overview of the geology and paleoenvironments of the more southerly Paraná–Paraguay River system, the third largest on the continent. Dating information from both palynology and paleoflora is used to evaluate paleoclimates across the basin. The first four chapters set the stage for the next five sections, with Chapter 5 (J. S. Albert, H. J. Bart Jr., and R. E. Reis) providing an analysis of species richness within the context of cladal diversity to address the interesting question of why some taxa are so diverse while others are so strongly conservative. Chapter 6, authored by H. López-Fernández and J. S. Albert, investigates the evidence from multiple sources on the origin of the modern neotropical freshwater ichthyofauna during the Paleogene. This summary provides insights into the factors that led to the diversification of this fauna and, equally important, points out many yet-to-be resolved questions. In the next chapter (7), J. S. Albert and T. P. Carvalho carry the analysis further via a quantitative biogeographic analysis based on a Brooks parsimony analysis of the aquatic ecoregions within South America (Abell et al. 2008) using data from 32 fish taxa comprising over 300 species. Evidence demonstrates that the modern distribution of the fauna represents both geodispersal and vicariance. These results also address numerous other issues (including taxon pulse hypotheses) and enable us to estimate the longevity of the species richness of the modern Amazonian fish fauna. Chapter 8 by D. D. Bloom and N. R. Lovejoy highlights the impact of marine incursions on the biogeographic patterns of South American freshwater fishes and the temporal sequence of the marine-derived lineages resulting from such incursions. Chapter 9 by F. C. T. Lima and A. C. Ribeiro summarizes the continental-scale factors associated with the shields, seaways, and foreland basins and the composite nature of various major basins both in terms of geology and biogeography. Rounding out the first major theme of the book is Chapter 10 by W. G. R. Crampton, which examines the diversity of the fish fauna and distribution of species from an ecological viewpoint based on information from multiple groups of electric knifefishes (Gymnotiformes). The author also advances a conceptual framework for evaluating
these questions within the context of a four-category classification of neotropical aquatic habitats.

The second part, on regional analysis, complements the contributions of the first with a series of papers focusing on geological episodes and/or distinct subunits of the region. The long-debated question of the permeability of the Amazon–Paraguay divide between the major river systems that lie along the boundary of those two basins is discussed in Chapter 11 by T. P. Carvalho and J. S. Albert. Species transfers between the rivers of the eastern portion of the Brazilian Shield and adjoining river systems are then analyzed by P. A. Buckup in Chapter 12. The complex geological history of the Guiana Shield and the hydrology of the numerous rivers draining that region are summarized by N. K. Lujan and J. W. Armbruster (Chapter 13), who also detail the extant interconnections (the Casiquiare and Rupununi Portals) and past drainage patterns reflected in present-day fish distributions. The Río Casiquiare, the river segment that joins the upper portions of the Río Negro (Amazon basin) with the upper Río Orinoco, and the interrelationships of the fish faunas in these drainages is the subject of Chapter 14 by K. O. Winemiller and S. C. Willis. Similarities between the basins are scrutinized using information from phylogeographic analysis and the distribution patterns of well-documented families present in both drainage systems. The continental fish faunas of the multiple river systems west and north of the Andes, the similarities between these faunas, and the species richness in the different basins (ranging from the smaller rivers of western Ecuador to the distinctly larger Río Magdalena and Lago Maracaibo) are summarized in Chapter 15 (D. Rodríguez-Olarte, J. I. Mojica, and D. C. Taphorn Baechle). In Chapter 16, S. Schaefer provides an in-depth analysis of an often forgotten aspect of the diversity of South American freshwater fishes—that of the fishes inhabiting the drainages and lakes of the Andean cordilleras—using evidence from all groups of resident fishes to arrive at innovative insights into the underlying patterns of faunal and area relationships. The final two chapters look at the fishes of nuclear South America (Chapter 17 by C. D. Hulsey and H. López-Fernández) and the Isthmus of Panama (Chapter 18 by P. Chakrabarty and J. S. Albert). This geologically and hydrologically complex region has a fish fauna that has long been the subject of speculation; these chapters evaluate the strengths or weaknesses of prior hypotheses and provide details on the relationships between this fauna and those of adjoining regions. Completing the book is a detailed and very useful glossary and an encompassing list of the literature cited, which, given the thoroughness of the various chapters, includes most of the significant literature dealing with neotropical freshwater fishes.

The editors and authors are to be congratulated for bringing together information from taxonomy, phylogeny, geology, paleontology, ecology, and other disciplines to provide a masterful summary of the multiple factors that probably contributed to the evolution of the freshwater neotropical ichthyofauna. I found the book and its layout visually pleasing, with the use of color for certain figures and plates adding to the information content of many chapters. The volume will prove an invaluable tool not only for researchers focused on the myriad wonders of South and Central American freshwater fish faunas but also those interested in the formation of the complex aquatic faunas in that region and general biogeographic patterns across the neotropics.

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A Review of “Fisheries Techniques, third edition.”
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Book Review


The new edition of Fisheries Techniques has finally arrived. For 30 years, previous versions of this text have functioned as the essential, go-to reference on basic questions regarding fisheries sampling and analysis. Furthermore, the book is frequently deployed as the principal textbook for introductory fisheries courses at universities offering a fisheries science curriculum. Sixteen years have elapsed since the publication of the previous edition, and many chapters were in great need of updating due to technological and conceptual advancements.

Owners of all three editions will immediately notice the growth in the size of the book over time (from 467 pages in 1983 to 732 pages in 1996 and 1,009 pages now). While all of the chapters were completely rewritten, the arrangement of the book is very similar to that of the previous editions, which should provide a level of familiarity for long-time users. Only two chapters were removed (“Sampling with Toxicants” and “Field Examination of Fishes”), and one chapter was added (“Fish Kill Investigation Procedures”). Thus, the type of information in this text has not changed dramatically, but the depth of coverage has.

Readers will probably find the updated and expanded information to be highly useful and timely. Noteworthy changes include the integration of zooplankton into the chapter on fish eggs and larvae and the addition of plants to the chapter on invertebrates (this being the oddest marriage of topics in the book). There also appears to be increased emphasis on ecological principles in fisheries (e.g., the chapter on diets is now titled “Diets and Energy Flow”). Freshwater mussel sampling is a welcome addition to this text, as is the inclusion of stable isotope approaches. Cutting-edge underwater imaging technologies, such as ultrasound imaging and dual-frequency imaging sonar are discussed. A list of standard weight equations is included for calculating relative weight data; however, equations published after 2004 were not included. Throughout the book, there appears to be a coordinated increase in the use of photographs and sidebar examples, which are especially welcome changes for teaching purposes.

I had informal conversations with four fisheries scientists regarding the new edition of this book. All remarked that it is an excellent contribution and will be especially valuable for advanced students and younger fisheries professionals. One had already used the book to teach an introductory fisheries course for undergraduates and, not surprisingly, noted the usefulness of the examples for pedagogy. It was also appreciated that the chapter on data management was updated, especially given that the previous edition discussed data storage on outdated technologies like floppy disks. An international scientist suggested that the book is biased toward North American fisheries and ecosystems but that it is still widely applicable. Two scientists commented that marine fisheries, especially coastal marine fisheries, are underrepresented. However, one noted that this is not necessarily a bad thing, as a comprehensive book covering all environments and fishery types would probably be too large and unwieldy to be accessible. All remarked about the length of time that it took for this edition to become available, as many had apparently been waiting for the new edition for years.

Ultimately, this book is simply an outstanding contribution to the fisheries literature, and the editors and chapter authors should be commended for their efforts. The book will probably be owned by almost every serious scientist in the field for years to come. It will also be wonderful to have an updated textbook for introductory fisheries coursework...at least for the next 7-10 years, until the need for a fourth edition arises.

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A Review of “Scientific Communication for Natural Resource Professionals.”

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BOOK REVIEW

Scientific Communication for Natural Resource Professionals.

Communication is the lifeblood of science. However, it can also be a daunting task, especially for students and young professionals. Recognizing this, the Southern New England Chapter of the American Fisheries Society (SNEC–AFS) held a writing workshop in January 2013. The workshop featured presentations by two prominent experts at the Northeast Fisheries Science Center, senior scientist Fred Serchuk and technical editor Jarita Davis. In addition, attendees were given a copy of the new AFS book Scientific Communication for Natural Resource Professionals, edited by Cecil A. Jennings, Thomas E. Lauer, and Bruce Vondracek. The SNEC–AFS asked several of the students to review the book in order to practice some of the writing techniques that they had learned at the workshop.

Scientific Communication for Natural Resource Professionals is an excellent desktop companion for any student or young professional. This short book is reasonably priced and contains a wealth of information. Its overall purpose is to facilitate scientific communication by students and early-career natural resource professionals. The editors and authors achieve this objective, providing important information useful to the target audience. The book consists of a series of contributed papers, allowing readers to reference examples as needed instead of having to read the text from start to finish. While the book covers many topics, most of it focuses on various aspects of manuscript preparation, ranging from the determination of authorship to statistical usage, figure generation, and responding to reviewers’ comments. Other topics include making oral and poster presentations, becoming an effective reviewer, and communicating in e-mails and memos. Probably the only topic not covered is how to write a book review, but we figured that out.

The book opens with a brief history of writing from cuneiform through the advent of the printing press to the development of the “World Wide Web” which provides a background for the medium of scientific communication. Scientific Communication walks the reader through the process of writing a peer-reviewed paper. The second chapter addresses the often neglected topic of determining authorship. Except in the case of the first author (the person who writes the paper), the criteria for determining authorship are often ambiguous at best. This chapter provides an excellent guide, with 13 recommendations that include the criteria put forth by the International Committee of Medical Journal Editors.

Chapter 3 provides an overview of the steps in crafting an informative scientific paper, beginning with journal selection and proceeding through manuscript compilation and submission. This is a thorough and informative chapter that sets the stage for the subsequent chapters relating to the individual elements of crafting a manuscript. This broad review is followed by a chapter about clear and concise scientific writing that identifies common mistakes in style, usage, grammar, and punctuation.

In subsequent chapters, the book addresses individual aspects of a manuscript. Parts of these chapters are a labor to read, but the information is highly valuable. The fifth chapter provides several tips for managing the literature search, reminding readers of the importance of evaluating the credibility of sources found online. Chapter 6 provides guidance on the presentation of statistics in a manuscript, something that is often difficult to do in ways that will make them accessible to the reader. Although this chapter is a tough read, the information it offers about describing statistics in the Methods section and incorporating them into the Results is insightful. The subsequent chapter goes into graphic design at some length. The material in this chapter does not reflect the current array of software tools and publishing formats available due to the rise of digital publications and supporting materials, giving it a dated feel. However, the strength of the chapter is the arguably timeless set of concepts and guidelines regarding figures.

After covering the various aspects of manuscript preparation, Scientific Communication reminds students of the importance of disseminating their research among the scientific community via published papers rather than leaving them in thesis form. Although this chapter is very useful, its title is misleading. It suggests that the chapter will center on ways to convert a thesis into a manuscript, but the chapter actually provides little advice along this line: most of it deals with ways to facilitate subsequent manuscript preparation while one is writing a thesis, which is essentially covered in a previous chapter. The inclusion of topics such as how to pare down a thesis, focus the writing, and select the figures to include in a journal submission would have been valuable to the many students who have already completed their theses.

Other aspects of publishing a paper are addressed in the following chapters, which describe journal selection and the peer review process. Chapter 9, on journal selection, highlights why authors choose to submit to one journal rather than another. This chapter provides examples of research results that could be published in widely different journals based on the emphasis of the research. While helpful, the examples are somewhat redundant. Complementing this chapter, Chapter 10 provides step-by-step guidance on revising a manuscript, whether it needs minor,
major, or multiple revisions. By breaking the process down into manageable steps, it provides helpful advice on handling what can be a daunting and difficult task.

Scientific communication is not entirely about writing manuscripts; oral presentations are also a major part of it. These are covered in Chapter 11, which contains sound advice about the style of presentation that is preferable given the audience and the amount and type of data to be presented. This chapter is an excellent guide for someone new to professional meetings. After all, presenting research can often be more daunting than conducting it.

There is also a chapter about writing a review paper. The chapter discusses the various elements in crafting a review paper and highlights the differences between such a paper and a typical manuscript, noting that the goal of a review paper is to synthesize a wealth of information so that professionals in other disciplines can utilize it without having to consult the pertinent references.

The final chapter covers peer reviewing manuscripts, which over the course of a natural resource professional’s career is as important as publishing. This chapter provides straightforward, insightful commentary on the ethical and functional responsibilities of the reviewer, including detailed instructions for reviewing each section of the paper. The author weaves personal experiences and humor into the discussion, while laying out a detailed road map for reviewers. We recommend keeping this chapter close at hand when you are reviewing a paper.

Overall, Scientific Communication for Natural Resource Professionals is an effective instructional guide to communicating in our field. Although the subject matter is at times bland and there is some unnecessary overlap between chapters, the book is a welcome desktop companion to those in the natural resource profession. We highly recommend it not only to students and young professionals but also to seasoned veterans as a guide through the daunting task of communicating science.

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ERRATUM

Please make the following correction in a recent issue of this journal:


Page 455. The first sentence in the first full paragraph should read as follows:

Splitting time (t) between Umpqua Chub from the Smith River and Umpqua River based on the IMa model was estimated to be 196 years before present (90% credible interval; 90% CI = 44–340) assuming no migration between rivers and 188 years before present (90% CI = 20–396) allowing for migration between rivers.