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ARTICLE

Use of Mini-Fyke Nets for Sampling Shallow-Water Fish Communities in Florida Lakes

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Abstract
We evaluated mini-fyke nets for sampling shore-based (SB; <1 m deep) fish communities in Florida lakes. Specifically, we wanted to determine the most effective deployment method and sample size required for adequately characterizing fish communities in these habitats. Shallow SB (0.15–0.6 m) net sets, in which nets were not completely submersed, collected significantly more individuals and a larger proportion of poeciliids. However, deep SB (0.6–1.0 m) net sets, in which nets were completely submersed, collected a larger proportion of centrarchids, cyprinids, and cyprinodontids. Net placement also significantly affected the overall catch and composition of samples. Nets placed in locations away from the lake boundary tended to collect actively schooling fishes such as Threadfin Shad Dorosoma petenense and cyprinids. Nets placed next to the lake boundary tended to collect species associated with shallow, vegetated habitats, particularly poeciliids, at greater frequencies. In some cases, the collection of these fishes was unique to a particular deployment method. Our results suggest that in long-term monitoring of Florida’s shore-based lentic fish communities, nets should be placed in SB waters with the lead extending to the lake boundary. Although long-term sampling objectives may vary, we determined that a sampling target of 30 net sets was sufficient for characterizing the fish community in terms of percentage composition, species richness, and species diversity. Furthermore, we recommend the continued use of additional gears to fully characterize littoral fish communities.

In 2006, the Florida Fish and Wildlife Conservation Commission established a standard protocol for sampling lentic fishes in approximately 30 Florida systems (Bonvechio 2009). This protocol uses a variety of gears and techniques, including otter trawls, boat electrofishing, and gill nets, to target fishes inhabiting different habitats (Bonvechio et al. 2008; 2009; 2012). Some protocols were developed to monitor target fish populations, such as important sport fishes, whereas others were chosen to track changes in fish communities. For example, the winter gill-net protocol is used to monitor pelagic species such as Threadfin Shad Dorosoma petenense in offshore areas, whereas boat electrofishing in the fall is used to monitor nearshore (<2 m depth) fish communities (Bonvechio et al. 2009, 2012). Previously, no protocol was in place for assessing shallow-water fish communities, which typically contain non-sport fish species and juvenile fishes not commonly sampled with other gears.

A variety of gears has been used to sample shore-based (SB; <1 m) fish communities, each with its own drawbacks.
Historically, block nets (i.e., a curtain of netting set around the periphery of typically up to an acre of water; Tugend and Allen 2004), Wegener rings (Wegener et al. 1974; Moyer et al. 1995), and throw traps (Chick et al. 1992; Chick and McIvor 1994) have been used in Florida waters. However, these gears cannot be properly deployed or secured in areas of dense vegetation or woody structure, and may be ineffective on bare substrates due to fish avoidance. Furthermore, Wegener rings and block nets typically involve the use of the fish toxicant rotenone, which has been increasingly discouraged due to public concerns (Finlayson et al. 2000). Despite the success of seines for sampling in SB habitats, they, too, are ineffective in areas with dense vegetation or structure due to snagging and rolling (Pierce et al. 1990; Lapointe et al. 2006; Clark et al. 2007). Airboat electrofishing has been deemed effective in these habitats, but similar to other electrofishing methods, it is biased toward larger fishes (Chick et al. 1999). Consideration of these issues and results of preliminary sampling efforts prompted us to further investigate mini-fyke nets for utility in our statewide monitoring program.

Unlike other gears considered, mini-fyke nets with small (≤6 mm) mesh netting may be effective for monitoring fish communities in a wide variety of SB habitats. Clark et al. (2007) noted that these nets were deployable in all of the study’s 22 floodplain lakes of the White River in Arkansas, lakes characterized by complex habitat including dense vegetation and woody debris. Furthermore, mini-fyke nets have been compared with other gears for assessing fish community structure. They tended to collect more fish and more species of fish than other gears, including electrofishing, gill nets, and seines (Clark et al. 2007; Eggleton et al. 2010; Cvetkovic et al. 2012). Weaver et al. (1993) also found that this gear resulted in better descriptions of littoral fish communities than did gill nets or seines.

Given the success of mini-fyke nets in other regions, we chose to evaluate them for sampling SB fish communities in Florida lakes. Gear configuration, such as different fyke net meshes and shape (e.g., Krueger et al. 1998; Shoup et al. 2003), has previously been studied. However, the effect of different gear deployments on catch and resulting fish community descriptors, especially in areas with a diversity of habitats, has not been fully explored. Thus, our study objective was to evaluate the effectiveness of mini–fyke nets for sampling SB fish communities in three Florida lakes of different trophic states. More specifically, we wanted to (1) determine the most effective gear placement, in terms of catch and number of species collected, and (2) with the chosen gear placement, estimate the sample size needed for characterizing the SB fish community.

### METHODS

The three study lakes, Harris, Minneola, and Santa Fe, differed in size, trophic state, and coverage by aquatic macrophytes (Table 1). Net placement and sample size were evaluated for all three lakes, but only Lake Harris was included in the depth placement evaluation because it offered the only lake shoreline conducive to doing these comparisons. For all comparisons, we used a mini-fyke net with a modified design, hereafter referred to as “fyke net.” Each net consisted of three metal frames (0.6 × 0.6 m), two chambers (0.6 × 0.6 m), and a 0.9-m conical cod end. A lead (4.6 × 0.6 m) with float and lead lines extended into the first chamber, which contained a 6.4-cm bar-mesh exclusion panel and a 30.5-cm zipper to aid in excluding and removing large predators and accumulated debris from the net. The second chamber consisted of a funnel with a 5.1-cm excluder ring elevated 15.2 cm from the bottom. The entire net, including the lead line, was made of 3-mm nylon mesh. All nets were fished overnight, i.e., set during the afternoon (1200–1600 hours) and retrieved the following morning (0800–1100 hours). For all samples, fish were identified to species, counted, measured (mm TL), and weighed (g). Data were collected for each individual in the sample, except in cases of large fyke net catches, for which data were extrapolated from a subsample of measured individuals.

#### Depth placement

To evaluate depth placement, 30 pairs of fyke nets were set in Lake Harris in September 2009. For each pair, one net was set with the lead extending to the lake boundary and the first frame in water 0.15–0.6 m deep such that the net was not completely submersed (hereafter referred to as the “shallow SB” net set; Figure 1A). The second net was set with the lead extending to the lake boundary and the first frame completely submersed in water up to 1 m deep (hereafter referred to as the “deep SB” net set; Figure 1A). Nets of each pair were placed within 50 m of each other. Sites were chosen based on where the two depth placements could be made near

### TABLE 1. Water chemistry, physical, and biological metrics for the 2008–2012 mini-fyke-net study period of three Florida lakes. Included are the surface area (Size), average lake depth (Depth), percentage area coverage by aquatic macrophytes (PAC), average lakewide estimate of aquatic plant biomass, average chlorophyll-a concentration, and trophic state.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Size (ha)</th>
<th>Depth (m)</th>
<th>PACa</th>
<th>Plant biomass (kg/m²)</th>
<th>Chlorophyll a (µg/L)</th>
<th>Trophic stateb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harris</td>
<td>6,691</td>
<td>3.4</td>
<td>4</td>
<td>4</td>
<td>30</td>
<td>Hypereutrophic</td>
</tr>
<tr>
<td>Minneola</td>
<td>764</td>
<td>3.9</td>
<td>&lt;1</td>
<td>3</td>
<td>5</td>
<td>Mesotrophic</td>
</tr>
<tr>
<td>Santa Fe</td>
<td>2,011</td>
<td>5.1</td>
<td>&lt;1</td>
<td>10</td>
<td>14</td>
<td>Eutrophic</td>
</tr>
</tbody>
</table>

aPercentage of lake area coverage by aquatic macrophytes.
bBased on Forsberg and Ryding’s (1980) criteria.
MINI-FYKE NET SAMPLING 695

FIGURE 1. Schematic of experimental set-up for each mini-fyke-net deployment to evaluate shore-based fish communities: (A) side view of the depth placement evaluation, where nets were set either shallow (with the first frame partially exposed) or deep (with the first frame completely submerged) (the gray area indicates water) and (B) top view of fyke net pairs set in vegetated and beach habitats (with the lead extending to the lake boundary) or out (with the lead terminating away from the lake boundary) (gray area indicates vegetation).

Each other, and efforts were made to spatially distribute them throughout the lake.

Fyke-net placement (shallow versus deep water) was analyzed using a paired $t$-test for log$_{10}(x+1)$-transformed total catch data using Proc TTEST and a type I error rate of 0.05 (SAS Institute 2011). We also compared the community composition for the two placement types. First, we determined species richness, modified Simpson’s diversity index, percent similarity index (PSI) and Jaccard’s similarity index (JSI; Krebs 1999). We deemed community composition similar between the two placements if both the PSI and JSI values were at least 80. Second, we grouped fish by family, except for exotic species, which were included as a single group. We then compared the between-placement distributions of these groups in terms of number of individuals collected. A Fisher’s exact test was used due to low numbers of fish observed for some groups. This analysis was performed using Proc FREQ with a type I error level of 0.05 (SAS Institute 2011).

Shoreline placement.—The shoreline placement evaluation was conducted at Lake Harris in September 2008. We later sampled lakes Minneola and Santa Fe in July 2012 to gain a broader understanding of the effect of shoreline placement in other systems. For this comparison, a total of 20 pairs of fyke nets were set at each lake (Figure 1B). As with the depth placement evaluation, sites were chosen based on where treatments could be established within 50 m of each other. Half of these pairs were set in high vegetative cover (hereafter referred to as “vegetated” sets); the other half were set in sparsely vegetated sandy habitat (hereafter referred to as “beach” sets). For each vegetated set, one net was set with the lead extending to the lake boundary (“in”) and one net set adjacent to it with the lead extending to the outer band of the vegetation (“out”). For each beach set, one net was set with the lead extending to the lake boundary (“in”) and one net set adjacent to it with the lead in open water (“out”; Figure 1B). Because each pair of nets was set at the same site, a repeated-measures analysis of variance (ANOVA) was used to compare mean total catch among treatments. We treated site as our subject and included the fixed effects, fyke-net placement and habitat (vegetated versus beach), and a placement × habitat interaction term in the model. We chose an unstructured covariant structure for the MIXED procedure because this yielded the lowest Akaike information...
criterion (AIC) value (SAS Institute 2011). All analyses were performed with log_{10}(x + 1)-transformed catch data and type I error rate of 0.05. Community composition comparisons were also done, as previously described under depth placement.

Sample-size estimation.—Sampling for the sample-size evaluations was conducted at all three lakes in August and September 2008. The shoreline of each lake was split into 50-m sections using ArcGIS software, 50 of which were randomly selected for sampling. Based on previously collected data at four pilot lakes, all nets were set in water shallower than 0.6 m. The lead extended to the lake boundary, which was either the lake shoreline or to the edge of thick vegetation or structure deemed impassible by fish. To determine the sample size needed to adequately describe the fish community using fyke nets, we used the resampling procedure described in Bonvechio et al. (2009). This analysis was conducted separately for each lake, each resample consisting of a single fyke net sample from the 50 that composed the full data set. For each sample size, we resampled, without replacement, the full data set 1,000 times, and for each resample we calculated the community metrics. These metrics were then expressed as a ratio of the pooled lake value (i.e., with all 50 samples combined) and averaged over the 1,000 values. Our target sample size was equal to the minimum number of samples needed to come within 10% of the pooled lake value, on average, for species diversity and evenness. In these analyses, we included Simpson’s evenness index and the reciprocal of Simpson’s diversity index. We also compared the community composition between sample size and the pooled lake value, our target sample size being equal to the minimum number of samples needed to obtain average PSI and JSI values of 90%.

RESULTS

Of the 30 pairs of fyke nets set at Lake Harris for the depth placement evaluation, 2 pairs were omitted from the analyses due to Florida Gar *Lepisosteus platyrhincus* impeding the funnel, which prevented the nets from fishing during the entire night set. The mean log-transformed total catch was significantly greater for fyke nets set in shallow SB (<0.6 m) than in deep water (0.6–1 m; \( t = -3.09; \) df = 26, \( P = 0.005 \)), shallow-SB sets collecting, on average, 226 fish/set (SE, 104) versus 44 fish/set (SE, 20) in deep water (Table 2). Both deep-SB and shallow-SB sets collected the same number of species, and 79% of the species were taken in both set types. Each set type, however, provided different representations of this near-shore fish community (Table 2; Figure 2). The frequency distribution of fish groups differed significantly between depth treatments (Fisher’s exact test: \( P < 0.001 \)). The deep samples contained a larger proportion of centrarchids, cyprinids, and cyprinodontids and smaller proportion of poeciliids than the shallow sets (Figure 2).

We also compared catches for nets with different shoreline placements. Community composition generally differed between shoreline placements, although this difference was most pronounced for vegetated sites (Table 2; Figures 2, 3). In all lakes, shoreline placement (in versus out) did not significantly influence mean total catch in beach habitats (\( P > 0.05 \)), but results for vegetated sites were inconsistent. In the two most productive lakes (Harris and Santa Fe), mean total catch in vegetated habitats did not differ significantly between in- and out-sets (\( P > 0.05 \)), but significantly more fish were captured in out-sets at Lake Minneola (LSMEANS: \( t = -4.11; \) df = 36, \( P < 0.001 \)). Mean total catch was variable, coefficients of variation reaching as high as 252% (Table 2; Figure 4). Although in-sets often caught more fish than out-sets, this variability may have influenced our ability to detect significant differences among treatments. In all, in-sets collected slightly more species, ranging from 9 to 15 for beach in-sets and from 11 to 20 for vegetated in-sets; by comparison out-sets collected 7–17 species (beach) and 8–18 species (vegetated). Furthermore, the...
TABLE 2. Total catch (fish/net set) statistics for the mini-fyke-net study treatment pairs (i.e., deep versus shallow sets, in versus out for beach sets, and in versus out for vegetated sites) in three Florida lakes. The statistics are the number of net sets (N), reciprocal of Simpson’s diversity index (diversity), number of species collected (richness), percent similarity (PSI), and Jaccard’s similarity (JSI).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Lake</th>
<th>Mean</th>
<th>SE</th>
<th>CV</th>
<th>N</th>
<th>Diversity</th>
<th>Richness</th>
<th>PSI</th>
<th>JSI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep</td>
<td>Harris</td>
<td>44</td>
<td>20</td>
<td>243</td>
<td>28</td>
<td>3.35</td>
<td>25</td>
<td>53</td>
<td>79</td>
</tr>
<tr>
<td>Shallow</td>
<td>Harris</td>
<td>226</td>
<td>104</td>
<td>244</td>
<td>28</td>
<td>2.53</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Placement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beach, in</td>
<td>Harris</td>
<td>886</td>
<td>707</td>
<td>252</td>
<td>10</td>
<td>1.43</td>
<td>20</td>
<td>90</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>Minneola</td>
<td>22</td>
<td>21</td>
<td>95</td>
<td>10</td>
<td>4.09</td>
<td>9</td>
<td>66</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>Santa Fe</td>
<td>18</td>
<td>4</td>
<td>65</td>
<td>10</td>
<td>4.96</td>
<td>15</td>
<td>71</td>
<td>58</td>
</tr>
<tr>
<td>Beach, out</td>
<td>Harris</td>
<td>396</td>
<td>285</td>
<td>228</td>
<td>10</td>
<td>1.64</td>
<td>17</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Minneola</td>
<td>10</td>
<td>6</td>
<td>62</td>
<td>10</td>
<td>2.73</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Santa Fe</td>
<td>20</td>
<td>5</td>
<td>84</td>
<td>10</td>
<td>4.83</td>
<td>15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetated, in</td>
<td>Harris</td>
<td>141</td>
<td>42</td>
<td>94</td>
<td>10</td>
<td>2.90</td>
<td>20</td>
<td>32</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>Minneola</td>
<td>20</td>
<td>16</td>
<td>80</td>
<td>10</td>
<td>4.02</td>
<td>11</td>
<td>45</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Santa Fe</td>
<td>82</td>
<td>39</td>
<td>150</td>
<td>10</td>
<td>3.82</td>
<td>17</td>
<td>44</td>
<td>84</td>
</tr>
<tr>
<td>Vegetated, out</td>
<td>Harris</td>
<td>197</td>
<td>117</td>
<td>189</td>
<td>10</td>
<td>2.67</td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Minneola</td>
<td>55</td>
<td>40</td>
<td>73</td>
<td>10</td>
<td>3.53</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Santa Fe</td>
<td>31</td>
<td>6</td>
<td>59</td>
<td>10</td>
<td>5.33</td>
<td>18</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

FIGURE 3. Percentage composition of species groups collected in different mini-fyke-net deployments at Lakes Minneola and Santa Fe for in- versus out-sets in beach versus vegetated habitats.
TABLE 3. Sample size estimates for four metrics as estimated for the three Florida mini-fyke-net study lakes, where values represent the minimum number of samples needed to come within 10% of the whole lake value, on average, for values of 90% when compared with the pooled lake data set. See Table 2 for an explanation of the metrics.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Harris</th>
<th>Minneola</th>
<th>Santa Fe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diversity</td>
<td>10</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Evenness</td>
<td>27</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>PSI</td>
<td>39</td>
<td>27</td>
<td>26</td>
</tr>
<tr>
<td>JSI</td>
<td>23</td>
<td>20</td>
<td>23</td>
</tr>
</tbody>
</table>

frequency distribution of fish groups differed significantly between shoreline placements for all three lakes (Fisher’s exact test: $P < 0.001$). In general, out-sets collected active schooling species (e.g., Threadfin Shad) and cyprinids (primarily species of *Notropis*). In-sets typically collected species associated with shallow vegetated habitats at greater frequencies, in particular poeciliids (e.g., Least Killifish *Heterandria formosa* and Eastern Mosquitofish *Gambusia holbrooki*). Collection of some fishes was unique to a particular deployment method.

For our sample-size estimation, species diversity yielded the smallest values, ranging from 4 to 10 samples, whereas PSI yielded the greatest, reaching 39 (Table 3; Figure 5). Given our monitoring objectives, we suggest that a sample size of 30 would be sufficient for sampling SB fish communities within lakes using mini-fyke nets. At this sample size, all study lakes achieved target values for JSI, diversity, and evenness, and two out of three achieved target values for PSI. Still, at 30 samples, Lake Harris is estimated to achieve a PSI of 84%, on average, which is within reasonable range of our 90% target.

**DISCUSSION**

Mini-fyke nets are an attractive option for statewide monitoring, given the range in habitat types that can be encountered over a large geographic area and across multiple systems. Clark et al. (2007) effectively used mini-fyke nets in 22 floodplain lakes in Arkansas, most of which contained large amounts of woody debris. Driver et al. (2009) also noted the effectiveness of mini-fyke nets in sampling complex habitats with heavy vegetation and structure. But as with any gear, biases associated with fyke nets must be considered before they are adopted for broad-scale application in a long-term monitoring program. We evaluated the effects of different depth and shoreline placements of mini-fyke nets on catch and community composition in SB (≤1 m) habitats. We expected that depth and shoreline placements would influence fish catch in these habitats, but we assessed their applicability for the long-term monitoring program based on (1) number of species collected, and (2) total catch.

Our results show that both depth placement (shallow-SB versus deep-SB waters) and shoreline placement (in-sets versus out-sets) can significantly affect catch and the resulting characterization of fish communities in these shallow-water habitats. With all data combined, we detected 22 species at Lake Minneola, 28 at Lake Santa Fe, and 32 at Lake Harris. As has been seen in other studies, mini-fyke nets tended to collect smaller, mobile fishes (Fago 1998; Clark et al. 2007; Ruetz et al. 2007). We found that although shallow-SB sets with partially submerged nets resulted in the same species richness estimates as deep-SB sets, shallow sets collected a significantly larger number of fish. The effects of shoreline placement on total catch were inconsistent among sites, but placement appeared to play a more significant role in vegetated habitats. He and Lodge (1990) compared the effectiveness of minnow traps set at a
FIGURE 5. Resampling procedure means for estimating the sample size needed to adequately describe the fish community sampled by mini-fyke nets in Lakes Harris, Minneola, and Santa Fe. The means of the 1,000 resamples are graphed as functions of sample size for each metric, where (A) diversity and (B) evenness are expressed as ratios of the pooled lake value (i.e., with all 50 samples combined) and (C) the percent similarity index (PSI) and (D) Jaccard’s similarity index (JSI) indicate the similarity between the resampled data set and the full pooled data set.

Lake’s perimeter with that of traps set at a mid-lake location. They noted that catch rates were as much as 50 times higher at the lake’s perimeter. Overall, we found that placement had little effect on total catch. In vegetated habitats at Lake Minneola, the only instance for which we observed a difference, mean total catch was greater in the out-sets. In all lakes, however, the in-sets collected slightly more species at both beach and vegetated sites. One noteworthy observation was the collection of 10 times more Lake Eustis Pupfish Cyprinodon variegatus hubisi, an endemic species of special concern, in the in-sets than out-sets at Lake Harris, regardless of habitat type.

Large predators are often captured in entrapment gear (e.g., Wagner 1972; Rogers et al. 2003). Breen and Ruetz (2006) found that the presence of a predator did not influence catch, but longer soak times increased overall catch and probability of fish escapement. Predation inside the net was minimal and should not be considered a major concern, assuming that the capture of predators remains a rare event and does not vary greatly at a site. With both excluders in place, we encountered predators in our nets about 5% of the time; they included large salamanders Amphiuma spp., water snakes Nerodia spp., and most commonly, Florida Gar. However, during pilot work in which we only included the 5.1-cm excluder ring at the entrance of the second chamber, large predators such as American alligator Alligator mississippiensis, Bowfin Amia calva, and a variety of gars (all Lepisosteus) were regularly observed in the front chamber (Florida Fish and Wildlife Conservation Commission [FWC], unpublished data). Therefore, we recommend including both a 6.4-cm bar-mesh excluder net at the entrance of the first chamber and the 5.1-cm excluder ring at the entrance of the second chamber to prevent large predators from entering.

Although we were interested in identifying a single gear for our long-term monitoring program, every gear has limitations. Whenever possible, especially in detailed or targeted sampling, multiple gears should be used to more fully characterize the fish community (Barthelmes and Doering 1996; Fago 1998; Clark
et al. 2007). For example, in their study of 22 floodplain lakes, Clark et al. (2007), found that mini-fyke nets collected more species than seines but failed to capture all species present. In Fago’s (1998) comparison study of three gears which included mini–fyke nets, each of the sampling methods missed an average of four species per lake that another method captured. Furthermore, in a comparison with boat electrofishing and gill nets, Eggleton et al. (2010) reported that mini–fyke nets captured the largest number of unique species. With little data overlap, this gear was able to describe a component of littoral fish communities that the other gears could not. This was true in our study as well. For example, the Everglades Pygmy Sunfish \textit{Elasmobranchius evergladei} was unique to fyke-net sampling at Lake Santa Fe; the species had not been observed in littoral electrofishing samples since standardized sampling began in 2006 (FWC, unpublished data). Dissimilarity in fish assemblages caught by different gears ultimately results from inherent selectivity and efficacy of each gear in different habitats. Thus, it is apparent that multiple methods are needed to fully characterize littoral fish communities and, in particular, to maximize the detection of all species present.

In addition to highlighting the importance of standardizing factors such as soak time and gear configuration (Breen and Ruetz 2006; Fischer et al. 2010), our results demonstrate the importance of standardizing net-deployment techniques. Based on our results, for long-term monitoring of Florida’s SB (<1 m) fish communities, we recommend that mini-fyke nets be placed in shallow-SB areas (i.e., where they are not fully submersed) with the lead extending to the inshore edge of the lake (or dense vegetation). Although sampling objectives can vary over time (Marsh and Trenham 2008), our primary goal is to track trends in community metrics through time. We determined that a sampling target of 30 nets, randomly distributed along the shoreline of the lake, adequately characterized the fish community in terms of percentage composition, species richness, and species diversity. Furthermore, we recommend continued use of additional gears, including gill nets and electrofishing (Bonvechio 2009), to fully characterize fish communities in these lakes.

Although we focused specifically on Florida lakes in this study, we believe these findings are applicable to other SB systems where mini-fyke nets may be used. Because this gear can be placed in nearly any SB habitat and is effective for capturing fishes not vulnerable to other gears, it is an attractive option for inclusion in long-term monitoring programs. Statewide monitoring programs often extend over a large geographic area and incorporate systems with different habitat complexities; thus, the feasibility of deploying gear in a large range of conditions is an important factor to consider. However, every monitoring program should have its own set of defined goals, so that a statistically sound sampling design can be established (Legg and Nagy 2006). Here, we estimated sample size for our long-term monitoring program based on a suite of community descriptors, but the same approach can be used to explore other objectives and provide program-specific recommendations.

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A Semi-Automated Method for Monitoring Dam Passage of Upstream Migrant Yellow-Phase American Eels

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Abstract
Fish passage facilities at dams have become an important focus of fishery management in riverine systems. Given the personnel and travel costs associated with physical monitoring programs, automated or semi-automated systems are an attractive alternative for monitoring fish passage facilities. We designed and tested a semi-automated system for eel ladder monitoring at Millville Dam on the lower Shenandoah River, West Virginia. A motion-activated eel ladder camera (ELC) photographed each yellow-phase American Eel *Anguilla rostrata* that passed through the ladder. Digital images (with date and time stamps) of American Eels allowed for total daily counts and measurements of eel TL using photogrammetric methods with digital imaging software. We compared physical counts of American Eels with camera-based counts; TLs obtained with a measuring board were compared with TLs derived from photogrammetric methods. Data from the ELC were consistent with data obtained by physical methods, thus supporting the semi-automated camera system as a viable option for monitoring American Eel passage. Time stamps on digital images allowed for the documentation of eel passage time—data that were not obtainable from physical monitoring efforts. The ELC has application to eel ladder facilities but can also be used to monitor dam passage of other taxa, such as crayfishes, lampreys, and water snakes.

Fish passage facilities (often called fish ladders or fishways) at dams have become an important focus of fishery management in riverine systems (Schilt 2007; Roscoe and Hinch 2010). Monitoring of fish passage facilities includes estimation of passage efficiency, documentation of species composition, and determination of the counts and sizes of individuals (Roscoe and Hinch 2010; Noonan et al. 2012). An understanding of the impacts and benefits of a fish passage facility requires long-term monitoring, although Roscoe and Hinch (2010) reported that monitoring programs for many passage facilities were infrequent to nonexistent. Infrequent monitoring of passage facilities is often attributable, in part, to budgetary issues, but automated or semi-automated methods of monitoring can be used to reduce costs.

For some fish passage monitoring programs, counts and length measurements of individuals are recorded physically or with automated or semi-automated systems. Physical monitoring programs may involve trapping and counting the fish (Moser et al. 2011; Welsh and Liller 2013) or the use of trained observers to count fish from elevated viewpoints or with viewing windows (Dauble and Mueller 2000; Bowen et al. 2006). Fish lengths can be measured with a measuring board for trapped individuals or can be estimated visually for observed fishes. Automated or semi-automated fish counter designs include sonar (Braithwaite 1971), impedance (Liscom and Volz 1975), time-lapse video (Castignolles et al. 1994; Haro and Kynard 1997; Hiebert et al. 2000; Clabough et al. 2012), resistivity (Reddin et al. 1992; Smith et al. 1996; Gowans et al. 1999; Moser et al. 2011; Corbett et al. 2013), and optical methods (Beach 1978; Ewing et al. 1983; Shardlow and Hyatt 2004). Fish lengths can also be determined from some automated or semi-automated methods of fish passage monitoring (Shardlow and Hyatt 2004; Burwen et al. 2010). Given the personnel and travel costs associated with daily physical monitoring programs, automated or semi-automated systems are an attractive alternative for monitoring fish passage facilities.

In 2003, an eel ladder was installed at Millville Dam on the Shenandoah River, West Virginia, for upstream passage of American Eels *Anguilla rostrata* (Welsh and Liller 2013). From

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2004 to 2005, American Eels that used this ladder were physically counted each day (Welsh and Liller 2013). However, because this effort required a large amount of travel and field time, a semi-automated system was designed for eel ladder monitoring (Welsh 2014). The eel ladder camera (ELC) at Millville Dam takes a digital photograph of each American Eel as it passes through the eel ladder. The digital images are date- and time-stamped, which allows for a total daily count (24-h period) of eels that use the ladder as well as documentation of passage timing. The digital photographs also allow for measurement of eel TL via photogrammetric methods with digital imaging software. Our study objectives were to evaluate the accuracy and effectiveness of camera-based counts and photogrammetric length measurements of American Eels in comparison with physical counts and length measurements obtained by use of a measuring board.

METHODS

Design of the eel ladder camera system.—The ELC system consists of four main parts: a rectangular housing made from sheets of transparent thermoplastic, downspout adapters, a ramped platform, and a camera that is triggered by an infrared motion sensor (Figure 1). The lid and the floor were cut to extend beyond the distance between the two sides, which provided space to install elastic fasteners for the lid, and infrared motion sensor devices to the floor on the outside of the housing. The underside of the lid was fitted with rubberized weather stripping (2.5 cm wide × 6.4 mm thick) to ensure a watertight seal. Water-proof glue that was appropriate for use with thermoplastic and polyvinyl chloride (PVC) material was used for construction of the housing. The total length of the housing was 55.3 cm measured from the circular ends of the downspout adapters, and the inside dimensions of the housing were 11.4 cm wide × 8.9 cm high. Plastic mesh (8.4-mm mesh width) was attached to the top of the frame by using zip ties. Aluminum legs elevated the platform to 5.7 cm above the housing floor. The housing was spliced into a section of 10.2-cm, schedule-40 PVC pipe on the upstream side of the top of the eel ladder. The pipe and attached housing were sloped (10°) downward in an upstream direction. River water, which was pumped onto the bevel at the top of the eel ladder, flowed through the pipe and the attached housing. The river water within the housing flowed through the mesh ramp and underneath the mesh platform. To prevent theft
or vandalism, the section of pipe that contained the housing was enclosed inside a stainless-steel box with a lockable front door; 11.2-cm-diameter holes in the sides of the box allowed entry and exit of the 10.2-cm pipe.

The camera and infrared trigger were placed inside of the stainless-steel box. The camera system was an Olympus E-300 Evolt single-lens reflex camera (Olympus America, Inc., Center Valley, Pennsylvania) with a built-in flash and a 50-mm 1:2 macro lens. The camera was connected to an infrared motion sensor system (Phototrap, Amado, Arizona). Paired infrared motion sensors were mounted centrally (one on each side) on the extended floor outside of the housing and were directed across the mesh platform at an elevation of 6.4 mm above the mesh platform (Figure 1). The camera was positioned next to the housing and was angled upward toward a mirror that was mounted on the ceiling of the stainless-steel box. The mirror resulted in a wide photographic field of view, which was necessary given the confined space inside the box. The camera’s flash was turned on to illuminate the darkness inside the box. Digital images were recorded on a 2-GB compact flash card, necessary given the confined space inside the box. The camera’s flash was turned on to illuminate the darkness inside the box.

Counts and passage time of American Eels.—Counts of American Eels were conducted by removal and hand-counting of individuals from a net bag on the terminal upstream end of the eel ladder. Handling and counting of live American Eels proved to be a challenging task, and in some instances individual eels escaped without being counted. Camera-based counts were conducted by first downloading the images from the camera’s flash card to a computer, followed by viewing and counting the digital image of each American Eel. In a few instances, two or more American Eels were present in a single image. In some cases, multiple photographs were taken of a single American Eel, as determined based on a combination of the time stamp, comparison of body size, and the eel’s position on the mesh platform. After reaching the apex of the ladder, American Eels traveled down a PVC pipe to the ELC, and individuals were not able to swim back up this pipe to go down the ladder. To examine the accuracy of camera-based counts, percent differences were calculated between the camera-based counts and the physical counts of individuals from the terminal net bag. This comparison was done for six time periods: June 28–July 1, 2011; July 1–7, 2011; July 7–15, 2011; August 27–September 1, 2011; May 9–17, 2012; and July 12–16, 2013.

The time stamps on digital images from the ELC allowed for documentation of the times that eels passed through the ladder; passage time data are not obtainable from physical monitoring methods. Time-of-passage data were demonstrated for American Eels that passed the ladder during July 12–16, 2013, by plotting a histogram of passage time in 30-min increments.

Measurements of American Eel lengths.—To examine the accuracy of TL measurements from camera-based data, 251 American Eels were subsampled from the terminal net bag of the eel ladder on July 16, 2013. Before measurement, each American Eel was anesthetized with tricaine methanesulfonate (MS-222; 75 mg/L). The TL of each anesthetized individual was determined with three methods: physical measurement with a measuring board (TL1), photogrammetric measurement (TL2), and prediction based on linear regression (TL3). For TL1, eel TL was measured from the snout tip to the caudal end using a metric measuring board. We also placed each American Eel on the mesh platform of the ELC and used digital calipers (Mitutoyo Absolute Digimatic, Model CD-6-in CS) to measure the eel’s body width (BW1) at a location near the origin of the dorsal fin. We did not quantify measurement errors for TL1 and BW1. Using linear regression, we modeled TL1 and BW1 data to obtain a prediction equation of the form TL1 = a + (b·BW1), where a is the intercept and b is the slope. An overhead digital photograph of the eel (dorsal view) was taken while the eel was on the mesh platform. An effort was made to photograph the entire length of the eel’s body, but this was not always accomplished, particularly for larger individuals. Using simple photogrammetric methods, TL2 values were determined by digitizing via the segmented-line measurement option within ImageJ software (Schneider et al. 2012). The measurement scale for the digital image was set based on the known width of the aluminum crossbar of the ramped platform (12.7 mm). Similarly, we used the straight-line measurement option in ImageJ to measure BW (BW2) near the dorsal fin origin from the photographic image. Finally, TL3 values were predicted by inserting the photogrammetric measurements of BW (i.e., BW2) into the previously described linear regression equation. Length data were analyzed with JMP version 10.0.0 (SAS Institute, Inc., Cary, North Carolina).

Agreement and error in length measurements.—We used several approaches to compare BW2 with BW1; TL2 with TL1; and TL3 with TL1. First, we calculated the mean ± SE and the range of BW and TL from each data set. Next, concordance correlation coefficients (CCCs) from variance components were computed between BW1 and BW2, TL1 and TL2, and TL1 and TL3 (Carrasco et al. 2013) by using the Statistical Analysis System version 9.2 (SAS Institute). The CCC, a commonly used approach for assessing agreement between two measurement methods, is a standardized coefficient with a range of values from −1 (perfect disagreement) to 1 (perfect agreement; Lin et al. 2002, 2007; Carrasco et al. 2013). To aid in the interpretation of CCCs, we used descriptive pairwise plots of BW1 versus BW2, TL1 versus TL2, and TL1 versus TL3, which included a 45° reference line (Lin 1989). Lastly, error was calculated for BW2, TL2, and TL3 as simple differences: BW2 minus BW1, TL2 minus TL1, and TL3 minus TL1, respectively. Error values of BW2 were depicted graphically (y-axis) versus BW1 ordered by American Eel size (x-axis). Similarly, error values of TL2 and TL3 were depicted graphically (y-axis) versus TL1 ordered by eel size (x-axis). We also calculated the mean ± SE and ranges of error values for BW2, TL2, and TL3.
RESULTS

Counts and Time of Passage

Camera-based counts and physical counts of American Eels were compared for six time periods, and percent differences ranged from 0.0% to 16.5%. For small sample sizes, camera-based counts were consistent with physical counts: 1 versus 1 during May 9–17, 2012; 5 versus 5 during June 28–July 1, 2011; and 10 versus 10 during August 27–September 1, 2011. For larger sample sizes, camera-based counts exceeded physical counts. Percent differences between camera-based and physical counts were 11.1% (95 versus 85 eels) for July 1–7, 2011; 16.5% (177 versus 150 eels) for July 7–15, 2011; and 2.0% (1,184 versus 1,160 eels) for July 12–16, 2013. An unknown number of individuals escaped from the net bag during these three physical counts; hence, the count differences between methods were at least partially due to bias in the physical counts.

To demonstrate the ability of the ELC to document time-of-passage data, we analyzed time stamps associated with 1,184 digital images of individual American Eels that passed through the ELC during July 12–16, 2013. A frequency histogram demonstrated the nocturnal nature of American Eels and indicated a bimodal distribution, with the highest counts observed near postdusk and near predawn hours (Figure 2). The number of American Eels peaked at 117 individuals between 2200 and 2230 hours and at 111 individuals between 0400 and 0430 hours.

Total Length Measurements

Using measurements of BW1 and TL1 for 251 American Eels, we calculated the following linear regression equation: \( TL_1 = 71.15 + (16.58 \cdot BW_1) \) (SE of intercept = 4.1; SE of slope = 0.27; \( R^2 = 0.94 \), root mean square error = 15.7; Figure 3). This equation was used to predict TL3 from BW2. The mean ± SE and range of BW2 measured from the 251 individuals (14.9 ± 0.24 mm; 8.3–27.4 mm) were consistent with those of BW1 (14.8 ± 0.24 mm; 8.2–27.6 mm). The mean TL3 of the 251 individuals (317.4 ± 4.0 mm) differed by 0.7 mm from mean TL1 (316.7 ± 4.0 mm). The range of TL1 values (209.2–525.4 mm) was similar to the range of TL1 values (223–530 mm), although the minimum and maximum values for TL3 were 13.8 and 4.6 mm lower, respectively, than those for TL1.

Agreement and Error in Length Measurements

Photographs of full body lengths, which were required for TL2 measurements, were available for 236 of the 251 photographed American Eels. Although TL1 and TL3 measurements were examined for the sample size of 251 individuals (as described above), separate analyses of TL1 and TL3 from the 236 individuals were conducted to allow for direct comparison with TL2 measurements. The mean of TL2 (mean ± SE = 310.1 ± 3.5 mm) differed by 1.6 mm from mean TL1 (308.5 ± 3.5 mm) and by 0.5 mm from mean TL3 (309.6 ± 3.5 mm). Ranges were also similar for TL2, TL1, and TL3 (225.7–487.3, 223–486, and 209.2–483.5 mm, respectively). The CCCs for BW1 versus BW2, TL1 versus TL2, and TL1 versus TL3 exceeded 0.98, supporting near-perfect agreement between methods (Figure 4). However, TL2 had slightly higher agreement (based on CCC) and a lower error than TL3 when compared with TL1. Interestingly, TL2 was more precise but less accurate than TL3. A plot of TL2 error depicted a positive systematic shift (bias; Figure 5), wherein the mean of TL2 error was 1.6 mm compared with an unbiased mean of zero. Error in BW2 values relative to BW1 (i.e., BW2 – BW1) ranged from −2.2 to 1.6 mm (mean ± SE = 0.04 ± 0.05 mm). Error in TL2 values (i.e., TL2 – TL1) ranged from −4.8 to 7.1 mm (mean ± SE = 1.6 ± 0.15 mm),
FIGURE 4. Concordance correlation coefficients (CCCs) for (A) American Eel body widths (BW) obtained from photogrammetric measurements (BW2) compared with BWs measured using hand-held digital calipers (BW1); (B) TLs obtained from photogrammetric measurements (TL2) compared with TLs measured using a metric measuring board (TL1); and (C) TLs predicted from BW2 based on a linear regression equation (TL3) compared with TL1 values. Descriptive pairwise plots with a 45° reference line are used as a visual aid for interpretation of CCCs.

FIGURE 5. Error in (A) photogrammetric measurements of American Eel body width (BW2) relative to BWs obtained with digital calipers (BW1; error calculated as BW2 - BW1); (B) photogrammetric TL measurements (TL2) relative to TL measurements obtained with a metric measuring board (TL1; error calculated as TL2 - TL1); and (C) TLs predicted from BW2 based on a linear regression equation (TL3) relative to TL1 measurements (error calculated as TL3 - TL1). Distributions of error not centered on the zero reference line support measurement bias.
whereas error in TL3 (i.e., TL3 − TL1) ranged from −29.5 to 30.4 mm (mean ± SE = 0.74 ± 0.61 mm).

DISCUSSION

The ELC was an effective semi-automated method for monitoring dam passage of American Eels and was inexpensive relative to the costs of daily physical monitoring. First, the ELC was effective at photographing each passing American Eel, which eliminated the need for costly physical counts. Second, TLs of eels were accurately predicted from a linear regression equation based on photogrammetric measurements of BW (BW2), thus eliminating the need to handle and anesthetize American Eels for board measurements of TL. Lastly, the time stamps on digital images allowed for documentation of eel passage time; such data were unobtainable from physical monitoring efforts.

Passage Counts

The ELC has several desirable qualities as a fish counter. First, photographs are taken only when an American Eel passes through the ELC housing; thus, photographs may require less editing than time-lapse video, for which editing time often requires sorting through blank frames (Hatch et al. 1998). Second, the ELC overcomes issues with water turbidity because passing eels are ramped up onto a mesh platform and are photographed above the water level. The ramped mesh platform of the ELC is necessary because American Eels in the Shenandoah River often move upstream during high flows associated with turbid water conditions (Welsh and Liller 2013). Water turbidity reduces the effectiveness of some video and optical monitoring systems (Bizzotto et al. 2009). In addition to turbidity, higher river discharges can also decrease the efficiency of some counters due to increases in water depth, water velocity, and turbulence (Thorley et al. 2005). The water volume passing through the ELC is controlled by a water pump; therefore, water depth, velocity, and turbulence are constant within the thermoplastic housing and do not affect the ELC’s efficiency during high river discharges.

We have also observed several less-desirable qualities of the ELC as a fish counter. First, double-counting is possible if an American Eel loiters on the ramp platform, resulting in multiple photographs of the same individual. We suspect that some American Eels hesitated during passage through the ELC housing owing to the camera flash. However, multiple images of a single eel are easily determined based on a combined assessment of the time stamp, individual body size, and the eel’s position on the platform. Second, in a few rare cases, a large number of American Eels (>10) passed through the housing at the same time, producing some uncertainty in the total count. However, the semi-automated nature of the ELC is advantageous in such cases because the photo can be examined closely to sort out the number of individuals, whereas some automated systems are not able to count the passage of more than one fish simultaneously (Dunkley and Shearer 1982; Shardlow and Hyatt 2004). Third, the ELC does require periodic maintenance. We serviced the ELC at 2-week (14-d) intervals; servicing included cleaning the algae from the inside of the housing and downloading images from the flash card.

Total Length Measurements

The TLs of American Eels from photogrammetric measurements (TL2) and as predicted from the linear regression equation (TL3) were in close agreement with lengths obtained by using the metric measuring board (TL1). This finding validated the ELC-based methods of TL measurement, providing confidence for using the ELC as a replacement for physical measurement of TLs. In comparing measurement methods, we designated BW1 (caliper measurement) and TL1 as the “true” values, and we assumed that BW1 and TL1 were measured without error. Although measurement error in fish TL is common (Bunch et al. 2013), we believe that measurement error for the serpentine body form of anesthetized American Eels is minimal compared with the error in measurements of other fish body forms.

Photogrammetric measurements and predictions of TL were not possible for use with all individuals passing through the ELC housing. In some instances, an American Eel was photographed on its side, or only its caudal end was photographed; hence, photogrammetric measurements of BW were not possible in those cases. As previously described, in a few cases a large number of American Eels were observed to pass through the housing at the same time; this would make it difficult to obtain BW measurements for predictions of TL. Our results demonstrated that precision in TL measurements could be increased by using photogrammetric measurements of TL from photographs of the full body length as opposed to predicting TL from BW in a linear regression equation. However, the housing of our current ELC design would have to be adjusted (i.e., lengthened) to consistently capture the full body lengths of passing American Eels.

Accuracy, Precision, and Error in Photogrammetric Measurements

The TL2 measurements were more precise than TL3 but were less accurate and biased. Close agreement between TL3 and TL1 resulted, in part, from the strong linear regression relationship (R² = 0.94) between BW1 and TL1. In addition, photogrammetric measurements of BW (BW2) accurately represented the measurements from calipers (BW1). Photogrammetric measurements of TL (TL2) were only possible when the eel’s body was captured fully in the digital image. There are several possible explanations as to why TL2 was more precise but less accurate than TL3. One would expect precise estimates of TL2 because the photogrammetric measurements were obtained directly from photographs. For TL3, measurements were predicted from BW2, so individual variation in BW–TL relationships is reflected in the TL3 values. The positive systematic shift (bias) in TL2 error, where the mean error was 1.6 mm compared with an unbiased mean of zero, represented inaccuracy in the TL2 measurement relative to TL1. The bias in TL2 may have resulted from
inaccurate starting points of photogrammetric measurements on some individuals with protruding lower jaws. Protrusion of the lower jaw is probably less pronounced during board measurements because the tip of the eel’s snout is pressed to the vertical base at the zero point of the measuring board. Some TL measurements may have included the tip of the lower jaw, which would have resulted in slightly longer TL values. Alternatively, measurement error in TL may be associated with barrel distortion at the edges of the digital images or with optical aberrations of the lens (Mallon and Whelan 2007; Stamatopoulos and Fraser 2011; Alemán-Flores et al. 2014). Regardless of the cause, a systematic shift (inaccuracy) in a measurement can usually be fixed with calibration (Barnhart et al. 2007); however, in our case, increased consistency and accuracy in the starting and stopping points of photogrammetric measurements would likely remove this bias. Furthermore, the current ELC design at Millville Dam relies primarily on predicted TLs (TL) rather than photogrammetric measurements (TL) because only a small proportion of eel images include full body lengths.

The ELC was an effective method for monitoring the passage of American Eels at Millville Dam and was inexpensive relative to daily physical monitoring efforts. The ELC system costs less than US$1,500. Field sampling with the ELC required 1 d per 14-d time period compared with 14 d (including weekends) to obtain daily physical counts and measurements of TL with a measuring board. Processing of ELC data required examination of digital camera images, counts of those images, and measurements of images by using image analysis software. The amount of employee time that was required to process ELC data from a 14-d time period depended on the total number of images but never exceeded 2 d. Thus, for a 14-d period, employee time for the ELC method (3 d; i.e., 1 d of travel plus up to 2 d of data processing) was equivalent to approximately 21% of the time required for physical monitoring (14 daily site visits). During a 14-d period, travel time for the ELC method (1 d) was equivalent to approximately 7% of the time needed for daily physical sampling.

Precision of TL measurements could be improved by increasing the size of the current ELC housing, which would allow for full-body photographs and photogrammetric measurements of all passing American Eels. However, TL measurements were accurately predicted from photogrammetric measurements of BW, providing a suitable alternative to photogrammetric measurements of TL and supporting the applicability of the current ELC system for monitoring American Eel passage at facilities where larger monitoring equipment cannot be used due to space limitations. Given that passing individuals are ramped onto a mesh platform above the water level, the current design is not appropriate for monitoring the passage of most fish species. However, the ELC would likely work well at other eel ladder facilities. The ELC may also be applicable for monitoring the passage of lampreys (Petromyzontidae) at dams. Additionally, aquatic snakes and crayfishes can be monitored using this method, as individual northern water snakes Nerodia sipedon and virile crayfish Orconectes virilis were photographed by the ELC at Millville Dam.

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Managing a Marine Stock Portfolio: Stock Identification, Structure, and Management of 25 Fishery Species along the Atlantic Coast of the United States

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ARTICLE

Managing a Marine Stock Portfolio: Stock Identification, Structure, and Management of 25 Fishery Species along the Atlantic Coast of the United States

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Abstract

In this review, stock identification methods used, resulting stock numbers and boundaries, and assessment and management context were explored for all 25 species managed by the Atlantic States Marine Fisheries Commission (ASMFC). This included invertebrates and vertebrates distributed between Maine and Florida, with a few species ranging across all these states and some ranging into the Gulf of Mexico and the Canadian Maritimes. The effects of larval dispersal or mixing of adults in the marine environment were evident. Marine and catadromous spawners were recognized and treated as a unit stock (e.g., northern shrimp *Pandalus borealis*, American Eel *Anguilla rostrata*, Atlantic menhaden *Brevoortia tyrannus*, Bluefish *Pomatomus saltatrix*, Tautog *Tautoga onitis*), a metapopulation (American lobster *Homarus americanus*, Atlantic Herring *Clupea harengus*), or two stocks, north and south of Cape Hatteras, a major biogeographic boundary, (Black Sea Bass *Centropristis striata*, Scup *Stenotomus chrysops*, Red Drum *Sciaenops ocellatus*, Summer Flounder *Paralichthys dentatus*). Estuarine and anadromous spawners were structured and managed at a finer spatial scale (horseshoe crab *Limulus polyphemus*, Atlantic Sturgeon *Acipenser oxyrinchus*, American Shad *Alosa sapidissima* and the river herrings Blueback Herring *A. aestivalis* and Alewife *A. pseudoharengus*, and Spotted Seatrout *Cynoscion nebulosus*). A broad suite of stock identification methods have been applied to ASMFC species and reviewed here in five categories: life history traits, other phenotypic traits, genetic traits, natural marks, and applied marks. An interdisciplinary mix of methods has been achieved for a few species (Striped Bass *Morone saxatilis*, Winter Flounder *Pseudopleuronectes americanus*), but only a few or no stock identification methods have been applied to others (Spiny Dogfish *Squalus acanthias*, Hickory Shad *A. mediocris*, Spot *Leiostomus xanthurus*, Spanish Mackerel *Scomberomorus maculatus*). Clinal phenotypic variation has contributed to several long-standing debates about stock structure; some of these have been recently reevaluated as a unit stock (Atlantic Croaker *Micropogonias undulatus*, Weakfish *Cynoscion regalis*), and others are still debated. For some ASMFC species, other priorities (e.g., bycatch) dominate the uncertainty of the assessment or management process. Otherwise, stock identification remains a research priority for most of these species. Continued research of this subject should consider (1) research priorities tabulated by ASMFC review panels, (2) strategic use of interdisciplinary stock identification methods, (3) use of experiments or reaction norms to separate phenotypes from genotypes, (4) genetic surveys at a seascape scale, (5) demonstration of contingent (nongenetic) structure and its implications for management, and (6) simulation modeling. Obstacles to adopting finer-scale structure into assessments or management of ASMFC fisheries include: (1) multiple stock units are apparent but boundaries are not clear, (2) monitoring requirements for smaller areas or for mixed-stock catches are not cost effective, or (3) mixing rates within a metapopulation or across biogeographic boundaries are poorly described.

Fisheries exploit stocks of fish, and historically, fishery stock units were defined by patterns in fishing activity alone. This created, and in many cases continues to create, mismatches of biological processes and management action (Halliday and Pinhorn 1990; Lear 1998; Waldman 2005a). Recognition of a “harvest stock,” or similar terms, where the effects of exploitation on

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one stock is independent of another stock, is an improvement in terminology but does little to clarify the biological basis of a stock (Hammer and Zimmermann 2005). A stock should comprise all age-classes, be self-reproducing, and express at least one distinguishing biological feature (Lebedev 1967). Phenotypic information has a long history of use in defining stocks, particularly the use of vital rates to measure and manage independent population units, but additional work is often required to distinguish a genetic versus ecophenotypic basis for such variation (Secor 2005; McBride 2014). The genetic basis for defining stocks has broad utility for fisheries management, but strictly genetic definitions are confounded by low levels of gene flow (i.e., straying), recent colonization events, poor sampling coverage, low resolution of pioneering genetic methods, and difficulty of incorporating purely genetic data into the management process (Grunwald et al. 2008; Waples et al. 2008; Reiss et al. 2009). One existing definition that captures a modern synthesis of both phenotype and genotype is “a group of organisms whose demographic/genetic trajectory is largely independent of other such groups” (Waples 1998). Herein, I use the term stock in this modern context to recognize it as a biological population that is subject to the effects of fishing.

Defining a stock’s spatial boundaries is the first step of the assessment process (NRC Committee on Fish Stock Assessment Methods 1998). Misspecification of the number of stocks can obscure the stock–recruitment relationship (Frank and Brickman 2000). Incorrect stock boundaries or poorly known mixing rates confound estimates of immigration and emigration (Hammer and Zimmermann 2005). When multiple stocks are fished as a simple aggregate, not only is the measurement of stock dynamics confounded, smaller stocks are at risk of overexploitation or extinction (Ricker 1958; Hilborn 1985; Smedbol and Stephenson 2001; Reich and DeAlteris 2009). Loss of genetic diversity is a concern, particularly with regard to small stocks for which there is typically insufficient data to assess their status (Slaney et al. 1996; Olsen et al. 2008; Hu and Wroblewski 2009). Regardless of genetic structure, preserving phenotypic stock or contingent structure can enhance stock productivity, resilience, and stability (Secor et al. 2009; Pettigas et al. 2010; MacCall 2012).

In response to the increasing demands for identifying stock units, development of pertinent methods has steadily progressed (Cadrin et al. 2005, 2014a). Traditional methods, such as the use of life history parameters, morphometrics, or parasites as natural markers, are still part of the toolbox (Baldwin et al. 2012; McAdam et al. 2012; Zischke et al. 2013; Cadrin et al. 2014a). New technologies, such as otolith microchemistry, single-nucleotide polymorphisms, or electronic tags, have greatly expanded the toolbox (Hodgins-Davis et al. 2007; Rooker et al. 2007; Walther et al. 2008; Cadrin et al. 2014a). Experimental methods investigating reaction norms are becoming more feasible (Swain et al. 2005; Conover and Baumann 2009; Heino 2014), and a suite of methods exists for analyzing mixed-stock fisheries data (Prager and Shertzer 2005). In a growing number of cases, an interdisciplinary set of methods or simulation modeling has improved confidence in our understanding of stock structure (Coyle 1997; Abaunza et al. 2008, 2014; Cadrin et al. 2014b; Kerr and Goethel 2014).

Herein, I review the marine stock portfolio managed by the Atlantic States Marine Fisheries Commission (ASMFC) (ASMFC 2013a, 2013b, 2013c). The ASMFC operates under the authority of the Atlantic Coastal Fisheries Cooperative Management Act to develop fishery management plans (FMPs) for 25 invertebrate and finfish species that reside in coastal waters along the U.S. east coast from Maine to Florida (e.g., Richards and Rago 1999; Table 1; Figure 1; Table A.1 in the Appendix). Both traditional and advanced stock identification methods have been applied to this marine stock portfolio. Initial FMPs of these species-based stock structure determinations were developed from extensive literature reviews, and the ASMFC continues to recognize the importance of this information by requesting and incorporating new research into stock structure determinations. Several types of stock structure are evident within this species portfolio. Most of these species are distributed across more than one major biogeographic region (Acadian, Virginian, and Carolinian: Briggs 1974; Ayvazian et al. 1992; Gabriel 1992) among a mosaic of bottom types or within a hydrodynamic milieu. These distributions may either induce connectivity between regions or promote disjunct stock structure along a latitudinal cline. Conversely, many ASMFC-managed species spawn in the open ocean, migrate seasonally in marine waters, and show little or no evidence of genetic structure. In over a third of the cases, these conditions support a single stock unit. Continued research is likely to reveal additional stock complexity, either in the underlying genetic structure or in the make-up of the conditionally based (nongenetic) contingents. Although challenges exist for uncovering and applying such new information into assessment and management, further evolution in research and application is still likely because of ongoing advances in the resolution or cost-effectiveness of stock identification methods, as well as because of our expanding awareness of the genetic and phenotypic complexity of stock structure and its value for the management of sustainable fisheries.

This review addresses these claims in seven sections. The first (Methods) provides an outline of how I reviewed the literature, which is followed with a brief summary of relevant terms and concepts of what stock structure looks like in open marine systems (Background). The largest section (Species Synopses) uses a standard format to state the recognized stock structure, summarize the supporting evidence, and highlight specific issues of each of the 25 ASMFC species. The next three sections are critiques. The first (Review of Methods Used) is of stock identification methods applied to ASMFC species, using the rubric of Cadrin et al. (2005); the second (Stock Structure Types) is of the diversity of stock structure among ASMFC species; and the third (Managing Stock Structure) is a perspective on the accomplishments and challenges ahead for managing these interjurisdictional fisheries. This assemblage provides a dynamic set of
FIGURE 1. The Atlantic coast of the United States. Individual coastal states are outlined and identified (FL, Florida; GA, Georgia; SC, South Carolina; NC, North Carolina; VA, Virginia; MD, Maryland; DE, Delaware; NJ, New Jersey; NY, New York; CT, Connecticut; RI, Rhode Island; MA, Massachusetts; NH, New Hampshire; ME, Maine). Other prominent locations mentioned in the text are identified, and the 50-fathom isobath is drawn to indicate the edge of the continental shelf.
TABLE 1. The interaction between spawning grounds and stock structure for 25 fishery species managed by the Atlantic States Marine Fisheries Commission. See Table A.1 for more complete taxonomic information and supplemental information about species ranges, life cycles, stock structure, methods for stock identification, and research and management status.

<table>
<thead>
<tr>
<th>Stock structure type</th>
<th>Marine</th>
<th>Estuarine</th>
<th>Freshwater$^c$</th>
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<tr>
<td>Unit</td>
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<tr>
<td></td>
<td>Northern shrimp$^a$</td>
<td>Weakfish</td>
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<td>Spiny Dogfish$^a$</td>
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<td>American Eel</td>
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<td>Atlantic Croaker</td>
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<td>Tautog</td>
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<td>Spanish Mackerel</td>
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<td>Metapopulation</td>
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<td>American lobster</td>
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<td></td>
<td>Atlantic Herring</td>
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<tr>
<td>Multiple populations (latitudinal)$^b$</td>
<td>Black Sea Bass</td>
<td>Horseshoe crab</td>
<td>Atlantic Sturgeon</td>
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<tr>
<td></td>
<td>Scup</td>
<td>Spotted Seatrout</td>
<td>American Shad</td>
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<td></td>
<td>Red Drum$^d$</td>
<td>Winter Flounder$^d$</td>
<td>Hickory Shad</td>
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<td></td>
<td>Summer Flounder</td>
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<td>Blueback Herring</td>
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</table>

$^a$A unit stock in U.S. waters only; managed as separate stocks internationally.

$^b$Marine spawners have a disjunct stock boundary near Cape Hatteras; the multistock estuarine and freshwater spawners have finer-scale structure (i.e., regional to river-specific).

$^c$Anadromous fishes.

$^d$Spawns both in estuaries and nearshore marine.

case studies to explore the continued value of traditional stock identification methods, the uptake of new methodologies, the diversity of stock structure types in marine fishes, and the application of this information to manage these fisheries sustainably. A concluding section (Summary) includes recommendations for future research directions.

METHODS

To write this review, I have relied on my own experience (∼30 years) of working with marine and diadromous fishes along the North American east coast, from the Gulf of Maine to the Gulf of Mexico, including experience as a state of Florida representative on ASMFC’s technical committees. I also consulted with several others for discussion and feedback (see Acknowledgments).

In searching the literature, I started with the ASMFC website, where I reviewed the materials available under “Fisheries Management” (ASMFC 2013a). I also integrated into this review two recent summaries of stock status and research priorities (ASMFC 2013b, 2013c). The methods used to investigate each species’ stock structure have been individually reviewed at one time or another as part of the original FMPs (ASMFC 2013a; MAFMC 2013). These documents are important historical records that provide details, and occasionally corrections, of original studies and changing approaches and interpretations about stock structure. In a multispecies, multimethod review such as this I can only summarize this information (Tables 1, A.1) and leave the specifics to be found in these supporting documents.

Finally, I reviewed selected examples from related books, namely Cadrin et al. (2005), Kritzer and Sale (2006), and Cadrin et al. (2014a). Some papers were easily found, whether in the gray literature (e.g., Cadrin et al. 2004; NEFSC 2013) or the peer-reviewed literature (e.g., Waldman et al. 1988, 1997; De-Celles and Cadrin 2011). Many papers were only discovered by using an iterative approach with Boolean logic when searching the web (Eells et al. 2012).

BACKGROUND

The species managed under the authority of the ASMFC are distributed across a wide latitudinal range (Figure 1; Table A.1), so they are affected by a range of environmental conditions and geologic history. Average winter (February) temperature increases from 2.8°C (Eastport, Maine; 44.5°N) to 22.8°C (Miami Beach, Florida; 25.5°N), approximately 1°C per 1°N (Figure 2). This temperature gradient is discontinuous, particularly near the coast, where it is disrupted by capes that create biogeographic boundaries (Briggs 1974; Friedland and Hare 2007; Briggs and Bowen 2012). Seasonal temperature fluctuations within the Middle Atlantic Bight are
among the most extreme in the world (\sim from http://www.nodc.noaa.gov/dsdt/cwtg/. Beach, Florida (FL). See Figure 1 for locations. Data are for 2012, downloaded from http://www.nodc.noaa.gov/dsdt/cwtg/.

FIGURE 2. Seasonal temperature gradient along the Atlantic coast of the United States. Seasonal temperatures from January (J) to December (D) are plotted for Eastport, Maine (ME); Portsmouth Harbor, New Hampshire (NH); Woods Hole, Cape Cod (CC), Massachusetts; Lewes, Delaware (DE); Cape Hatteras (CH), North Carolina; Savannah Beach, Georgia (GA); and Miami Beach, Florida (FL). See Figure 1 for locations. Data are for 2012, downloaded from http://www.nodc.noaa.gov/dsdt/cwtg/.

Given this environmental backdrop and life history variation, several types of stock structure may be expected among these species. The simplest is that of a single or unit stock. A unit stock would be perpetuated by high rates of mixing (i.e., gene flow) within the stock area. This may occur at one life stage, such as by dispersal of an early life stage, or by large home ranges and random mating by adults, or by more than one life stage (Hare 2005; McBride 2014). Dispersal of early life stages or straying by adults can also lead to vagrancy, an inability to return to spawning grounds to mate (Sinclair 1988; McBride and Able 1998; McBride and Horodysky 2004). Migrants from different stocks may periodically mix, such as on feeding grounds, which may overlap with the fishing grounds and thereby complicate stock identification or assignment of stock-specific landings (McQuinn 1997; Rooker et al. 2007). At a more complex level, a metapopulation may exist, resulting in demographic or phenotypic heterogeneity but genetic homogeneity. In a metapopulation, local populations reside in specific habitat patches and interpatch connections exist but are not so strong as to negate local population dynamics (Sale et al. 2006). Acceptance of a metapopulation structure shifts the emphasis on managing total spawning biomass to maintaining some level of biomass in each spawning component.

Physical barriers within a species’ geographic range can lead to stock structure. This can be expected at a macroscale, particularly as related to prominent points along the coast (i.e., capes), which are typically associated with abrupt changes in hydrography and environmental conditions. Along the east coast of the United States, major faunal breaks occur at Cape Canaveral (Florida), Cape Hatteras (North Carolina), and Cape Cod (Massachusetts) (Figure 1). Stock boundaries can also occur at a smaller scale. For example, Cunningham et al. (2009) described an isolation-by-distance pattern among Pacific Cod Gadus macrocephalus extending from Washington State to the Aleutian Islands; however, in fjords, which represent sharp barriers to migration and larval dispersal, Pacific Cod were genetically distinct.

Life history or behavioral differences can also contribute to stock structure (Sherwood and Grabowski 2010). When individuals have a strong association with a specific spawning ground, either remaining there (indolence) or returning there after a dispersed or migratory period (philopatry), stocks can arise from reproductive isolation. Philopatry can arise from natal homing, which is caused by imprinting on a specific environmental cue experienced when young, or by repeat homing, which is facilitated by young fish learning spawning routes from older fishes (Fromentin and Powers 2005; MacCall 2012). Differences in spawning location and timing can maintain reproductive isolation even for fish within the same river system. This is evident in the genetic discreteness of nonanadromous and anadromous forms of Oncorhynchus mykiss in the same river of Oregon (Zimmerman and Reeves 2000), or between odd and even year spawning stocks of the biennial Pink Salmon O. gorbuscha (Beacham et al. 2012). In the open marine environment, subtle behaviors related to depth preferences in spawning habitat can contribute to fine-scale structuring within the spawning ground of Icelandic (Atlantic) Cod G. morhua (Grabowski et al. 2011). These behaviors do not need to be genetically determined (Secor 2005). A conditional response, such as growth rate, may determine whether an individual becomes resident or migratory among diadromous species (Thorpe 1987; Jonsson and Jonsson 2003). Within Chesapeake Bay, the initial physiological
condition of White Perch *Morone americana* had permanent consequences that affected their behavior, growth, and survival as adults, resulting in a portion of the population residing in freshwater and another portion migrating between natal, freshwater habitats and brackish habitats (Kerr et al. 2009). Model simulations revealed that the resident contingent contributed mostly to population stability whereas the dispersive contingent contributed mostly to productivity and resiliency (ability to rebuild from an overexploited state; Kerr et al. 2010a).

Ready solutions to define, identify, and monitor stock structure are much needed for sustainable management. Stock structure can be dynamic, even lost, as many populations become overfished (Ames 2004; Wright and Trippe 2009; Fowler 2011). Stock boundaries may shift in response to environmental change (Nye et al. 2009). Mismatches between genetic units and fishery units persist (Laikre et al. 2005; Reiss et al. 2009), and a better understanding of phenotypic variability within and between stocks is necessary to determine fishery yields, use maturity data to calculate spawning stock size, or understand how conditional or culturally transmitted life history traits contribute to stock productivity, resilience, or stability (Petitgas et al. 2010; MacCall 2012). The following review of species, methods, and patterns of stock structure captures in time the practice of stock structure identification and its application in regard to fishery management of 25 species along the U.S. east coast.

**SPECIES SYNOPSES**

The following species synopses are in phylogenetic order. Each synopsis briefly describes (1) a species’ geographic range, (2) a statement about its stock structure, (3) data supporting its stock structure, (4) how such information affects stock assessment and management, and (5) what research priorities remain in relation to stock structure (see also Table A.1).

**Invertebrate Species**

Horseshoe crab *Limulus polyphemus* is distributed from the Gulf of Maine to the Gulf of Mexico. Habitat use, genetics, size, and thermal tolerance vary with latitude, and in Atlantic waters, four stocks (southeast, Delaware Bay, New York, and New England) are recognized. Horseshoe crabs reside year-round in estuaries of the Gulf of Maine (Moore and Perrin 2007; Schaller et al. 2010), so they do not migrate out into the gulf (Botton and Ropes 1987). Farther south, horseshoe crabs are distributed both within estuaries and on the continental shelf (Botton and Ropes 1987; Swan 2005). A survey of microsatellite DNA loci reveal an isolation-by-distance pattern (King et al. 2005), with a strong break near northeastern Florida (Saunders et al. 1986). Delaware Bay and the Chesapeake Bay, the two most important spawning areas, are genetically distinct (Pierce et al. 2000). Horseshoe crabs spawn in estuaries, laying eggs in sand (Leschen et al. 2006), and their larvae have limited dispersal even within the estuary (Botton and Loveland 2003). Smaller adults are found at both the northern and southern extremes (Riska 1981; Sekiguchi and Shuster 2009), and horseshoe crabs from southern Florida cannot survive temperatures typical of Massachusetts, and vice versa (Mayer 1914; Sekiguchi and Shuster 2009). Abundance, harvest pressure, population trends, and regulations vary greatly among the regions (ASMFC 1998b; Smith et al. 2009). The Delaware Bay population is of particular concern because of an ecological link between horseshoe crab spawning and shorebird migrations (Smith et al. 2006), and stock discrimination is an ongoing concern because at least a portion of the landings in several neighboring states can be attributed to this bay (ASMFC 2012b). Sampling near Delaware Bay, Cape Hatteras, and in southern Florida is still a research priority to determine stock boundaries and mixing dynamics (King et al. 2005; ASMFC 2009b, 2013c).

American lobster *Homarus americanus* is distributed as a stock complex in U.S. and Canadian waters, representing a metapopulation (Fogarty and Botsford 2006). Three stocks (Gulf of Maine, Georges Bank, and southern New England) are recognized in U.S. waters, but more are plausible, especially with regard to inshore and offshore components of these populations (ASMFC 2010a). Regulations are applied to nine smaller management areas (ASMFC 2013b). Stocks are defined by migration patterns, location of spawners, and the dispersal and transport of larvae. There is evidence of morphological and genetic differences between stock areas, as well as differences between coastal and offshore areas. In some stock areas, coastal lobsters are smaller (Chen et al. 2006), move less (Haakonsen and Anoruo 1994), have a distinct morphology (Cadrin 1995), and are genetically distinct (Crivello et al. 2005; Hodgins-Davis et al. 2007); these patterns are less evident in Canadian waters (Hare 2005). Patterns of larval dispersal suggest that the coastal and offshore components are not independent (Hare 2005), and there are transient and resident lobsters within stock areas (Geraldi et al. 2009). Fogarty and Botsford (2006) summarized the evidence indicating that inshore areas, where fishing effort is highest, receive recruitment subsidies from offshore areas. Recently, a lower abundance reference point was set for the southern New England stock, because environmental changes in this region are predicted to impede efforts to rebuild this stock to historical levels (ASMFC 2010a, 2013b). One stock-related priority still recognized by the ASMFC is to align the American lobster management areas with the areas used to aggregate landings (ASMFC 2013c).

Northern shrimp *Pandalus borealis* is managed as one stock (Gulf of Maine) in U.S. waters (ASMFC 2011a). This is the southernmost stock of a species that is also managed in Canadian waters and throughout the north-central and northeastern North Atlantic Ocean (Fogarty and Botsford 2006; Richards et al. 2012). There is little evidence of genetic structure in Canadian or northeastern Atlantic waters (summarized by Fogarty and Botsford 2006), but the timing of shrimp spawning in different areas suggests local adaptation, because this timing matches the different regional peaks in food suitable for larvae (Koeller et al. 2009). Worm and Myers (2003) reported large-scale coherence
in population biomass trends among northern stock areas, but biomass of the Gulf of Maine stock fluctuates independently of these northern stocks, suggesting a lack of connectivity between the U.S. Gulf of Maine and other stocks. Specific biomass declines in the Gulf of Maine are associated with notably warmer temperatures in the 1950s and in the past decade (Shumway et al. 1985; Richards et al. 2012). Understanding the mechanistic links between climate and northern shrimp recruitment is the focus of most research priorities for this species rather than stock structure (ASMFC 2013b, 2013c).

**Dogfish, Sturgeon, Eel**

Spiny Dogfish *Squalus acanthias* is distributed worldwide on continental shelves, at boreal and temperate latitudes. In the western North Atlantic Ocean, it is most abundant from Nova Scotia to Cape Hatteras (Stehlik 2007; Veríssimo et al. 2010). The ASMFC comanages Spiny Dogfish as a unit stock together with the Mid-Atlantic Fishery Management Council (MAFMC) and the New England Fishery Management Council (NEFMC; ASMFC 2002a, 2012a). No genetic differentiation is evident along the North American east coast (Annand and Beanlands 1986; Campana et al. 2007; Veríssimo et al. 2010), but the evidence is either restricted to allozymes or to global phylogeographic surveys that have not sampled intensively along the U.S. east coast (McCauley et al. 2004). This suggests that additional work with more information-rich genetic markers at a seascape level is warranted. In an extensive review of tagged fish, Campana et al. (2007) observed a mixing of Canadian and U.S. Spiny Dogfish in the Gulf of Maine. They proposed a metapopulation structure with at least one sink population in Canada. An ongoing mark–recapture study shows extensive mixing of both sexes between the Gulf of Maine, Georges Bank, and the Middle Atlantic Bight (Northeast Fisheries Science Center, National Marine Fisheries Service, unpublished data). Campana et al. (2009) reported that Spiny Dogfish has low reproductive potential in Canadian waters, so ecophenotypic differences along a latitudinal gradient are possible. Continued research of genetic stock structure, migration patterns, and mixing rates remains a high priority research area (ASMFC 2013c).

Atlantic Sturgeon *Acipenser oxyrinchus* is anadromous and spawns in rivers from eastern Canada to Florida (Waldman et al. 2002; McBride and Matheson 2011). Five population segments are presently recognized, but as few as a single to as many as nine distinct population segments have been proposed (ASMFC 1998a; Grunwald et al. 2008; Kocik et al. 2013). There is clinal variation in growth and age at maturity (Smith 1985; Smith and Clugston 1997), and most rivers contain genetically distinct populations (Wirgin et al. 2000; Waldman et al. 2002; Grunwald et al. 2008). They are philopatric, but during the marine phase, tagged fish are known to move considerable distances away from natal systems and straying is evident (Dovel and Bergstrom 1983; ASMFC 1998a; King et al. 2001). All five population segments are listed as endangered or threatened in the USA, and the species is managed under a moratorium on directed fishing from Maine through Florida (Kocik et al. 2013). Research priorities related to stock structure are focused on regional stock enhancement by aquaculture or discrimination of stocks in nontarget bycatch (ASMFC 2013c).

American Eel *Anguilla rostrata* is catadromous and inhabits aquatic habitats of the North American Atlantic coast from Canada to Florida, as well as Gulf of Mexico drainages (Tesch 1977; Vélez-Espino and Koops 2010; McBride and Matheson 2011). American Eel is managed as a unit, coastwide stock from Maine to southern Florida, with the future potential for joint management with Gulf of Mexico and Canada (ASMFC 2000). Although the classical view is that *Anguilla* species reside in freshwater habitats for many years, there is mounting evidence of contingents arising from partial migration, where a portion of the stock moves between freshwater and estuarine habitats, and other individuals may not even leave marine habitats (Secor 2005; Jessop et al. 2008). There is a latitudinal gradient in size, age, and reproduction (Oliveira 1999), but this appears to be driven by productivity gradients and distance from the spawning grounds (Vélez-Espino and Koops 2010). This species’ genetic structure appears to be persistently panmictic (Tseng et al. 2006; Gagnaire et al. 2012), and stock structure research is not listed as a priority (ASMFC 2013c). The chronic, depleted state of this fishery species has led to a petition to list it as endangered, and most research priorities are focused on improving fishery, habitat, and life history information (ASMFC 2013b, 2013c).

**Shad and River Herrings**

Shad and river herrings (*Alosa* species, subfamily Alosinae) are all anadromous. Data collection and assessment are heavily biased towards American Shad *Alosa sapidissima*, where regional stocks are recognized and state-specific assessments have been completed (ASMFC 2007). Historically, American Shad was found in about 130 rivers, but it is found in only about half (70) of these today as a result of habitat loss (Limborg et al. 2003), and its fishery status is considered depleted (ASMFC 2013b). Interpretation of genetic stock structure of shad and river herrings is confounded by the common, historic practice of stock transfers between rivers and between states. In U.S. waters, genetic structure of American Shad is apparent at only the regional scale (Nolan et al. 2003; Hasselman and Limburg 2012), whereas in Canada, where artificial stock transfers were not common, genetic population structure is evident at the river scale (Hasselman et al. 2009, 2010). American Shad exhibit philopatry (Hollis 1948; Melvin et al. 1986; Walther et al. 2008), which would support river-specific populations. Latitudinal variations in life history characteristics are evident from Canada to Florida (Leggett and Carscadden 1978; Limburg et al. 2003); meristic and morphometric parameters also vary with latitude (Melvin et al. 1992). Research priorities related to stock structure emphasize using native broodstock when restoring stocks by aquaculture to preserve genetic integrity and the potential for stock-specific adaptive phenotypes (ASMFC 2013c).
Hickory Shad *A. mediocris* is distributed from the Gulf of Maine to Florida but appears to spawn only as far north as Maryland (Murro 2002a; Harris et al. 2007; Murauskas and Rulifson 2011). There are no specific data on genetic structure or philopatry of Hickory Shad, but river-specific stock structure is assumed by proxy. Although there have been anecdotal reports that this species’ abundance is increasing (Waldman 2006), no comprehensive, coastwide assessment of Hickory Shad exists, and few states have assessed this species in local waters. River herrings (Blueback Herring *A. aestivalis* and Alewife *A. pseudoharengus*) also appear to be philopatric (Gahagan et al. 2012). They demonstrate genetic structure at least at a regional scale, where three Alewife stock complexes and four Blueback Herring stock complexes are recognized (Palkovacs et al. 2014).

For all Alosinae, concerns about cryptic overexploitation of small populations via ocean fisheries, particularly those targeting Atlantic Herring *Clupea harengus* and Atlantic Mackerel *Scomber scombrus*, has led to modification of the original FMP and reinstated a more river-centric approach to management (ASMFC 1999, 2013c; McBride and Holder 2008; Davis and Schultz 2009; Bethoney et al. 2013; Cronin-Fine et al. 2013). Recently, a determination to list river herrings as threatened failed (NOAA 2013), but concerns continue because river-specific data are not available for all stocks, especially for the smaller stocks (ASMFC 2007, 2009a, 2012c, 2013c). Morphometric analysis appears to be emerging as a promising, readily available tool to discriminate stocks of the river herrings (Cronin-Fine et al. 2013).

**Other Herrings**

Atlantic Menhaden *Brevoortia tyrannus* is distributed from Canada to southern Florida, and tag returns demonstrate extensive migrations above the Atlantic Continental Shelf (Ahrenholz 1991). As many as three stocks have been postulated based on morphometric and meristic data (Ahrenholz 1991), but these appear to be ecophenotypes. Atlantic Menhaden have a homogeneous genetic population in Atlantic waters (Lynch et al. 2010), and presently, it is managed as a unit stock (ASMFC 2001). Although its larvae and juveniles are strongly associated with estuaries, spawning occurs from estuarine to open-shelf habitats resulting in widespread dispersal of propagules (Ahrenholz 1991; Epifanio and Garvine 2001; Warlen et al. 2002). The fishery was historically distributed coastwide; however, in recent years over half the landings come from Chesapeake Bay, so this region has become the focus of stock assessment and management (ASMFC 2011b; Lynch et al. 2011; Smith and O’Brien 2011). Most research priorities are focused on collecting spatially explicit data within the broad, unit stock area, and using multispecies models to assess this forage species in an ecosystem context (ASMFC 2013c).

Atlantic Herring is distributed in a complex of spawning populations on both sides of the Atlantic Ocean, representing metapopulation stock structure (McQuinn 1997; Hare and Richardson 2014). In U.S. waters, assessment and allocation of catch recognizes four management areas comanaged with the NEFMC (Kritzer and Liu 2014). These management areas are defined by spawning, movement of the fish, and harvesting and processing by the fishery: inshore Gulf of Maine, offshore Gulf of Maine, Georges Bank, and a southern coastal stock (i.e., south and west of Cape Cod) (ASMFC 2006). Genetic evidence supports isolation by distance among U.S. and Canadian stocks, but there is little evidence for natal homing and specific evidence of mixing in the Gulf of Maine (Kornfield and Bogdanowicz 1987; McPherson et al. 2001, 2003; Hare 2005). Similar recruitment patterns along the Maine and New Brunswick coasts are evident on the west side of the Bay of Fundy, such that U.S. assessments include these transboundary data (Shepherd et al. 2009). Stocks can be discriminated successfully on a variety of phenotypic characters, including life history characteristics, such as growth, reproductive biology, and geographic distributions, as well as morphometric and meristic characters (Lea 1919; Messieh 1972; Cadrin et al. 2004; Stevenson and Scott 2005). Fishery allocations are distributed by management areas to apportion catch among mixed shoals of herring stocks and to prevent overfishing of discrete, particularly smaller, spawning units (ASMFC 2013b; Kritzer and Liu 2014). Data limitations about mixing rates between spawning components hamper full actualization of policies aimed at managing herring metapopulation structure, so tagging, morphometrics, and related stock identification research remain a priority (Smedbol and Stephenson 2001; Secor et al. 2009; ASMFC 2013c).

**Striped Bass and Black Sea Bass**

Striped Bass *Morone saxatilis* is anadromous in the northern part of its range, north of the Carolinas (Waldman et al. 1997, 2012; McBride and Matheson 2011). The ASMFC manages Striped Bass as a stock complex, where three primary producer areas (Chesapeake Bay, Delaware Bay, and Hudson River) are distinct stocks contributing to a coastal migratory group (ASMFC 2013b). More stocks are plausible. River-specific stock structure along the U.S. Atlantic coast is documented by both phenotypic and genetic traits (Waldman et al. 1988, 1997; Waldman 2005b). In addition, Secor et al. (2001) identified riverine, estuarine, and coastal contingents in the Hudson River. Thus, there is stock structure between estuaries and substructure (contingents) within estuaries. Estuaries in North Carolina are provisionally considered a fourth source of coastal migrants, both because tagged Striped Bass from North Carolina estuaries make limited movements into coastal waters, and fish tagged in the north foray into coastal waters of North Carolina (ASMFC 2003). The fishery exploits mixed stocks in coastal waters. The composition of landings, even in major producer areas, is not monitored, so the effect is to manage this fishery as a single stock. In the past, when the Chesapeake Bay stock was considered overfished, a coastwise mortality on fishing Striped Bass was imposed (Richards and Rago 1999). As this stock was rebuilt, the fishing ban was lifted. Special regulations for the Chesapeake Bay region and North Carolina estuaries are
presently in effect as a management equivalency, accounting for a lower size limit in these regions. Tagging methods are still regarded as a research priority to investigate migratory rates and pathways and the resulting stock composition (ASMFC 2013c).

Black Sea Bass spawns on the continental shelf from Cape Cod to the Gulf of Mexico in association with reef structure (Drohan et al. 2007; Fabrizio et al. 2014). Black Sea Bass is considered a unit stock north of Cape Hatteras, where the ASMFC comanages this stock with the MAFMC. Subpopulation structure of this northern stock is unresolved (NEFSC 2012), where several lines of evidence suggest more than one stock: (1) mitochondrial DNA polymorphisms exist within the exploitable stock from North Carolina to Massachusetts (McCartney et al. 2013), (2) ecophenotypes exist and are observable with meristic and morphometric characters (Shepherd 1991), and (3) different migratory contingents exist and either migrate north–south between the northern and southern portions of the Middle Atlantic Bight or undertake shorter, onshore–offshore migrations within the southern portion of the bight (Musick and Mercer 1977; Hood et al. 1994; Moser and Shepherd 2009). Across the species’ range, persistent genetic differences are evident between Atlantic populations north and south of Cape Hatteras, as well as between the Atlantic Ocean and Gulf of Mexico (Bowen and Avise 1990; Roy et al. 2012; McCartney et al. 2013). South of Cape Hatteras Black Sea Bass are smaller and nonmigratory (Wenner et al. 1986; Hood et al. 1994); this southern stock is managed by the South Atlantic Fishery Management Council, as part of their snapper–grouper complex (SAFMC 2013). A variety of stock identification approaches are still regarded as research priorities: otolith microchemistry, genetic tools, and tagging (ASMFC 2013c).

**Bluefish and Scup**

Bluefish *Pomatomus saltatrix* ranges along the eastern coast of North America from the Gulf of Maine to Gulf of Mexico (Shepherd and Packer 2006). In Atlantic waters, Bluefish is comanaged as a single, unit stock with the MAFMC (MAFMC 1998), but historic determinations had suggested that this species has a more complex stock structure. Adultst undergo extensive seasonal migrations above the continental shelf, and their spawning produces multiple intraannual cohorts, primarily during the spring and summer, and to a minor extent in the autumn (Kendall and Walford 1979; McBride and Conover 1991; McBride et al. 1993). Two processes appear to create pulses in these Bluefish cohorts: individuals are capable of spawning multiple times in a year (Robillard et al. 2008), and differential larval mortality or vagrancy may occur at certain times of the year (Hare and Cowen 1993). The spring-spawned cohort is typically dominant, and individuals of this cohort attain a larger size by their first winter (McBride and Conover 1991; Munch and Conover 2000). Lund (1961) counted Bluefish gill rakers and concluded that there are multiple phenotypic stocks along the Atlantic coast (Massachusetts–Florida). Tagging data also suggest contingent structure among adult Bluefish, where adults of different sizes migrate differentially: smaller fish migrate largely north–south in nearshore waters, whereas larger fish migrate more offshore and do not migrate as far south in the winter (Lund and Maltezos 1970; Shepherd et al. 2006). These size-specific migratory patterns are postulated to arise from different physiological conditions among age-classes (Wuenschel et al. 2012). No genetic structure is evident along the U.S. east coast, despite a prolonged spawning season that produces intrannual cohorts of variable abundance, meristics that vary with latitude, and migratory patterns that vary with size-class (Graves et al. 1992a; Graves 1998). However, relative to the attention paid to other ASMFC species, the genetic data available for Bluefish appears rather limited. No research priority directly targets stock structure issues, but the ASMFC prioritizes efforts to improve or coordinate spatially explicit sampling (ASMFC 2013c).

Scup *Stenotomus chrysops* was initially regarded as two species, one each north and south of Cape Hatteras (Steimle et al. 1999). These species have now been combined and the population north of Cape Hatteras, where the fishery is concentrated, is comanaged as a single, unit stock by the ASMFC and the MAFMC (MAFMC 1996). Meristic, morphometric, and tagging data have suggested contingent populations of Scup occupy waters north and south of Cape Hatteras (Mayo 1983; Love and Chase 2009; Chase 2011). The fishery operates in the northern region, where abundance is highest. Coastal spawning and seasonal movements by adults create conditions for gene flow, and there is specific evidence of northern fish migrating south of Cape Hatteras. No stock structure research is identified as a priority (ASMFC 2013c), but Chase (2011) notes that seasonal mixing appears offset from the spawning period, so further investigation of genetic structure appears warranted.

**Sciaenids**

Spotted Seatrout *Cynoscion nebulosus* spawns in estuaries from Chesapeake Bay to the Gulf of Mexico (Roumillat and Brouwer 2004; Smith et al. 2008). This species is managed by the ASMFC as individual stock units at the state level, from Maryland to eastern Florida, because of an isolation-by-distance genetic structure, estuarine spawning, limited movements outside of estuaries, and differences in growth and mortality (ASMFC 1984a, 2011c). An isolation-by-distance genetic pattern is evident, whether measured with general proteins or allozymes (Weinstein and Yerger 1976; Ramsey and Wakeman 1987) or with microsatellites (Wiley and Chapman 2002; Ward et al. 2007). Spotted Seatrout show limited movements, rarely leaving the estuary. Size and growth rates vary between estuaries but interpretation of stock-specific effects are confounded by different sampling biases, environmental conditions, and fishing mortality rates (Iversen and Tabb 1962; Murphy and Taylor 1994; Murphy and McMichael 2003). Delineation of discrete spawning groups and limited movements of tagged fish have received most attention in the Gulf of Mexico (reviewed by Ward et al. 2007; Lowerre-Barbieri et al. 2009). A recent study that sampled 21 microsatellites from Spotted Seatrout sampled
at 18 sites between Texas and North Carolina identified three genetic stocks in the southeastern United states: (1) from Texas to Apalachicola Bay (western Florida); (2) from Apalachicola to Biscayne Bay (eastern Florida); and (3) from Sebastian Inlet (eastern Florida) to Morehead City (North Carolina; S. Seyoum, Florida Fish and Wildlife Conservation Commission [FWC], unpublished data). Determining mixing rates between North Carolina and Virginia and how hypothermal (winter) mortality may affect genetic diversity are still research priorities (ASMFC 2011c, 2013c).

Weakfish *Cynoscion regalis* spawns in estuaries during summer but migrates offshore during winter (Nye et al. 2008). It is managed as a unit stock from Cape Cod to eastern Florida, and while there is evidence of two stocks, defining a stock boundary has proven elusive (ASMFC 1985; NEFSC 2009). Multiple lines of evidence, such as clinal differences in meristic, morphometric, age, and growth patterns as well as tagging studies, support at least a north and south ecophenotype (ASMFC 1985). No genetic stock structure is evident throughout this range, whether based on allozymes, mitochondrial DNA, or microsatellites (Crawford et al. 1988; Graves et al. 1992b; Cordes and Graves 2003). Thorrold et al. (2001), using otolith microchemistry methods, reported philopatry among a majority of 1- and 2-year-old Weakfish from New York to Georgia. In summary, an isolating effect of philopatry at young ages should create conditions for separate stocks, but mixing among older age-classes appears sufficient to homogenize the genetic structure. Research employing tagging methods is considered a priority to further investigate stock identification, mixing, and overwintering patterns (ASMFC 2013c).

Spot *Leiostomus xanthurus* ranges from the central Middle Atlantic Bight south to the Gulf of Mexico. Spot is considered a unit stock from Delaware to eastern Florida, but this is a particularly data-poor species for assessment (ASMFC 2013b, 2013c). What little is known about Spot includes the following: Spot spawns above the continental shelf and spends its first year in estuaries (Govoni and Pietrafesa 1994); larvae can be dispersed from south to north of Cape Hatteras (Flores-Coto and Warlen 1993); larger and older fish exist in the northern part of their range (ASMFC 1987a). Measuring the extent of stock mixing during autumn with genetic and tagging studies has long been a research priority (ASMFC 1987a, 2011c, 2013c).

Atlantic Croaker *Micropogonias undulatus* is distributed from New Jersey to eastern Florida, and into the Gulf of Mexico. Separate assessments, north and south of Cape Hatteras, were completed until 2003, but have since been done on a coastwide basis (ASMFC 2013b; Munyandorero 2014). Separate assessments were based on life history information that fish north of Cape Hatteras spawn earlier, mature later, grow larger, and live longer than conspecifics south of Cape Hatteras (White and Chittenden 1977; ASMFC 1987b); however, subsequent analyses did not find larger, older fish north of Cape Hatteras (Barbieri et al. 1994). Parasite data also supported existence of two stocks, one north and one south of Cape Hatteras (Baker et al. 2007), but otolith microchemistry data did not (Thorrold et al. 1997). Lankford et al. (1999) reported evidence of substantial gene flow between these putative stock areas, based on a survey of mitochondrial DNA variations. In addition, Lankford and Targett (2001a) employed the unusual but rigorous approach of a single laboratory experiment to disentangle genetic and phenotypic effects on growth and cold tolerance in young-of-the-year Atlantic Croaker (i.e., a common garden experiment using fish collected from Delaware, North Carolina, and Florida). These results suggest that northern fish have a genetically determined higher capacity for growth or are better able to tolerate colder temperatures, but this variation among individuals does not manifest itself as local adaptation. The temperature-mediated effects expected to affect juvenile survival can indeed predict abundance and distribution (Lankford and Targett 2001b; Hare and Able 2007), but offshore spawning and coastwide movements of adults appear sufficient to mix the genotypes among northern and southern locales. Although collaborative, coastwide studies to examine genetic structure, migration patterns, and mixing rates are still considered high research priorities, the main source of uncertainty in this fishery assessment is the high but difficult-to-measure bycatch rates of Atlantic Croaker in the penaeid shrimp fishery (ASMFC 2010b, 2011b, 2013b).

Red Drum *Sciaenops ocellatus* spawns in estuaries and coastal habitats from Chesapeake Bay to Gulf of Mexico drainages (Johnson and Funicelli 1991; Murphy and Crabtree 2001). The Atlantic stock of Red Drum is managed as two units, north and south of the North Carolina–South Carolina border. This split is based largely on life history differences (e.g., maximum age), an isolation-by-distance genetic pattern, and tagging data. Red Drum in North Carolina grows longer and lives longer than conspecifics to the south (Ross et al. 1995). Atlantic and Gulf populations are genetically distinct, whether based on allozymes, mitochondrial DNA, or microsatellites (Gold et al. 1994; Seyoum et al. 2000; Gold and Turner 2002); this pattern was also evident with otolith microchemistry (Patterson et al. 2004). Genetic structure follows an isolation-by-distance pattern from Florida to North Carolina (Gold et al. 1999). Specific evidence for the stock boundary comes in the form of tagging data. Adults move well out into the coastal environment, and although little mixing of tagged fish occurs between neighboring states, mixing occurs at higher rates in the northern part of the range, specifically between North Carolina and Virginia (ASMFC 1984b, 2002b; Bachelier et al. 2009). Continued tagging studies are considered a research priority to clarify how movements affect abundance, mortality, and mixing of Red Drum stocks (ASMFC 2013c).

**Tautog and Mackerel**

Tautog *Tautoga onitis* ranges from Canada to the Carolinas but is most abundant from Cape Cod to Chesapeake Bay (Steimle and Shaheen 1999). This species is managed as a unit stock (ASMFC 1996) based on data showing restricted
movements by adults and genetic homogeneity. Tautogs reside year-round in association with deeper (<75 m) hard-bottom habitat, but individuals also move inshore (<10 m) seasonally (Hostetter and Munroe 1993; Arendt et al. 2001; Munroe 2002b). Orbach and Gaffney (2000), using mitochondrial DNA and nuclear (intron) DNA, found no significant genetic differentiation to support more than a unit stock. Tuckey et al. (2007) reported lower mortality rates offshore of the Chesapeake Bay than farther north in the mid-2000s, but these lower mortality rates did not persist and have not changed the status of a unit stock. Stock structure research regarding this data-poor species is not considered a priority (ASMFC 2013c).

Spanish Mackerel Scromberomorus maculatus ranges from New York to Florida and throughout the Gulf of Mexico (Collette 2002). The Atlantic stock is assessed and comanaged with the South Atlantic Fishery Management Council (SAFMC) as a unit stock from New York to eastern Florida (ASMFC 1990, 2011c). Spawning is protracted, from May to September, in depths < 40 m above the continental shelf (Collins and Stender 1987). No genetic structure has been detected across this geographic range using mitochondrial DNA and nuclear (intron) DNA (Buonaccorsi et al. 2001), but stock identification research is still regarded as a priority research area for this species, specifically to explore finer-resolution genetic structure (ASMFC 2011c, 2013c).

Flounders

Summer Flounder Paralichthys dentatus spawns above the continental shelf from Georges Bank to Florida (Able et al. 1989; Packer et al. 1999). The ASMFC comanages Summer Flounder with the MAFMC as a unit stock from North Carolina northward, where over 70% of the harvest is landed in New York and New Jersey (ASMFC 1982; MAFMC 1991; Terceiro 2011). The issue of stock structure has focused on populations north and south of Cape Hatteras, where broad evidence, including larval distributions, meristic and morphometric data, and movements inferred from tagging, suggested ecophenotypes exist. In a common garden experiment, Burke et al. (2000) reported some physiological differences in larval growth between fish from south and north of Cape Hatteras, but these differences were not consistent across temperatures or relative to predictions. In another laboratory experiment using juveniles, Malloy and Targett (1994) reported higher growth rates and higher growth efficiencies, but decreased tolerance to cold temperature for Summer Flounder from North Carolina compared with fish from Delaware Bay. Kraus and Musick (2001) summarized additional evidence for possible spawning groups above the shelf, latitudinal variation in growth rates, and movement patterns to suggest that at least two stocks exist coastwide. Although some adults returned to their tagged area between years (Caposella et al. 2013), fish leaving estuaries also disperse broadly in shelf habitats (Henderson 2012), and Jones and Quattro (1999) report no genetic structure north or south of Cape Hatteras. Stock-structure-related research priorities are now focused on approaches that could identify mixing rates around Cape Hatteras (ASMFC 2013c).

Winter Flounder Pseudopleuronectes americanus exhibits dramatic life history variability throughout its range, from Labrador to North Carolina. In the United States, three stocks are assessed, but this number has been higher in the past and life history variations exist within the coastal stocks. DeCelles and Cadrin (2011) summarized interdisciplinary evidence supporting stock structure, including meristic and morphometric data, parasite markers, little movement—particularly north to south—inferred from tagging, and differences between growth and maturity. Common garden experiments demonstrate genetically based growth rate differences between stocks (Butts and Litvak 2007). Analysis of microsatellite characters demonstrates genetic differences between Georges Bank and the other Canadian stocks (McClelland et al. 2005; Wirgin et al. 2014). Recently, McElroy et al. (2013) documented temporally stable differences in productivity (i.e., annual fecundity) between all three U.S. stocks, and McBride et al. (2013) and Winton et al. (in press) demonstrated inter- and intrastock variation in age at maturity. Historically, the ASMFC managed three of four U.S. stocks: the Gulf of Maine, southern New England, and the Mid-Atlantic stocks (ASMFC 1992). The last two stocks were combined (ASMFC 2005) into a southern New England stock which appears to have two contingents: estuarine residents and estuarine–nearshore migrants (Sagarese and Frisk 2011). An early analysis of microsatellite loci suggest fine-scale stock structuring of Winter Flounder at this southern range (Crivello et al. 2004), but a more recent analysis using microsatellite and single-nucleotide polymorphic loci did not find support for more than three U.S. stocks (Wirgin et al. 2014). In the Gulf of Maine, coastal spawning is increasingly recognized but the effects of mixing between spawning groups within this region are unclear (DeCelles and Cadrin 2010; Fairchild et al. 2013). The Georges Bank stock, found offshore, is managed by the NEFMC; the phenotype of this offshore stock is so different from the coastal stocks that it was once proposed as a separate species (Chase 2014). Continued investigation of stock structure, particularly for the coastal stocks, remains a research priority (ASMFC 2013c).

REVIEW OF METHODS USED

Methods used to identify stock structure of ASMFC species fell into five broad categories: life history traits, other phenotypic traits, genetic traits, natural marks, and applied marks (Cadrin et al. 2005). All species have not been treated equally in terms of the breadth and depth of methods used to explore stock structure; a few ASFMC species have been investigated rather exhaustively whereas others have received almost superficial treatment. Where more intensive research has been applied, rather complex patterns have emerged, such as in metapopulation structure for American lobster and Atlantic Herring, or contingent structure for American Eel, Striped Bass, and Winter Flounder. Experimental methods, although rarely applied, have
been particularly helpful in teasing apart ecophenotypes from genotypes, such as for horseshoe crab, Atlantic Croaker, and Winter Flounder. Therefore, methods do affect our confidence in indentifying and managing stock structure.

Life history characteristics, such as distribution and abundance, age and growth, and reproductive traits, are often the most historically rich kinds of information available because these traits are measured, and sometimes routinely monitored, to estimate vital rates used in assessment (Costello et al. 2012; McBride, 2014). The coarse-scale distribution of spawning grounds is well documented for all ASMFC species (Table 1). At one extreme, marine spawners are associated with a unit stock or metapopulation, and at the other extreme, anadromous species are associated with river-specific genetic units that are treated at least as regional stock complexes. Life history data were typically part of early stock definitions established in the initial FMPs developed by the ASMFC, but such descriptive data can be simply demonstrative of ecophenotypes that no longer justify separate stock status. The use of experimental approaches to test for stock-specific effects of temperature on mortality (horseshoe crab) or growth reaction norms (Atlantic Croaker, Winter Flounder) have been particularly effective for partitioning phenotypic and genotypic sources of stock integrity.

There is also a rich history of using meristic and morphometric methods to define ASMFC and other fishery stocks (Cadrim and Friedland 2005; Waldman 2005b; Cadrim 2014; Chase 2014; Stransky 2014). These methods have waned presumably because of the numerous studies already published, leaving little room for new information to be uncovered, together with the potential for existing variation to be an ecophenotypic signal unrelated to genetic structure or assessment needs. Nonetheless, a truss network approach has been recently fruitful in separating regional stock units for Alewife and Scup (Love and Chase 2009; Chase 2011; Cronin-Fine et al. 2013).

Application of genetic methods is very uneven across ASMFC species. At one extreme, analysis of broad spatial and temporal patterns with a number of different genetic markers has occurred for horseshoe crab, Atlantic Sturgeon, American Shad, Striped Bass, Weakfish, and Red Drum. Still, the genetic structure of some other “data-rich” species, such as American lobster, remain poorly known (Hodgins-Davis et al. 2007), or for Arctic Sturgeon (Helyar et al. 2011; ICES 2012; MacKenzie and Abaunza 2014), and an International Council for the Exploration of the Sea working group is actively exploring and promoting the strategic use of parasite taxonomy and genetics for stock identification (ICES 2012). Fatty acid profiles have been used to identify stocks of Striped Bass (Grahl-Nielsen and Mjaavatten 1992), and such biochemical markers, including amino acids, may hold promise with other species (Riveiro et al. 2011; Grahl-Nielsen 2014). Using otolith chemistry to associate habitat and connectivity of fishes has become more popular recently, contributing to stock identification of several species (American Shad, Striped Bass, Weakfish, and Red Drum). Its increasing cost-effectiveness is promising for continued use, especially in identifying contingents or metapopulation structure, where genetic signals between spawning units are confounded by even low levels of gene flow (Patterson et al. 2004; Kerr and Campagna 2014).

Many stock definitions of ASMFC species are based on tag returns, although much of this can only be found in the gray literature or as summarized in the original FMPs. Tag returns often only confirm what can already be inferred from seasonal
distributions, but strategic use of tags to explore connectivity of metapopulations or parallel life histories of contingents is still very relevant today (Sécor 1999; DeCelles and Zemeckis 2014). Many recent ASMFC FMPs still prioritize tagging research for investigating mixing at stock boundaries (i.e., for Spotted Seatrout: ASMFC 2011c, 2013c). Cape Hatteras or Cape Cod are routinely used as stock boundaries because of their association with biogeographic patterns rather than with specific evidence, so tagging studies near these locales may be particularly useful. The use of electronic tags is still typically directed at investigating habitat use (Aunins and Olney 2009; Grothues et al. 2009; DeCelles and Cadrin 2010), but as these data accumulate, their use for stock identification is growing (Rooker et al. 2007; Bacheler et al. 2009; DeCelles and Zemeckis 2014).

Simulation modeling is emerging as a complementary tool to understand stock-specific population dynamics (Kerr and Goethel 2014). Fogarty (1998) explored the metapopulation dynamics of American lobster, particularly the role that spawning by offshore populations plays in recruitment to inshore populations. Kerr et al. (2010b) explored a general model for simulating stock structure processes and applied this to a simple metapopulation example of Atlantic Herring. Henderson (2012) used different tagging approaches with Summer Flounder to explore how small-scale behaviors influence large-scale population movements and distributions.

Among the methods outlined in Cadrin et al. (2005), few have not been used repeatedly with different ASMFC species. Marking of otoliths of ASMFC species has occurred but not for stock identification purposes (Volk et al. 2005; Duffy et al. 2012); considering that the mass marking of juveniles has many applications for measuring homing rates and survival (e.g., Keefer et al. 2008), this method has considerable potential. An a priori, strategic, interdisciplinary research program (e.g., Abaunza et al. 2008, 2014) has not been applied directly to any ASMFC species, but Striped Bass and Winter Flounder have received ad hoc interdisciplinary reviews (Waldman et al. 1988, 1997; DeCelles and Cadrin 2011; Cadrin et al. 2014b).

**STOCK STRUCTURE TYPES**

As expected, a variety of stock structure patterns exist in U.S. waters among these 25 species (Tables 1, A.1). Much of this diversity is easily related to coastal hydrographic and life history processes. Two marine spawners, American lobster and Atlantic Herring, are recognized as metapopulations. This helps integrate the latitudinal and onshore–offshore spawning components with the potential for both larval dispersal and adult movements. Most other marine spawners are recognized as single stocks. Spot is considered a unit stock on very weak evidence. Otherwise, the evidence is fairly robust for Spiny Dogfish, American Eel, northern shrimp, Atlantic Menhaden, Bluefish, Atlantic Croaker, Tautog, and Spanish Mackerel (Table 1). The high number of unit stocks among marine spawners was not entirely expected, since a complex structure exists for many marine spawners in the North Atlantic (e.g., Ames 2004; Reiss et al. 2009). There is always the suspicion that a lack of evidence for more than one stock leads to an incorrect conclusion of a unit stock (Abaunza et al. 2014), and unresolved issues about contingent structure exist for some of these same species. Nonetheless, the high seasonal variability in temperature, specifically within the Middle Atlantic Bight, is the dominant mechanism that drives large-scale, north–south or onshore–offshore, migrations for many of these species. These movements disrupt conditions for reproductive isolation, particularly in terms of isolation by distance, but may promote conditions for establishing contingent structure, evident in Black Sea Bass, Bluefish, and Scup. Some of these same species have relatively long planktonic larval durations and considerable larval dispersal, which reduces the potential for stock structure even further. Other unresolved questions regarding the marine species generally fall into three categories: continuous or disjunct clinal stock structure, variation in vital rates between Cape Cod and Cape Hatteras, or mixing rates of individuals around capes.

Red Drum and Winter Flounder spawn in both estuaries and in the nearshore coastal environment and demonstrate relatively limited coastal movements. Their stock structure is correspondingly more complex than that for strictly marine spawners. Sufficient evidence exists to manage Red Drum as separate stocks north and south of Cape Hatteras (Bacheler et al. 2009). Winter Flounder probably comprises dozens of biological populations in the southern New England region where spawning is concentrated in estuaries, but there are resident and migratory contingents. The spawning groups of Winter Flounder in six New York estuaries are small enough to show symptoms of inbreeding (O’Leary et al. 2013).

Among the strict estuarine spawners there is well recognized stock structure. Horseshoe crab is managed by four latitudinally segmented stocks. This scale of structure is only a problem for the Delaware Bay stock where landings are highest. Fisheries in multiple states harvest individuals of this stock, and there are overlapping ecosystem concerns regarding migratory birds, specifically the red knot Calidris canutus. Spotted Seatrout is assessed at the state level because of its limited movements outside estuaries, whereas Weakfish is not, presumably because philopatry and the potential for genetic structure break down when older weakfish migrate offshore.

Anadromous species show stock structure at the river level. Nonetheless, while there is evidence of philopatry for Atlantic Sturgeon, American Shad, the river herrings, and Striped Bass, there is also evidence of straying and the knowledge that much of the fishing mortality occurs on mixed-stock complexes in the ocean. Consequently, stock units have been set at a regional rather than a river-specific scale.

**MANAGING STOCK STRUCTURE**

The ASMFC incorporate stock structure into the management of these 25 exploited species reasonably well. Implementation of each FMP included a review of research and knowledge
about stock structure (ASMFC 2013a). Further debate about stock structure of individual species takes place largely through peer-review panels and the primary literature (reviewed herein). There are many example of timely uptake of new information, as advocated by Cadrin et al. (2014b).

I found it difficult to develop a simple metric to define success, based on some association between knowledge of stock structure with stock status. This review does summarize the stock status and status of these 25 species. About one-third (eight) of these species are not overfished and over half (15) are not experiencing overfishing (Table A.1); however, there is marked uncertainty about both stock structure and status for several species. Furthermore, overfishing or an overfished status was evident at the adoption of some FMPs that stated good knowledge of stock structure, and for many species priorities other than stock structure are driving the research needs for assessment and management (ASMFC 2013c). Instead of focusing independently on developing such a metric, I highlight a few issues to guide further consideration of the intersection of research and the application of stock structure in an assessment and management context.

The anadromous fishes, most of which are in a depleted status, show that much more could be done. The concerns about shad and river herrings as bycatch in ocean fisheries are con-founded by a lack of real-time methods to discriminate between stocks in the fishery catch. Improved methods that would address these concerns should allow a more nuanced approach in the future for these species (Waldman et al. 2012; Cronin-Fine et al. 2013). Palkovacs et al. (2014) promoted a two-pronged approach of defining river herring stocks with genetic tools and monitoring them by using more traditional demographic traits. In the case of Atlantic Sturgeon, low levels of abundance, a moratorium on directed fishing, and evidence of straying by adults has culminated in managing distinct population segments by region (Grunwald et al. 2008; Kocik et al. 2013). In the case of Striped Bass, where the fishery is largely in coastal waters, stocks are recognized by the FMP, but as no stock is considered overfished and stock composition cannot be managed cost-effectively in real time, the species is managed at a coastwide level. These factors have resulted in managing the fisheries of some anadromous species in a binary regulatory manner (Richards and Rago 1999). Directed fishing is allowed when all stocks are not overfished or overfishing is not occurring—as is presently the case for Striped Bass—but is not allowed (i.e., a fishing moratorium) when these thresholds are crossed for even one stock—as is presently the case for Atlantic Sturgeon and in the past for Striped Bass. Recent efforts to list river herrings or close the stocks to fishing failed; as an alternative, Bethoney et al. (2013) and Courmane et al. (2013) explored an approach that monitors bycatch of depleted stocks of shad and river herrings in real time and develops control rules to stop fishing when bycatch is excessive.

Although metapopulation structure is recognized in American lobster and Atlantic Herring, much remains to be considered in terms of understanding its dynamics and the effectiveness of area-specific harvest control rules to preserve metapopulation structure. American lobster management is area-specific, taking the form of several coastal areas, where 90% of the landings occur, and an offshore area (ASMFC 1997); however, the management boundaries do not conform precisely with stock boundaries, which complicates data collection and stock assessment (ASMFC 2013c). Similar questions arise for Atlantic Herring (Kritzer and Liu 2014). Reiss et al. (2009) documented the inertia of historical stock designations and noted the tradeoffs between rigid and simple management versus the dynamics of flexible management structures.

The issue of mixing rates is not limited to these two metapopulations. Mixing rates around faunal breaks or between jurisdictional boundaries is a frequently recognized research priority by the ASMFC. Regarding Winter Flounder, the potential for genetic diversity between some individual estuaries, as well as different migratory contingents within estuaries, exceeds the resolutions of fishery data. Defining smaller stock units will have little effect on assessment if monitoring of catch, effort, and other fishery parameters do not occur at a similar scale (Reiss et al. 2009).

Although individual states can often adopt a specific management plan for their coastal waters, including to declare de minimis (exempt from regulations if their state contributes <1% of coastwide landings), each state’s harvest policies may also be governed by agencies other than the ASMFC. A state’s territorial seas do not typically extend beyond 3 mi (4.8 km) in Atlantic Ocean waters, but many of the species treated here are distributed across the shelf, requiring interaction with the regionally based federal fishery management councils. The NEFMC is the lead council on FMPs for Atlantic Herring and Winter Flounder; the MAFMC is the lead council for Spiny Dogfish, Black Sea Bass, Bluefish, Scup, and Summer Flounder; the SAFMC is the lead council on Spanish Mackerel (ASMFC 2013b).

The distribution of several species extends beyond the ASMFC’s range of governance and into the Canadian Maritimes or the Gulf of Mexico as well (Table A.1). In most cases, Canadian populations are considered separate stocks and their assessments are independent of U.S. stock assessments. Notable exceptions are Atlantic Herring, such that data for the west side of the Bay of Fundy are part of the U.S. stock assessment, and as proposed for Spiny Dogfish, which may be a sink population in Canada relative to a larger, possibly metapopulation structure along the North American east coast. Among the several species that are distributed along both the east and west coasts of Florida, fish on each coast are treated as separate populations—some are recognized as subspecies—and are governed by the ASMFC and the Gulf States Marine Fisheries Commission, respectively. Only American Eel has the potential to be comanaged by both commissions as a common species in both regions.

Given this governance framework and the costs of identifying stocks and implementing stock-specific monitoring and management, the ASMFC demonstrates considerable
accomplishment. One measure of success is that almost one-third (seven) of these managed species do not prioritize continued stock research (Table A.1; ASMFC 2013c). For Scup, the temporal allocation of fishing effort is more of a concern than is its spatial allocation (ASMFC 2013b). About half the ASMFC-managed species support active recreational fisheries, and recreational landings can be dominant for a few (e.g., Bluesh, Tautog), such that these species’ research priorities are focused on better characterization of the recreational catch. In the case of Atlantic Croaker, for which the ASMFC continues to identify stock structure as a research priority, there are competing priorities, such as discard mortality. There are so little data for Hickory Shad that it could benefit from additional research, not just regarding stock structure, but in nearly all areas related to assessment.

The following trends will increase our confidence in identifying and understanding the value of stock structure to manage sustainable fisheries: (1) strategic integration of methods to disentangle genetic from phenotypic variation; (2) improved cost-effectiveness of advanced methods, notably genetic markers, otolith microchemistry, and artificial tags; (3) simulation models to evaluate the effects of different stock structure types on assessment and management processes. Aside from the concrete concept that stock structure reflects some degree of reproductive isolation, the growing recognition of nongenetic contingent structure, e.g., in American Eel, Striped Bass, Black Sea Bass, Bluesh, Scup, and Winter Flounder so far, is also likely to have broad implications.

SUMMARY

In an attempt to improve our understanding and the application of stock structure in marine fisheries, this review provides a glimpse of how a specific set of species has been treated. It attempts to point out how methods that may be unfamiliar to some researchers could be complementary to those methods that may be more familiar. And it notes the tradeoffs that exist in putting such research into practice by assessment scientists and resource managers. Initial FMPs developed by the ASMFC, often in conjunction with federal management councils, included rigorous reviews of the available stock identification data. These were used to inform stock assessments and management policy, and the ASFMC continues to request and readily incorporate new data and information to manage these coastal fisheries. Marine spawners are treated as a single stock, two stocks, or a metapopulation, whereas estuarine and freshwater spawners are typically assessed and managed at a finer scale. Nonetheless, the stock structure of some species is still poorly known or the available data are conflicting and not resolved. Continued research of this subject should consider (1) research priorities tabulated by ASMFC review panels, (2) strategic use of interdisciplinary stock identification methods, (3) use of experiments or reaction norms to separate phenotypes from genotypes, (4) genetic surveys at a seascape scale, (5) demonstration of contingent (non-genetic) structure and its implications for management, and (6) simulation modeling. Obstacles to adopting finer-scale structure into management of ASMFC fisheries include: (1) multiple stock units are apparent but boundaries are not clear, (2) monitoring requirements for smaller areas or for mixed-stock catches are not cost effective, or (3) mixing rates within a metapopulation or across biogeographic boundaries are poorly described.

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### Appendix: Supplemental Information on the ASMFC Fishery Species

### TABLE A1. Tabulation of species managed by the Atlantic States Marine Fisheries Commission, grouped by order and family, identifying aspects of their natural history and stock identity, and how this relates to their stock status and management (ASMFC 2013a, 2013b, 2013c). Black Drum Pogonias cromis was added as a managed species in 2013 but is not included here because the first coastwide stock assessment is not planned until 2015. The ASMFC also manages several coastal sharks as a species complex but these are not considered herein because of data limitations. Life cycle characterizes if a species is resident in marine (Mar), estuarine (Est), or both (Mar-Est) habitats and where its spawns if different (in parentheses); diadromous species are assigned as either anadromous (Anad) or catadromous (Catad), based on whether they spawn in freshwater or marine habitats, respectively. Striped Bass migrates strictly within freshwater (Potamodromous; Pot) in the southern part of its range.

<table>
<thead>
<tr>
<th>Species</th>
<th>Latitudinal range</th>
<th>Life cycle</th>
<th>ASMFC stocks</th>
<th>Other stocks</th>
<th>Stock identification methods</th>
<th>Overfished</th>
<th>Overfishing</th>
<th>Research priority</th>
<th>Other</th>
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<tbody>
<tr>
<td>Xiphosura, Limulidae</td>
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<td></td>
<td></td>
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<tr>
<td>Horseshoe crab</td>
<td>21°N–44°N</td>
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<td>Lat (4)</td>
<td>GoMex</td>
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<td>Unknown</td>
<td>Y</td>
<td></td>
</tr>
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<td>Decapoda, Nephropidae</td>
<td>41°N–51°N</td>
<td>Mar</td>
<td>Meta (3[9])</td>
<td>Canada</td>
<td>LHda, LHag, LHre, PMo, GEmo, GEmo, AmCt, AmMt</td>
<td>GOM: N</td>
<td>GBK: N</td>
<td>SNE: Y</td>
<td></td>
</tr>
<tr>
<td>American lobster</td>
<td>42°N–82°N</td>
<td>Mar</td>
<td>Unit</td>
<td>Canada +</td>
<td>LHda, GEmo, GEmo</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Squaliformes, Squalidae</td>
<td>56°S–73°N</td>
<td>Mar</td>
<td>Unit</td>
<td>Canada</td>
<td>LHda, LHre, GEmo, AmCt</td>
<td>N</td>
<td>N</td>
<td>Y</td>
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<td>Spiny Dogfish</td>
<td>10°S–50°N</td>
<td>Anad</td>
<td>River (5 DPS)</td>
<td>Canada</td>
<td>LHda, LHre, GEmo, AmCt</td>
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<td>N</td>
<td>Listed</td>
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<tr>
<td>Atlantic Sturgeon</td>
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<td>Catal</td>
<td>Unit</td>
<td>Canada, GoMex</td>
<td>LHda, LHag, LHre, GEmo, GEmo</td>
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<td>Unknown</td>
<td>N</td>
<td></td>
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<tr>
<td>Anguilliformes, Anguillidae</td>
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<td></td>
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<td></td>
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<td></td>
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<td></td>
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<tr>
<td>American Eel</td>
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<td>River</td>
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<td>LHda</td>
<td>Y</td>
<td>Unknown</td>
<td>Y</td>
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<tr>
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<td>Anad</td>
<td>River</td>
<td>Canada</td>
<td>LHda, PHmo, GEmo</td>
<td>Y</td>
<td>Unknown</td>
<td>Y</td>
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<tr>
<td>Alewife</td>
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<td>Anad</td>
<td>River</td>
<td>Canada</td>
<td>LHda</td>
<td>Y</td>
<td>Unknown</td>
<td>Y</td>
<td></td>
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<tr>
<td>Hickory Shad</td>
<td>22°N–61°N</td>
<td>Anad</td>
<td>River</td>
<td>Canada</td>
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<td>Y</td>
<td>Unknown</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>Atlantic Menhaden</td>
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<td>Mar-Est (Mar)</td>
<td>Unit</td>
<td>Canada</td>
<td>LHda, LHre, PHmo, GEmo, AmCt</td>
<td>Unknown</td>
<td>Y</td>
<td>N</td>
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<tr>
<td>Atlantic Herring</td>
<td>33°N–80°N</td>
<td>Mar</td>
<td>Meta (4)</td>
<td>Canada +</td>
<td>LHda, LHre, PHmo, PMo, PHmo, PHmo, GEmo, GEmo, NMhc, NMhc, NMua, AmCt</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>OI</td>
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<tr>
<td>Perciformes, Moronidae</td>
<td>24°N–51°N</td>
<td>Anad (Pot)</td>
<td>Unit (North [3])</td>
<td>GoMex</td>
<td>LHda, LHre, PHmo, PHmo, PHmo, PHmo, GEmo, GEmo, NMhc, NMhc, NMua, AmCt</td>
<td>N</td>
<td>N</td>
<td>Y</td>
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(Continued on next page)
### Table A1. Continued.

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<th>Speciesa</th>
<th>Latitudinal rangeb</th>
<th>Life cycle</th>
<th>ASMFC stocks(^c)</th>
<th>Other stocks(^d)</th>
<th>Stock identification methods(^e)</th>
<th>Overfishedf</th>
<th>Overfishingf</th>
<th>Research priority(^g)</th>
<th>Otherh</th>
</tr>
</thead>
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<tr>
<td>Perciformes, Serranidae</td>
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<tr>
<td>Black Sea Bass</td>
<td>25° N–45° N</td>
<td>Mar</td>
<td>Unit (North)</td>
<td>SAFMC, GoMex</td>
<td>LHda, LHag, LHre, PHme, PHno, GEmo, AMct</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>Cont, Herm, Reef</td>
</tr>
<tr>
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<td>44° S–45° N</td>
<td>Mar-East (Mar)</td>
<td>Unit</td>
<td>GoMex</td>
<td>LHda, LHag, LHre, PHme, GEmo, AMct</td>
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<td>N</td>
<td>N</td>
<td>Cont</td>
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<tr>
<td>Perciformes, Pomatomidae</td>
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<tr>
<td>Scup</td>
<td>25° N–46° N</td>
<td>Mar</td>
<td>Unit (North)</td>
<td>GoMex</td>
<td>LHda, LHag, PHme, PHno, AMct</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Cont</td>
</tr>
<tr>
<td>Spotted Seatrout</td>
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<td>Est</td>
<td>Lat (State)</td>
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<td>LHda, LHag, LHre, GEal, GEmo, AMct</td>
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<tr>
<td>Weakfish</td>
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<td>Mar-East (Est)</td>
<td>Unit</td>
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<td>LHda, LHag, LHre, PHme, PHno, GEal, GEmo, NMhc, AMct</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
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<tr>
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<td>Unit</td>
<td>GoMex</td>
<td>LHda, LHag, LHre</td>
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<td>Unknown</td>
<td>Y</td>
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<td>Red Drum</td>
<td>0° N–43° N</td>
<td>Mar-East</td>
<td>Lat (2)</td>
<td>GoMex</td>
<td>LHda, LHag, LHre, GEal, GEmo, NMhc, AMct</td>
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<td>Unknown</td>
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<td>Perciformes, Labridae</td>
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<tr>
<td>Tautog</td>
<td>31° N–46° N</td>
<td>Mar</td>
<td>Unit</td>
<td>GoMex</td>
<td>LHda, LHag, GEmo</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>Reef</td>
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<tr>
<td>Perciformes, Sciaenidae</td>
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<tr>
<td>Spanish Mackerel</td>
<td>19° N–44° N</td>
<td>Mar</td>
<td>Unit</td>
<td>GoMex</td>
<td>LHda, LHag, GEla</td>
<td>N</td>
<td>N</td>
<td>Y</td>
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<tr>
<td>Summer Flounder</td>
<td>29° N–45° N</td>
<td>Mar-East (Mar)</td>
<td>Unit (North)</td>
<td>GoMex</td>
<td>LHda, LHag, LHre, LHrn, PHme, PHno, GEal, GEmo, AMct</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td></td>
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<tr>
<td>Pleuronectiformes, Pleuronectidae</td>
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</tbody>
</table>

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\(^{a}\)Nomenclature follows Page et al. (2013), McLaughlin et al. (2005), and Sekiguchi and Shuster (2009).

\(^{b}\)Latitudinal range is from FishBase (www.fishbase.org), Shumway et al. (1985), Sekiguchi and Shuster (2009), and Currie and Schneider (2011).

\(^{c}\)ASMFC stock structure characterizes how the Commission manages this species: as distinct population segment (DPS; an aggregate of regional spawning groups); river-specific groups (River); at the state level (State); by latitudinally defined groups (Lat); a metapopulation (Meta); or a single unit (Unit). Several species are only managed by the ASMFC north of Cape Hatteras (North), either because that is where the coastal fishery exists (Striped Bass) or is concentrated (Scup, Summer Flounder), or little mixing is apparent north and south of this cape (Black Sea Bass); in such cases, southern stocks are managed by separate authorities. The number of stocks is provided (in parentheses) with an additional number of management units [in brackets], if greater than one or not at the state level.

\(^{d}\)Other regional management agencies responsible for these species are indicated as occurring in the Gulf of Mexico (GoMex), the South Atlantic Fishery Management Council (SAFMC) Canada (Canada), or Canada and other nations in the North Atlantic Ocean (Canada + ).

\(^{e}\)Categories of evidence identifying stock structure for each species. Life history evidence is related to distribution and abundance (LHda), age and growth (LHag), reproduction (LHre), and experimental demonstration of a reaction norm (LHrn). Phenotypic evidence is related to meristics (PHme), morphometrics (PHmo), or hardpart morphology (PHhm; i.e., scales or otoliths). Genetic evidence is grouped as based on karyotype (GEka), protein allozymes (GEal) or more direct molecular markers (GEmo). Natural markers include parasites (NMpa), hardpart chemistry (NMhc), or fatty acid profiles (NMfa). Applied marks are indicated as conventional tags (AMct) or electronic tags (AMet).

\(^{f}\)Identifies stock status in terms of overfished and overfishing (Y = yes; N = no; Unknown) as discussed in ASMFC (2013b). Specific stocks are identified as Gulf of Maine (GOM), Georges Bank (GBK), and southern New England (SNE).

\(^{g}\)Identifies stock structure related research priorities (Y = yes; N = no) as discussed in ASMFC (2013c).

\(^{h}\)Special characteristics are identified as: contingents (Cont), hermaphroditic (Herm), listed as threatened or endangered (Listed), offshore–ins hore larval source dynamics (OI), partial migration (Part), reef-associated habitat preference (Reef), or viviparity (Vivip).
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Effects of Age at Treatment on Oxytetracycline Mark Formation in Larval Northern Pike


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MANAGEMENT BRIEF

Effects of Age at Treatment on Oxytetracycline Mark Formation in Larval Northern Pike

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Abstract

Oxytetracycline (OTC) immersion treatments were evaluated at the Waterville State Fish Hatchery (Waterville, Minnesota) for producing fluorescent marks on larval Northern Pike *Esox lucius* otoliths. A pilot marking trial conducted with 7-d-posthatch (dph) larvae resulted in poor mark efficacy and prompted further investigation on the treatment of younger larvae and modification of the treatment by use of osmotic induction to promote better mark formation. Northern Pike treated within 24 h post-hatch had significantly higher mark efficacies and marked otolith intensities than did Northern Pike treated at later life stages. Similar to the pilot marking trial, immersion of 7-dph fry in OTC solution resulted in poor mark efficacy, in which only 38% of the inspected fry possessed visible marks and most of the marks that were visible appeared faint. Simple immersion of newly hatched fry in OTC solution resulted in 91% marking success, and 65% of the visible marks appeared either clear or intense. The poorer mark efficacy on 7-dph fry suggests that differences in mark formation were more dependent on contemporaneous physiological processes than on otolith size. Osmotic induction prior to OTC immersion had a much weaker effect on mark intensity than did age-class of treatment in the study.

Northern Pike *Esox lucius* serve as important keystone predators in many aquatic ecosystems across North America (Casselman and Lewis 1996) and provide considerable recreational value due to their abundance and vulnerability to anglers (Paukert et al. 2001). Many natural populations have become vulnerable, however, to the effect of cultural eutrophication and habitat loss over the past half century (Casselman and Lewis 1996). Beyeler and Williams (1973) suggested that development of marshy habitat surrounding lakes has greatly reduced Northern Pike spawning habitat, and Forney (1977) reported that the loss of suitable spawning habitat has caused the virtual elimination of Northern Pike stocks in several systems.

Natural resource agencies have traditionally responded to declining natural reproduction by stocking fry or fingerlings (Schramm and Piper 1995), but difficulties differentiating stocked and wild Northern Pike during assessment sampling complicates evaluation of stocking success. Conventional marking techniques, such as fin clips and tags, can be used to differentiate fingerling-stocked Northern Pike in a population but are not practical for marking the much smaller and very numerous fry (Nielsen 1992).

Oxytetracycline (OTC) immersion marking, which has recently been approved by the U.S. Food and Drug Administration (FDA) for use on potential food fish (FDA 2011), may be a practical alternative for marking the much smaller and very numerous larval Northern Pike. The OTC immersion marking process is a batch-marking technique where large numbers of fish are immersed in an OTC solution of up to 700 mg/L for a maximum of 6 h (FDA 2011). The OTC binds with proteins in the blood and is incorporated into newly forming bones (Frost et al. 1961). When subjected to ultraviolet light, the OTC-marked bones emit a yellow-gold fluorescence that is detectable through epifluorescent microscopy (Weber and Ridgway 1962; Brooks et al. 1994). Oxytetracycline immersion marking has been shown to produce detectable fluorescent marks on the larvae of several fish species (Dabrowski and Tsukamoto 1986; Lorson and Mudrak 1987; Muth and...
Bestgen 1991; Secor et al. 1991; Brooks et al. 1994) that can remain visible for many years (Jenkins et al. 2002; Logsdon et al. 2009).

The OTC immersion process may be further enhanced by immersion of the larval Northern Pike in a concentrated salt solution immediately preceding immersion in the OTC solution. This experimental process, called osmotic induction (Mohler 2003), has been shown to reduce the immersion period necessary to produce both tetracycline and calcein marks in the elvers of the European Eel Anguilla anguilla (Alcobendas et al. 1991), calcein marks in larval and juvenile salmonids (Mohler 2003; Negus and Tureson 2004), and alizarin red marks in Golden Perch Macquaria ambigua (Crook et al. 2007, 2009). In addition, Crook et al. (2009) found that fish immersed in salt solution prior to alizarin red immersion had more intense marks when evaluated 100 d after treatment than did the fish immersed only in alizarin red and not subjected to the osmotic induction. Although osmotic induction is not currently approved by the FDA for use with OTC on potential food fish, Crook et al. (2009) suggested that the simplicity and speed of the process for enhancing fluorescent chemical marking could make it appealing for large-scale hatchery use in the future.

The opportunities for marking larval fish are limited by how long the fish are retained in the hatchery and are best conducted with the least amount of additional handling or interruption of normal hatchery operations (Logsdon et al. 2004). Consequently, an ideal time to mass-mark larval fish is during collection and transportation of the fish for stocking (Secor et al. 1991, Brooks et al. 1994). Northern Pike eggs hatch after incubation for approximately 180 temperature units (TU; number of degrees Fahrenheit that the water temperature is above 32°F multiplied by number of days). After the initial activity associated with hatching, the larval Northern Pike enter a sedentary period of yolk sac absorption for approximately 150 cumulative TU before they begin actively swimming again (Pierce 2012). After yolk sac absorption, often corresponding with 5–7 d posthatch (dph), the fry can no longer be retained in the hatching jars and are stocked into lakes or nursery ponds. The purpose of this study was to evaluate the potential of using OTC immersion for marking stocked Northern Pike fry by evaluating (1) the efficacy of a 6-h immersion in 700 mg/L OTC solution for producing fluorescent marks on both 7-dph and newly hatched (<24 h posthatch) Northern Pike, and (2) whether preimmersion in a 2.5% salt solution (osmotic induction) enhances mark formation at either age.

METHODS

Pilot marking trial.—A pilot marking trial was conducted in 2008 by immersing 7-dph fry in 700 mg/L OTC solution for 6 h at 10°C immediately before transporting the fry for stocking. The Northern Pike were treated at the Waterville State Fish Hatchery (Waterville, Minnesota) with a method similar to that first described by Brooks et al. (1994) but modified by use of the maximum FDA allowable OTC concentration and immersion period.

A bulk solution of 700 mg/L active OTC (Fielder 2002; Lucchesi 2002; Logsdon et al. 2004) was first prepared using Terramycin-343 (Pfizer, New York). The solution was then buffered to pH 6.8 with sodium phosphate dibasic (Sigma, St. Louis, Missouri) and a silicon-based surfactant (No-Foam; Argent Chemical, Redmond, Washington) was added at a concentration of 0.04 mL/L to reduce foaming. Fry age was derived from the time the eggs began to hatch. The vast majority of pike eggs within a single hatchery jar hatched within 24 hr of the onset of the first eggs hatching. The Northern Pike were treated directly in the containers used to transport fry for stocking: collapsible 19-L clear plastic water jugs with the caps modified by the addition of valve stems to facilitate inflation with oxygen. The fry were enumerated by weight and combined with the OTC solution in each container at a density of approximately 438–614 fry/L. To allow room for oxygen infiltration, a maximum of approximately 7,000 fry and 11.4 L of OTC solution were combined in each container. The fry remained immersed in the OTC solution for 6 h, during which time care was taken to reduce fry exposure to sunlight and to limit temperature fluctuation. During the 2009 marking trial, the water temperature was 12.2°C.

At the end of the 6-h immersion period, a sample of approximately 3,500 treated fry was transferred to a raceway in the fish hatchery; the remainder of the treated fry were stocked into nearby lakes. The Northern Pike not released were fed cultured brine shrimp three times daily for 10 d to allow time for mark formation (Logsdon et al. 2004) and to decrease the influence of autofluorescence. Untreated fish from the same hatch date were also held in a raceway for 10 d to serve as controls. At the end of the 10-d grow-out period, a sample of 100 fry was removed from each raceway and each fry was inspected for the presence of fluorescent marks.

OTC mark inspection.—All sampled Northern Pike were inspected in blind trials where prepared otoliths from treated and untreated fish were chosen randomly, their identities being concealed during inspection. Examination of Northern Pike fry for the presence of a mark was conducted following the methods of Secor et al. (1991), Brooks et al. (1994), and Logsdon et al. (2004). The sagittal otoliths were first removed from the fry and wiped dry. They were then secured to a glass microscope slide with cyanoacrylate cement. Otoliths were cleared with Type DF immersion oil for initial inspection. If no mark was detected during initial inspection or a faint/clear mark was detected, the otoliths were polished with either 600- or 1,000-grit sandpaper in attempts to detect or enhance the mark. The exposed growth rings were then viewed with an epifluorescent microscope equipped with fluorescent lighting and filter blocks designed to optimize tetracycline fluorescence (Bumgardner 1991; Brooks et al. 1994). The specific system used was the Nikon Eclipse E-400 microscope with B-3A filter cube (505-nm dichroic mirror, 420–490-nm exciter filter, and 520-nm barrier
filter), 10× and 20× objectives (100× and 200× total magnification), and a 100-W mercury UV light source. Identified marks were rated with a system similar to that of Weber and Ridgway (1967), assigning grades of absent to the fish when no mark was evident, faint when a mark was present but not clearly visible, clear when the mark was readily visible but not vivid, and intense when a mark was both readily visible and vivid.

**Experimental marking trials.**—The OTC treatments conducted during the pilot marking trial failed to produce adequate marks on the otoliths of the inspected Northern Pike fry. Consequently, a series of experimental trials were conducted during 2009 to determine whether brighter, more consistent marks could be obtained by treating the fry at a younger age or by preceding immersion in the OTC solution with immersion in a salt solution (osmotic induction).

Four separate OTC marking trials were conducted in 2009. The first was a replicate of the pilot marking trial where 7-dph fry were treated by immersion in OTC at 700 mg/L for 6 h using the afore-mentioned methods. The second experimental marking trial differed from the pilot marking trial by the use of osmotic induction. Before immersion in the OTC solution, the 7-dph Northern Pike fry treated during the second trial were immersed for 30 s in a 25 g/L salt solution (Hi-Grade evaporated salt; Cargill, Minneapolis, Minnesota). The fry were then given a 5-s rinse in freshwater and immediately transferred to the OTC solution for 6 h. The third trial differed from the pilot marking trial in that the fry were treated within 24 h of hatching (newly hatched fry). The fourth experimental trial was also conducted with newly hatched fry but included osmotic induction as described for the second experimental trial.

Approximately 5,000–7,000 fry were treated during each experimental trial. Following the trials, the fry were held in raceways with supplemental feeding for 10 d and then inspected in blind trials with untreated fish, using the methods described for the pilot marking trial.

**Data analysis.**—Ordinal multinomial logistic regression models, also known as proportional odds models (Venables and Ripley 2002), were used to model the proportion of otoliths in each of the four categories of mark intensity as a function of both age at treatment and osmotic treatment status. This model accounts for the natural ordering of the intensity categories and assumes that two factors, age and osmotic treatment, have a consistent effect on changing a mark’s intensity from category to category. To determine which factors affected mark intensity, a model containing an age × osmotic treatment interaction was compared with all possible submodels, using Akaike information criterion (AIC) scores (Burnham and Anderson 2002). The AIC scores gave a relative measure of fit among the candidate models, allowing identification of which factors were associated with differences in mark intensity. The model with the lowest AIC score was chosen as the best model, and models with AIC scores within 4 of the lowest AIC score were viewed as having some support in the data. Models with AIC scores that exceeded the lowest AIC score by greater than 10 were viewed as having very little support in the data.

**RESULTS**

Immersion of 7-dph fry in 700 mg/L OTC solution for 6 h during the pilot marking trial in 2008 resulted in poor mark efficacy. Only 11 of the 100 inspected fish from the pilot study possessed visible marks, and 10 of the marks that were detected appeared faint (Table 1). No false marks were observed on any of the untreated fish inspected as controls.

All of the experimental treatment trials conducted in 2009 resulted in some individuals that possessed visible marks, but none of the experimental treatments resulted in 100% mark efficacy (Table 2). Mark efficacy varied among treatment groups, and mark intensity varied both among treatment groups and among individuals within a treatment group. As with the pilot study in 2008, no false marks were observed on any of the untreated fish in 2009.

Similar to the pilot marking trial, immersion of 7-dph fry in 700 mg/L OTC solution for 6 h during the first experimental trial in 2009 also resulted in poor mark efficacy. Only 38% of the inspected fry from the first 2009 experimental trial possessed visible marks, and most of the marks that were visible appeared faint. Addition of osmotic induction to the treatment procedure failed to increase mark efficacy for 7-dph fry. Only 34% of

<table>
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<th>Absent</th>
<th>Faint</th>
<th>Clear</th>
<th>Intense</th>
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</thead>
<tbody>
<tr>
<td>OTC only</td>
<td>89</td>
<td>10</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>None (controls)</td>
<td>100</td>
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**TABLE 1.** Results of the 2008 pilot study showing the intensity of fluorescent marks observed during blind trial examination of otoliths from untreated Northern Pike (controls) and Northern Pike treated with oxytetracycline (OTC) at 7 d posthatch.

**TABLE 2.** Results of the 2009 age/treatment study showing the intensity of fluorescent marks observed during blind trial examination of otoliths from untreated Northern Pike (controls) and Northern Pike treated with oxytetracycline (OTC) only or treated by osmotic induction of OTC at either 7 d or <24 h posthatch (newly hatched).

<table>
<thead>
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<tr>
<td><strong>7-dph fry</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OTC only</td>
<td>62</td>
<td>29</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Osmotic induction</td>
<td>66</td>
<td>22</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>None (controls)</td>
<td>200</td>
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<table>
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<td><strong>Newly hatched fry</strong></td>
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<td></td>
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<td>OTC only</td>
<td>9</td>
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<td>17</td>
</tr>
<tr>
<td>Osmotic induction</td>
<td>1</td>
<td>28</td>
<td>36</td>
<td>35</td>
</tr>
<tr>
<td>None (controls)</td>
<td>200</td>
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</table>
TABLE 3. Comparisons of multinomial logistic regression models for predicting mark intensity from age of fish and treatment type. Presented are the explanatory variables for each model, the degrees of freedom (df), AIC scores, and differences in AIC between each model and that with the lowest AIC score (ΔAIC). The lowest AIC identifies the model with the best fit to the data. Sample size was 400 for all models.

<table>
<thead>
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<th>Model</th>
<th>df</th>
<th>AIC</th>
<th>ΔAIC</th>
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</thead>
<tbody>
<tr>
<td>Intercept-only (null model)</td>
<td>3</td>
<td>1,077.1</td>
<td>213.0</td>
</tr>
<tr>
<td>Osmotic induction</td>
<td>4</td>
<td>1,076.9</td>
<td>212.8</td>
</tr>
<tr>
<td>Age</td>
<td>4</td>
<td>867.9</td>
<td>3.8</td>
</tr>
<tr>
<td>Age × osmotic induction</td>
<td>5</td>
<td>866.6</td>
<td>2.5</td>
</tr>
<tr>
<td>Age × osmotic induction</td>
<td>6</td>
<td>864.1</td>
<td>0</td>
</tr>
</tbody>
</table>

The best-fitting multinomial regression model of mark intensity contained both age at treatment and osmotic induction in addition to their interaction (Table 3); however, models with age only and age plus osmotic induction had AIC scores within 4 of the best-fitting model. The models indicated a strong effect of age at treatment on mark intensity. Including osmotic induction treatment, in contrast, had different, and much weaker, effects on mark intensity for the two age-classes in the study. For fish treated as newly hatched fry, osmotic induction produced the highest mark efficacy of the study. Only one Northern Pike treated during the fourth experimental treatment trial had no visible mark, and 71% of the marks from this group were rated either clear or intense.

The results of the current study indicate that such was not to be the case. Not only did treatment of 7-dph Northern Pike result in poorer marks than treatment of newly hatched fry, but mark efficacy on 7-dph Northern Pike was not increased by the use of osmotic induction. The poorer mark efficacy on 7-dph fry suggests that differences in mark formation were more dependent on contemporaneous physiological processes other than otolith size.

Growth is one such process that has been reported to affect OTC mark formation. Dabrowski and Tsukamoto (1986) reported lower mark efficacy and formation of narrower OTC bands on the otoliths of larval Peled Coregonus peled than on those that were held at 16.8°C than on those that were held at 16.8°C. Harrison and Heidinger (1998) also reported fainter marks formed on the otoliths of juvenile Walleyes that were purposely starved 5 d before and after treatment than on those that experienced faster growth from being fed to satiation.

The newly hatched Northern Pike fry treated during the current study possessed well-developed yolk sacs at the time of treatment, whereas the 7-dph fry were transitioning to exogenous feeding (Piper et al. 1982). Although cultured brine shrimp were offered to the 7-dph larvae prior to fry transition to exogenous feeding, it is possible that growth slowed during the transition. Slower growth is particularly likely because forage was provided only three times daily and the 7-dph fry had to expend energy to capture and digest their new source of nourishment. A concomitant decrease in otolith growth would probably have diminished the width of the OTC deposition ring in the otoliths of the 7-dph Northern Pike whether treated by simple immersion in OTC or by osmotic induction as well.

The osmotic induction procedure (Mohler 2003) takes advantage of rapidly changing osmotic gradients to increase the absorption of the OTC solution. Fish exposed to a hypersaline...
environment experience water loss from body fluids due to diffusion across the gills, skin, and kidneys (Conte 1969; Holliday 1969; Smith 1982). Abruptly moving the fish from the hypersaline environment to the OTC solution then reverses the osmotic gradient and results in increased absorption of the OTC solution as water is replaced via diffusion in the opposite direction (Alcobendas et al. 1991; Mohler 2003). The OTC that enters the fish tissue then binds with proteins in the blood and is subsequently incorporated into new bone growth during the calcification process (Frost et al. 1961). The osmotic induction treatments conducted during the current study may have, in fact, increased the OTC concentrations in tissues of both newly hatched and 7-dph fry, but a paucity of new otolith growth in the 7-dph fry could have formed mark formation.

The results of this study illustrate the importance of conducting efficacy tests not only on the species of interest but also on the life stage that is intended to be marked. The OTC immersion process underwent rigorous testing of mark efficacy and safety prior to approval for use on finfish by the FDA (USFWS 1996). Even so, the maximum FDA-allowable OTC concentration and immersion period failed to produce suitable marks on 7-dph Northern Pike fry. Failure to recognize and account for poor OTC mark efficacy in recruitment studies could lead to inflated estimates of natural reproduction and subsequently mask the effects of spawning habitat loss.

Although growth has been implicated as the cause of the poor mark formation on 7-dph fry, confirmation of this effect is beyond the scope of our experimental design. Consequently, we recommend that additional research be conducted on the metabolic processes that accompany yolk sac absorption in Northern Pike and on how these processes might affect OTC absorption and deposition in otoliths. This would benefit not only Northern Pike research but also other species having a similar early life history. Further research may reveal opportunities to mark fish within hatchery jars and thus decrease additional handling required to immerse fish in OTC. We recommend that samples of fish from each OTC treatment episode be held in raceways or ponds to confirm mark formation prior to use of the recapture data for management purposes. Furthermore, fish mortality associated with OTC immersion should be documented when OTC is to be used to evaluate stocking success.

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REFERENCES


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Assessment of Subyearling Chinook Salmon Survival through the Federal Hydropower Projects in the Main-Stem Columbia River

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Abstract

High survival through hydropower projects is an essential element in the recovery of Pacific salmon *Oncorhynchus* spp. populations in the Columbia River. High dam passage survival is also a regulatory requirement under the 2008 Biological Opinion (BiOp; established under the Endangered Species Act) on Federal Columbia River Power System operation. The BiOp requires dam passage survival to be at least 0.96 and at least 0.93 for spring and summer out-migrating juvenile salmonids, respectively, and to be estimated with an SE of 0.015 or lower. An innovative virtual/paired-release design was used to estimate dam passage survival, which was defined as survival from the upstream face of a dam to the tailrace mixing zone. A coordinated four-dam study was conducted during the 2012 summer out-migration using 14,026 subyearling Chinook Salmon *O. tshawytscha* out-migrants with surgically implanted acoustic micro-transmitter tags. The release–recapture design consisted of 9 different release locations and 14 different detection arrays. Each of the four estimates of dam passage survival exceeded BiOp requirements, with values ranging from 0.9414 to 0.9747 (SE = 0.0031–0.0114). The virtual/paired-release design illustrated here has potential applicability wherever dam passage survival of migrant juvenile fish stocks must be estimated.

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Salmonid stocks have declined in the Columbia River for over a century due to overfishing, habitat loss, invasive species, and fragmentation caused by dam construction and irrigation withdrawals. There are 14 major hydropower projects on the Columbia and Snake rivers and many more projects on their tributaries. Currently, 13 stocks of Pacific salmon *Oncorhynchus* spp. or steelhead *O. mykiss* in the Columbia River basin are listed as threatened or endangered under the 1973 Endangered Species Act (ESA). In 1980, the Northwest Power and Conservation Council (then the Northwest Power and Planning Council) stated in the Northwest Power Act (officially the Pacific Northwest Electric Power Planning and Conservation Act) that its Fish and Wildlife Program was developed “to protect, mitigate, and enhance fish and wildlife, including related spawning grounds and habitat, on the Columbia River and its tributaries” (Northwest Power Act of 1980, section 4[h][1][A], U.S. Statutes at Large 94:2708), while providing an “adequate, efficient, economical, and reliable power supply” (section 2[2], U.S. Statutes at Large 94:2697).

The 2008 Biological Opinion (BiOp) by National Oceanic and Atmospheric Administration Fisheries regarding the operation of the Federal Columbia River Power System specified the actions necessary to avoid jeopardy for the ESA-listed stocks of Pacific salmon. Among these actions are performance-based criteria for dam operations. Survival of migrating salmonids through dams must be at least 96% for spring migrants and at least 93% for summer migrants, and survival must be confirmed with SE estimates of 1.5% or lower. Similar criteria were already established for public-utility-operated dams through habitat conservation plans with Federal Energy Regulatory Commission relicensing agreements (Skalski et al. 2012). A major distinction, however, was that the survival criterion in the 2008 BiOp was for dam passage (i.e., dam face to tailrace), whereas the habitat conservation plan criterion included passage through the reservoir plus the dam.

Restricting the survival estimates to dam passage required isolating the survival process to a relatively small segment of the river in a manner that still permitted valid inference to out-migrating juvenile salmonids. Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic micro-transmitter (AMT) tags were selected because of their small size, high detection rates, and flexibility in establishing detection arrays (McMichael et al. 2010) as well as the large available code set. The study design involved integrating the requirements of a release–recapture model with the capabilities of the AMT tag and the regulatory definition of passage survival. A virtual/paired-release–recapture design was specifically developed for this task (Skalski et al. 2010b).

A key element of the study design is the detection of AMT-tagged fish entering the dam as would typical migrants. Passive tag technologies (e.g., PIT tags, coded wire tags, etc.) are incapable of detection across the entire face of a dam, and releasing fish at the dam face does not ensure that arrival and passage distributions will be typical of in-river migrants. Instead, upriver releases of AMT-tagged fish are used to obtain nominal arrival at the dam, and a dense, three-dimensional (3D) hydrophone array at the dam face is used to record their entrance. These fish that are known to have entered the dam form what we call a “virtual release,” and they are used to estimate survival through the dam to a downstream detection location based on standard release–recapture methods (Burnham et al. 1987; Skalski et al. 1998). The term “virtual release” is used to distinguish this tagged group from actual release groups that are self-contained and whose members are prespecified at the time of release.

The limitations of tagging studies once again play into the design of these compliance studies. It is inappropriate to use a tailrace detection array to estimate survival through the dam by using just the virtual release and a single release–recapture design. Fish that die during dam passage with still-active tags would bias the estimate of dam passage survival upward. It would also be inappropriate to form a paired-release–recapture design by pairing the virtual release group (i.e., that goes through the dam) with a tailrace release group. The reason is that fish in the virtual release will have had time to express any postrelease handling or tagging mortality before the pairing, whereas a fresh tailrace release would not express any handling effect until after the pairing. Such a tagging study would again bias the estimate of dam passage survival upward. Instead, the virtual release is used to estimate survival through the dam and to a tailwater array that is located far enough downstream to avoid false-positive detections of fish that die during dam passage but still have active tags. To estimate mortality beyond the tailrace mixing zone, a classic paired-release–recapture study (Burnham and Anderson 1984) is performed with tag releases in the tailrace and at the first downstream detection array (Skalski et al. 2010b). This design could potentially be used at any hydropower project site where dam passage survival must be estimated for active migrant fish stocks.

In this paper, we illustrate compliance studies based on investigations of subyearling Chinook Salmon *O. tshawytscha* at four hydropower projects in the main-stem Columbia River during 2012. The 2012 study also illustrates how a multiple-dam investigation can be coordinated to provide economy of scale when assessment of multiple projects is required.

**STUDY AREA**

The study area is located in the lower Columbia River from the uppermost release location at river kilometer (rkm) 503 (33 rkm upstream of McNary Dam) to the last detection array at rkm 86 (148 rkm below Bonneville Dam; Figure 1). The Columbia River is 2,000 km long, and its largest tributary is the Snake River. The Columbia River is the fourth-largest river by volume and the seventh-longest river in the United States. The river drains an area of about 670,000 km². There are 14 hydroelectric dams on the main-stem Columbia River and over 150 dams in the Columbia River basin. During the study period, total volume discharge at McNary Dam (the uppermost dam included in the
study) ranged from 8.7 to 11.7 kilo cubic meters per second (kcms; i.e., 1,000 m$^3$/s).

**McNary Dam**

McNary Dam, which includes a navigation lock, powerhouse, spillway, and two adult fish ladders, spans 2,245 m across the river at rkm 470. The spillway is 399 m long and contains 22 vertical lift gates. The powerhouse has 14 turbine units. The dam has a powerhouse hydraulic capacity of 6.6 kcms and a nameplate generating capacity of 980 MW. The dam’s reservoir, Lake Wallula, extends 103 km upstream on the mid-Columbia River to the confluence of the Columbia and Yakima rivers and 68 km up the Snake River to Ice Harbor Dam.

**John Day Dam**

John Day Dam is located at rkm 348 and includes a navigation lock, spillway, powerhouse, and adult fish passage facilities on both the Washington and Oregon shorelines. The project has 16
turbine units and a 374-m spillway with 20 gates. The project has a total length of 602 m. The hydraulic capacity of the dam is 9.1 kcms, with a nameplate generating capacity of 2,160 MW. The reservoir it creates, Lake Umatilla, extends upriver 122 km to McNary Dam.

The Dalles Dam

The Dalles Dam is located at rkm 309 and spans the 2.4-km distance between the Washington and Oregon shorelines. The project consists of the dam, navigation lock, spillway, powerhouse, and adult fish passage facilities on both state shorelines. The hydroelectric project includes 22 turbine units and a 420-m spillway with 23 spill gates. The Dalles Dam has a powerhouse hydraulic capacity of 10.6 kcms and a nameplate electrical generating capacity of 1,780 MW. The dam’s 38.6-km-long reservoir, Lake Celilo, extends to John Day Dam.

Bonneville Dam

Bonneville Dam is located at rkm 234 and includes two powerhouses, two navigation locks, a spillway, and adult fish passage facilities on the shorelines of both Washington and Oregon. The spillway is 442 m long and contains 18 spill gates. The project has a powerhouse hydraulic capacity of 8.2 kcms and a nameplate power generation capacity of 1,050 MW. The associated reservoir, Lake Bonneville, extends 77 km upstream to the base of The Dalles Dam.

METHODS

The successful development of survival studies in the Federal Columbia River Power System resulted from the integration of policy, biology, acoustic technology, and statistics (Figure 2). The 2008 BiOp provided the definitions of dam passage survival, survival targets, and precision limits that molded the virtual/paired-release design used in the compliance studies (Skalski et al. 2010b). That design, in conjunction with the properties of acoustic tags, specified the number and location of the hydroacoustic arrays that were needed to detect fish passage through the dam and downstream.

Concurrent with the development of the field design, miniaturization of the acoustic tags allowed for the tagging of a more realistic distribution of smolt sizes and the tagging of fish stocks that comprise smaller individuals (i.e., subyearling Chinook Salmon; McMichael et al. 2010). Tag size reduction was essential in order to tag a representative sample of the fish and to make inferences about the run-of-the-river juvenile population. Surgical methods were also investigated to identify the best incision and suture procedures for tag retention and fish recovery (Deters et al. 2010, 2011; Panther et al. 2011).

A final component of the study preparation was the development of software to (1) process the volumes of acoustic signals into detection events and capture histories and (2) turn those capture histories into estimates of dam passage survival (Figure 2). Among the software developed for these efforts was Program ATLAS (Active Tag-Life-Adjusted Survival; www.cbr.washington.edu/analysis/apps/atlas), which can incorporate tag life data into the release-recapture analyses.

Release–Recapture Design

The virtual/paired-release design (Skalski et al. 2010b) was selected for estimating dam passage survival because it can be used to isolate survival between the dam face and tailrace within the context of using acoustic technology. The release–recapture design begins with the release of fish at a location far enough upriver that the fish can distribute themselves as would naturally migrating fish when they arrive at the dam (Figure 3). A dense hydrophone array (Weiland et al. 2011) at the face of the dam is then used to identify those fish that survived to and passed into the dam (Deng et al. 2011). These fish form a virtual release

FIGURE 2. Schematic of the elements contributing to the design, implementation, and analysis of the Juvenile Salmon Acoustic Telemetry System (JSATS) survival compliance studies conducted at Columbia River hydropower projects (BiOp = Biological Opinion; ATLAS = Program ATLAS [Active Tag-Life-Adjusted Survival]; ˆS = estimated survival).
FIGURE 3. Schematic of a virtual/paired-release design used to estimate dam passage survival of juvenile salmon at four Columbia River hydropower projects. Releases ($R$) and detection arrays (dashed line) are indicated, along with estimated survival ($S$), detections ($p$), and joint probabilities of survival and detection ($\lambda$) in the final reaches ($V_1 = \text{virtual release group}$). Dam passage survival is estimated by the quotient $S_{\text{Dam}} = S_1/(S_2/S_3)$.
The single-release estimate from the virtual release (i.e., $\hat{S}_V$) is then estimated as the quotient of the single-release estimate from the virtual release (i.e., $\hat{S}_1$) to the paired-release estimate of survival (i.e., $\hat{S}_2/\hat{S}_3$) below the dam:

$$\hat{S}_{\text{Dam}} = \frac{\hat{S}_1}{\left( \frac{\hat{S}_2}{\hat{S}_3} \right)} = \frac{\hat{S}_1 \hat{S}_3}{\hat{S}_2}. \quad (1)$$

The 2012 study of subyearling Chinook Salmon was conducted as a coordinated study at four sequentially located hydropower projects on the main-stem Columbia River (Figure 4). Instead of the nominal 12 releases needed for the survival assessment (i.e., 3 releases x 4 dams), the study was performed by using only nine release locations. This economy of scale was achieved by allowing fish from any of the above-dam release locations to be potentially used in forming the virtual release at a downriver project. Sample sizes for the below-dam paired releases ($R_i$; Figure 4) were reduced in anticipation of the greater precision in the estimate of $S_1$ at downriver hydropower projects (i.e., $R_1, R_2 > R_4, R_3 > R_6, R_7$). Because of the large discharge volumes and shallow tailwater environment below Bonneville Dam, several actions were taken to increase precision; one such action was to increase the sample sizes of the below-dam releases, $R_8$ and $R_9$. Other actions included increasing the density of hydrophones at arrays below the dam and using tags with a shorter pulse repetition interval (PRI).

**Handling, Tagging, and Release Procedures**

**Acoustic micro-transmitter tags and PIT tags.**—The AMT tags used during the summer 2012 study were Advanced Telemetry Systems Model SS300 acoustic tags; each tag was 10.7 mm long, 5.21 mm wide, and 3.03 mm thick and weighed 0.304 g in air. One lot of AMT tags was used for releases upstream of Bonneville Dam (i.e., $R_1-R_7$), and another lot was used for releases below the dam (i.e., $R_8$ and $R_9$). Fish released upstream of Bonneville Dam had AMT tags with a nominal transmission rate of 1 pulse every 3 s (i.e., PRI = 3 s) and a nominal tag life of about 23 d. To increase detection probabilities below Bonneville Dam for the $R_8$ and $R_9$ releases, those fish received AMT tags with a 2-s PRI, which reduced the nominal tag life to about 15 d.

Each juvenile Chinook Salmon was also tagged with a Biomark HPT12 PIT tag (12.5 mm long; 0.100-g weight in air). The PIT tags were used to identify fish that had to be censored in the survival study because they entered barge transportation or juvenile sampling facilities during their downstream migration.

Such fish were right-censored at the upstream hydrophone array where they were last detected.

**Fish source.**—All subyearling Chinook Salmon used in the study were obtained from the juvenile bypass system at John Day Dam. The Pacific States Marine Fisheries Commission diverted fish from the juvenile bypass system into an examination trough as described by Martinson et al. (2006). Fish were selected for surgical implantation of AMTs if they met the following criteria: (1) fish length was at least 95 mm but less than 300 mm, (2) there were no severe malformations or injuries, and (3) descaling was less than 20%. The length frequency of the tagged fish was compared with the length frequency of subyearling Chinook Salmon that were sampled by the Fish Passage Center at the John Day Dam juvenile fish sampling facility. The mean FL of tagged fish was 113 mm compared with 111 mm for fish that were sampled at the monitoring facility. Tag burden (i.e., tag weight/fish weight) for these subyearling Chinook Salmon smolts ranged from 0.7% to 4.0%, with an average value of 2.1%. Adams et al. (1998) recommended a tag burden of less than 5% for fish smaller than 120 mm.

**Surgery procedure.**—The fish that were to receive AMT tags and PIT tags were anesthetized in a 24.6-L “knockdown” bucket with fresh river water and an 80-mg/L concentration of tricaine methanesulfonate (MS-222). Each fish was weighed and measured before surgery.

During surgery, each fish was placed ventral side up, and a gravity-fed anesthesia supply line was placed into its mouth. The anesthesia (MS-222) dosage during surgical tagging was 40 mg/L. A 5–7-mm incision was made in the body cavity along the linea alba at a site that was 3–5 mm anterior of the pelvic girdle. The PIT tag was inserted first, followed by the AMT tag. Both the AMT tag and the PIT tag were inserted toward the anterior end of the fish. The incision was closed with two interrupted stitches using 5-0 Ethicon Monocryl monofilament suture. After the incision was closed, the fish were placed in a dark, 24.6-L transport bucket filled with aerated river water. Fish were transported to postsurgery holding tanks (continuously supplied with fresh river water), where they were held in transport buckets for 12–36 h before being transported for release into the river. The loading rate was 5 fish/bucket.

**Release procedures.**—All fish used in the survival study were transported by truck to release locations (Figure 3). The transport times from the tagging location to the release locations at a hydropower electric project were adjusted to be similar in duration. The transport travel times depended on dam location and ranged from 20 min (i.e., John Day Dam) to 140 min (Bonneville Dam). Upon arrival at a release site (Figure 3), fish buckets were transferred to a boat for transport to five release locations spanning the width of the river, and equal numbers of buckets of fish were released at each of the five locations.

Releases occurred for 33 consecutive days. Releases alternated between daytime and nighttime (every other day) over the course of the study. The timing of releases at the release sites was staggered to help facilitate downstream mixing. The first release above McNary Dam occurred on June 13, 2012, and
FIGURE 4. Schematic of releases (R) and detection arrays (dashed lines) used in the coordinated compliance studies conducted at four Columbia River hydropower projects, along with the reach survival to be estimated (S) and the numbers of subyearling Chinook Salmon in the release groups. Numbers of fish in the virtual releases (V) are shown in parentheses (rkm = river kilometer).
the last release below Bonneville Dam took place on July 22, 2012.

Acoustic signal processing.—Cabled hydrophone arrays were used at the dam faces, and autonomous hydrophone arrays were used within tailwaters. Coded transmissions from the AMT tags were recorded in raw data files on cabled arrays to allow for precise time synchronization of signals for 3D tracking; on autonomous arrays, transmissions from the tags were recorded as decoded signals. The files were periodically downloaded and processed to produce a data file of acceptable detection events. At the cabled arrays, detections from all hydrophones within a dam face array were combined for processing. Data filters were used to convert the AMT tag code receptions to detection events. A multipath filter eliminated redundant AMT tag signals due to reflection. A multiple-detection file retained receptions only if the same AMT tag code was received at another hydrophone in the same array within 0.3 s. The reasoning was that detections at separate hydrophones in the same cabled array within 0.3 s (i.e., \( \approx 450 \text{-m range} \)) were likely from the same AMT tag transmission. The PRI was considered within the range of transmission frequencies for the JSATS AMT tags. A detection event required at least six AMT tag codes to be received within 47.8 s (for the 3-s PRI tag) or within 32.2 s (for the 2-s PRI tag) depending on the tag lot. Autonomous receivers were processed separately from the cabled arrays and independently from other autonomous receivers. The multipath and PRI filters described above were applied to the autonomous receivers. The occurrence of at least four AMT tag signals within 47.8 s (for the 3-s PRI tag) or within 32.2 s (for the 2-s PRI tag) was required in order for an acoustic signal to be accepted as an AMT tag detection event at autonomous receivers.

Acoustic micro-transmitter tag life studies.—Two different AMT tag lots were used during the investigation (one for releases \( R_1\)–\( R_7 \) and another for releases \( R_8 \) and \( R_9 \)). The two lots of AMT tags differed in their signal PRIs; one lot had a 3-s PRI, and the other lot had a 2-s PRI. During AMT tag activation, 98–99 tags were systematically set aside from each tag lot for tag life studies. The AMT tags were placed in river water, activated, and monitored continuously until failure. The AMT tag life curves were subsequently fitted to each data set to provide AMT tag life corrections to the Cormack–Jolly–Seber (CJS) estimates of reach survival.

Releases of dead, tagged fish.—Dead fish into which active AMT tags had been surgically implanted were released below the spillway at each dam to assess the assumption that the first detection arrays used by the virtual release groups were far enough downstream to avoid false-positive detections due to fish that died during dam passage with active AMT tags. The spillway release locations were used because they were considered the hydraulic environment most likely to result in dead, tagged fish floating downstream. Between 30 and 41 dead fish with AMTs were released below each dam over the course of the investigation.

Statistical Methods

Estimates of dam passage survival.—Maximum likelihood estimation was used to estimate dam passage survival at each dam based on the virtual/paired-release design. The capture histories from all of the daily replicate releases (both daytime and nighttime) were pooled to produce reach survival estimates. A joint likelihood model was constructed as the product of multinomial distributions describing the capture histories of the separate release groups (e.g., \( V_1, R_2, \) and \( R_9 \)). If the virtual release group was composed of fish from multiple upstream release locations, then all fish were assumed to have common survival and capture processes but different tag life corrections. In the case of Bonneville Dam, the different tag lots used above and below the dam also had separately estimated tag life corrections.

The joint likelihood that was used to model the three release groups was initially fully parameterized. Each of the three releases was allowed to have unique survival and detection parameters downstream. If precision with the fully parameterized model was adequate (i.e., \( SE \leq 0.015 \)), as was the case here, then no further modeling was performed. Skalski et al. (2013) demonstrated that there is no precision advantage in using a reduced-parameter model when detection rates are very high, as occurs in studies using AMT-tagged fish. This approach preserves both the precision and the robustness of the estimation process. The tag life correction methods of Townsend et al. (2006) were used to adjust the perceived survival estimates from the CJS model for tag failure. All calculations were performed using Program ATLAS. The variance of \( \hat{S}_{\text{Dam}} \) was estimated in a two-step process (Seber 1982:9) that incorporated uncertainty in the tag life corrections and in the release–recapture processes.

Tag life analysis.—For each AMT tag lot, the four-parameter vitality model of Li and Anderson (2009) was fitted to the failure time data. The vitality model tends to fit AMT tag failure times well because it allows for early random failure due to manufacturing defects as well as the anticipated battery failure later on.

For \( V_1 \) based on fish that were known to have arrived at the dam face and with active AMT tags, the conditional probability of an AMT tag being active downstream given that the tag was active at the dam face was used in the tag life adjustment for that release group. The conditional probability of an AMT tag being active at time \( t_1 \) given that it was active at time \( t_0 \) was computed by the quotient

\[
P ( t_1 | t_0 ) = \frac{P ( t_1 )}{P ( t_0 )},
\]

where \( P(t_0) \) is the unconditional probability that the AMT tag was active when detected at the dam face detection array; and \( P(t_1) \) is the average unconditional probability that the AMT tag was active at a downstream detection site.

Tests of assumptions.—Several tests of assumptions were performed to ensure the validity of the release–recapture study. Downstream mixing of the release groups was examined at
shared downstream detection locations to assess whether the releases shared common survival processes. Subtle differences in handling and surgical implantation techniques can have an effect on the survival of AMT-tagged juvenile salmonids used in the estimation of dam passage survival. For this reason, surgeon effects were evaluated in two ways. First, contingency table tests were performed to assess the extent to which surgeon effort was balanced across release locations. For instance, an undetected surgeon effect concentrated in one of the release groups could bias the survival estimates. Second, the single release–recapture model was used to estimate reach survival for fish that received AMT tags implanted by different individuals. The analysis evaluated whether there was any consistent pattern of reduced reach survival among tagged fish in relation to the particular surgeon(s) that implanted the tags.

For \( k \) independent reach survival estimates, a test of equal survival was performed using the \( F \)-test,

\[
F_{k-1,\infty} = \frac{s^2_S}{\sum_{i=1}^k \text{Var}(\hat{S}_i | s)}
\]

where \( s^2_S = \sum_{i=1}^k (\hat{S}_i - \bar{S})^2/k - 1 \) with \( \bar{S} = \sum_{i=1}^k \hat{S}_i/k \).

Delayed tagging effects or time-dependent effects of tag burden could affect the formation of a virtual release group that is composed of fish from multiple upstream release locations. Consequently, downstream reach survival and cumulative release survival were compared among fish that were released from different upstream locations. The \( F \)-test (equation 2) was used to evaluate whether reach survival estimates were homogeneous regardless of upstream release locations. If heterogeneity was detected, the uppermost release groups with lower survival would be eliminated from the formation of the virtual release groups (i.e., \( V_1 - V_4 \)).

**RESULTS**

**Assumptions**

Assessment of the assumptions found that downstream mixing of all release groups was good. Figure 5 illustrates the downstream mixing of releases \( V_1, R_2, \) and \( R_3 \) associated with the study at McNary Dam. Comparable downstream mixing was observed at the other three dams. Of the 131 dead, tagged fish that were released at the four dam locations, none was detected downstream, suggesting that the locations of arrays for detecting releases \( V_1 - V_4 \) were far enough downriver to avoid false-positive detections.

Chi-square tests of homogeneity found that surgeon effort was balanced among release groups at all locations. No surgeon effects were detected based on tests of homogeneous survival for the fish that received AMTs implanted by the different surgeons.

**FIGURE 5.** Frequency distribution (proportion) plots of downstream arrival timing for subyearling Chinook Salmon releases (\( V_1 = \) virtual release [solid line]; \( R_2 \) and \( R_3 = \) paired releases [dotted and dashed lines, respectively]) at three detection arrays: (A) river kilometer (rkm) 422, (B) rkm 349, and (C) rkm 325 (see Figure 4). All times are adjusted relative to the release time of \( V_1 \).
Tests of delayed tag effects or time-dependent tag burden effects found no difference in downstream survival of releases \(R_1-R_7\), through rkm 234. This permitted all available fish to be used from the virtual releases at McNary, John Day, and The Dalles dams. However, mortality below Bonneville Dam was greater among releases \(R_1-R_3\) than among the other release groups. Consequently, we only used fish from upstream releases \(R_4-R_7\) when forming the virtual release group for Bonneville Dam.

**Tag life corrections.**—The vitality function of Li and Anderson (2009) fit the failure time data for both tag lots (Figure 6). For the JSATS AMT tags with a 3-s PRI, the average tag life was 23.3 d. For AMT tags with a 2-s PRI, the average tag life decreased to 15.0 d.

In all cases, the probability of an AMT tag being active at a downstream detection array was estimated to be greater than 0.99. Consequently, tag life corrections to the CJS survival estimates were relatively small.

**Estimates of Dam Passage Survival**

Separate analyses were performed to assess compliance with BiOp survival standards at each dam. The survival standard for subyearling Chinook Salmon was \(\hat{S}_{\text{Dam}}\) of at least 0.93 with an SE of 0.015 or less.

**McNary Dam.**—Survival for \(V_1\) through McNary Dam and 48 km of tailwater below the dam (see Figure 4; \(V_1\) to \(R_3\)) was estimated at 0.9149 (SE = 0.0057; Table 1). Survival from the tailrace mixing zone (see Figure 4; rkm 468) to the face of John Day Dam (rkm 349; i.e., through Lake Umatilla) was estimated from the \(R_2\) release as 0.8864 (SE = 0.0086). In turn, survival from rkm 422 to the face of John Day Dam (rkm 349) was estimated based on the \(R_1\) release and was 0.9443 (SE = 0.0066). Consequently, the virtual/paired-release design estimated dam passage survival through McNary Dam as

\[
\hat{S}_{\text{Dam}} = \frac{0.9149}{0.8864} = 0.9747 \quad (\text{SE} = 0.0114).
\]

In other words, survival through the dam, tailrace, and 46 km of tailwaters was estimated based on \(V_1\) as 0.9149 (SE = 0.0057). Survival below the dam in those extra 46 km of tailwaters, as estimated from the paired release (i.e., \(\hat{S}_2/\hat{S}_3\)), was 0.9387 (SE = 0.0112). This ratio then produced a dam passage survival estimate of 0.9747, which is above the BiOp standard for estimated survival and is associated with an SE less than 0.015.

**John Day Dam.**—Based on the virtual release \((V_2)\) composed of fish from releases \(R_1-R_3\) and the below-dam paired releases of \(R_4\) and \(R_5\), dam passage survival at John Day Dam was estimated as

\[
\hat{S}_{\text{Dam}} = \frac{0.9414}{0.9387} = 0.9747 \quad (\text{SE} = 0.0031).
\]

Unlike the McNary Dam study, very little (i.e., \(\approx 0\)) mortality was estimated for the extra 21 km of tailwaters below John Day Dam based on the releases \(R_4\) and \(R_5\). The paired-release survival point estimate for the reach below the dam (1.0041; SE = 0.0052) was set to 1.0, resulting in the dam passage survival estimate being equated to the survival of the \(V_2\) group through the dam and 24 km downstream.

**The Dalles Dam.**—The virtual release group at The Dalles Dam \((V_3)\) was composed of fish from releases \(R_1-R_3\) in conjunction with the below-dam releases of \(R_6\) and \(R_7\). In all cases, the probability of an AMT tag being active at a downstream detection array was estimated to be greater than 0.99. Consequently, survival estimates for the \(V_3\) group met the survival standard (\(\geq 0.93\)) without the help of the tailwater correction. Estimated survival through the downstream tailwaters was very high (i.e., 0.9949; SE = 0.0063).
TABLE 1. Survival estimates ($\hat{S}$; SE in parentheses) for the three release groups of subyearling Chinook Salmon (virtual release $V_1$ and paired releases $R_2$ and $R_3$; see Figures 3, 4) and the resulting estimates of dam passage survival ($\hat{S}_{\text{Dam}}$) at each of the four Columbia River hydropower projects that were included in the 2012 Juvenile Salmon Acoustic Telemetry System compliance study.

<table>
<thead>
<tr>
<th>Project</th>
<th>$\hat{S}_{V1}$</th>
<th>$\hat{S}_{R2}$</th>
<th>$\hat{S}_{R3}$</th>
<th>$\hat{S}_{\text{Dam}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>McNary</td>
<td>0.9149 (0.0057)</td>
<td>0.8864 (0.0086)</td>
<td>0.9443 (0.0066)</td>
<td>0.9747 (0.0114)</td>
</tr>
<tr>
<td>John Day</td>
<td>0.9414 (0.0031)</td>
<td>0.9966 (0.0033)</td>
<td>0.9925 (0.0039)</td>
<td>0.9414 (0.0031)</td>
</tr>
<tr>
<td>The Dalles</td>
<td>0.9420 (0.0028)</td>
<td>0.9886 (0.0048)</td>
<td>0.9937 (0.0041)</td>
<td>0.9469 (0.0059)</td>
</tr>
<tr>
<td>Bonneville</td>
<td>0.9693 (0.0031)</td>
<td>0.9953 (0.0063)</td>
<td>1.0037 (0.0050)</td>
<td>0.9739 (0.0069)</td>
</tr>
</tbody>
</table>

Bonneville Dam.—Indications of tag burden effects on release groups $R_1$–$R_3$ at or below Bonneville Dam resulted in the use of only releases $R_4$–$R_7$ in the formation of the virtual release group ($V_4$) for the Bonneville Dam study. The virtual release was coupled with the paired releases below the dam (i.e., $R_8$ and $R_9$) to estimate dam passage survival:

$$\hat{S}_{\text{Dam}} = \frac{0.9693}{0.9953} \frac{0.9693}{0.9953} = 0.9737 (SE = 0.0069).$$

Again, this study indicates relatively low mortality in the tailwaters. Furthermore, the $V_4$ survival estimate of 0.9693 (SE = 0.0031) meets the BiOp survival standard, despite including the survival effects from an additional 77 km below the project tailrace.

DISCUSSION

The successful completion of the 2012 subyearling Chinook Salmon compliance studies at the four main-stem Columbia River hydropower projects is only one element of evaluation efforts. Two consecutive trials at a dam must be successful (i.e., $\hat{S} \leq 0.93$; SE $\leq 0.15$) for a summer fish stock to meet dam passage survival standards. This was the case for subyearling Chinook Salmon at The Dalles and Bonneville dams. In 2010, dam passage survival was estimated to be 0.9404 (SE = 0.0091; Skalski et al. 2010a) at The Dalles Dam and 0.958 (SE = 0.0055; Ploskey et al. 2011) at Bonneville Dam. Additional survival trials with subyearling Chinook Salmon are currently scheduled for summer 2014 at the other two dams. Furthermore, the replicate trials must be performed in years when flows are in the middle 90% of the historical distribution of discharge values. Analogous compliance studies using yearling Chinook Salmon and steelhead stocks must also be performed during the spring out-migration.

In addition to the acoustic detection arrays illustrated in Figure 4, the study also included autonomous arrays in the forebay and tailrace mixing zones, typically 1–2 km above or below each dam. The autonomous arrays, along with the 3D array at each dam face, permitted specific passage route assignment, evaluation of fish behavior in three dimensions, and estimation of forebay residence time, tailrace egress time, spill passage efficiency (i.e., fraction of fish passing through the spillway) and forebay–tailrace survival. Collectively, these measures are known as the Fish Accords performance measures, and their purpose is to help ensure that fish passage performance through the dams does not degrade over time after the compliance testing is completed.

This performance-based approach to salmon recovery can be costly. The large tag–release sizes of the compliance studies are the result of tight precision requirements (i.e., $SE \leq 0.015$) and the need to use three release groups (e.g., $V_1$, $R_2$, and $R_3$) in order to isolate dam passage survival. However, coordinated multiple-dam investigations, as illustrated here, can reduce expenses. The compliance studies were performed at four dams using nine release locations instead of 12, resulting in a 25% reduction in fish tagging and related costs.

Under this performance-based approach, once compliance at a dam has been demonstrated, the test conditions become the planned dam operations within the limitations of available water and power demand. Subsequent changes in dam operations could require reevaluation, such as occurred at Rock Island Dam when spill was reduced from 20% to 10% (Skalski et al. 2012). However, in the lower Columbia River, hydrologic conditions could require reevaluation, such as occurred at Rock Island Dam when spill was reduced from 20% to 10% (Skalski et al. 2012). Consequently, dam operations, including spill targets, are subject to the vagaries of nature. In summer 2012, spill target levels were exceeded throughout the studies at McNary and Bonneville dams and were in excess at the beginning of the studies at John Day and The Dalles dams due to a high-flow year. Uncontrollable environmental factors can make test conditions difficult to achieve and will assuredly affect the planned operational conditions at a dam after compliance testing is completed. These uncertainties will be addressed, in part, by the multiple years of testing that are required to examine three fish stocks—at least twice each—at the eight federally operated dams. Between 2010 and 2012, 26 compliance tests were performed at six of the eight dams. Of these tests, 22 met the intended survival standard for the fish stock. Additional testing is scheduled through at least 2016. During these 7 years of scheduled testing, the range of river conditions will help to verify the robustness of the results. This large bank of tests will be used to determine the impact of dam operations on smolt out-migration success.
and will provide the necessary information to help prioritize and guide future recovery actions for the ESA-listed salmonid stocks in the Columbia River basin.

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Comparative Swimming Performance of Five Catostomus Species and Roundtail Chub

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PLEASE SCROLL DOWN FOR ARTICLE
Abstract.—Decreased habitat connectivity and competition with nonnative species have led to declines of many freshwater fishes. An understanding of swimming performance can aid in the conservation of these fishes; however, acquiring sufficient numbers of rare and threatened species to perform swimming studies can be logistically challenging and ecologically costly. In order to determine whether swimming data for common sucker species may be substituted for that of similar but rare sucker species, we compared the swimming abilities of two rare western catostomids, Bluehead Sucker *Catostomus discobolus* and Flannelmouth Sucker *C. latipinnis*, as well as one catostomid with a less well understood status, Mountain Sucker *C. platyrhynchus*, with those of the common White Sucker *C. commersonii* and Longnose Sucker *C. catostomus*. We also examined Roundtail Chub *Gila robusta* because they are often included in conservation efforts involving Bluehead Sucker and Flannelmouth Sucker. The critical swimming velocities (*U*<sub>crit</sub>), standardized by body length, of Bluehead Sucker and Longnose Sucker differed significantly from those of White Sucker. However, there was no significant difference between the *U*<sub>crit</sub> of Mountain Sucker, Flannelmouth Sucker, and White Sucker. During constant acceleration trials, Bluehead Sucker exhibited the greatest swimming ability, reaching a mean maximum velocity of 4.56 ± 1.28 body lengths per second (BL/s; mean ± SD), followed by Mountain Sucker (3.56 ± 0.57 BL/s), White Sucker (3.28 ± 0.90 BL/s), Longnose Sucker (2.97 ± 0.31 BL/s), and Flannelmouth Sucker (2.22 ± 0.42 BL/s). Additionally, key behavioral differences in the swimming behaviors of the fishes studied were observed. We conclude that swimming performance data for common White Sucker should not be used in place of data for rarer species. Comprehensive swimming studies should be conducted on individual sucker species before implementing conservation strategies involving fish passageways or barriers.

The Rocky Mountain region of the western USA is home to a variety of native catostomid species. However, some species, including Bluehead Sucker *Catostomus discobolus*, Flannelmouth Sucker *C. latipinnis*, and Mountain Sucker *C. platyrhynchus* have experienced decreases in range and population size (Bezzerides and Bestgen 2002; Compton 2007; Schultz and Bertrand 2012). Bluehead Sucker and Flannelmouth Sucker, along with Roundtail Chub *Gila robusta*, are classified by the Wyoming Game and Fish Department as native species status 1 (NSS1), or rare species with declining and vulnerable habitat, and are thus the subjects of a range-wide conservation agreement between Arizona, Colorado, Nevada, New Mexico, Utah, and Wyoming state fisheries agencies (Utah Department of Natural Resources 2006). These species are regionally referred to as the “three species” and managed as a species group rather than individually (Utah Department of Natural Resources 2006). White Sucker *C. commersonii* is common throughout the region and has been introduced into many habitats that were formerly...
restricted to the above-mentioned species. Longnose Sucker *C. catostomus* is an uncommon introduced sucker in many of the regions’ watersheds.

Catostomid populations throughout North America face declines resulting from a variety of factors including decreased habitat connectivity and hybridization with introduced species (Cooke et al. 2005). Within the Rocky Mountain region, human impacts, such as land use, nonnative fish introductions, habitat fragmentation, and altered flow regimes, are probable reasons for observed declines (Bestgen and Propst 1989; Martinez et al. 1994; Propst and Gido 2004; Bestgen et al. 2006; Compton et al. 2008). Introductions of nonnative fishes can affect native catostomids through predation (e.g., Burbot *Lota lota*), competition (e.g., Longnose Sucker), and hybridization (e.g., White Sucker) (Sweet and Hubert 2010; Gardunio et al. 2011).

Problems with habitat fragmentation may be resolved by the removal or modification of instream barriers to allow unrestricted up- and downstream movements by the catostomids. Conversely, the creation of instream barriers may impede invasions of nonnative fish into critical catostomid habitat. To design effective fish passage structures or barriers, it is critical to understand the different swimming abilities of target fish species (Hyde 2007). Different species of fish exhibit a variety of endurance levels, maximum swimming speeds, and unique swimming behaviors that affect their ability to pass different barrier sizes and configurations. Unfortunately, studies that evaluate the swimming abilities of fish in relation to passage capability often require large numbers of fish (e.g., 240 individuals per species: Ficke et al. 2011). Collecting large numbers of sensitive species such as Bluehead Sucker and Flannelmouth Sucker may be infeasible due to the challenge of locating healthy populations. In such cases, one possible alternative is to use a more common and closely related species as a surrogate, provided the species have similar swimming performances.

Suitable surrogate species may be identified through swimming ability studies that require fewer fish (e.g., ≤20 individuals per species: this study) than complete, passage-focused studies. The critical swimming methodology (*U* _crit_) approach is a commonly used test of aerobic swimming endurance that uses a stepped velocity increase (Brett 1964; Beamish 1978). Because of its standardized methodology and frequent usage, this method is ideal for interspecific comparisons. The *U* _crit_ does not, however, provide data that are directly applicable to fish passage or barrier design beyond a measurement of the maximum aerobic velocity a fish can maintain for a fixed amount of time. Comparisons using *U* _crit_ can also require fewer fish to produce statistically meaningful values than other methods such as fixed velocity tests to compare aerobic swimming endurance (Hammer 1995). The constant acceleration test (CAT; Reidy et al. 1995) method is shorter in duration and estimates a maximum velocity that is closer to the maximum sprinting speed of the fish (Farrell 2008); the top velocity in a constant acceleration test could be considered a sprinting velocity and would be powered by the fast-glycolytic (anaerobic) muscles. The CAT approach is also useful in identifying swimming gait transitions (e.g., from steady swimming to unsteady or burst-and-glide swimming).

The availability of Bluehead Sucker, Flannelmouth Sucker, and Mountain Sucker held for a captive rearing study presented us with a unique opportunity to conduct swimming ability tests on rare catostomid species. Our primary research goal was to determine whether the swimming performance and behavior of the more common White Sucker and Longnose Sucker are interchangeable with those of Bluehead Sucker, Flannelmouth Sucker, and Mountain Sucker using *U* _crit_ and CAT tests. The secondary goal of our study was to measure and compare the *U* _crit_ of the “three species”—Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub—to determine whether they have similar swimming performances or whether one species’ swimming performance could be the driving factor when designing fish-passage structures.

**METHODS**

*Fish sources and care.—* The White Suckers we used were collected using two Smith-Root LR-24 backpack electrofishers on May 7, 2012, from Spring Creek (South Platte River watershed: UTM zone 13T, 493071 E, 4490414 N, NAD83) in Fort Collins, Colorado. Thirty-six White Suckers were transferred to a 416-L rectangular tank receiving constant flows of aerated well water at the Colorado State University Foothills Fisheries Laboratory (FFL). They were then tempered to the test temperature (8.0°C) from the stream temperature of Spring Creek (10.4°C) over 1 h. The fish were allowed to acclimate to the laboratory environment and study temperature for 25 d. The White Suckers were fed frozen bloodworms to satiation and were visually checked for signs of stress (abnormal coloration, behavior, or an unwillingness to feed) or disease daily. Several fish exhibited stress-indicative coloration and others did not respond to food for several days after being brought into the laboratory, but all fish appeared healthy and were actively feeding at least 2 weeks before we began conducting trials.

All other fishes used were provided by the Wyoming Game and Fish Department (WYGF). These fishes were part of an ongoing captive-holding and growth study being conducted by WYGF at the University of Wyoming Red Buttes Environmental Biology Laboratory (RBEBL); because this was their primary use, there was little emphasis on collecting fish of similar size. Longnose Suckers (*n* = 65) were collected by backpack electrofishing from the inlet of North Crow Reservoir (South Platte River watershed: UTM zone 13T, 484121 E, 4563317 N, NAD83) northeast of Laramie, Wyoming, on June 3, 2010. Mountain Suckers (*n* = 161) were collected by backpack electrofishing from Littlefield Creek (Little Snake River watershed: UTM zone 13T, 296466 E, 4591709 N, NAD83) near Rawlins, Wyoming. Bluehead Suckers (*n* = 50) were collected with trap nets from Ringdal Reservoir (Green River watershed: UTM zone 12T, 587468 E, 4556642 N, NAD83) near Green River, Wyoming, on August 10, 2010. Flannelmouth Suckers were...
collected from the Little Sandy River (Green River watershed: UTM zone 12T, 641532 E, 4684090 N, NAD83), also near Green River, Wyoming, on two occasions in 2011 (August 18, \( n = 6 \); October 1, \( n = 51 \)) by backpack electrofishing. Roundtail Chub were collected from Muddy Creek (Little Snake River watershed: UTM zone 13T, 269755 E, 4590969 N, NAD83) on two occasions in 2011; 10 were collected on July 14, and 40 were collected on October 19.

After collection, all fish were transported directly to the RBEBL in purpose-built fish-hauling tanks. Before transport, hauling tanks were filled with water from a hatchery or dechlorinated municipal water source. The use of water from these sources reduced the likelihood of transporting invasive invertebrates, vertebrates, plants, or disease pathogens in water from the collection site. Water in the hauling tank was kept cool and was added, when necessary, to maintain a temperature similar to that at RBEBL. Salt was dissolved in the stocking tanks (1% NaCl concentration by water weight) to reduce hauling stress and as a prophylactic treatment for external parasites. All fish were initially held in 1.2-m-diameter circular tanks; however, Longnose Suckers and Mountain Suckers were moved to separate 0.6-m-diameter tanks on June 7, 2011, and held at initial densities of 20.7 and 6.4 kg/m³, respectively. The Bluehead Suckers were moved to a 4.6-m-long rectangular tank shortly after entering the laboratory and were held at a density of 1.6 kg/m³. The Flannelmouth Suckers were split into two 1.2-m-diameter circular tanks and held at a density of 7.9 or 9.5 kg/m³. The Roundtail Chub were held in a 0.6-m-diameter circular tank. All fish were held at low densities and the holding arrangement was determined by available circular tanks at RBEBL. All fish were monitored for signs of stress and disease throughout the time they were held in the laboratory. It is important to note that the original collection of all species other than the White Sucker was done for an unrelated study, and thus there was no emphasis placed on collecting a wide range of total lengths, as was done for the White Sucker.

The suckers used were identified upon capture by personnel experienced in catostomid fish identification using meristic counts and morphometric characteristics to phenotypically identify the fish to species. Additionally, Bluehead Suckers from Ringdal Reservoir, Flannelmouth Suckers from Little Sandy Creek, and Roundtail Chub from Muddy Creek have been analyzed for genetic purity during previous studies (Douglas and Douglas 2007a, 2007b; Gelwicks et al. 2009). Bluehead Suckers from Ringdal Reservoir are isolated from White Suckers and are 100% genetically pure. While hybridization of Flannelmouth Suckers with White Suckers from Little Sandy Creek does occur, it was determined that phenotypic identification, when compared with genotypic identification, was correct for 99% of Bluehead Suckers and 86% for Flannelmouth Suckers (Gelwicks et al. 2009). Also, the accuracy of these identifications for a subsample of the suckers held for this study was confirmed genetically using high-throughput DNA sequencing and analysis of genetic clustering (E. Mandeville, University of Wyoming, personal communication). Based on the genetic analyses, visual identification was found to be 100% accurate for the fish we used for the swimming trials.

The water source at the RBEBL is a natural spring supplying water that ranges between 6.1°C and 7.8°C, and all tanks were supplied by this source. All suckers at the RBEBL were offered a daily diet consisting of algae wafers, algae plates (natural algal cultures on Plexiglas plates), and two pellet diets specifically formulated for June Sucker Chasmistes liorus and Razorback Sucker Xyrauchen texanus at the U.S. Fish and Wildlife Service’s Bozeman Fish Technology Center, Bozeman, Montana. They are commercially produced by Skretting USA (Tooele, Utah) and are the primary diets for hatchery-reared June Suckers and Razorback Suckers. Roundtail Chub were offered daily rations of June Sucker and Razorback Sucker pellets and frozen bloodworms.

Swimming protocol.—All swimming trials (at both the RBEBL and FFL) were conducted in the same 90-L swim tunnel (model 90, Loligo Systems, Tjele, Denmark). In both locations, the swim tunnel was supplied with air-saturated, flow-through water (ca. 0.5–1.0 L/min) from the same source that supplied the fish-holding tanks. Water velocity in the swim tunnel is directly related to the frequency output of the variable speed motor, as displayed on the digital motor controller. We calibrated the flume prior to conducting swimming trials by measuring the water velocity as a function of motor controller output and developed a calibration curve that allowed repeatable velocity settings.

A random catostomid species was selected daily for all catostomid \( U_{\text{crit}} \) and CAT trials conducted at the RBEBL. The swim tunnel was disinfected overnight with Virkon Aquatic (Western Chemical) prior to each swimming session involving a different species to prevent disease transmission between species. The \( U_{\text{crit}} \) trials were conducted with 18 Bluehead Suckers (13.1–37.4 cm TL), 13 Flannelmouth Suckers (25.6–34.4 cm TL), 18 Longnose Suckers (12.7–35.8 cm TL), 22 Mountain Suckers (9.7–16 cm TL), 20 White Suckers (10.6–26.5 cm TL), and 20 Roundtail Chub (11.5–25.9 cm TL). Ten constant acceleration trials using each species were also conducted.

For each trial, a fish was selected at random from the appropriate holding tank and measured (SL, FL, and TL in centimeters, wet weight in grams). The fish was then placed in the swim tunnel, an opaque black screen was placed over the forward portion of the swim chamber to provide cover and encourage rheotaxis, and the velocity was set to 0.5 body lengths per second (BL/s; based on TL) for \( U_{\text{crit}} \) trials, or 10 cm/s for CAT experiments. Velocity increases were started after the >1-h recovery period. For \( U_{\text{crit}} \) trials, the velocity was increased by 0.5 BL/s every 10 min. Velocity steps were related to fish TL to account for the varied size distributions among the different species (Table 1). For the constant acceleration trials, fish were first subjected to an immediate velocity increase from 10 to 40 cm/s, and then the velocity was subsequently increased by 4 cm/s every 24 s, producing an acceleration rate of 10 cm s⁻¹ min⁻¹.
All fish were kept under constant remote observation during the trials for proper swimming behavior using a video camera and monitor. Fish often “cheated” by resting against the rear mesh of the swim chamber. When this occurred, the current was either momentarily reversed or pulsed (rapid upwards increase of 10–15 cm/s for <10 s) and returned to the test velocity to encourage the desired swimming behavior. If fish were able to hold a static, nonswimming position at lower velocities through fin and mouth placement the behavior was allowed, as it is a natural behavior employed by some species in flowing environments. Trials were terminated when the fish either became impinged on the rear mesh, or would no longer hold position in the swim chamber without resting against the rear mesh, after four consecutive attempts to restore normal swimming or holding behavior with the techniques described above.

The numbers of fish tested per species for the \( U_{\text{crit}} \) and CAT trials varied because of the limited availability of some of the species. We tested at least 13 individuals per species for the \( U_{\text{crit}} \) trials and 10 fish per species for the CAT experiments (Tables 1, 2).

Digital video of each trial was recorded with a GoPro Hero 2 HD camera (GoPro Products) for later analyses. After each trial, fish were removed from the swim tunnel, lightly anesthetized in a 25-mg/L solution of tricaine methanesulfonate (MS-222), weighed, marked with a small pelvic fin clip to eliminate repeated trials, and returned to their respective holding tank. No fish were used in more than one CAT or \( U_{\text{crit}} \) trial.

Data analyses.—All individual \( U_{\text{crit}} \) values were calculated using

\[
U_{\text{crit}} = U_i + \left( \frac{T_i}{T_{ii}} \right) U_{ii}
\]

Brett (1964), where \( U_i \) is the highest velocity that the fish was able to maintain for the whole time increment, \( U_{ii} \) is the velocity increment (0.5 BL/s), \( T_i \) is the time elapsed at the terminal velocity increment, and \( T_{ii} \) is the time increment between velocity steps (10 min). Relative \( U_{\text{crit}} \) estimates (i.e., length-adjusted \( U_{\text{crit}} \)) were created for each fish by dividing the \( U_{\text{crit}} \) by the TL of individual fish. Comparisons of both of these values were then made among all sucker species and among Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub.

All statistics were calculated using JMP version 5.0 (SAS Institute, Cary, North Carolina). Differences in TL, wet weight, length, weight, and least-squares (LS) means calculated from relative critical swimming velocities regressions for the \( U_{\text{crit}} \) study on Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, Mountain Sucker, White Sucker, and Roundtail Chub. Identical lowercase letters indicate equivalences between the five catostomid species, while identical uppercase letters indicate equivalences among Bluehead Suckers, Flannelmouth Suckers, and Roundtail Chub. Values are means \( \pm \) SDs.

### TABLE 1. Temperature, length, weight, and least-squares (LS) means calculated from relative critical swimming velocities regressions for the \( U_{\text{crit}} \) study on Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, Mountain Sucker, White Sucker, and Roundtail Chub. Identical lowercase letters indicate equivalences between the five catostomid species, while identical uppercase letters indicate equivalences among Bluehead Suckers, Flannelmouth Suckers, and Roundtail Chub. Values are means \( \pm \) SDs.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size (n)</th>
<th>Holding temperature ( ^{\circ} \text{C} )</th>
<th>Test temperature ( ^{\circ} \text{C} )</th>
<th>TL (cm)</th>
<th>Wet weight (g)</th>
<th>LS mean of ( U_{\text{crit}} ) (BL/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bluehead Sucker</td>
<td>18</td>
<td>7.8 ( \pm ) 0.05 yZ</td>
<td>7.8 ( \pm ) 0.06 zZ</td>
<td>20.2 ( \pm ) 7.19 yxY</td>
<td>118.9 ( \pm ) 153.43 zyZY</td>
<td>3.3 zZ</td>
</tr>
<tr>
<td>Flannelmouth Sucker</td>
<td>13</td>
<td>7.5 ( \pm ) 0.10 xX</td>
<td>7.8 ( \pm ) 0.04 yZ</td>
<td>29.5 ( \pm ) 2.80 zZ</td>
<td>192.5 ( \pm ) 53.69 zZ</td>
<td>2.8 zyxZ</td>
</tr>
<tr>
<td>Longnose Sucker</td>
<td>18</td>
<td>7.7 ( \pm ) 0.10 y</td>
<td>7.8 ( \pm ) 0.08 z</td>
<td>23.9 ( \pm ) 6.05 y</td>
<td>185.2 ( \pm ) 143.73 z</td>
<td>2.6 y</td>
</tr>
<tr>
<td>Mountain Sucker</td>
<td>22</td>
<td>7.7 ( \pm ) 0.08 y</td>
<td>7.8 ( \pm ) 0.12 z</td>
<td>13.0 ( \pm ) 2.01 w</td>
<td>26.3 ( \pm ) 12.07 x</td>
<td>2.4 zyx</td>
</tr>
<tr>
<td>White Sucker</td>
<td>20</td>
<td>8.0 ( \pm ) 0.26 z</td>
<td>7.6 ( \pm ) 0.41 y</td>
<td>17.4 ( \pm ) 5.46 x</td>
<td>69.8 ( \pm ) 61.43 yx</td>
<td>1.9 x</td>
</tr>
<tr>
<td>Roundtail Chub</td>
<td>20</td>
<td>7.6 ( \pm ) 0.06 Y</td>
<td>7.7 ( \pm ) 0.05 Y</td>
<td>16.7 ( \pm ) 3.96 Y</td>
<td>47.8 ( \pm ) 35.20 Y</td>
<td>2.1 Y</td>
</tr>
</tbody>
</table>

**ANOVA P-value comparison**

- Catostomid comparison: \(<0.0001\) 0.0128 \(<0.0001\) \(<0.0001\)
- “three species” comparison: \(<0.0001\) \(<0.0001\) \(<0.0001\) \(<0.0006\)

### TABLE 2. Comparison of the maximum velocities reached by five species of western intermountain suckers when tested using a constant acceleration trial protocol. Values are means \( \pm \) SDs; letters indicate statistically significant differences between the five sucker species \( (n = \text{sample size}) \).

<table>
<thead>
<tr>
<th>Species</th>
<th>( n )</th>
<th>Test temperature ( ^{\circ} \text{C} )</th>
<th>TL (cm)</th>
<th>Wet weight (g)</th>
<th>Maximum velocity reached (cm/s)</th>
<th>Maximum velocity reached (BL/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Longnose Sucker</td>
<td>10</td>
<td>7.6 ( \pm ) 0.05 yx</td>
<td>23.8 ( \pm ) 2.89 y</td>
<td>149.6 ( \pm ) 52.8 yz</td>
<td>70.8 ( \pm ) 11.4 y</td>
<td>2.97 ( \pm ) 0.31 yx</td>
</tr>
<tr>
<td>Mountain Sucker</td>
<td>10</td>
<td>7.7 ( \pm ) 0.0 zyx</td>
<td>13.8 ( \pm ) 2.22 w</td>
<td>30.6 ( \pm ) 15.6 y</td>
<td>48.2 ( \pm ) 6.14 x</td>
<td>3.56 ( \pm ) 0.57 y</td>
</tr>
<tr>
<td>White Sucker</td>
<td>10</td>
<td>7.6 ( \pm ) 0.36 x</td>
<td>17.3 ( \pm ) 5.02 xw</td>
<td>65.1 ( \pm ) 58.6 y</td>
<td>53.2 ( \pm ) 5.35 x</td>
<td>3.28 ( \pm ) 0.90 y</td>
</tr>
<tr>
<td>Bluehead Sucker*</td>
<td>10</td>
<td>7.9 ( \pm ) 0.14 z</td>
<td>21.7 ( \pm ) 7.89 yx</td>
<td>134.9 ( \pm ) 196.3 y</td>
<td>91.7 ( \pm ) 16.3 z</td>
<td>4.56 ( \pm ) 1.28 z</td>
</tr>
<tr>
<td>Flannelmouth Sucker*</td>
<td>10</td>
<td>7.9 ( \pm ) 0.05 zy</td>
<td>32.2 ( \pm ) 4.33 z</td>
<td>283. ( \pm ) 142.1 z</td>
<td>70.8 ( \pm ) 13.6 y</td>
<td>2.22 ( \pm ) 0.42 x</td>
</tr>
</tbody>
</table>

*Designated as “three species” suckers.
holding temperatures, and trial temperatures among species were compared among species with one-way ANOVA. Linear models were used to test for species, fish length (using TL), and interaction effects on absolute $U_{\text{crit}}$ and the relative $U_{\text{crit}}$ across the different catostomid species and for the “three species.” When significant differences ($P < 0.05$) were indicated, Tukey’s post hoc analyses were used to identify treatment means that were significantly different from others.

We plotted fish TL versus absolute and relative $U_{\text{crit}}$ and used linear regression to fit lines to the resulting plots. The same approach was used to illustrate the relationship between the five sucker species’ TL and their gait transition velocities. Finally, we graphically compared the relationship between TL and the $U_{\text{crit}}$ and $U_{\max}$ of the five sucker species using this same approach, albeit with logarithmic lines of best fit.

Videos of the critical swimming trials were analyzed to identify gait transitions. The transitions and endpoints of interest were the maximum station-holding velocity ($U_{\text{SH-max}}$), maximum aerobic swimming velocity (the transition from steady to burst swimming; $U_{\text{A-max}}$), and maximum (impingement) velocity ($U_{\max}$). The $U_{\text{SH-max}}$ was identified as the highest velocity at which fish could maintain position without any backward slippage, to account for exploratory and velocity-refuge-seeking behaviors that occurred throughout earlier portions of the trial. Each of these transition velocities were then plotted against TL. Analyses of variance and Tukey’s analyses were also used to compare the fish lengths (TL), wet weight, holding temperatures, and trial temperatures of the CAT trials. We observed an interesting behavior in some species wherein the high-friction surface of the lips was used to aid station-holding ability. We refer to this behavior as mouth holding. To provide a quantitative measure of this behavior among species, the total time that the behavior was employed and the maximum velocity at which it was effective were also recorded.

**RESULTS**

**Critical Swimming Speed**

*Catastomid comparison.*—Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, and Mountain Sucker all exhibited significantly different critical swimming velocities across a range of sizes (Table 1; Figure 1), and differences in the way that critical swimming velocity changed with size, as shown by the varying slopes of the regression lines in Figure 1. The effects of species ($P < 0.0001$) and TL ($P = 0.0057$) on $U_{\text{crit}}$ were both significant; however, the interaction effect between species and TL on $U_{\text{crit}}$ was not significant. Similarly, the effects of species ($P < 0.0001$) and TL ($P < 0.0001$) on relative $U_{\text{crit}}$ were again significant, but the interaction was not. There were significant differences in both test and holding temperatures among the five sucker species, though they were all within $0.5^\circ \text{C}$ of each other (Table 1). There were significant differences in both TL and wet weight among all five species (Table 1).
All suckers, with the exception of Flannelmouth Sucker, showed definite length versus $U_{\text{crit}}$ relationships, wherein larger fish achieved higher absolute $U_{\text{crit}}$, but lower relative $U_{\text{crit}}$ (Figure 1). However, the effect of TL on $U_{\text{crit}}$ was only significant for Bluehead Sucker ($P = 0.0500$), Mountain Sucker ($P = 0.0229$), and White Sucker ($P = 0.0004$). The effect of TL on the relative $U_{\text{crit}}$ (BL/s) was significant for Bluehead Sucker ($P < 0.0001$), Flannelmouth Sucker ($P = 0.0407$), and Longnose Sucker ($P = 0.0003$). There was an apparent, but not significant, negative relationship between $U_{\text{crit}}$ and TL for Flannelmouth Sucker (Figure 1). Based on the TL versus relative $U_{\text{crit}}$ linear relationship least-squares means, only Bluehead Sucker and Longnose Sucker were significantly better swimmers than White Sucker, while Flannelmouth Sucker and Mountain Sucker did not significantly differ from any other species (Table 1).

Three-species comparison.—When comparing Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub, there was a significant species effect on both $U_{\text{crit}}$ ($P < 0.0001$) and relative $U_{\text{crit}}$ ($P < 0.0001$). Among all three species, there was only a significant length (TL) effect on relative $U_{\text{crit}}$ ($P < 0.0001$; Table 1). The interaction effect was not significant for either model. As with the catostomid $U_{\text{crit}}$ comparison, there were significant differences in TL, wet weight, and both holding and test temperatures among all species (Table 1).

Similar to the suckers studied, except for Flannelmouth Sucker, Roundtail Chub showed a significant positive relationship between TL and $U_{\text{crit}}$ ($P = 0.0500$), and a significant negative relationship between TL and the relative $U_{\text{crit}}$ ($P < 0.0001$). Bluehead Sucker appeared to again have the highest overall relative $U_{\text{crit}}$, and Roundtail Chub the lowest. Based on the least-squares means generated from the linear relationships between TL and relative $U_{\text{crit}}$, Bluehead Sucker were significantly faster swimmers than Roundtail Chub; however, Flannelmouth Sucker were not significantly different from either species (Table 1).

**Constant Acceleration**

The constant acceleration experiments provide information on the maximum relative swimming velocities of the five sucker species. The fastest of the sucker species was the Bluehead Sucker, followed by the Mountain Sucker, White Sucker, Longnose Sucker, and the Flannelmouth Sucker (Table 2). Interestingly, while the Bluehead Sucker was also the fastest species in the critical swimming velocity trials, the order of the remaining species is different. The three major swimming categories used by the suckers were station holding, steady (aerobic) swimming, and burst-and-glide (anaerobic or unsteady) swimming. For all fish, all transition velocities appeared to increase with TL; however, the relationships were not significant (Figure 2). The transitions did not always follow the expected trend wherein fish would move from station holding to steady swimming, to burst-and-glide swimming, and finally become impinged at the $U_{\text{max}}$. Bluehead Sucker and Mountain Sucker transitioned from steady to burst-and-glide swimming at velocities lower than the $U_{\text{SH-max}}$, while, according to the relationship between TL and $U_{\text{crit}}$, Flannelmouth Sucker reached $U_{\text{max}}$ before $U_{\text{A-max}}$. For White Sucker, the trend appears as expected for smaller fish, but then is essentially reversed for larger fish. We also noted that the relative $U_{\text{max}}$ was always higher than the relative $U_{\text{crit}}$ for fish of similar size (Figure 3).

The constant acceleration trials showed distinct differences in swimming behavior among the five sucker species. Station holding was used more frequently by Bluehead Sucker, Flannelmouth Sucker, and Longnose Sucker than by Mountain Sucker and White Sucker, but Mountain Sucker used station holding more frequently than White Sucker (Table 3). Also, two different types of station holding were observed. Fish either used simple fin placement and body form to maintain position on the swimming chamber floor or walls, or they used the high friction surface of their lips and possibly suction to increase their ability to maintain a static position. Bluehead Sucker used mouth holding most frequently and at much higher velocities than other species (Table 3). The other sucker species tested used limited mouth holding, with the notable exception of White Sucker, which was not observed to employ the behavior (Table 3).

**DISCUSSION**

This comparative study on the aerobic and anaerobic swimming performance of catostomid fishes found in the

### TABLE 3. Relative frequencies of different swimming behaviors for five species of suckers in the U.S. intermountain region.

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of fish that exhibited station holding</th>
<th>Proportion of fish that exhibited mouth holding</th>
<th>Mean ± SD percentage of whole trial spent mouth holding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bluehead Sucker</td>
<td>1.0</td>
<td>1.0</td>
<td>45.0 ± 21.1</td>
</tr>
<tr>
<td>Flannelmouth Sucker</td>
<td>0.9</td>
<td>0.5</td>
<td>3.6 ± 5.2</td>
</tr>
<tr>
<td>Longnose Sucker</td>
<td>0.9</td>
<td>0.8</td>
<td>4.2 ± 2.9</td>
</tr>
<tr>
<td>Mountain Sucker</td>
<td>0.7</td>
<td>0.7</td>
<td>8.7 ± 8.6</td>
</tr>
<tr>
<td>White Sucker</td>
<td>0.2</td>
<td>0.0</td>
<td>0 ± 0</td>
</tr>
</tbody>
</table>
FIGURE 2. Constant acceleration trial gait transition velocities (grey circles = maximum station-holding velocity, grey squares = steady swimming to burst swimming transition velocity, and solid triangles = impingement velocity) plotted against TL for Bluehead Sucker, Flannelmouth Sucker, Longnose Sucker, Mountain Sucker, and White Sucker (BHS, FMS, LNS, MTS, and WHS, respectively). Lines represent linear lines of best fit.
U.S. Intermountain region revealed substantial species-level differences in aerobic and anaerobic swimming ability and in swimming behavior. These interspecific differences suggest that natural resource managers should carefully evaluate whether data from one sucker species could be used as a surrogate for another species. This approach might work when substituting performance data from a slower species, like White Sucker, for that of a faster species, like Bluehead Sucker, when designing a fish passage structure, but the same substitution might be ill-advised when designing a velocity barrier.

The experiments showed that the five sucker species tested represent a continuum of aerobic swimming ability, with Bluehead Sucker reaching the highest aerobic velocities when tested at temperatures of 7.5–8.0°C, followed by Flannelmouth Sucker.
Longnose Sucker, Mountain Sucker, and White Sucker. While we did observe significant differences among holding and test temperatures, the temperature ranges were small (0.5°C and 0.2°C, respectively), and were probably not biologically significant. The differences between the five species are such that they could be placed into three overlapping groups: the fast-swimming Bluehead Sucker and Flannelmouth Sucker, the medium-speed Flannelmouth Sucker, Longnose Sucker, and Mountain Sucker, and the slow-swimming Mountain Sucker and White Sucker. This overlapping performance illustrates the challenge with using performance data from one sucker species when designing an instream barrier or passage structure for another species.

The designer of a fish passage structure could use a conservative approach and substitute data from one of the “slow-swimming” species, like a White Sucker, to establish design criteria for a structure designed to pass a fast-swimming species, like a Bluehead Sucker. The designer could be fairly confident that Bluehead Sucker in the same size range as the White Sucker (10.6–26.5 cm TL) from which the performance data were gathered would be capable of successfully passing the structure. Conversely, trying to use the same data to design an instream fish barrier would not be recommended, because of the substantial difference in performance between the two species, and because one generally wants to prevent passage of 100% of the target species, not just the average member of that species. However, fish trying to negotiate a potential barrier tend to use their fast-glycolytic or anaerobic muscles, so it is important that those values also be considered.

In terms of anaerobic swimming or sprinting ability, the study also showed a continuum of top velocities among the five species, though the order was somewhat different. Therefore, from a barrier design point of view, using performance data from one of the slower species (e.g., Flannelmouth Sucker) to establish critical barrier velocities might result in a barrier that fails to prevent the upstream movement of a faster species. This is because they can either achieve a higher sprinting velocity or can maintain an equivalent velocity for a longer period of time (endurance at velocities above aerobic levels was not quantified in this study). Not only do the different sucker species have different aerobic and anaerobic swimming abilities, they also display different swimming behaviors, which would further complicate any attempts to use data interchangeably between species.

The swimming behaviors of the five species of sucker were notably different, and again formed a continuum from species wherein all individuals used some form of station-holding behavior (Bluehead Sucker) to White Sucker, where only 20% of tested fish used station-holding behavior. Interestingly, more than 50% of the individual fish in every sucker species tested except White Sucker used station-holding behavior and perhaps gained some energetic advantage by doing so. Fishes that can hold their position in the swimming flume without using their trunk musculature to do so presumably expend less energy than those that use active swimming to maintain position. Thus, one possible reason for the relatively poor performance of the White Sucker in the critical swimming velocity experiments relative to the other species is simply that, unlike the other species, most of the White Suckers swam continuously and thus expended their aerobic energy more quickly. This may also explain why Bluehead Suckers were able to clearly outperform the other four species, given that they spent an average of 45% of their time using station-holding behaviors. From a management standpoint, these differences in swimming behavior deserve consideration when designing passage and barrier structures. Fish that use station holding would be more capable of ascending an instream structure because they would be able to use nonswimming behaviors to hold their position to rest, whereas species that swim continuously would find the same ascent more energetically costly and might fatigue before successfully completing passage.

When viewed individually, the five sucker species generally showed the expected relationships between swimming performance and fish size, where larger fish reached higher absolute swimming velocities, while smaller fish reached higher relative swimming velocities. The one exception to this was the Flannelmouth Sucker, which did not show a significant positive relationship between TL and critical swimming velocity. This likely results from the lack of a wide range of tested sizes (TL range, 25.6–34.4 cm) rather than representing the first documented case of length-independent swimming ability. The different slopes of the regression lines showing the relationship between fish size and relative swimming ability provide further evidence for the contention that sucker swimming ability cannot be readily interchanged between species. Species such as the Bluehead Sucker show a much more rapid decline in performance than do species like White Sucker, though the reason for this difference is not known.

Our results compare favorably with data from other sources. Ficke et al. (2012) measured mean relative \( U_{\text{crit}} \) values ranging from 1.8 to 2.5 BL/s for White Suckers 90–158 mm TL, acclimated to 15°C and also from Spring Creek in Fort Collins, Colorado. The performance of White Suckers of similar size used in this study falls within the same range, suggesting that \( U_{\text{crit}} \) is a repeatable measure for this species. Flannelmouth Suckers from 105 to 123 mm TL swum at 10°C had a mean \( FV_{50} \) (velocity at which 50% of individuals cannot swim for a full 30 min) of 38.3 cm/s (Ward et al. 2002). This value is similar to the \( U_{\text{crit}} \) for Mountain Suckers of the same size that we evaluated. This suggests that smaller Flannelmouth Suckers also have a higher \( U_{\text{crit}} \) than smaller White Suckers. Ward et al. (2003) used a swimming procedure with a stepwise increase in velocity similar to the CAT trials used in our study and found that the average maximum velocity reached for Bluehead Suckers 61.5–81.5 mm TL was 86.62 cm/s. This velocity corresponds well with the predicted values for impingement velocity of 60–80-mm fish that we measured.

The so-called “three species” (Bluehead Sucker, Roundtail Chub, and Flannelmouth Sucker) co-occur in parts of the upper
Colorado River system and are often the subject of multispecies management efforts, so comparisons of their swimming abilities are appropriate. Bluehead Sucker was the fastest species, followed by the Flannelmouth Sucker and the Roundtail Chub when relative aerobic swimming ability was compared. As one might expect, the two sucker species were able to use station holding during the $U_{\text{crit}}$ experiments, while the Roundtail Chub swam continuously and did not attempt to do so. Myrick and Cech (2000) reported a similar phenomenon in a study comparing the swimming performance of Sacramento Suckers C. occidentalis with that of three large-bodied cyprinids native to California. Interestingly, another large cyprinid, the Sacramento Splittail Pogonichthys macrolepidotus, has been reported as using oral grasping to hold position in swimming flumes (Young and Cech 1996), so perhaps our flumes did not provide an appropriate surface for Roundtail Chub to display such behavior.

The sprinting abilities of Roundtail Chub were not tested, so it is not possible to speculate on whether they would still be slower swimmers than the two sucker species. Nevertheless, if Roundtail Chub aerobic performance data were used to design a fish passage structure, it is likely that such a structure would be passable for the two sucker species. Realistically, it is unlikely a passage structure would be designed with such low velocities (~35 cm/s), so the measurement of Roundtail Chub performance at fixed velocities above their maximum aerobic speed is recommended. The ideal approach for designing such structures would be to first conduct laboratory tests of potential fishway designs to determine how the combinations of swimming ability and swimming behavior interact to affect passage success. The second step would be to conduct field trials using some form of telemetry (e.g., PIT-tagged fish and antenna arrays built into the test fishways) to measure field swimming performance. Castro-Santos (2004) suggests that laboratory studies often underestimate true swimming performance.

Our $U_{\text{crit}}$ study offers an estimation of the sustained swimming ability of the five sucker species. The $U_{\text{crit}}$ value theoretically represents the velocity that a fish could maintain for long periods of time (Brett 1964). However, it may often be infeasible to design a passage structure with a gentle enough slope to produce these low velocities (Katopodis 2005). Luckily, fish can typically reach substantially higher velocities than their $U_{\text{crit}}$ velocities. The constant acceleration test offers a better estimation of the maximum velocity a fish can achieve (impingement velocity), but this is still an underestimation of maximal sprinting velocity because the process of accelerating to the maximum velocity fatigues the fish, limiting its performance at higher velocities (Farrell 2008). There are other limitations to using $U_{\text{crit}}$ alone in fishway design such as different designs may have better attraction and induce passage attempts with greater frequency (Castro-Santos 2004).

Additionally, we only tested the performance of the five sucker species and Roundtail Chub under one set of environmental conditions. Temperature is directly linked to swimming performance, and fish generally have a temperature range where performance is maximized (Beamish 1978; Batty and Blaxter 1992). If these fishes had been tested at higher temperatures (within the species’ preferred thermal ranges) it is likely that swimming velocities and stamina would also have increased. For instance, Ward et al. (2002) found a 40% increase in the swimming ability of Flannelmouth Suckers between 10°C and 20°C. However, Myrick and Cech (2000) reported that the critical swimming velocities of 19–20-cm TL Sacramento Suckers tested at 10, 15, and 20°C were temperature independent and point out that of the fishes tested in their study Sacramento Suckers occupy the widest elevational and latitudinal gradients and thus may have a broader thermal range over which their swimming performance is optimized.

Our results may also have been influenced by the unavoidable necessity of using fish that had been held under laboratory conditions for different time intervals prior to testing. The swimming performance of certain catostomids can decrease in association with long periods of time between the time when the fish are captured and the swimming tests are conducted (Ward et al. 2002). However, because White Suckers spent the shortest amount of time (25 d) in the laboratory prior to study yet still exhibited relatively poor swimming ability compared with other species that were held for much greater amounts of time (1–2 years), we remain confident in the trends observed wherein White Sucker critical swimming velocity was consistently lower than that of the other sucker species.

While our study does provide useful information on the relative abilities of the five tested sucker species and Roundtail Chub, it should be viewed as a pilot study. A more thorough evaluation of swimming performance should be conducted on each of the five sucker species to better inform fishway or barrier design. This future study should combine measurements of swimming endurance at fixed velocities (fixed velocity tests) with tests of fish performance in scaled-down fishways so that the effects of fish behavior can be integrated with their swimming performance. Additionally, this study should be conducted on all life stages and sizes of the target species. At a minimum, this type of study should be conducted for the White Sucker if designing structures for passage of all of these suckers is the main objective for future conservation work.

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for fish care. Additional technical assistance was provided by A. Ficke, E. Gardunio, and other members of the Colorado State University Fish Physiological Ecology Laboratory.

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North American Journal of Fisheries Management

An Egg-Per-Recruit Model to Evaluate the Effects of Upstream Transport and Downstream Passage Mortality of American Eel in the Susquehanna River

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ARTICLE

An Egg-Per-Recruit Model to Evaluate the Effects of Upstream Transport and Downstream Passage Mortality of American Eel in the Susquehanna River

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Abstract

Dams and their associated effects on the migration and mortality of the American Eel Anguilla rostrata have been implicated as a significant factor in the current depleted status of the species along the Atlantic coast of North America. Female American Eels that mature in areas below dams may be smaller and have lower fecundity than individuals that mature in more upstream reaches of a river system. However, increased mortality associated with downstream migration through hydroelectric turbines may negate any reproductive advantage afforded to American Eels occupying areas upstream of hydroelectric facilities. We developed an American Eel egg-per-recruit (EPR) model to investigate how various levels of upstream and downstream passage may affect the reproductive output from rivers with hydroelectric facilities. We applied our model to the Susquehanna River and found that if American Eels are passed upstream of multiple dams on the river, cumulative downstream passage survival must be $\geq 33\%$ for the upstream passage to be beneficial; otherwise, upstream passage is likely to result in an EPR deficit when compared with no passage. Cumulative downstream passage survival would need to increase substantially above 33% to have a high probability of making any gains in terms of EPR. Our EPR modeling framework can be adapted to other systems and used to make recommendations for necessary upstream and downstream passage for the conservation of American Eels in rivers impacted by hydroelectric facilities.

The distribution and survival of American Eels Anguilla rostrata within a river system can be largely influenced by the location and number of dams (Levesque and Whitworth 1987; Goodwin and Angermeier 2003; Verreault et al. 2004; Machut et al. 2007; Hitt et al. 2012). American Eels restricted to areas below dams live in higher densities, leading to reduced survival, modified sex ratios, and reduced growth rates (Oliveira and McCleave 2000; Larinier 2001; Strickland 2002; Verreault et al. 2004; Machut et al. 2007). American Eels that are able to move above dams may experience injuries and mortality once they mature and migrate downstream (at the silver eel life stage) through turbines at hydroelectric plants (Carr and Whoriskey 2008; Brown et al. 2009; Welsh et al. 2009). In rivers where American Eels must successfully pass through several hydroelectric facilities during downstream migration, cumulative mortality can be 37–82%, depending on the number of dams and dam-specific passage mortality (McCleave 2001; Verreault and Dumont 2003). When passage mortality is combined with...
mortality due to commercial fisheries, escapement of spawning American Eels is further reduced. Verreault and Dumont (2003) estimated that commercial fishing caused 22% of the total mortality experienced by American Eels leaving the St. Lawrence River, Ontario. The overall effect of dams on the coastwide population of American Eels is uncertain but is believed to be a significant factor in their current depleted status (Atlantic States Marine Fisheries Commission 2012).

Because of the potential mortality associated with hydroelectric facilities during downstream migration of American Eels, managers often question the efficacy of passing them upstream of hydroelectric facilities if individuals could grow and mature below dams. Could passing American Eels upstream of dams actually lead to a reduction in reproductive output from a river due to mortality associated with hydroelectric facilities? Such questions often arise during development and relicensing of hydroelectric facilities by the Federal Energy Regulatory Commission under the Federal Power Act. Fisheries agencies are responsible for recommending appropriate mitigation actions to the Federal Energy Regulatory Commission, and recommendations often need to be made without complete data (Railsback et al. 1990). To gain a better understanding of the effects of hydroelectric facilities on American Eel reproductive output from a river, we developed an egg-per-recruit (EPR) model to investigate the effects of various levels of upstream and downstream passage. Egg-per-recruit models are commonly used in fisheries management to estimate the lifetime reproductive potential of a recruit under various levels of fishing mortality and to set fishery management benchmarks that preserve some percentage of the reproductive output from an unexploited population (Boreman 1997; Boreman and Friedland 2003; Goodyear 2003). The International Council for the Exploration of the Sea (ICES 1997) recommended that fishing mortality reference points from per-recruit models (egg and spawning-stock biomass per recruit) be set at levels that would preserve 30% of the exploited population \( (F_{30\%}) \) as a lower limit reference point for data-poor stocks and that management, under a precautionary approach, should increase this level to something greater than 30% to ensure a low probability that the realized \( F \) is not sustainable. Boreman (1997) recommended using \( F_{30\%} \) as a reference point for North American sturgeons (family Acipenseridae) and Paddlefish Polyodon spathula. Also, ICES (2001) suggested the use of \( F_{50\%} \) in the management of European Eels Anguilla anguilla and this level was used in a stock assessment of American Eels in the Potomac River (Fenske et al. 2011).

Very little is known about the life history of American Eels within the Susquehanna River because there have been virtually no American Eels in the watershed since the construction of Conowingo Dam in 1928. Occasional stockings of American Eels occurred upstream of Conowingo Dam between 1936 and 1980 by the Pennsylvania Fish and Boat Commission, and a limited trap and transport effort above Conowingo Dam began in 2008 by the U.S. Fish and Wildlife Service. American Eels recruit to the lower river at age 2 (Normandeau Associates 2011) at approximately 115 mm in length (SRAFRC 2013). An eel ramp at Conowingo Dam permits capture of these recruits below the dam. At issue is a proposal to capture and transport these juvenile American Eels by truck above York Haven Dam and stock them in the upper Susquehanna River watershed. Based on demographic studies in other systems, individuals that are transported upstream of York Haven Dam will likely have different life histories than those that remain below Conowingo Dam, including a differing proportion of females, delayed maturation, and larger size (Goodwin 1999; Oliveira et al. 2001; Morrison and Secor 2003). Here we employ a novel application of an EPR model for American Eel to assess the local population effect of upstream transport and provide insight on the level of downstream survival required to produce an overall favorable outcome as described by having a positive effect on the number of eggs per recruit.

**STUDY AREA**

The Susquehanna River drains over 69,930 km\(^2\) and represents 43% of the Chesapeake Bay watershed (Susquehanna River Basin Commission 2006). Moving upriver from Chesapeake Bay, American Eels encounter four main-stem hydroelectric dams on the Susquehanna River: Conowingo, Holtwood, Safe Harbor, and York Haven (Figure 1). The Muddy Run pumped storage facility, located between Conowingo and Holtwood dams, also has the potential to cause mortality to migrating American Eels and is treated as an additional hydroelectric facility in our modeling of downstream mortality. American Eels have been essentially excluded from the entire Susquehanna River watershed since the construction of Conowingo Dam at river kilometer 16. Historically, American Eels supported a substantial commercial fishery in the Susquehanna River (Pennsylvania State Commissioners of Fisheries 1883) and they comprised 50% of the fish biomass in some mid-Atlantic tributaries (Ogden 1970). The loss of American Eels from the Susquehanna River has likely had impacts on ecosystem function within the watershed. For example, young American Eels are prey for other predatory species and then switch to being top predators as they grow (Ogden 1970; Denoncourt and Stauffer 1993). While resident in the freshwater systems, American Eels also serve as hosts to freshwater mussels like the eastern elliptio Elliptio complanata (Lellis et al. 2013). While restoring the ecological integrity of the watershed is important, ensuring some level of downstream passage survival such that upstream passage does not negatively impact overall egg production from the system is also desired.

**METHODS**

Typical EPR models pertain to females of iteroparous species and assume all female recruits will share the same life history strategy in terms of maturity and mortality schedules, as well as sex ratios. However, for American Eels maturity, mortality, and sex ratios can vary along a river gradient, which can affect
the results of per-recruit analyses (Alonzo and Mangel 2005). Thus, we attempted to account for this variability in life history within our EPR model by allowing the proportion of recruits that become female, as well as growth, fecundity, maturity, and mortality rates, to differ between areas downstream and upstream of the first dam. Contrary to traditional EPR models that define recruits as only female individuals, in our application of an EPR model to American Eels, we define a recruit as any individual that encounters the first upstream fish passage barrier on a river system. The actual proportion of total individuals that become female depends upon the level of upstream fish passage.

**Generalized American Eel EPR model.**—The American Eel EPR model begins with some number of total recruits at age \( i \) to the base of an upstream passage barrier \( (N_i) \), and the resulting number of females downstream and upstream of the barrier is as follows:

\[
N_{f,i,\text{down}} = N_i \cdot (1 - P) \cdot F_r \quad \text{and} \quad N_{f,i,\text{up}} = N_i \cdot P \cdot F_r,
\]

where \( N_{f,i,\text{down}} \) and \( N_{f,i,\text{up}} \) are the number of female \( f \) age \( i \) recruits in each reach (downstream or upstream), \( P \) is the proportion of age \( i \) recruits that are moved above the barrier either volitionally or via trap and transport, and \( F_r \) is the proportion of age \( i \) recruits in each reach \( r \) that become female.

Because American Eels are semelparous and leave the system once mature, the number of females remaining within subsequent age-classes in a reach is a function of natural mortality within the reach and the proportion that remain immature:

\[
N_{f,i,r} = N_{f,i-1,r} \cdot (1 - \rho_{i-1,r}) \cdot e^{-M_{i-1,r}},
\]

where \( N_{f,i,r} \) is the number of females of age \( i \) in reach \( r \), \( \rho_{i,r} \) is the proportion of females that are mature at age \( i \) in reach \( r \), and \( M_{i,r} \) is the natural mortality of females of age \( i \) in reach \( r \).

The number of eggs produced by an age-class of females is as follows:

\[
E_{f,i,r} = \rho_{i,r} \cdot \theta_{i,r} \cdot N_{f,i,r} \cdot S_r,
\]

where \( \theta_{i,r} \) is the fecundity of a female of age \( i \) in reach \( r \) and \( S_r \) is the cumulative downstream survival during migration as a function of the number of dams American Eels must pass during migration \( (S_r = 1.0 \text{ if there are no dams}) \).

The total number of...
eggs per recruit is the sum of all the eggs produced over all age-classes and all reaches divided by the number of recruits:

\[ \text{EPR} = \sum_{i=1}^{n} \frac{E_{f, i, r}}{N_i}. \]

**Application to Susquehanna River American Eels.**—We parameterized our model using a combination of empirical data on American Eel collected in the Susquehanna River and literature-derived values (Table 1; Figure 2). Because trap and transport efforts in the Susquehanna River began as recently as 2008, specific life history information of this population is lacking. However, we believe the literature-derived parameters we used are representative because we used parameters obtained from systems in relatively close geographic proximity to the Susquehanna River and we attempted to match parameters from other studies based on the relative location along a river gradient where they were collected to where we applied them in our model of the Susquehanna River (e.g., large lower-river areas versus smaller upriver areas). We assumed that a lower proportion of American Eels that remained below Conowingo Dam would become female compared with those that were transported by truck to above York Haven Dam (Table 1). The proportion of American Eels that became female upstream of York Haven Dam was equivalent to growth rates transported upstream. The growth rate for American Eels transported above York Haven Dam was equivalent to growth rates from upstream areas in the Hudson River (Morrison and Secor 2003) and Shenandoah River, Virginia (Goodwin 1999). Maturity in each reach was modeled as a function of length by logistic regression:

\[ \rho_{i, \text{down}} = \frac{1}{1 + e^{(-10.43 + 0.02 L_{i, r})}} \]

and \[ \rho_{i, \text{up}} = \frac{1}{1 + e^{(-13.83 + 0.02 L_{i, r})}}, \]

where \( L \) is the total length (mm) of a female of age \( i \) in the downstream or upstream reach. The downstream maturity schedule followed that of the general stock assessment model employed by the Atlantic States Marine Fisheries Commission (ASMFC 2012), and the upstream maturity schedule was derived from maturity-at-size data from the Shenandoah River (S. Eyler, unpublished). These two models assume that American Eels that remain downstream mature at a smaller size than those that are transported upstream. Fecundity was also modeled as a function of length (cm) and was the average of two published functions (Barbin and McCleave 1997; Tremblay 2009):

\[ \theta_{i, r} = \frac{(308.32 \cdot L_{i, r}^{2.93} + 18.20 \cdot L_{i, r}^{3.64})}{2} \]

**TABLE 1.** Life history parameters used in the EPR model for Susquehanna River American Eel.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of recruits to Conowingo Dam</td>
<td>2</td>
<td>Normandeau Associates 2011</td>
</tr>
<tr>
<td>Length of recruits to Conowingo Dam</td>
<td>115 mm</td>
<td>SRAFRC 2013</td>
</tr>
<tr>
<td>Growth rate downstream of Conowingo Dam</td>
<td>72.5 mm/yr (range: 65–80)</td>
<td>Morrison and Secor 2003; Fenske et al. 2010</td>
</tr>
<tr>
<td>Growth rate upstream of York Haven Dam</td>
<td>38.5 mm/yr (range: 34–43)</td>
<td>Goodwin 1999; Morrison and Secor 2003</td>
</tr>
<tr>
<td>Proportion female downstream of Conowingo Dam</td>
<td>( F_r = 0.68 ) (range: 0.64–0.72)</td>
<td>K. Whiteford, Maryland Department of Natural Resources, unpublished data</td>
</tr>
<tr>
<td>Proportion female upstream of York Haven Dam</td>
<td>( F_r = 1.00 ) (range: 0.80–1.00)</td>
<td>Goodwin and Angermeier 2003; Morrison and Secor 2003</td>
</tr>
<tr>
<td>Age-specific natural mortality</td>
<td>( M_{i, r} = 0.492 \cdot W_{i, r}^{-2.88} ) (±10%)</td>
<td>ASMFC 2012</td>
</tr>
<tr>
<td>Ratio of downstream to upstream natural mortality</td>
<td>2.0 (range: 1.0–3.0)</td>
<td>Assumed</td>
</tr>
<tr>
<td>Fecundity</td>
<td>( \theta_{i, r} = \frac{(308.32 \cdot L_{i, r}^{2.93} + 18.20 \cdot L_{i, r}^{3.64})}{2} )</td>
<td>Barbin and McCleave 1997; Tremblay 2009</td>
</tr>
<tr>
<td>Maturity schedule downstream of Conowingo Dam</td>
<td>( \rho_{i, r} = \frac{1}{1 + e^{(-10.43 + 0.02 L_{i, r})}} )</td>
<td>ASMFC 2012</td>
</tr>
<tr>
<td>Maturity schedule upstream of York Haven Dam</td>
<td>( \rho_{i, r} = \frac{1}{1 + e^{(-13.83 + 0.02 L_{i, r})}} )</td>
<td>S. Eyler, unpublished</td>
</tr>
<tr>
<td>Weight–length relationship</td>
<td>( W_{i, r} = 0.000000344 \cdot (L_{i, r}^{3.27}) )</td>
<td>ASMFC 2012</td>
</tr>
</tbody>
</table>
Natural mortality was modeled as a function of weight at age (Lorenzen 1996; ASMFC 2012):

\[ M_{i,r} = 0.492 \cdot W_{i,r}^{-2.88}, \]

where \( W_{i,r} \) is the weight of an age \( i \) American Eel in reach \( r \) and was estimated from the general weight–length equation (ASMFC 2012):

\[ W_{i,r} = 3.44 \times 10^{-7} \cdot L_{i,r}^{3.27} \]

The natural mortality of American Eels that remained downstream of Conowingo Dam was assumed to be greater than that of those that were transported above York Haven Dam because
American Eel predators in larger estuary waters are rarely found in tributaries (Buckel and Conover 1997; Griffin and Margraf 2003; Walter and Austin 2003; Machut et al. 2007). Therefore, upstream natural mortality \( (M_{\text{up}}) \) was modeled by dividing the natural mortality by an assumed ratio of downstream-to-upstream natural mortality \( (\pi) \) for each age- or size-class.

Cumulative downstream passage survival during migration as mature silver eels \( (S_r) \) was a function of the survival at each hydroelectric facility:

\[
S_r = S_{SYH} \cdot S_{SSH} \cdot S_H \cdot S_{MR} \cdot S_C,
\]

where \( S_{SYH}, S_{SSH}, S_H, S_{MR}, \) and \( S_C \) are the proportional downstream survivals at the York Haven, Safe Harbor, Holtwood, Muddy Run, and Conowingo hydroelectric facilities, respectively. We assumed downstream passage survival was the same at each hydroelectric facility in our application of the EPR model because we wanted to determine target downstream passage survivals that could be recommended consistently for all hydroelectric facilities.

We attempted to capture the uncertainty in life history parameters for American Eels in the Susquehanna River by conducting Monte Carlo simulations of EPR that allowed life history parameters to vary according to uniform distributions (Table 1). The proportion of downstream recruits that became female \( (F_r) \) varied from 0.64 to 0.72, and the proportion of upstream recruits that became female ranged from 0.80 to 1.0. The ratio of downstream to upstream natural mortality \( (\pi) \) ranged from 1.0 to 3.0, and expected values of natural mortality in each reach were allowed to vary by \( \pm 10\% \). A base simulation was conducted in which no recruits were transported above Conowingo Dam (hereafter termed Base-EPR). This simulated a “do nothing” scenario to compare with other combinations of upstream trap and transport \( (P) \) and cumulative downstream survival \( (S_r) \). Rates. Also, we simulated the theoretical maximum EPR (hereafter termed Max-EPR) assuming there were no hydroelectric facilities on the Susquehanna River (i.e., 100% upstream and downstream passage). We simulated trap and transport rates from below Conowingo Dam to upstream of York Haven Dam ranging from 10% to 100% combined with downstream passage survival at each of the five dams of 10–100% (cumulative downstream passage survivals of 0.00001–100%). The model was developed in R (version 2.12.2) and was used to conduct 10,000 iterations of each simulated scenario. Simulation results were summarized as a median EPR, percent change from Base-EPR, and percent of Max-EPR.

RESULTS

The EPR for American Eel in the Susquehanna River was dependent upon both the percentage of recruits to Conowingo Dam that were trapped and transported above York Haven Dam as well as downstream passage survival at each of the five main-stem dams. Median Base-EPR, assuming no upstream passage, was 567,291 (5th–95th percentile = 466,812–676,442). Median Max-EPR, assuming 100% upstream and downstream passage, was 1,793,011 (573,520–2,924,411). The potential benefits of upstream trap and transport depended on downstream passage survival. When downstream passage survival was less than approximately 80% at each hydroelectric facility (33% cumulative downstream survival), EPR was actually higher with lower levels of upstream transport. That is, transporting American Eels upstream lowered the overall productivity of American Eels in the system, as measured by EPR, when cumulative downstream survival was 33% or less. It was not until downstream passage survival exceeded 80% at each hydroelectric facility that more upstream trap and transport (Figure 3) provided potential gains over the Base-EPR.

Estimates of the change from Base-EPR and the percent of Max-EPR varied widely, as evident in the wide range (90th percentile) on the simulated distributions (Figures 4, 5). The distributions of the change from Base-EPR overlapped zero for all scenarios with less than 100% upstream and downstream passage (Figure 4). Increasing both upstream transport and downstream passage survival also increased productivity, as measured by the percent of Max-EPR (Figure 5). Various combinations of upstream and downstream passage resulted in the median percent of Max-EPR being at least 50%, all of which required at least 90% downstream survival at each hydroelectric facility. The distributions of the percent of Max-EPR were also highly skewed to the right and point estimates occasionally exceeded 100% Max-EPR.
DISCUSSION

Our model outputs suggest that if any American Eels are passed upstream of a barrier, cumulative downstream passage survival must reach some critical level; otherwise, total reproductive output from a system may actually be lowered by passing American Eels upstream. We call this critical level the “break-even threshold.” Compared with the lower reaches of a river system, a greater proportion of American Eels become female in further upstream reaches and attain a greater size and fecundity due to being in lower densities. However, when downstream passage survival is below the break-even threshold, the gains in reproductive potential coincident with occupying more upstream reaches is negated by the cumulative mortality suffered during downstream migration of the silver eels. In our application of the EPR model to the Susquehanna River population, the break-even threshold of cumulative downstream passage survival is approximately 33% (80% at each of the five hydroelectric facilities). At the break-even threshold, we would expect EPR to be...
greater than the Base-EPR (i.e., the “do nothing” management approach of leaving American Eels below the dams) approximately 50% of the time. In order to have a high probability of making gains in the reproductive output of American Eels by moving them above dams, downstream passage survival will need to increase above the break-even threshold. The break-even threshold of downstream passage survival, as well as the point when some high probability of making gains in EPR is realized, will vary from system to system depending on the life history of American Eels in a particular system and the model parameters used. If emigrating American Eels are required to pass more hydroelectric facilities, the downstream passage survival at each hydroelectric facility will need to increase in order to realize any reproductive benefit from upstream passage or transport.

Even with relatively high downstream passage survival at each hydroelectric facility, a large difference between the expected EPR and the maximum EPR (the idealized situation with no dams on the system) likely exists. We found that 70% upstream trap and transport and 90% downstream passage survival at each of the five hydroelectric facilities was the lowest combination of upstream and downstream rates that reached a median percent of Max-EPR of 50%. This suggests that achieving a predam level of reproductive output is unlikely, even with a moderate level of upstream passage and the best-engineered downstream passage. Upstream passage rates on the Susquehanna River are unknown and downstream passage survival has been estimated at only two of the five hydroelectric facilities. Eyler (2012) estimated downstream passage survival of 90% at Conowingo Dam, and in a reanalysis of data collected at the Muddy Run pumped storage facility (Exelon 2012), downstream passage survival was 88% (J. A. Sweka, unpublished). These observed downstream passage survival rates are greater than the break-even threshold, and if downstream passage survival is similar at the other hydroelectric facilities, trap and transport of American Eels to areas upstream of the five hydroelectric facilities should result in an increase in reproductive output from the Susquehanna River. However, reproductive output would still remain well below the maximum expected if there were no hydroelectric facilities on the river.

We acknowledge that our expected levels of EPR for the Susquehanna River reflect the EPR only for American Eels emigrating from the river. As American Eels continue their seaward migration from the Susquehanna River, they will also experience fishing mortality throughout the Chesapeake Bay, and this was not accounted for in our model. There are no commercial American Eel fisheries upstream of Conowingo Dam, and our objective was to specifically evaluate the effects of hydroelectric facilities on the reproductive potential of American Eels from the river. The inclusion of fishing mortality should also be considered to gain a full understanding of the effects that human activities play in the dynamics of American Eels. Fishing mortality could and should be added to this model in applications to other systems for which estimates of fishing mortality are available.

Our American Eel EPR model was most sensitive to the differences between upstream and downstream growth, the natural mortality rates, and the proportions of American Eels that become female. If the growth rate upstream was higher and more similar to the growth rate downstream, the break-even threshold would decrease because American Eels will reach maturity faster and emigrate at younger, more abundant ages. We assumed that American Eels that were trapped and transported upstream would experience lower natural mortality because of fewer predators capable of consuming them in this section of river, and we incorporated this by varying the ratio of downstream-to-upstream natural mortality for a given size between 1.0 and 3.0. If the true upper bound on this range is lower and upstream natural mortality is more similar to downstream mortality, then expected EPR would increase at a slower rate as downstream passage survival increases and the break-even threshold increases. Finally, if the actual proportion of American Eels upstream that become female is lower and more similar to the downstream sex ratio, the break-even threshold for downstream passage would increase because fewer individuals would be females. Thus, future research to gain better parameter estimates for this type of modeling exercise should focus on quantifying the actual life history parameters in the system being modeled and the difference in life history parameters of American Eels occupying areas upstream and downstream of dams.

Downstream passage survival is difficult to assess and can be influenced by the physical structure of intakes and turbines, as well as their operating procedures (Haro et al. 2003; Welsh et al. 2009). We used a general specification of overall downstream passage survival at each hydroelectric facility on the Susquehanna River that includes survival through turbines as well as survival over dam spillways. Modeling the fate of tagged American Eels (e.g., radio or balloon tags) under various operational procedures and diurnal flow conditions may help tease apart the various components of overall downstream passage survival. If routes of passage are determined under various river flow conditions and mortality through each route quantified, actual estimates of downstream passage survival for future modeling efforts would be available, assuming the sample sizes in these studies were adequate to sufficiently reduce the error associated with the survival estimates. If downstream passage requirements are not met, operational modifications and guidance structures can be implemented to minimize mortality at the hydroelectric projects (e.g., Haro et al. 2003).

Upstream passage efficiency (or the proportion of American Eels that are trapped and transported) can be difficult to assess because the abundance below a dam is usually unknown and highly variable due to interannual recruitment variability. Policies that require an absolute number of individuals to be passed annually are possible, but the proportion of the population represented by this number will still be unknown in many cases. In such situations, our EPR model is limited in making inferences about the expected gain in reproductive output over a “do
nothing” strategy, wherein no individuals are passed upstream. Estimates of the proportion of the population actually passed upstream are needed for this model to be most useful in making recommendations for both upstream and downstream passage and survival. However, even with this unknown, the break-even threshold from this model provides a minimum downstream passage survival required if any individuals are passed upstream. In cases where the proportion of American Eels passed upstream is not known, managers may opt to set cumulative downstream benchmarks that preserve some percentage of the reproductive output of those individuals passed upstream. For example, ICES (2001) suggested the use of a fishing mortality benchmark for European Eels that preserved 50% of the spawning stock biomass ($F_{50\%}$), and management of European Eels has actually implemented a 40% escapement target that includes all sources of anthropogenic mortality (ICES 2012).

Egg-per-recruit models have traditionally been used in setting reference points for fishing mortality, but here we illustrate they can also be used to establish reference points for other sources of anthropogenic mortality, such as hydroelectric facilities. Our American Eel EPR model could easily be adapted to other systems for which the potential effects of dams on American Eels are in question and also for questions about the effects of dams on other species. Application to anadromous species, as opposed to the catadromous species in our study, would apply downstream passage mortality to both out-migrating juveniles and postspawning adults if the species was iteroparous. The effects of upstream passage could be accounted for by multiplying an upstream passage rate by age-specific fecundity values, assuming individuals that do not pass upstream of barriers do not spawn or spawn with lower success. There may be cases in which the reproductive benefits provided by upstream passage are negated by mortality associated with downstream passage at either the emigrating-juvenile stage or postspawning adult stage. An example of such an occurrence was seen in modeling efforts by Harris and Hightower (2012) in which the potential for restoration of American Shad Alosa sapidissima in the Roanoke River, North Carolina and Virginia, was not enhanced through trap and transport efforts due to the current habitat conditions and inadequate downstream passage survival.

Data on the American Eel along Atlantic coast drainages is generally deficient in supplying the information necessary for predictive population models (ASMFC 2012). Our EPR model provides a framework for evaluating the potential effects of upstream and downstream passage on the reproductive output of American Eels from a river system when data to model actual population numbers are not available. However, much uncertainty remains for even the most basic of life history parameters for this species, which can be observed for the Susquehanna River population, and future research should be aimed at gaining better estimates of these life history parameters. Nevertheless, this EPR model framework could be easily adapted to other systems to provide defensible decisions regarding fish passage requirements when other information is lacking.

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Otolith Daily Increment Deposition in Age-0 Smallmouth Bass Reared in Constant and Fluctuating Water Temperatures

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Abstract

We reared embryos and larvae of Smallmouth Bass *Micropterus dolomieu* in constant and diel fluctuating water temperatures (mean of 20°C) to clarify when otolith first daily increments were deposited and the periodicity of increment formation. Unlike the results of previously published studies, we found that first-increment formation began at hatching rather than 7–11 d later at swim-up. We confirmed that increment deposition was daily and extended the daily increment validation period from 21 d to 30 d posthatch. Accurate and precise age estimation was possible for Smallmouth Bass reared in both constant and fluctuating temperature environments, as age estimates rarely varied more than 1 d from true age. We also found consistent estimated ages using either left or right sagittae and showed relationships for Smallmouth Bass total length as a function of age, and otolith diameter as a function of total length. Otolith daily increment counts allow accurate and precise estimates of Smallmouth Bass age, which enables determination of hatch date, timing of spawning, and growth rate. These findings may assist with the management of this species, as well as provide information that can be used to disadvantage reproductive success of invasive Smallmouth Bass.

The number of daily increments in fish otoliths, patterns of increment deposition, and otolith growth may record life history events such as hatching, growth, periods of physiological stress, movements, and changes in water temperature or food abundance (Pannella 1971; Campana and Neilson 1985; Bestgen et al. 2006; Falke et al. 2010). Such information is particularly useful for fishes that are captured for commercial or recreational use, or for those that are rare and endangered, because understanding life history and ecological processes can contribute to their improved management and conservation.

Validation studies are required to enhance the accuracy and precision of information obtained from otoliths, particularly the timing of deposition of the first increment and the frequency (daily or otherwise) of increment formation (Beamish and McFarlane 1983; Campana 2001). Accurate predictions of the hatch time of young fish that are derived from otolith microincrement analyses may be especially important when managers attempt to influence year-class strength of a species. For example, understanding the reproductive timing of invasive populations of Smallmouth Bass *Micropterus dolomieu* in the Green River, Colorado and Utah, would allow for appropriately timed disruption of spawning via nest destruction, mechanical removal of adults, or by-flow manipulations that might reduce the survival of embryos and young (Winemiller and Taylor 1982; Ridgway and Friesen 1992; Jager et al. 1993; Knoteck and Orth 1998). Using embryos reared in the laboratory at 20–22°C and larvae reared at 17–23°C, but presumably not under a regular daily temperature fluctuation, Graham and Orth (1987) reported that first-increment deposition occurred at swim-up (7 d posthatch) and that increment deposition in larvae was daily for 14 d after swim-up. However, their age estimates for Smallmouth Bass larvae that were sacrificed on the same day and that were presumably the same age, varied widely. For example, estimates of age for Smallmouth Bass larvae that were 10 d after swim-up (e.g., should have had 10 daily age increments) ranged from 7 to 14 d, variation which they attributed...
to difficulty in distinguishing between daily and subdaily rings (increments). Graham and Orth (1987) also reported that the clarity of otolith increments of laboratory-reared Smallmouth Bass was lower than that of wild individuals, which may have contributed to variable age estimates.

While aging wild Smallmouth Bass from the Yampa River, Colorado, for another project, we found an inconsistency in previously reported aging techniques. We suspected that either the daily increment formation rate for Smallmouth Bass reported in Graham and Orth (1987) was different than one per day or that deposition of the first otolith increment occurred prior to swim-up. First-increment formation at hatch with a daily deposition pattern is the norm in many fishes, including Largemouth Bass *M. salmoides* (Campana and Neilson 1985; Isely and Noble 1987 [but see Miller and Storck 1982]; Bestgen and Bundy 1998). Therefore, we undertook our validation study to (1) document the timing of first-increment deposition in Smallmouth Bass, (2) determine if increment deposition rate in Smallmouth Bass sagittae was one per day, (3) understand the effects of temperature on initial and daily increment formation and otolith growth, (4) determine if left and right sagittae differed in rate of increment deposition, and (5) expand the validation period for otolith age estimation to 30 d.

**METHODS**

We collected fertilized Smallmouth Bass eggs from a pond at the Colorado Parks and Wildlife Hatchery in Wray, Colorado, on June 10, 2010. Hatchery-cultured broodfish were placed in ponds earlier in the spring and allowed to spawn naturally over existing pond substrate or gravel-filled containers. After Smallmouth Bass broodfish deposited eggs, the broodfish were removed from the ponds and the larvae were left to hatch and grow. We suctioned 670 eggs from a single nest with a baster and transported them in aerated coolers to the Aquatic Research Laboratory at Colorado State University, Fort Collins, Colorado. Taking all eggs from a single nest increased the likelihood that they were in a similar developmental state and that hatching would occur in a relatively short time period. Knowing that larvae hatched in a relatively short time frame was essential to interpreting when otolith formation and first-increment deposition occurred in Smallmouth Bass larvae. Observations showed eggs were in a similar and early stage of development (no somites or other readily identifiable early life stage features present), perhaps just fertilized and within 12 h old. The temperature of the pond when eggs were collected was 24°C.

Eggs were sorted from debris and divided in approximately equal numbers into four 2-L flow-through tanks. Two randomly chosen tanks were maintained at a constant 20°C water temperature, and two tanks were subjected to a fluctuating temperature treatment with a mean daily temperature of 20°C and diel fluctuation of ±2°C (see Bestgen and Bundy [1998] for more details on experimental setup); measured minima and maxima were 18°C and 23°C. In fluctuating tanks, temperature change was gradual over several hours and the diel change minimally approximated that for the Yampa River, Colorado, in early summer when Smallmouth Bass were spawning (U.S. Geological Survey Gauge 09251000). The diel light cycle was 14 h light : 10 h dark. The drip water supply to flow-through tanks was sufficient to change water volume about every 90 min. Live nauplii of brine shrimp *Artemia* spp. were hatched daily, and Smallmouth Bass larvae fed to satiation twice per day after jaw formation was noted.

We observed development daily and removed embryos that had fungus or were dead. Most hatching occurred on June 13 for both treatments and the 13 eggs that did not hatch that day were moved to a separate constant temperature tank, where they then hatched 1 d later on June 14. The separation of fish with different hatching dates was important to make inferences to timing of otolith formation and first-increment deposition. Most larvae (about 90%) in fluctuating tanks died on June 13, and we supplemented those with larvae from the constant temperature tanks. Thus, valid comparisons between temperature treatments could be achieved because larvae were subjected to their correct treatments since the day of hatch.

Five live eggs or larvae from each temperature treatment were preserved daily in late morning from June 11 until June 30 in 100% ethanol. Only healthy embryos or larvae were selected. After June 30, preservation continued every third day until no fish remained. The 13 embryos that did not hatch until June 14 were preserved last, and their later hatch date was adjusted in analyses. Preserved samples were labeled with date, time, and treatment type. After experiments were completed, preserved samples were reassigned random numbers so that fish sample date was unknown when the reader was counting otolith increments. We treated individual fish as independent experimental replicates (e.g., Bestgen and Bundy 1998). We randomly selected three fish from each sample and used samples collected the first 5 d posthatch (June 13–18), samples collected every other day from June 19 to 30, and samples from every third day after that. We measured each fish with electronic calipers to the nearest 0.01 mm TL. Both left and right sagittal otoliths were extracted and mounted on separate microscope slides (Stevenson and Campana 1992). Otoliths were fixed to the slide with cyanoacrylate glue that bonded to glass and were then polished using lapping film (0.3–12.0-micron grit size). A compound microscope fitted with a calibrated ocular micrometer was used to measure the maximum diameter of each sagitta, typically from the tip of rostrum to the postrostrum (Stevenson and Campana 1992). Core diameter was measured at 320 × magnification and was the maximum diameter of the first distinct and dark band surrounding the primordia. Counts of otolith microincrements were at 320 × magnification; immersion oil placed on the otolith increased increment clarity. Increments were counted in the sagittal plane of each otolith...
and one increment consisted of one light band and one dark band (the L-zone and D-zone, after Kalish et al. 1995).

Reader One (first author) counted increments in all left and right sagittae one time to gain familiarity with otolith growth and aging. Reader Two (second author) reread several of those otoliths to confirm age estimates. All counts by each reader were performed blind to the true age or any knowledge of the specimen, measured otolith size, or preservation date. The first reader then conducted a second series of three consecutive increment counts for each otolith, again in a blind fashion; those counts were averaged to determine the final increment count for each otolith. The mean difference between the first and second otolith readings, calculated only after all readings were completed, was 0.03 increments with a range of −1 to +2 increments. The maximum difference between Reader One and Reader Two was ±1 increment, demonstrating the validity of having a single reader conduct all increment counts.

We used analysis of covariance (ANCOVA) to compare slope and intercept of age estimates as a function of known age, using water temperature regime (fluctuating and constant) as the covariate. We then used regression to estimate the effects of constant and fluctuating temperature regimes on relationships of increment count as a function of age in days posthatch (true age). We also used regression to evaluate if increment counts were different for the left and right sagittae of individual fish. All statistical analyses were conducted using SAS statistical software (SAS Institute 2012; version 9.3).

RESULTS

Observations showed that embryo development proceeded at similar rates for fish in constant and fluctuating temperature treatments. Movement of embryos in each treatment was first detected on June 12, and most hatching began and was completed on June 13. Thus, hatching occurred about 4 d after embryo collection and likely within 5 d of fertilization; mean TL of 1-d-old larvae was 5.6 mm. Both sagittae and lapilli were easily observed in just-hatched live fish under a dissecting microscope at 10× magnification. The eyes of larvae were pigmented by June 16, 3 d posthatch, and a few fish were attempting to swim. Pectoral fins were noted on June 17, followed by the formation of jaws and a functional mouth on June 18. All larvae were buoyant (gas bladder inflated), swimming in the water column, and actively feeding on June 22, 9 d posthatch, when mean TL was 8.5 mm.

Constant and fluctuating thermal regimes had no effect on otolith microstructure or fish length but had a small effect on the diameter of the otoliths. The ANCOVA showed that the timing of first-increment deposition and increment deposition rates were not different in otoliths of fish from constant or fluctuating temperature treatments for the relationship of estimated age (increment counts) as a function of true age (days posthatch; Table 1). Consequently, increment counts for fish in both treatments were combined for further analyses. Additionally, slopes and intercepts for relationships of estimated age as a function of true age were similar when compared for left and right sagittae. Thus, the median increment count of the right and left sagittae (three readings each) was used as the estimated age for each fish in subsequent analyses. Likewise, TL of Smallmouth Bass larvae as a function of true age in the two temperature treatments was similar. Finally, the ANCOVA showed that sagittae in fish from the fluctuating temperature treatment grew only slightly faster than in fish in the constant temperature treatment, and otoliths from fish in the fluctuating temperature treatment were only about 8% larger.

The least-squares regression relationship, estimated using combined data from constant and fluctuating temperature treatments and the median values from left and right sagittae, supported the idea that increment deposition began at hatching and continued at a rate of one per day through 30 d posthatch (Table 2). This was true because the slope and intercept parameter values were close to 1 and 0, respectively ($P = 0.606$ and $P = 0.656$), and estimated age from increment counts showed little variation over the range of true ages (CV [100 · SD/mean] = 4.5%; Figure 1). Observations of otolith margins of fish preserved 1 d posthatch (June 14) showed a small but distinct light–dark band, which also supported the notion that first-increment deposition occurred the day of hatching (Figure 2).

DISCUSSION

Validation studies continue to be a necessary precursor for obtaining reliable information from fish otoliths, particularly for investigations that use daily increments (Beamish and McFarlane 1983; Campana and Neilson 1985; Campana 2001). We verified earlier findings of the validation study by Graham and Orth (1987), who suggested otolith microincrement deposition in Smallmouth Bass was daily, and we were able to obtain both accurate and precise estimates of age (Rice 1987; Campana 2001). Our findings also extended the period of validation, based on known-age specimens, from 21 to 30 d posthatch.
TABLE 2. Least-squares statistics for regression relationships of the following: (1) Smallmouth Bass total length (TL; mm) as a function of days since hatching (true age) with fish from constant and fluctuating temperature regimes combined, (2) sagittae diameter (µm; mean of left and right sagittae) as a function of true age for fish from constant and fluctuating temperature regimes, and (3) otolith increment counts (estimated age in days) as a function of true age with fish from constant and fluctuating temperature regimes combined (P-value for significance test of slope not significantly different from 1). True ages were the median age from left and right sagittae (three counts each) in all cases.

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Intercept (SE, P)</th>
<th>Slope (SE, P)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) TL–true age</td>
<td>5.56 (0.084, &lt;0.0001)</td>
<td>0.304 (0.006, &lt;0.001)</td>
<td>0.971</td>
</tr>
<tr>
<td>(2) Sagittae diameter–TL</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant temperature</td>
<td>−270 (14, &lt;0.0001)</td>
<td>47 (1.4, &lt;0.001)</td>
<td>0.971</td>
</tr>
<tr>
<td>Fluctuating temperature</td>
<td>−280 (15, &lt;0.0001)</td>
<td>48 (1.6, &lt;0.001)</td>
<td>0.963</td>
</tr>
<tr>
<td>(3) Estimated age–true age</td>
<td>−0.043 (0.095, 0.656)</td>
<td>0.997 (0.007, 0.606)</td>
<td>0.996</td>
</tr>
</tbody>
</table>

Daily increment deposition is routinely observed in the otoliths of many fishes (Campana and Neilson 1985; Campana 2001), and we found increments in Smallmouth Bass otoliths from both temperature treatments to be clear and easy to read. While even a 30 d validation period is relatively short, the finding that wild Smallmouth Bass deposit clear and easily identifiable otolith increments suggests that reliable aging is possible as long as fish are actively growing, typically when water temperatures are $>10^\circ$C (Graham and Orth 1987). Smallmouth Bass otoliths will be useful to estimate recruitment, growth, and survival of larvae relative to biotic and abiotic stressors (Crecco and Savoy 1985; Bunnell et al. 2003; Bestgen et al. 2006).

A major departure of our findings from those of Graham and Orth (1987) was that increment deposition began at hatching rather than at swim-up. Timing of first-increment deposition (daily or annual) is an important aspect of any aging or validation study because, as Campana (2001) noted, a correctly defined starting point is needed or age determinations will be wrong by a constant amount. We first suspected discrepancies in the timing of first-increment deposition based on the presence of increments positioned close to the nucleus in otoliths from wild Smallmouth Bass in the Yampa River, Colorado. Those included just-hatched, preswim-up fish, which, according to Graham and Orth (1987), should not have readily identifiable daily increments. We also suspected that the wide variation in age estimates of laboratory-reared Smallmouth Bass in Graham and Orth (1987) derived from confusion regarding the identification of daily or subdaily increments. Similarly, Miller and Storck (1982) suggested that “prolarval rings” (a minimum of seven increments are visible in their Figure 1) in Largemouth Bass otoliths were present at hatching but were difficult to see when fish were older because otoliths became increasingly opaque.

![Figure 1](image1.png)  
**FIGURE 1.** Relationship of estimated age, based on otolith daily increment counts, as a function of true age for early life stages of Smallmouth Bass reared at a constant 20°C and a fluctuating 20±2°C for 30 d posthatch.

![Figure 2](image2.png)  
**FIGURE 2.** Photograph of a Smallmouth Bass otolith at 80× magnification showing 11 daily increments (marked with the black dots). The inset is an otolith from a 1-d-old Smallmouth Bass larvae at 160× magnification showing the otolith core diameter terminating in a hatch check band (A; the “A” is over the middle of the otolith core) and the first daily increment (B), deposited after 1 d of life, consisting of a light band outside the hatch check and the dark outer margin.
and the rings would not be visible in later life. Isely and Noble (1987) later confirmed the deposition of first otolith increments at hatching in Largemouth Bass. Specimens used by Graham and Orth (1987) were from an irregularly fluctuating environment (17–23°C) over 14 d after swim-up that might have caused deposition of irregular increments of varying clarity and thus yielded results different from ours.

The potential bias caused by the assumption that first-increment deposition in Smallmouth Bass begins at swim-up rather than hatching depends, in part, on the specific use of otolith information. The range of time from hatch to swim-up was reported as 7–11 d (Graham and Orth 1987; Ridgway and Friesen 1992); time to swim-up in our study was 9 d at 20°C. Thus, estimation of hatch dates based on subtracting increment-based fish ages from fish capture date could be biased by as much as 7–11 d and affect comparisons of hatch timing in disparate geographic areas, such as Virginia, South Dakota, and Ontario (e.g., Ridgway and Friesen 1992; Sabo and Orth 1995; Phelps et al. 2008). Further, estimation of growth rates based on the size of fish at capture could be biased low, again if changes in fish length posthatching (about 5.5 mm TL) are divided by the number of daily increments counted and inflated by adding an additional 7 (or up to 11) d. The relative bias would be greatest for relatively young fish and decrease for older fish since the proportion of days before swim-up to total age would decrease over time. The bias induced by this method would be increased if the length at swim-up (8.5 mm TL), rather than the length at hatching (5.5 mm TL), was used to determine the change in length to capture, as was done by Phelps et al. (2008), because the divisor for the daily growth calculation was the number of days between hatching and capture, not swim-up and capture. Regardless, investigators may wish to assess if potential aging bias for young Smallmouth Bass affected the conclusions of previous studies.

Our specific purpose for estimating Smallmouth Bass age using otoliths was to predict periods of reproduction relative to environmental cues so that spawning and hatching periods can be predicted. This would allow for appropriately timed disturbances in places like the dam-regulated Green River, where flow spikes could reduce reproductive success and disadvantage invasive Smallmouth Bass populations. Accurate and precise age estimation will allow managers to correctly time disturbances that target specific portions of the reproductive effort and aid in reducing the negative effects of Smallmouth Bass on native fishes in the upper Colorado River basin.

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REFERENCES


Multidecadal Evidence of Recovery of Nearshore Red Drum Stocks off West-Central Florida and Connectivity with Inshore Nurseries

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Abstract

The importance of defining and quantifying ontogenetic movements and connectivity between juvenile and adult populations, especially for exploited species, has been well documented. Furthermore, the persistence of strong year-classes can be used to track the success of regulations that contribute to the increased survival and escapement of fish into the adult population. Size and age structures of Red Drum *Sciaenops ocellatus* were documented within the Tampa Bay estuary, in southwest Florida, using haul seines and trammel nets (1989–2008), and in nearshore Gulf of Mexico waters using a commercial purse seine (2005–2008). In the estuary, juvenile Red Drum (<100-mm TL) were collected from low-salinity backwater areas, and peaks in the annual relative abundance were apparent. In the estuary, Red Drum older than age 4 (>800-mm TL) were rare. Red Drum from nearshore gulf waters ranged from 2 to 35 years of age (674–1,074-mm TL), but most were greater than age 4. After back-calculating ages from Red Drum collected in the estuary and in nearshore gulf waters, we found that specific year-classes of Red Drum, driven by strong juvenile recruitment, were disproportionately represented in the adult spawning stock. We evaluated the long-term effectiveness of fishing regulations as a tool for rebuilding local adult Red Drum stocks by comparing data on size and age structures with results from earlier research conducted in the same geographic area. Adult Red Drum in nearshore waters off Tampa Bay were significantly longer, heavier, and older than were individuals collected a decade earlier, suggesting rebuilding of local Red Drum stocks. These observations validate the utility of long-term, multigear monitoring efforts to track populations from the estuary to nearshore coastal waters.

The importance of defining and quantifying ontogenetic movements and connectivity between juvenile and adult populations, especially for exploited species, has been well documented (Heck et al. 1997, 2003; Beck et al. 2001). Such research provides scientists, conservationists, and fisheries managers with a better understanding of species-specific habitat utilization through ontogeny (i.e., nursery areas) and empirical support for the protection and conservation of these habitats (Beck et al. 2001; Gillanders et al. 2003). Despite the importance of understanding these connections, few studies have focused on more than one life history phase (Gillanders et al. 2003). To effectively manage species with complex life histories (i.e., shifting habitats with age), however, it is important to integrate data from all life history phases and to develop a sampling design that successfully monitors species throughout their ontogeny (Beck et al. 2001; Gillanders et al. 2003).

Estuaries on the Gulf of Mexico (hereafter, “Gulf”), such as Tampa Bay, are important nursery areas for Red Drum *Sciaenops ocellatus* (Sykes and Finucane 1966; Yokel 1966; Peters and McMichael 1987; Scharf 2000; Bacheler et al. 2008). In the eastern Gulf, juvenile Red Drum (age 0) use low-salinity backwater areas (e.g., tidal rivers) as primary nurseries (Peters and McMichael 1987), growing quickly during their first year and reaching an approximate TL of 350 mm (Murphy and Taylor 1989).
1990). As they grow, Red Drum gradually disperse from backwater areas into the main bay and between the ages of 1 and 4 generally use common estuarine habitats in the bay (e.g., oyster bars, mangrove shorelines, grass flats; Peters and McMichael 1987). By age 5, most Red Drum have reached maturity and aggregate near the mouth of the estuary before recruiting into nearshore adult populations (Murphy and Taylor 1990). Adult Red Drum often form large pelagic schools along the Gulf and Atlantic coasts (Beckman et al. 1988; Murphy and Taylor 1990; Pafford et al. 1990; Ross et al. 1995), where they are most easily sighted during the fall (August–November), when they congregate near inlets and estuary mouths to spawn (Beckman et al. 1988; Murphy and Crabtree 2001). Red Drum have been estimated to live more than 40 years in most of their range (Beckman et al. 1988; Murphy and Taylor 1990; Ross et al. 1995).

During the 1980s, Red Drum became an extremely popular food fish, and due to extensive harvests, Gulf stocks were assessed and had been classified as overfished before the end of the decade (Swingle et al. 1984; Goodyear 1987; Beckman et al. 1988; Murphy and Taylor 1990; Murphy and Munyandorero 2008). Escapement rates Gulf-wide had dramatically declined and annual fishing mortality on the spawning stock had risen to greater than 20% by 1986 (Goodyear 1987). These findings led to the implementation in Florida and other Gulf states of a series of restrictive fishing regulations on Red Drum, including moratoria, size and bag limits, and cessation of sale (Murphy and Crabtree 2001). In the late 1990s, 10 years after an 18-month closure of the fishery, Murphy and Crabtree (2001) analyzed the age structure of the adult Red Drum population in nearshore waters off Tampa Bay. Offshore schools were dominated by two year-classes (1986 and 1989), which correlated closely with high estuarine recruitment, facilitated by restrictive fishing regulations implemented during those years (Murphy and Crabtree 2001). Offshore schools also had an extremely compressed age structure, attributed primarily to recruitment overfishing during the early to mid-1980s (Murphy and Crabtree 2001). These data were instrumental in the subsequent estimation of historic Red Drum escapement rates for the Florida Gulf Coast and were an impetus for maintaining stringent fishing regulations for this species (Murphy and Munyandorero 2008).

We examined relative abundance data for juvenile, subadult, and adult Red Drum collected in Tampa Bay and adjacent Gulf waters from 1989 through 2008 to determine whether trends in juvenile and subadult Red Drum relative abundance were subsequently reflected in the age structure of adult populations. The persistence of strong year-classes throughout ontogeny into the adult population can allow tracking of the success of regulations designed to increase survival and escapement of fish into the adult population (Bacheler et al. 2008). As a further measure of regulatory success and Red Drum stock recovery, we compared our data on size and age structure with data from a study conducted a decade earlier that found a compressed age structure, containing few fish more than 12 years old (Murphy and Crabtree 2001). If Florida Red Drum stocks are recovering, we would expect to see (1) persistence of strong juvenile year-classes into the nearshore adult population (evidence of adequate escapement) and (2) expanded size and age structure in the offshore population (evidence of escapement and improved survival of adult fish).

**METHODS**

*Field collections.*—We collected and analyzed long-term, fisheries-independent data on Red Drum in the Tampa Bay estuary to determine patterns in size and age structure and in year-class abundance (Figure 1). Tampa Bay (∼886 km²), located on Florida’s west-central Gulf coast, is a shallow (average depth < 5 m), tidally mixed estuary characterized by mangrove or marsh grass shorelines and extensive mud or sand flats often populated with sea grasses. We used a multiple-gear sampling approach, including haul seines and trammel nets to facilitate collection of Red Drum at multiple life stages. Haul seine sampling sites were selected at random following standardized protocols, which included stratifying monthly sampling effort by depth and habitat type (McMichael 1991; Flaherty and Landsberg 2011). From 1989 through 2008, we targeted young of the year (age-0) and small juvenile Red Drum in bay and tidal river habitats by using small haul seines (21.3 m long, 3.2-mm-knotless nylon mesh; hereafter, “small seines”; McMichael 2008; Flaherty and Landsberg 2011; Figure 1a). All Red Drum from small-seine samples were enumerated and a subsample measured for length (mm SL). We targeted large juvenile and subadult Red Drum (100–800-mm TL) using large haul seines (183 m long, 38-mm-knotted nylon mesh; hereafter, “large seines”) from 1996 through 2008 along shoreline habitats of the bay (McMichael 2008; Winner et al. 2010; Figure 1b). A subsample of Red Drum was retained from large-seine sets for life history analyses (see below), and the remainder of the fish were enumerated, measured for length (mm SL), and released alive.

Schools of subadult and young adult Red Drum (∼500–1,000-mm TL) were targeted during July–January in seagrass areas of lower Tampa Bay from 1993 through 1998 and again from 2003 through 2008 (Figure 1c). Schools were located visually and then encircled and captured with a 548.6-m-long × 2.4-m-deep nylon-mesh trammel net. This net consisted of one inside mesh (117.5-mm mesh size, #12 twisted nylon twine) and two outer mesh walls (356-mm-mesh size, #18 twisted nylon twine). The net had a 9.5-mm black polypropylene float line with small bullet floats spaced 762 mm on center, and a #50 leadcore rope along the base of the net. A subsample from each school of Red Drum was retained for life history analyses, and the remainder of the fish were enumerated, measured for length (mm TL), and released alive.

We contracted with a spotter pilot and commercial purse seine vessel to locate, capture, and sample schools of adult Red Drum in nearshore Gulf waters. Methods of searching (e.g., area, season), fishing, and subsampling were similar to those of Murphy and Crabtree (2001). The pilot conducted visual aerial surveys over nearshore Gulf waters between John’s Pass and Longboat.
Key, Florida (Figure 1c), from the beach to approximately 15 km from shore. Search effort was divided between two zones based upon distance from shore (0–5 km and 5–15 km). Aerial surveys were 2 h in duration and were typically conducted from August to December of each year from 2005 through 2008 to coincide with the fall Red Drum spawning season (Murphy and Taylor 1990; Wilson and Nieland 1994; Murphy and Crabtree 2001). If a school of Red Drum was sighted, the pilot contacted the purse seine vessel, relaying the geographical coordinates of the school. Once the purse seine vessel arrived on location,
it encircled the fish with its gear and gathered a subsample of approximately 100 Red Drum for life history analyses.

**Processing Red Drum life history samples.**—All Red Drum retained for life history analyses were iced and taken back to the laboratory where they were measured (mm TL), weighed (kg, total weight and gonad weight), and sexed. We removed sagittal otoliths and determined ages of Red Drum by using observed annulus counts, which were adjusted assuming an October 1 hatch date, following methods described by Murphy and Taylor (1990) and Murphy and Crabtree (2001). Since no Red Drum were retained from the small-seine samples, no data are available on sex ratio, weight, or age for those samples.

**Analytical methods.**—We calculated mean CPUE (fish/100 m$^2$) for age-0 Red Drum in small-seine collections and used an ANOVA ($\alpha = 0.05$; SAS Institute 2006a) to compare CPUE spatially between primary nursery areas and the main bay. Red Drum catch demographics (i.e., length, weight, age) were calculated and summarized independently by gear type for small-seine, large-seine, trammel-net, and purse-seine samples. Length frequency plots were constructed by gear type and included all individuals collected. When a subsample of Red Drum was measured for length at a given sampling site, applicable to haul seine samples only, known measurements were proportionally allocated to the unmeasured portion. When necessary (i.e., for individuals released in the field for which only SL was recorded), SL was converted to TL using length–length regressions published by Murphy and Taylor (1990). We calculated length statistics and used a Kolmogorov–Smirnov two-sample test (KS test; $\alpha = 0.05$; Sokal and Rohlf 1981; SAS Institute 2006a) to compare length frequency distributions between sexes within each gear type. Spatial variation in Red Drum lengths within the bay was statistically compared among large-seine samples to identify ontogenetic differences in habitat use. Large-seine samples were assigned to the upper bay (above 27°49′N), the middle bay (between 27°42′N and 27°49′N), or the lower bay (below 27°42′N; Figure 1b). Red Drum TL statistics were summarized and compared among these bay areas using a one-way ANOVA and a post hoc comparison of least-squared means using the Tukey adjustment for multiple pairwise comparisons ($\alpha = 0.05$, SAS Institute 2006a).

Weight frequency plots were constructed by gear type for large-seine, trammel-net, and purse-seine samples. Weight data used for purse-seine plots included only those individuals that were sampled because released individuals were not measured; however, for large seines and trammel nets, both subsampled individuals and those measured for length and released alive were included. Weight of released individuals was estimated utilizing the regression equation

$$\log_{10}(\text{total weight}) = -8.1457 + 3.0522 \cdot \log_{10}(\text{TL}; n = 14,076, r^2 = 0.999),$$

established by regressing log-transformed length and weight data from historical Red Drum collections (1993–2011) made by the Fisheries-Independent Monitoring (FIM) program at the Fish and Wildlife Research Institute (FWRI) in the Tampa Bay estuary (McMichael 2008). We calculated total weight statistics and used a KS test ($\alpha = 0.05$; SAS Institute 2006a) to compare weight frequency distributions between sexes within each gear type (using only individuals for which sex data were available).

We used the ages of subsampled Red Drum to construct age frequency plots by gear type and sex. Additional age data were generated for large-seine and trammel-net collections using lengths of Red Drum that were measured in the field and released alive. These fish were assigned ages using gear-specific age–length keys constructed from aged fish from large-seine and trammel-net samples. We calculated age statistics and used a KS test ($\alpha = 0.05$; SAS Institute 2006a) to compare age frequency distributions between sexes within each gear type (using only individuals for which sex data were available).

We compared the nearshore adult Red Drum size and age structures observed in this study with those observed by Murphy and Crabtree (2001), who conducted similar purse-seine sampling of Red Drum in the same geographic region. We used a one-way ANOVA ($\alpha = 0.05$; SAS Institute 2006a) to compare lengths, weights, and ages to test for changes in Red Drum mean size and age within the nearshore adult population as determined from purse-seine collections.

We calculated gonadosomatic indices (GSI, [gonad weight/total weight] \times 100; Wilson and Nieland 1994) for all Red Drum subsampled from large seines, trammel nets, and purse seines. We then plotted mean monthly GSI by gear type and sex to evaluate temporal patterns. An ANCOVA ($\alpha = 0.05$; SAS Institute 2006a) was used to model variation of GSIs during the spawning season (August–November) between the inshore (within Tampa Bay) and nearshore (Gulf waters) Red Drum populations. Gear type was used as a proxy of habitat (categorical variable), with large-seine and trammel-net data representing the inshore population and purse-seine data representing the nearshore population. The ANCOVA was run using TL as a covariate within the model including only Red Drum of 500–900-mm TL, since these sizes were prevalent in both habitats.

To monitor year-class strength, we developed relative abundance indices of juvenile Red Drum recruitment into the Tampa Bay estuary. Data from monthly stratified-random, small-seine surveys conducted in Tampa Bay from 1989 through 2008 were used to provide an annual index of relative abundance for age-0 Red Drum (McMichael 2008). To best estimate age-0 recruitment into Tampa Bay, only data collected during the peak recruitment period (October–December; Peters and McMichael 1987) of age-0 Red Drum (<40-mm SL) were analyzed. The relative abundance of age-0 Red Drum represented annual recruitment and was computed using a generalized linear model with a negative binomial distribution to adjust for the effects of spatial and temporal variability between samples (McMichael 2008). Location, time, and environmental variables were treated as either classification variables (zone, year, month, gear, deployment technique, sediment type, and presence or absence of bottom vegetation) or covariates (water temperature, salinity,
depth) in the analyses. The GLIMMIX procedure (SAS Institute 2006b), which fits generalized linear models and allows for nonnormal data, was used to complete all analyses. Water temperature, salinity, and depth data were natural log transformed (log\((X + 1)\)) before analysis. With the exception of year, all variables that were not significant (\(\alpha > 0.05\)) were dropped and the analysis repeated. Least-squares adjusted means and SEs were calculated for each year. Relative abundance was calculated as the median annual number of Red Drum per net haul. Median values were determined from the least-squares adjusted means by multiplying the SE by a random normal deviate (\(\mu = 0, \sigma = 1\)) and adding it to the least-squares mean. These data were then back-transformed (\(\text{ex}\)), and the process was repeated 500 times for each year to create a sampling distribution of back-transformed means.

We assigned a year-class (e.g., birth year) to all subadult and adult Red Drum by subtracting the fish’s age from the date of capture. Year-class frequency distributions were constructed by gear type (i.e., large seine, trammel net, and purse seine). Peak years in juvenile recruitment were qualitatively compared with year-class data for subadult and adult Red Drum collected within Tampa Bay and nearshore Gulf waters to track the persistence of strong year-classes through ontogeny (i.e., across gear types). Year-class frequencies were also qualitatively compared between the present study and a study by Murphy and Crabtree (2001) to evaluate the persistence of strong year-classes over time within the nearshore adult Red Drum population.

RESULTS
Small-Seine Collections
We collected 23,312 Red Drum during monthly small-seine sampling (11,512 net sets) in Tampa Bay from 1989 through 2008 (Table 1). The small-seine catch was dominated by smaller juvenile Red Drum, with 95% of the fish measuring less than 100-mm TL (Figure 2). Small Red Drum were more abundant within primary nursery areas of Tampa Bay. Mean CPUE of age-0 Red Drum was significantly higher (greater than six times higher) in primary nursery areas than in the main bay (ANOVA: \(F = 57.1; \text{df} = 1, 11,510; P < 0.0001\)). Even though Red Drum up to 750-mm TL were collected with the small seine, larger Red Drum were rarely captured in this gear (\(< 1%\) of Red Drum collected were \(> 200\)-mm TL).

Since no Red Drum were sampled from small-seine samples, no sex ratio, weight, or age information was available for individuals collected with this gear. However, based upon our recorded length data (99% of the Red Drum collected were \(< 200\)-mm TL) and the literature (Peters and McMichael 1987; Murphy and Taylor 1990), we estimate that Red Drum collected with the small seine would typically weigh less than 0.5 kg and be less than a year old (age-0 fish).

<table>
<thead>
<tr>
<th>Gear type, sex</th>
<th>TL (mm)</th>
<th>Total weight (kg)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>Min</td>
</tr>
<tr>
<td>Small-haul seine</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>All</td>
<td>23,312</td>
<td>58.2</td>
<td>17.5</td>
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<tr>
<td>Large-haul seine</td>
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<td></td>
</tr>
<tr>
<td>Male</td>
<td>381</td>
<td>526.7</td>
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</tr>
<tr>
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<td>421</td>
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</tr>
<tr>
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<tr>
<td>Male</td>
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<td>683.0</td>
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<tr>
<td>Female</td>
<td>741</td>
<td>691.0</td>
<td>459</td>
</tr>
<tr>
<td>All</td>
<td>5,582</td>
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<td>328</td>
</tr>
<tr>
<td>Purse seine (current study)</td>
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<td></td>
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</tr>
<tr>
<td>Male</td>
<td>456</td>
<td>918.3</td>
<td>678</td>
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<td>Female</td>
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<tr>
<td>All</td>
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<td>674</td>
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<tr>
<td>Purse seine (Murphy and Crabtree 2001)</td>
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<td>690</td>
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</tr>
<tr>
<td>All</td>
<td>905</td>
<td>911.7</td>
<td>685</td>
</tr>
</tbody>
</table>

* For fish not weighed, a total weight was calculated using a TL to total weight regression equation (see details in Methods).

* For fish not aged, an age was assigned using a gear-specific age length key (see details in Methods).
Large-Seine Collections

A total of 2,412 Red Drum was collected during monthly large-seine sampling (3,055 net sets) within Tampa Bay between 1996 and 2008 (Table 1). Red Drum ranged from 52- to 875-mm TL, with approximately 90% measuring more than 200-mm TL (Figure 2). Of the 2,412 Red Drum collected, 802 Red Drum were subsampled from large-seine samples for life history analyses. Among these subsamples, the male-to-female sex ratio was 1.0:1.1. Mean TL of females was longer than that of males, and length frequency distributions were significantly different.
between males and females (KS test: $D_{max} = 0.10, P < 0.05$; Table 1). Mean TL of Red Drum differed significantly among bay areas (ANOVA: $F = 37.5; df = 2, 2,409; P < 0.0001$). Red Drum collected in the lower bay (mean = 482.0-mm TL; SE = 5.0) were longer than those from the middle bay (mean = 412.0-mm TL; SE = 11.6) and the upper bay (mean = 422.1-mm TL; SE = 5.5), which did not differ. Red Drum total weight ranged from 0.001 to 6.8 kg, with a mean of 1.2 kg (Table 1; Figure 3).

**FIGURE 3.** Weight frequency distributions of Red Drum collected using large seines, trammel nets, and purse seines in Tampa Bay and nearshore Gulf of Mexico waters. The total number of Red Drum weighed (N) is noted for each sampling type.
and did not differ significantly between males and females (KS test: $D_{max} = 0.09, P > 0.05$). Red Drum collected in the large seine ranged in age from 0 to 6.5 years, and more than 90% of these were 3 years of age or younger (Table 1; Figure 4). Age did not differ significantly between males and females in the large-seine samples (KS test: $D_{max} = 0.09, P > 0.05$).

**Trammel-Net Collections**

We collected mainly subadult or young adult Red Drum ($N = 5,582$; Table 1) during directed trammel-net sampling (207 net sets) in Tampa Bay from 1993 through 1998 and from 2003 through 2008. Red Drum ranged from 328- to 1,051-mm TL, with 99% of the individuals caught measuring
more than 500-mm TL (Table 1; Figure 2). Of these 5,582 Red Drum, 1,510 were subsampled for life history analyses. The male-to-female sex ratio of Red Drum from trammel-net samples was 1:1, and the length frequency distributions were not significantly different between sexes (KS test: $D_{\text{max}} = 0.06$, $P > 0.05$). Red Drum total weight ranged from 0.4 to 11.9 kg, with a mean total weight of 3.5 kg (Table 1; Figure 3), and did not differ significantly between males and females (KS test: $D_{\text{max}} = 0.07$, $P > 0.05$). Red Drum collected in trammel nets ranged in age from 0 to 14 years; however, most (95%) were between the ages of 2 and 4 years (Table 1; Figure 4). Red Drum ages did not differ significantly between sexes in trammel-net samples (KS test: $D_{\text{max}} = 0.07$, $P > 0.05$).

**Purse-Seine Collections**

A contracted spotter pilot conducted 97 flights searching for Red Drum, including 31 flights in 2005, 12 flights in 2006, 47 flights in 2007, and 7 flights in 2008. These flights totaled nearly 200 h of search time, and the pilot sighted 17 schools of Red Drum during our study period. Most of these sightings were made between September and November (14 schools), with an additional 2 schools sighted in December and one in January. However, in 2005, no Red Drum schools were spotted. This was attributed to a major red tide (Karenia brevis) that occurred from the summer of 2005 through the spring of 2006 in the Tampa Bay area (DuPont et al. 2010; Flaherty and Landsberg 2011). Although search time was allocated evenly between search areas (0–5 km and 5–15 km from the shoreline), the majority of Red Drum schools (71%) were sighted in waters between 5 and 15 km from shore and ranging in depth from 6 to 9 m. The pilot visually estimated that the number of Red Drum per school ranged from 250 to more than 5,000. From 2006 through 2008, the contracted purse seine vessel was able to sample six of the sighted schools (Figure 1c). Fish were subsampled from a single school of Red Drum during 2006 (December 19, $N = 118$), two schools during 2007 (September 17, $N = 105$; September 26, $N = 172$), and three schools during 2008 (September 15, $N = 136$; October 2, $N = 141$; October 7, $N = 149$).

We subsampled 821 Red Drum from purse seines for life history analyses, including 456 males and 365 females (sex ratio of 1.2:1.0; Table 1). Fish ranged from 674- to 1,074-mm TL, with a mean of 922.5-mm TL (Table 1; Figure 2). Length frequency distributions did not differ between sexes (KS test: $D_{\text{max}} = 0.05$, $P > 0.05$). Red Drum ranged in total weight from 2.9 to 13.1 kg, with a mean of 8.3 kg (Table 1; Figure 3). The weight distributions of male and female Red Drum were not significantly different (KS test: $D_{\text{max}} = 0.07$, $P > 0.05$). Red Drum ranged in age from 3 to 35 years, with a mean of 11.9 years (Table 1; Figure 4). Age structure did not differ significantly between sexes in purse-seine samples (KS test: $D_{\text{max}} = 0.03$, $P > 0.05$).

Statistical comparison of our purse-seine data with work by Murphy and Crabtree (2001) shows that the size structure of adult Red Drum in nearshore waters off Tampa Bay has changed. Although the general range of length and weight is similar to historic estimates (Murphy and Crabtree 2001), mean TL (911.7–922.5 mm; ANOVA: $F = 10.43$; df = 1, 1,723; $P = 0.0013$) and mean total weight (7.7–8.3 kg; ANOVA: $F = 39.85$; df = 1, 1,720; $P < 0.0001$) have both increased significantly over the past decade (Figures 2, 3). Murphy and Crabtree (2001) reported a mean age of 9.8 years (minimum 3.0 years, maximum 30.4 years), with very few Red Drum older than age 12 in the nearshore population (Table 1; Figure 4). Ten years later, we found that the mean age has significantly increased to 11.9 years (ANOVA: $F = 70.85$; df = 1, 1,723; $P < 0.0001$) and that the proportion of older fish within the population (≥12 years) has increased from 26.6% (Murphy and Crabtree 2001) to 47.4% (Figure 4).

**Temporal and Spatial Variation in Reproductive Condition**

We observed seasonal variations in GSIs for both male and female Red Drum across all gear types (Figure 5). Peaks in GSIs typically occurred during September and October, coinciding with the Red Drum spawning season. During the spawning season, GSIs were significantly different between inshore and nearshore habitats for both female and male Red Drum (ANOVA, females: $F = 405.58$; df = 5, 832; $P < 0.0001$; males: $F = 1,221.20$; df = 5, 866; $P < 0.0001$). Red
Drum collected in nearshore Gulf waters (i.e., purse-seine collections) had significantly higher GSIs than similar-sized (500–900-mm TL) Red Drum collected in Tampa Bay (i.e., large-seine and trammel-net collections).

Year-Class Strength and Connectivity between Juvenile and Adult Populations

Although strong year-classes were evident in 1991, 1995, and 2002, annual relative abundance of juvenile Red Drum in Tampa Bay was variable and generally fluctuated only slightly from 1989 through 2008 (Figure 6). These strong year-classes were followed by a relatively large decline in abundance of juvenile Red Drum in 1992 and 1996, and by a steady but gradual decline from 2003 through 2005.

Red Drum year-class frequency distributions constructed by type of gear revealed peaks in year-class strength in Tampa Bay and nearshore Gulf waters (Figure 6). Year-classes represented within large-seine and trammel-net samples ranged from 1990 to 2008 and from 1982 to 2006, respectively. Our purse-seine samples collected in nearshore Gulf waters contained Red Drum year-classes ranging from 1973 to 2005. Murphy and Crabtree (2001) reported year-classes ranging from 1966 to 1995. Red Drum year-classes prior to 1984 were relatively rare in the present study (<1% of catch) and in the study by Murphy and Crabtree (2001; 12% of catch).

We found that specific year-classes of strong juvenile recruitment were disproportionately represented in both subadult stocks within the estuary (e.g., trammel-net catch) and in adult stocks in nearshore Gulf waters (e.g., purse-seine catch; Figure 6, gray bars). The persistence of strong year-classes within the adult population over time was also evident when comparing peaks in year-class strength between the present study and Murphy and Crabtree (2001). Murphy and Crabtree (2001) reported strong year-class peaks in both 1986 and 1989, and these same year-classes were persistent within our purse-seine collections a decade later (Figure 6, hashed gray bars).

DISCUSSION

Ontogenetic Habitat Shifts

Our use of multiple gear types specifically designed to target a variety of habitats and life history stages of Red Drum helped us document population connectivity and ontogeny from the estuary to nearshore Gulf of Mexico waters. Changes in relative abundance and the progression of size- or age-classes among separate habitats are commonly used to infer movement and habitat connectivity for estuarine-dependent species (Gillanders et al. 2003). Nevertheless, many studies have not obtained sufficient sampling coverage across a broad enough range of habitats and life history stages to satisfactorily characterize ontogeny.

We were able to document spatial and temporal trends of juvenile Red Drum in their primary nursery habitats as well as long-term trends in age-0 relative abundance in the estuary. Juvenile Red Drum typically recruit into low-salinity backwater areas (e.g., tidal creeks and rivers) in estuaries on the Gulf coast (Sykes and Finucane 1966; Yokel 1966; Peters and McMichael 1987; Scharf 2000; Bacheler et al. 2008). We found that most Red Drum (95%) utilizing these primary nursery habitats were age-0 fish of less than 100-mm TL. Results from our baywide small-seine collections also showed that mean catch rates for age-0 Red Drum were significantly higher in primary nursery areas than were those in the main bay. Some studies have shown that larger juveniles up to 450 mm in SL (543-mm TL, approximately age 2) may still frequent these primary nursery habitats (Peters and McMichael 1987; Ross et al. 1995; Adams and Tremain 2000). We also found this to be true, but rare, within our small-seine collections; only 1% of the Red Drum collected within primary nursery habitats was of more than 200-mm TL. The paucity of Red Drum of more than 200-mm TL in our small-seine catch can be partly attributed to gear selectivity (i.e., gear avoidance by larger fish). Previous work by FIM scientists in these same primary nursery habitats using hook-and-line gear showed that sublegal Red Drum (200–400-mm TL) were most prevalent in or near tidal creeks and rivers and backwater habitats (Flaherty et al. 2013).

Results from long-term monthly sampling with the large seine along estuarine shoreline habitats (e.g., mangroves, emergent vegetation, fringing oyster bars, sea grass flats) indicated that large juvenile Red Drum began recruiting to these areas between the ages of 6 months and 1 year (150–300-mm TL) and used these habitats until age 3 or 4 (500–800-mm TL). Previous studies also found that age-0 Red Drum gradually moved into deeper basins or bayous within rivers and creeks or ventured into shallow shoreline areas in the bay as they grew (Simmons and Breuer 1962; Peters and McMichael 1987; Flaherty et al. 2013). Peters and McMichael (1987) reported that Red Drum between the ages of 1 and 4 years used these common estuarine habitats within Tampa Bay.

The ontogenetic movement of Red Drum from nursery habitats into the higher salinity areas near the mouth of the estuary was reflected in our large-seine samples, which collected significantly larger (TL) Red Drum in lower Tampa Bay compared with those collected in the middle and upper bay. Flaherty et al. (2013) reported a similar trend of larger Red Drum collected from higher-salinity areas within the lower bay. Also, our trammel-net collections in lower Tampa Bay were dominated by subadult Red Drum (600–800-mm TL, 2–4 years old). These aggregations of subadult and young adult Red Drum in the grass flats of lower Tampa Bay were most common during the fall (August–November). Recent Red Drum mark-and-recapture studies in Tampa Bay also support the ontogenetic shift toward the lower bay as Red Drum grow and develop (Switzer et al. 2009); twice as many individuals originally tagged in the upper estuary had moved toward the lower estuary. These individuals were frequently recaptured in lower Tampa Bay but were also found in passes associated with the barrier islands north of Tampa Bay, in Sarasota Bay, and as far away as the Charlotte Harbor estuary (Switzer et al. 2009).
FIGURE 6. Indices of annual relative abundance of juvenile (age-0) Red Drum collected in small seines from 1989 through 2008 (top plot). Box plots represent the 25th and 75th percentiles, the vertical line extends from the 10th to the 90th percentile, and the horizontal line within each box plot indicates the median estimate. The five lower plots reflect the year-class percentage–frequency distributions of Red Drum collected using large seines, trammel nets, and purse seines in Tampa Bay and nearshore Gulf of Mexico waters. The total number of Red Drum aged and assigned a year-class (N) is noted for each sampling type. Gray-shaded areas within the background of the gear-specific plots represent the years during which sampling was done (e.g., large-seine sampling conducted from 1996 to 2008). Trammel-net year-class data are presented in two plots (1993–1998; 2003–2008) to facilitate interpretation of data. Years of peak juvenile (age-0) recruitment are marked as gray solid bars within each gear-specific plot. Prominent year-class peaks in the nearshore adult Red Drum population reported by Murphy and Crabtree (2001) are marked with gray hashed bars for comparison with the purse-seine plot from our current study. Some year-classes represented in large-haul seine (1990) and trammel-net (1982–1987) samples are not visible within these plots due to scaling (e.g., <0.05%).
Results from our analyses and previous studies indicate that the vast majority of Red Drum have completed their migration into nearshore coastal waters by age 5 (>800-mm TL, Yokel 1966; Murphy and Taylor 1990; Murphy and Crabtree 2001; Powers et al. 2012). The ontogenetic shift of subadult Red Drum from the lower estuary to the adult population in nearshore coastal waters was reflected in both our trammel-net and purse-seine collections. Our trammel-net collections in lower Tampa Bay showed a marked decrease in Red Drum from age 4–5, with very few Red Drum older than age 5 collected in the bay. In contrast, we found that Red Drum in nearshore Gulf waters were generally older than age 5 and of more than 800-mm TL (Figure 4). Even though subadult Red Drum ages 3 and 4 were found in our Gulf of Mexico purse-seine catch, they were rare (age 3: 2% of catch; age 4: 5% of catch). Similarly, Murphy and Crabtree (2001) reported that age-3 and age-4 fish made up only 7% of their overall catch. Others have collected small numbers of young Red Drum mixed in with the nearshore adult population and surmised that Red Drum of age 2 to age 4 are infrequent in the nearshore adult populations and that they do not fully recruit into the nearshore populations until at least age 5 (Simmons and Breuer 1962; Beckman et al. 1988; Pafford et al. 1990; Wilson et al. 1992). The mechanisms that determine when an individual fish will leave the estuary (e.g., size, age, state of maturity) and join the adult population are poorly understood. The movement from juvenile to adult habitats may be associated with reproduction or an ontogenetic or seasonal habitat shift relating to changing ratios of mortality risk and growth rate (Gillanders et al. 2003). Our observations of GSIs suggest that reproductive state may play a role in triggering migration of an individual from the bay to nearshore waters. Red Drum (500–900-mm TL) collected in the lower bay exhibited GSI values and trends reflective of immature fish or fish that were not actively involved with spawning; similar-size fish in nearshore waters exhibited GSI values and trends reflective of mature fish, peaking during the known spawning season and at levels seen by previous researchers for mature fish in the Gulf (Wilson et al. 1992; Wilson and Nieland 1994; Powers et al. 2012). In the northern Indian River Lagoon, on the east coast of Florida, Reyier et al. (2011) used acoustic telemetry to document that a majority of mature Red Drum remained within the lagoon–estuary year-round, suggesting true estuarine reproduction; we did not detect evidence of such behavior on the Gulf side of Florida. The dramatic differences in estuary morphologies between the Indian River Lagoon (i.e., lagoon–few inlets) and Tampa Bay (i.e., barrier island–multiple inlets) likely contribute to observed differences in Red Drum movement patterns and spawning-related behaviors, although causative factors are at present unclear. Detailed mark-and-recapture (e.g., otolith microchemistry, sonic tracking, and external tagging) and reproductive studies of Red Drum of migration age (3–5 years) would provide valuable insight into the dynamics of Red Drum escapement and connectivity between juvenile and adult habitats (Gillanders et al. 2003; Patterson et al. 2004).

Our multigear sampling design also provided evidence of correlation and persistence of strong year-classes across multiple life history stages. Juvenile Red Drum recruitment or year-class strength can vary greatly from year to year (Rooker et al. 1998; Scharf 2000; McMichael 2008). The persistence of strong year-classes through ontogeny into the adult population can be used as a tool to track how strongly regulations and environmental management contribute to increased survival and escapement of fish into the adult population (Bacheler et al. 2008). Our Red Drum indices of relative abundance from 1989 through 2008 documented peak juvenile recruitment in 1991, 1995, and 2002. We found that all 3 years of peak age-0 abundance persisted over time and were evident in subadult stocks in the estuary (trammel-net collections) and in adult stocks in nearshore Gulf waters. Furthermore, the peaks and general pattern of year-class frequency in our trammel-net samples were not only reflective of age-0 abundance indices but also year-class patterns seen in our purse-seine samples from nearshore gulf waters. In contrast, peaks in age-0 abundance were not consistently reflected in our large-seine samples collected within the estuary. In fact, year-class abundance for large-seine samples was fairly similar from 1995 through 2006, with only a few peaks that were not reflective of age-0 abundance trends. This disconnect between age-0 abundance and year-class strength seen in our large-seine samples could be attributed to a variety of factors, including variation in natural mortality of age-0 Red Drum and their subsequent recruitment to the gear. Our data suggest that Red Drum fully recruit to the large seine at age 2. Variation in age (between age 0 and age 2) at which Red Drum migrate from primary nursery areas into the main bay, could have a direct impact on cohort accessibility to our large-seine sampling. We also found that in several years of poor age-0 abundance, the associated year-classes were strongly represented in both our large-seine (i.e., 1996–2001, 2005, and 2006) and purse-seine samples (i.e., 1997, 1998, and 2000). This type of result illustrates the complexity of the connective relationship between age-0 recruitment and the adult population. Juveniles of smaller cohorts may benefit from density-dependent growth and survival while in primary nursery areas (Rooker et al. 1998; Scharf 2000) or reductions in fishing mortality within the estuary (e.g., reduced fishing pressure; Murphy and Crabtree 2001). Year-class strength in nearshore adult populations may also reflect contributions from multiple estuaries, which may vary in age-0 recruitment success. Thus, in years of poor recruitment in Tampa Bay, there could be improved escapement from neighboring estuaries that could contribute to the nearshore adult Red Drum population in this region of the eastern Gulf of Mexico. Although we found considerable variation in year-class strength within the adult population, we also found that some strong year-classes remained proportionately dominant over time. For example, Murphy and Crabtree (2001) documented strong year-classes in both 1986 and 1989, and these year-classes persisted within our nearshore purse-seine samples, collected 10 years later. These findings demonstrate that when estuarine Red Drum
populations are afforded regulatory protections, we can track escapement to the offshore spawning population, as evidenced by the persistence of strong year-classes over decades.

**Stock Recovery**

Life history data from adult Red Drum collected in nearshore waters off Tampa Bay provided evidence of continued stock recovery in the eastern Gulf of Mexico. Coastal proximity of adult Red Drum schools off Tampa Bay was similar to that noted for historic collections; all of the Red Drum schools we sampled were within a few nautical miles of locations sampled by Murphy and Crabtree (2001; Figure 1c). The ratio of male to female Red Drum within the adult population was consistent with historical estimates for Gulf Red Drum of a 1:1 ratio (Wilson and Nieland 1994; Murphy and Crabtree 2001). Although the general range of Red Drum lengths and weights was similar to historic values (Murphy and Crabtree 2001), mean TL and total weight have both increased significantly over the past decade (Figures 2, 3), further supporting the idea that stocks that have continued to recover.

A marked increase in relative numbers of older fish in the nearshore population off Tampa Bay also supports the idea of continuing recovery of the Red Drum stock (Figure 4). Collections of Red Drum by Murphy and Taylor (1990) during a period of heavy exploitation and with little-to-no regulation (early 1980s) identified a maximum age of Red Drum of only 24 years. Implementation of highly restrictive management measures during the mid to late 1980s resulted in an increase of the maximum age to 30 years, as reported by Murphy and Crabtree (2001). We found that the mean and maximum age of adult Red Drum in nearshore Gulf waters has increased significantly over the past decade, corroborating our conclusion that Red Drum stocks are recovering. The maximum age of Red Drum populations off Tampa Bay remains similar to estimates from the northern Gulf of Mexico (34–39 years; Wilson and Nieland 1994; Powers et al. 2012) but are lower than ages estimated from nearshore waters off North Carolina (maximum age: 56 for males, 52 for females; Ross et al. 1995), which may simply be evidence of regional variation between populations or an indication that adult Red Drum populations in this region of the Gulf may not yet have fully recovered.

Continued recovery of eastern Gulf of Mexico Red Drum stocks, as suggested by our study, is likely attributable to the long-term benefits of both state and federal regulation of fisheries, which have been followed by reductions in fishing mortality (Murphy and Crabtree 2001; Powers et al. 2012). In Florida, juvenile Red Drum enter the fishery at 15–18 months and are fully recruited by 24 months (legal slot: 457–686-mm TL), and by age 3 most Red Drum have outgrown the legal slot size (Murphy and Munyandorero 2008). Increased natural recruitment likely plays a significant role in rebuilding Red Drum populations (Sissenwine 1984; Dingsør et al. 2007; Bacheler et al. 2008). Nevertheless, strong juvenile recruitment does not always result in a concomitant increase to overall fishery productivity. There are very likely other limiting factors to recruitment than spawning stock biomass, such as carrying capacity of the environment, variation in physiochemical processes, natural and manmade perturbations, competition for resources, predator–prey relations, and fishing mortality (Rooker et al. 1998; Murphy and Crabtree 2001; Flaherty and Landsberg 2011). For example, Murphy and Crabtree (2001) documented high age-0 recruitment during the early 1980s, but due to lax fishing regulations and high fishing pressure within the estuary at the time, few of these fish recruited into the nearshore adult population.

In association with declining Red Drum populations, Florida implemented strict management measures in the late 1980s that included a combination of bag limits (i.e., 1 fish-person\(^{-1}\cdot\text{d}^{-1}\)), slot limits (457–686-mm TL), moratoria (i.e., 1986: 3 months; 1987: 6 months; 1988: 12 months), and permanent prohibition of commercial sales. Collectively, these regulatory measures reduced fishing mortality among subadult Red Drum and likely contributed to the survival of more Red Drum to maturity in the adult, nearshore population.

Although evidence suggests that Red Drum populations have recovered over the past two decades, increasing fishing pressures are of concern and should be monitored relative to harvest and catch-and-release mortality to ensure that this recovery continues. Fishing effort has increased markedly throughout Florida, from approximately 500,000 directed Red Drum trips per year in 1990 to nearly 2.25 million trips in 2006 (Murphy and Munyandorero 2008). Despite this dramatic increase in fishing effort directed toward Red Drum, the number of Red Drum being harvested has decreased substantially. Since 1989, approximately 473,000 Red Drum have been harvested annually along the Florida Gulf coast, compared with peak landings of nearly 1.4 million before fisheries regulations were implemented for this species (Murphy and Crabtree 2001; Murphy and Munyandorero 2008). In a largely catch-and-release fishery, postrelease mortality can contribute significantly to overall fishing mortality. Current research in Tampa Bay shows that estimates of postrelease mortality of Red Drum are relatively low (~6%; Flaherty et al. 2013). Fishing mortality estimates (F) were greater than 0.80 before the late 1980s and, following the establishment of regulations, have averaged 0.15 (Murphy and Munyandorero 2008). Recent recovery in Florida’s Red Drum populations has led to subsequent relaxing of recreational fishing regulations in the northern regions of the state where escapement rates have exceeded the FW C’s 40% escapement threshold for the past 20 years.

In summary, we found that a multigear approach, using a variety of gears specifically suited to capture target species at specific life stages, is an effective way to monitor a diverse array of habitats used by Red Drum throughout their ontogeny. Long-term monitoring of age-0, juvenile, and subadults allowed us to assess the success of recruitment within, and subsequent escapement from, the estuary. This inshore monitoring approach should be supported by periodic subsampling of adult stocks in nearshore waters, which has now been shown to be useful in...
assessing the condition (e.g., size and age structure) of the adult population and linking peak young of the year recruitment with the rebuilding of adult populations on a multidecade scale.

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Long-Term Population Response of Triploid Grass Carp Stocked in Piedmont and Coastal Plain Reservoirs to Control Hydrilla

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PLEASE SCROLL DOWN FOR ARTICLE
Abstract

The triploid Grass Carp Ctenopharyngodon idella has been used to control hydrilla Hydrilla verticillata infestations in southern U.S. reservoirs for several decades. After eliminating hydrilla in the water column, Grass Carp must be maintained in sufficient densities to control hydrilla regrowth from the tuber banks in the hydrosoil. We monitored the long-term response of triploid Grass Carp populations that had eliminated hydrilla within the water column in two Piedmont (Lake Norman and Mountain Island Lake, North Carolina) and two Coastal Plain reservoirs (the Santee Cooper system comprising Lakes Marion and Moultrie, as well as the connecting canal in South Carolina). Triploid Grass Carp stocked in Lake Norman and Mountain Island Lake exhibited slow growth and erratic, but potentially high, mortality. Due to erratic survival in the two Piedmont reservoirs, we could not estimate mortality using a catch curve. Fish stocked into the Santee Cooper system not only grew larger and faster, they also persisted (i.e., significant numbers of age-16–21 fish were collected during sampling in 2011). We hypothesize that Piedmont reservoirs without hydrilla in the water column and with little naturally occurring aquatic vegetation have a very low carrying capacity for triploid Grass Carp. Consistent, long-term survival of triploid Grass Carp in the Santee Cooper system may be due to available food provided by hydrilla regrowth in the water column, floating vegetation, and less-palatable, native, submersed vegetation. Hydrilla management in systems with residual plant food could involve estimating an average mortality rate and maintaining enough fish (i.e., about one fish per four hectares of surface area) to control hydrilla regrowth. In Piedmont reservoirs, possible management alternatives could include maintenance stockings based upon (1) yearling stocking rates that were successful in the past, (2) stocking determined from indirect measures of mortality such as from von Bertalanffy growth equation parameters, or (3) stockings derived from measures or indices of abundance such as counts conducted at night by bowfishers.

Grass Carp Ctenopharyngodon idella were introduced into the USA during the 1960s to control unwanted aquatic vegetation in small impoundments (Sutton and Vandiver 1986; Kirk 1992). However, diploid (fertile) fish were not widely used in larger, open bodies of water (primarily to control hydrilla Hydrilla verticillata) because of concerns about the establishment of reproducing populations, migration into environmentally sensitive areas, and impacts on nontarget aquatic vegetation (Guillory and Gasaway 1978; Noble et al. 1986; Leslie et al. 1987; Bain 1993). Concerns over adverse effects were especially warranted in peninsular Florida, where maintaining low levels of submersed aquatic vegetation is typically desirable and complete elimination of all submersed vegetation by Grass Carp has been documented (Leslie et al. 1987; Hoyer et al. 2005; Cassani et al. 2008).

The development of the triploid (sterile) Grass Carp increased their utility for controlling hydrilla in large impoundments (Allen and Wattendorf 1987; Wattendorf and Anderson 1987).
The first large-scale use of triploid Grass Carp was in the Santee Cooper system, South Carolina (Lakes Marion and Moultrie, and the connecting canal). A series of studies performed in these reservoirs from 1992 to 2004 provided useful information for aquatic plant managers. The following is a synopsis of these studies. Bowfishers provided a cost-efficient method of sample collection, and age-estimation techniques were refined using sectioned lapillar otoliths (Morrow et al. 1997). Age and growth studies monitored stocking success, growth, mortality, population size, and lifespan of triploid Grass Carp (Kirk et al. 2000; Kirk and Socha 2003). Angler responses to hydrilla management, gauged with angler creel surveys, suggested strong sentiment favoring hydrilla (Henderson et al. 2003). Movements of triploid Grass Carp into coastal rivers were evaluated using telemetry (Kirk et al. 2001). After triploid Grass Carp eliminated hydrilla in the water column, maintenance densities of about one fish per four hectares reservoir-wide controlled hydrilla regrowth from tubers in the hydrosoil (Kirk and Henderson 2006).

As a partial consequence of developmental studies in the Santee Cooper reservoirs, triploid Grass Carp became a significant hydrilla management tool in the southern reservoirs (Cassani et al. 2008; Manuel et al. 2013). Triploid Grass Carp were used in the successful management of hydrilla in Lake Marion, Lake Moultrie, and Lake Murray in South Carolina (Kirk and Henderson 2006; Manuel et al. 2013); Lake Austin and Lake Conroe in Texas (Klussman et al. 1988; Webb et al. 1994; Chilton et al. 2008); and Belews Lake, Mountain Island Lake, Lake James, Lake Norman, and Lake Wiley in North Carolina (Manuel et al. 2013). Triploid Grass Carp are being evaluated in Lake Gaston, Virginia–North Carolina, (Stitch et al. 2013) and in Claytor Lake, Virginia.

Understanding the long-term population response of triploid Grass Carp stocked to control hydrilla is important to achieve management goals. For example, studies in Florida have suggested that this fish persists too long and removal techniques need to be perfected (Thomas et al. 2006; Cassani et al. 2008; Hetrick and Langeland 2012). In other reservoirs (e.g., the Santee Cooper reservoirs, Lake James, and Lake Conroe), hydrilla returned after initial control was achieved (Chilton et al. 2008; Manuel et al. 2013), probably from regrowth of the tuber banks, rather than from the reintroduction by boaters. Thus, long-term hydrilla control will depend upon maintaining Grass Carp densities sufficient to deplete all regrowth from the hydrilla tuber bank for an extended yet undefined period.

In this study, we described two very different long-term triploid Grass Carp population responses where hydrilla had been eliminated in the water column. One focus area included two Piedmont reservoirs (Mountain Island Lake and Lake Norman) in North Carolina used for recreation, water supply, and power production by Duke Energy Corporation. The other area was the Santee Cooper system (Lakes Marion and Moultrie, and the connecting canal), which typifies multi-use, shallow, Coastal Plain reservoirs. The differences in triploid Grass Carp population responses between Piedmont and Coastal Plain systems may provide insight into maintenance stocking strategies in other regions of the country.

**METHODS**

**Study area and background.**—The study sites (Figure 1) included the Santee Cooper reservoirs in South Carolina and Lake Norman and Mountain Island Lake in North Carolina. The Santee Cooper reservoirs are a shallow Coastal Plain system covering approximately 77,000 ha. The reservoirs have a history of aquatic vegetation infestations that became much more serious after hydrilla was discovered in the early 1980s. Initially hydrilla was treated with registered herbicides, but when this approach failed triploid Grass Carp were stocked beginning in 1989. Even after initiating the use of triploid Grass Carp, hydrilla continued to expand and eventually infested 22,000 ha. A total of 768,500 fish were stocked between 1989 and 1996 and effectively eliminated hydrilla in the water column during 1996 and 1997. Triploid Grass Carp initially eliminated most submersed vegetation but substantial amounts of both floating and emergent vegetation remained in the system. Over the subsequent years, hydrilla remained controlled and native submersed aquatic vegetation became reestablished covering approximately 10% of the reservoirs (Kirk and Henderson 2006). By 2007, significant hydrilla coverage returned and triploid Grass Carp were again stocked. Despite stockings and the use of herbicides, hydrilla continued to expand and a total of 39,900 fish were stocked from 2007 to 2011 in an attempt to control the expanding hydrilla.

Mountain Island Lake is a 1,490-ha impoundment constructed during 1924 to supply drinking water to the greater Charlotte, North Carolina, area. Like nearby Lake Norman, this reservoir is typical of Piedmont reservoirs operated by Duke Energy Corporation for some form of power production. Submerged native aquatic vegetation is paltry and based upon the depth profile, hydrilla has the potential to infest about 25% of the surface area (Manuel et al. 2013). Hydrilla, discovered during 2000, was interspersed with brittle naiad *Najas minor*. The infestation was treated with registered herbicides and triploid Grass Carp at a rate of 42 fish per vegetated hectare. Hydrilla continued to expand until it displaced the brittle naiad, covered approximately 455 ha, and occupied most of the suitable habitat. By 2002, 32,000 triploid Grass Carp had been stocked and hydrilla was eliminated in the water column. Maintenance stockings continued (see Table 1) and hydrilla has not reappeared in the reservoir (Manuel et al. 2013).

Lake Norman covers 14,760 ha and was impounded during 1963. Hydrilla was first detected in this heavily developed reservoir during 2000. The infestation was aggressively treated with herbicides for the next 4 years. In addition to herbicide treatments, approximately 6,120 triploid Grass Carp were stocked during 2004, and all 180 ha of hydrilla were eliminated within a year. Maintenance stockings to prevent regrowth have continued (see Table 1). The hydrilla management plan for Lake Norman is considered a success. Hydrilla could have potentially covered...
3,600 ha but was eliminated at approximately 1% coverage by using an integrated approach of herbicides and triploid Grass Carp (Manuel et al. 2013).

Collections and analysis.—Studies conducted during the 1990s in the Santee Cooper reservoirs and in Lake Guntersville, Alabama, revealed that Grass Carp can be collected cost effectively by skilled bowfishers (Morrow and Kirk 1997; Morrow et al. 1997). Bowfishers operated at night using specialized tackle and boats employing gasoline generators to power a bank of lights. Bowfishers using these specialized techniques were able to collect fish in Lake Norman and Mountain Island Lake during 2010. These fish were compared with those collected earlier in the Santee Cooper system. Growth rates of triploid Grass Carp for the Santee Cooper reservoirs were obtained from Morrow et al. (1997), who described their growth during 1994. A later collection during 1998 depicted the population age structure and mortality 2 years after hydrilla had been eliminated in the water column (Kirk et al. 2000). An additional collection was made during 2011 to evaluate early survival of triploid Grass Carp stocked to control resurgent hydrilla.

Direct comparisons of year-class strengths of triploid Grass Carp must account for yearly differences in the number of fish stocked (e.g., about 50,000 triploid Grass Carp were stocked into the Santee Cooper reservoirs during 1993, and 152,500 were stocked during 1994). Due to unequal yearly stocking, age structure was described by adjusting the number of fish collected using a conversion factor to yield an adjusted number. The adjusted number of collected Grass Carp would allow the assumption of equal recruitment and the development of a total mortality estimate using a catch curve (Ricker 1975).

Age and growth techniques were developed by Morrow et al. (1997). Fish collected by bowfishers were returned to laboratory facilities operated by the Duke Energy Corporation or the South Carolina Department of Natural Resources. There, the fish were weighed to the nearest 10 g and measured for TL to the nearest millimeter. Also, lapillar otoliths were extracted, and scales were removed near the base of the pectoral fin. The relationship between weight (W) and TL was developed using a power function (Ricker 1975): \( W = aTL^b \). Otoliths were embedded in Polybed 812 resin and sectioned at 0.70 mm by means of a Buehler Isomet slow-speed saw using a diamond wafering blade. Ages were estimated by counting annuli viewed with transmitted light using either a microscope or dissecting scope.
Two readers independently estimated the age and then came to an agreement on an assigned age.

Conditions for triploid Grass Carp growth in the Santee Cooper reservoirs during 1994 were considered to be nearly optimum—and served as a good benchmark for comparison with Piedmont reservoirs—because hydrilla was still expanding, and the preferred food for the carp was not limiting (Morrow et al. 1997). Comparisons of growth were made as follows: the assigned ages, determined from reading the otoliths, were used with corresponding scales for back-calculation of TL at annulus formation. This technique was described by Morrow et al. (1997) and used the Fraser–Lee method and a standard correction factor of 30 mm after Carlander (1982). Age-specific weights were then determined for each age-class using the weight–length relation and back-calculated lengths from each reservoir system. Von Bertalanffy growth equation parameters were developed from mean back-calculated TLs (von Bertalanffy 1938). We did not statistically compare growth from von Bertalanffy equations because of practical concerns (e.g., the complete lack of younger fish, ages 1–3, from the Piedmont reservoir collections) raised by Knight (1968) and Francis (1996).

RESULTS

A total of 160, 96, and 66 triploid grass carp were collected and their ages estimated for the Santee Cooper reservoirs, Mountain Island Lake, and Lake Norman, respectively. The number of triploid Grass Carp collected in the three systems and adjusted for equal recruitment is listed in Table 1. The Santee Cooper reservoirs showed declining numbers of triploid Grass Carp (except for a strong 1993 year-class), reflecting a total annual mortality rate of about 32%. Mountain Island Lake and Lake Norman showed erratic, unequal survival among age-classes. Some age-classes showed good survival and others either poor or no survival; as a result total mortality based upon a catch curve could not be calculated.

The weight-to-length relation in the Santee Cooper system reported by Morrow et al. (1997) included fish collected during 1992–1994 and was $W = 0.00000425TL^{3.185}$ ($N = 354$, $r^2 = 0.98$). The Lake Norman relation was $W = 0.000389TL^{2.483}$ ($N = 66$, $r^2 = 0.87$) and for Mountain Island Lake it was $W = 0.00073TL^{2.349}$ ($N = 96$, $r^2 = 0.73$).

Mean back-calculated lengths at annulus formation, variability in back-calculated lengths described using standard deviations, and age-specific weights are shown in Table 2. Data presented for the Santee Cooper system came directly from Morrow et al. (1997). Growth of Grass Carp in the Santee Cooper system is faster than either Lake Norman or Mountain Island Lake. Both lengths at age and age-associated weights (Table 2) are markedly less in Lake Norman and Mountain Island Lake and imply that stunting, or at least greatly diminished growth, has occurred. Growth equation parameters (Table 2) suggest that triploid Grass Carp in the Santee Cooper reservoirs grow bigger and achieved an asymptotic TL ($L_\infty$) about 200 mm greater than fish in Mountain Island Lake or Lake Norman.

During 2011, skilled bowfishers collected 82 triploid Grass Carp from the Santee Cooper reservoirs to monitor early survival. Of these fish, 71 fish were from the stockings between 1989 and 1996 and 11 were from the more recent stockings between 2007 and 2011. Using published mortality rates from Kirk and Socha (2003), we expect that only a very small number of the original stockings would remain. Thus, the collection of only 11 fish from the 2007–2011 stockings of approximately 39,900 fish suggests poor early survival. These 11 fish were far

<table>
<thead>
<tr>
<th>Santee Cooper reservoirs</th>
<th>Lake Norman</th>
<th>Mountain Island Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>Year</td>
<td>Number stocked</td>
</tr>
<tr>
<td>1</td>
<td>1998</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>1997</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>1996</td>
<td>76,800</td>
</tr>
<tr>
<td>4</td>
<td>1995</td>
<td>90,000</td>
</tr>
<tr>
<td>5</td>
<td>1994</td>
<td>152,500</td>
</tr>
<tr>
<td>6</td>
<td>1993</td>
<td>50,000</td>
</tr>
<tr>
<td>7</td>
<td>1992</td>
<td>100,000</td>
</tr>
<tr>
<td>8</td>
<td>1991</td>
<td>100,000</td>
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<tr>
<td>9</td>
<td>1990</td>
<td>100,000</td>
</tr>
<tr>
<td>10</td>
<td>1989</td>
<td>100,000</td>
</tr>
<tr>
<td>11</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
too few in number to allow age structure analysis or to develop a catch curve.

**DISCUSSION**

The survival rate of triploid Grass Carp stocked into the Piedmont reservoirs could not be directly determined using a catch curve because a major assumption could not be met, namely these systems did not have a relatively constant survival rate among year-classes (Ricker 1975). No triploid Grass Carp younger than age 4 were collected in either Lake Norman or Mountain Island Lake. These fish may have been too small—about 600 mm according to Morrow et al. (1997)—to be fully vulnerable to bowfishers and probably should not be considered in the analysis. Examining age-classes 4 and older shows some year-classes exhibited much better survival than others (e.g., the 2003 and 2006 year-classes in Mountain Island Lake, Table 1). The opposite was true in the 1998 Santee Cooper collection where, with the exception of the 1993 year-class, the population declined at a rate of about 32% annually (Kirk et al. 2000). The annual mortality rate estimated during 1998 was about midway among a series of mortality estimates ranging from 22% to 39% described by Kirk and Socha (2003). Additionally, the original stockings from 1989 to 1996 persisted for at least 16–21 years and dominated the collection made during 2011. The presence of these older fish suggests at least some plant food has consistently been available. These older cohorts (i.e., age 16) are similar to those reported by Stich et al. (2013) in Lake Gaston, which suggests that with adequate food significant numbers of triploid Grass Carp can persist longer than a decade as predicted by Kirk and Socha (2003).

While the mortality rates for the Piedmont systems cannot be determined using a catch curve, we believe it was higher than in the Santee Cooper reservoirs. We hypothesize that once hydrilla is eliminated from the water column these reservoirs typically support very limited food for triploid Grass Carp. For example, Duke Energy Corporation mosquito control crews generally measured less than 1% coverage of native submersed vegetation in their Piedmont reservoir surveys for hydrilla. We hypothesize that the fish stocked into these Piedmont reservoirs after hydrilla was eliminated in the water column suffered high mortality from starvation. This explanation is further supported by evidence of stunting (or at least very slow growth and reduced condition) provided by age-specific comparisons in Table 2. Assuming that triploid Grass Carp in Piedmont reservoirs were not fully vulnerable to collection until age 4, a fish collected in Mountain Island Lake at age 4 would have been about 530 mm TL and weighed about 2 kg. A similar triploid Grass Carp collected from Lake Norman would have been about 660 mm TL and weighed almost 4 kg, while a fish from the Santee Cooper system would have been about 900 mm TL and weighed about 10 kg.

Triploid Grass Carp carrying capacity in these two Piedmont reservoirs—after hydrilla elimination in the water column—is potentially very low and may not sustain a stocking density sufficient to control hydrilla regrowth from the tuber bank. Indirect evidence that these two Piedmont reservoirs may not be able to support the desired density of one fish per four surface hectares of the reservoirs follows. Triploid Grass Carp were stocked into both Piedmont reservoirs control hydrilla regrowth using annual mortality rates from the Santee Cooper reservoirs that averaged about 32% (Manuel et al. 2013). In retrospect, even this desired density of one fish per four hectares was probably not achieved because triploid Grass Carp in both reservoirs suffered erratic mortality (Table 1) and reduced growth (Table 2).

The long-term response of triploid Grass Carp stocked into the Santee Cooper system during 1989–1996 was markedly
different (Kirk et al. 2000; Kirk and Henderson 2006). Triploid Grass Carp finally eliminated hydrilla in the column during 1996–1997. Initially, these fish also consumed much of the remaining submersed aquatic vegetation, but abundant floating and emergent vegetation remained. Submersed vegetation rapidly returned to the system and within a few years after the elimination of hydrilla covered approximately 10% of each of the two reservoirs. Over time, as triploid Grass Carp densities declined below a critical threshold (estimated by Kirk and Henderson 2006 as about one fish per four hectares), more and more hydrilla in the water column returned, and by 2007 both herbicides and triploid Grass Carp were being employed to combat this infestation. The collection during 2011 demonstrated that some triploid Grass Carp were able to persist for long periods of time (16–21 years), and we believe they were supported by hydrilla regrowth from the 22,000-ha tuber bank, less palatable floating and submersed plant species, and the subsequent rapidly resuming hydrilla.

Survival of triploid Grass Carp used in maintenance stockings can vary widely and is likely site-specific. Therefore, maintaining densities sufficient to control hydrilla recolonization from the tuber bank will be challenging. Piedmont systems devoid of hydrilla have limited available food, which apparently leads to the erratic survival of fish stocked to control hydrilla regrowth. We suggest that it may not be possible to directly estimate mortality via a catch curve for triploid Grass Carp, and hence population density, in Piedmont reservoirs. The Santee Cooper system, and perhaps similar systems, apparently can provide sufficient forage from native vegetation or hydrilla regrowth to support triploid Grass Carp for decades. In these systems, reliable estimates of mortality and projections of population densities are possible.

We suggest, since mortality via a catch curve cannot accurately be measured in Piedmont systems, that yearly stockings adequate to control hydrilla be made for an extended period (at least a decade or more) after hydrilla has been eliminated in the water column. Recommendations on improving this approach include using methods other than a catch curve to estimate mortality and thus determine future maintenance stocking rates. One suggested method, using von Bertalanffy growth equation parameters (i.e., \( k \), the Brody growth coefficient) was used by Stich et al. (2013) to indirectly estimate triploid Grass Carp mortality in nearby Lake Gaston, North Carolina–Virginia. The second approach involves counts by bowfishers as a baseline of density. This approach too has merit because bowfishers have proven repeatedly their ability to not only detect but to collect triploid Grass Carp at very low densities. Both indirect measures of mortality using growth equation parameters and counts may be a significant improvement over annual stockings based upon no real estimate of mortality or density.

ACKNOWLEDGMENTS

We thank D. Sigmon, A. Todd, and the Tar Heel Fish Stickers Club of Statesville, North Carolina, for collecting triploid Grass Carp by bowfishing. Likewise we acknowledge K. Baker and M. Autin of the Duke Energy Corporation, and M. C. Martin from the South Carolina Department of Natural Resources who processed Grass Carp. Support for this study was provided by the Duke Energy Corporation and the U.S. Army Corps of Engineers’ Aquatic Plant Control Research Program. Detailed comments and recommendations from the reviewers significantly improved this manuscript.

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reservoir ecosystem. Texas Agricultural Experiment Station Miscellaneous Publication 1664.


Assessment of Fat Reserves Adequacy in the First Migrant Silver American Eels of a Large-Scale Stocking Experiment

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ARTICLE

Assessment of Fat Reserves Adequacy in the First Migrant Silver American Eels of a Large-Scale Stocking Experiment

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Abstract

An experimental stocking program in the St. Lawrence River–Lake Ontario system provided a unique opportunity to compare reproductive fitness of migrant silver American Eels Anguilla rostrata from the stocking program (SM) and wild migrants (WM), both of which were grown in the same location. Body size, muscle lipid stores, oocyte development, and morphometric indices of silvering were compared between SM and WM eels captured in the St. Lawrence River estuary. Migrant eels from the stocking program were smaller than wild migrants from the estuary, but their size was similar to migrating wild silver American Eels from their site of original capture on the Atlantic coast of New Brunswick and Nova Scotia. A bioenergetic model was used to estimate the costs of migration and reproduction and the duration of migration. The adequacy of the measured lipid reserves to meet these estimated energetic costs was assessed for SM and WM eels. Gonad maturation and stage of silvering for SM eels were less advanced than that for WM eels, and they had lower initial muscle fat reserves and higher estimated energetic requirements for migration as a consequence of their smaller size. It was estimated that 100% of the SM eels would not have adequate fat reserves for migration and reproduction, whereas 57% of the WM eels would have adequate reserves. Smaller-sized SM eels would take 1.6 times longer to reach the spawning grounds than WM eels and, thus, may not arrive in synchrony with these wild migrants. Thus, smaller-sized, out-migrating, stocked eels from the upper St. Lawrence River are less likely than wild migrants to complete successfully their migration and reproduction. These results support the recommendation to source and stock American Eels at sites where they have similar life strategies to increase the likelihood of successful silver eel escapement.

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Received November 27, 2013; accepted April 9, 2014
A decline in abundance and recruitment of American Eel *Anguilla rostrata* has been observed in the St. Lawrence River–Lake Ontario system (SLR/LO) in Canada over the last 30 years, albeit some recovery has been seen recently (COSEWIC 2012). The causes of this decline are still uncertain, but hypotheses include overfishing, habitat destruction, pollution, barriers to migration, mortality after passage through turbines, disease, invasive species, and changes in ocean currents (COSEWIC 2012). Two experimental offsetting measures to help the recovery of this species involved a trap and transfer program moving large-sized American Eels downstream from hydroelectric dams (Stanley and Pope 2010) and a stocking program of glass (larval) eels. The latter were obtained from the commercial fishery based along the Atlantic coast of New Brunswick and Nova Scotia and translocated to the Richelieu River, Quebec from 2005 to 2008 and into the SLR/LO from 2006 to 2010 (Figure 1; Verreault et al. 2010; Pratt and Threader 2011). The aim of these experimental offsetting measures was to develop and evaluate efficient ways to increase escapement of maturing silver-phase American Eels migrating to the Sargasso Sea from this important freshwater habitat for this species.

A monitoring program was initiated to evaluate the movement, growth rates, sex ratio, and health status of the stocked American Eels and their effect on escapement (Verreault et al. 2010; Pratt and Threader 2011). In fall 2009, six migrating, female, silver American Eels originating from the 2005 stocking program in the Richelieu River were caught by commercial fishermen in the St. Lawrence Estuary during the period of migration of naturally recruited, migrating, female silver eels. The stocked eels had grown exceptionally fast and by age 4+ measured between 570 and 668 mm in length and weighed between 387 and 675 g. The size and coloration of stocked migrating (SM) eels were similar to those reported for migrating, wild, female silver American Eels in the original site of their capture in Nova Scotia. Even though the color of SM eels was similar to that of the migrating wild (WM) eels, their size was smaller in the St. Lawrence Estuary where silverying-phase females were generally longer than 800 mm and weighed over 1.5 kg (Verreault et al. 2010). Histological evaluation of SM eel gonads was not performed at that time. In 2010, 2011, and 2012, increasing numbers (hundreds) of smaller silverying American Eels (TL < 700 mm) were intercepted in the commercial fishery in spite of their low vulnerability to the large mesh of the fishing weirs (G. Verreault, unpublished data).

At the end of their growth phase, yellow anguillid eels of the North American and European coasts of the Atlantic Ocean accumulate lipid reserves prior to metamorphosis to a silver phase and departure for long-distance migrations to the Sargasso Sea where they spawn and die (Tesch 2003). American Eels leaving from the most distant portion of Lake Ontario have to swim more than 5,500 km to reach their spawning site in the Sargasso Sea (COSEWIC 2012). Over their large geographic range, wild silver European Eels *A. anguilla* and American Eels exhibit different characteristics at the time of their departure for migration. As the distance from their spawning site increases, their body length, mass, and somatic lipid content increase, and they leave earlier (Oliveira 1999; Tesch 2003; van Ginneken and Maes 2005; Tremblay 2009; Jessop 2010; COSEWIC 2012). For example, female silver American Eels captured in the Savannah River Estuary, Georgia, at 1,580 km from the Sargasso Sea have a mean body length of 584 mm compared with >900 mm for silver eel migrants captured in the upper St. Lawrence River, Quebec, at 5,520 km from the Sargasso Sea (Jessop 2010). There is a concern that transferring glass American Eels to sites that are more distant from the Sargasso Sea than their site of origin (~3,000 to >4,500 km) would disrupt this ecological gradient, reducing the reproductive fitness of migrants originating from the stocking program compared with wild migrants from SLR/LO, even though eels from the differing sites are genetically identical as the species is panmictic (Côté et al. 2012).

It was unknown whether the small stocked silver American Eels would have normally developing gonads and adequate lipid reserves to complete their migration to the Sargasso Sea.

Stocking of European Eels in rivers and lakes has been used in Europe for decades to create or to sustain fisheries (Feunteun 2002). More recently, stocking was used as one measure for the recovery of the European Eel stock. In 2007, the European Commission initiated an Eel Recovery Plan requiring that by 2013 at least 60% of the commercial catch of European Eels less than 12 cm be made available for restocking (European Commission 2007). However, there is a lack of scientific information regarding the efficacy of stocking to increase silver eel abundance and escapement to the Sargasso Sea as most studies have focused on the contribution of stocking to commercial and sport fisheries (Taylor 2011).

One of the objectives of the experimental stocking program in the SLR/LO is to compare reproductive fitness of SM eels intercepted in the St. Lawrence Estuary and WM eels of known origin that have grown in the same location. This study examined the hypotheses that SM eels caught in 2010 had a lower capacity for successful migration and reproduction as a result of insufficient energetic reserves and inadequate or delayed metamorphosis and gonad maturation. Body size, muscle lipid stores, oocyte development, and morphometric indices of silverying were compared between SM and WM eels captured in the St. Lawrence Estuary during their fall migration. A bioenergetic model developed by Clevestam et al. (2011) for female European Eels was used to estimate individual costs of migration and reproduction and the duration of migration for each individual SM and WM eel. The adequacy of the measured lipid reserves to meet these estimated energetic costs was compared between SM and WM eels.

**METHODS**

Fish tagging and recapture.—Most of the WM eels were captured and marked as juveniles (TL, 319–582 mm) from 1997 to 2001 as they moved upstream on eel ladders installed on dams
FIGURE 1. Sites of collection (open circle) and of stocking (stars) of glass eels, of tagging (MS: Moses–Saunders dam; B: Beauharnois dam) of juvenile wild American Eels, and of recapture (solid circles) of stocked and wild migrant silver American Eels.

located on the SLR/LO (Table 1). Wild migrant American Eels were divided into two components based on their tagging origin: \(W_{M1}\) eels were tagged and returned to the SLR/LO above the Moses–Saunders generating station (GS) and \(W_{M2}\) eels were tagged and returned to Lake St. Francis between the Beauharnois GS and Moses–Saunders GS (Figure 1). The American Eels were individually marked via an injection of a PIT tag into the dorsal musculature or visceral cavity. The PIT tags contained a unique alphanumeric code that identifies individual fish upon recapture (Verdon and Desrochers 2003).

For the stocking program, glass eels were purchased from the commercial fishery based along the Atlantic coast of New Brunswick and Nova Scotia (Figure 1) and were maintained in quarantine pending the outcome of health-screening procedures, batched marked via immersion in a solution containing oxytetracycline (Alcobendas et al. 1991), and transported a distance of 900–1,100 km to the receiving water bodies (Verreault et al. 2010; Pratt and Threader 2011). From 2005 to 2010, approximately 6.8 million glass eels were stocked in the Richelieu River and the SLR/LO (Figure 1).

Maturing female silver American Eels were recaptured during their seaward spawning migration from September 4 to November 6, 2010, by commercial fishers using weirs installed at angles to the shoreline on the south shore of the St. Lawrence

<table>
<thead>
<tr>
<th>Categories</th>
<th>Year of capture and tagging (n)</th>
<th>Site of capture</th>
<th>Site of release</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild migrants</td>
<td>1997 (1), 1999 (14), 2001 (12)</td>
<td>Upper St. Lawrence River (Moses–Saunders Dam)</td>
<td>Same as site of capture</td>
</tr>
<tr>
<td></td>
<td>1998 (24)</td>
<td>Upper St. Lawrence River (Beauharnois Dam)</td>
<td>Same as site of capture</td>
</tr>
</tbody>
</table>
Estuary near Kamouraska, Quebec (Figure 1). Kamouraska is located approximately 650 km downstream from Lake Ontario and about 3,650 km from the Sargasso Sea (shortest distances between sites). Two WM eels (one WM1 and one WM2) were trapped at an upstream site in the St. Lawrence River close to Québec City (Figure 1). The fishers kept PIT-tagged eels in tanks filled with aerated freshwater. Small (TL < 80 cm) silver American Eels, possibly originating from the stocking programs, were recaptured by commercial fishers during the same period as the WM eel and were also retained in the tank.

**Fish processing.**—Eels were scanned for PIT tags by the Ministère du Développement durable, de l’Environnement, de la Faune et des Parcs (MDDEFP) and those with PIT tags or small migrants were transported to the MDDEFP laboratory located in Rivière-du-Loup, Quebec. Eels used for biochemical and histological analyses were kept alive and were processed on the day after transport.

The eels were anaesthetized with a clove oil solution (1 mL Eugenol, Sigma-Aldrich, Oakville, Ontario; 10 mL 95% ethanol; 20 L freshwater) and killed by decapitation. Total length (±0.5 mm), body mass (±0.05 g), and empty digestive tract (stomach and intestine) mass were measured. Horizontal (OD H) and vertical (OD V) orbital diameters (left eye) and left pectoral fin length were also measured using a caliper (±0.01 mm). Measurement of the eye diameters were made from the mar...

**Statistical analyses.**—Three silvering morphometric indices were calculated: the ocular index \( \left\{ O_I = 10^2 \cdot \pi \cdot [4^{-1} \cdot (OD_H + OD_V)]^2 \cdot TL^{-1} \right\} \) (Acou et al. 2005), the pectoral fin index \( \left\{ I_{PF} = 10^2 \cdot \text{left pectoral fin length} \cdot TL^{-1} \right\} \), and the digestive tract index \( \left\{ I_{DT} = 10^2 \cdot \text{digestive tract mass} \cdot \text{body mass} \cdot TL^{-1} \right\} \) (Durif et al. 2005).

Data did not meet assumptions of normality and variance homogeneity; therefore, nonparametric tests were used for comparisons among categories of American Eels. Morphometric, histological, and biochemical measurements and indices were compared using a Kruskal–Wallis (KW) test on ranked data followed, when data was significant, by multiple comparisons using Tukey’s studentized range test. The percentages of American Eels with oocyte atresia were compared using the Fisher’s exact test. The relationships among variables were explored by calculating Pearson’s correlation coefficients. A critical significance level of \( \alpha < 0.05 \) was used for all these tests (SAS Institute 2000).

The lipid reserves required for migration and for maturation were calculated for each individual using the approach described in Clevestam et al. (2011) for female European Eels. The optimal swimming speed \( (U_{opt}, \text{mm/s}) \) was based on swimming experiments performed on silver European Eels and is a function of body length (mm) (Palstra 2006; Palstra et al. 2007) as...
follows:

$$U_{opt} = 0.77 \cdot TL.$$  (1)

The optimal swimming speed is used to calculate the individual optimal cruising speed ($U_{ind}$, km/h) as

$$U_{ind} = 3.6 \cdot 10^{-3} \cdot U_{opt}.$$  (2)

Swimming distance ($D$) from Kamouraska to the spawning site in the Sargasso Sea was estimated as 3,650 km using Google Map and was used in the calculation of the individual swimming time ($T_{SWIM}$, h) as

$$T_{SWIM} = D \cdot U_{ind}^{-1}.$$  (3)

The individual initial fat reserve ($M_{FAT}$, g) was

$$M_{FAT} = 10^{-2}\% \text{ lipid} \cdot \text{body mass} \cdot 0.8 \text{ (skin and bone excluded).}$$  (4)

The cost of transport (COT) was estimated from the total amount of lipid spent during a 5,500-km European Eel migration divided by the number of hours spent swimming (105 d) (Palstra et al. 2006). This value was used to calculate the individual fat consumption for migration ($M_{FATMIG}$, g) as

$$M_{FATMIG} = 38.2 \cdot 10^{-6} \cdot \text{body mass} \cdot T_{SWIM}.$$  (5)

The cost of female maturation (COM = 57 g/kg) was derived from Palstra and van den Thillart (2010) and was used to calculate the individual fat consumption for maturation ($M_{FATMAT}$, g) as

$$M_{FATMAT} = 57 \cdot 10^{-3} \cdot \text{body mass}.$$  (6)

The percentage of lipids in muscle required for migration was $10^2 \cdot M_{FATMIG} \cdot (\text{body mass} \cdot 0.8)^{-1}$, and the percentage of lipids required for both migration and maturation were $10^2 \cdot (M_{FATMIG} + M_{FATMAT}) \cdot (\text{body mass} \cdot 0.8)^{-1}$. Finally, the percentage of the initial lipid reserves remaining after migration and maturation was $10^2 \cdot [M_{FAT} - (M_{FATMIG} + M_{FATMAT})] \cdot M_{FAT}^{-1}$.

**RESULTS**

**Morphometric Characteristics**

Among suspected SM eels, only those having a clearly fluorescent yellow mark on the otoliths as a result of oxytetracycline marking were kept for the analyses, as these individuals originated from the 2005–2006 stocking programs based on the mark and annuli counts. Body mass and TL of SM eels were markedly lower than that of WM eels (KW test: $\chi^2 = 78$, df = 2, $P < 0.0001$; Table 2). The ocular index and pectoral fin index were lower in SM eels compared with WM eels, whereas the digestive tract index was higher (KW test: $\chi^2 = 30$, 9, and 29, df = 2, $P \leq 0.01$; Table 3). Parasitic nematodes, Anguillicoloides crassus, were not found in the swim bladders of the WM or SM eels examined in 2010 and thus were not considered to be a factor affecting growth and condition in this study.

**Histological Indices of Maturity**

All WM eels captured in the St. Lawrence estuary in 2010 were migrant silver female eels undergoing gonad maturation (mean oocyte diameter > 0.13 mm, percent oocytes with cortical alveoli > 40%). All SM eels sampled for histological examination ($n = 30$) were also silver females undergoing gonad maturation. The mean oocyte diameter was significantly lower in SM eels compared with WM eels ($\chi^2 = 23$, df = 2, $P < 0.0001$; Table 3). The proportion of oocytes with cortical alveoli did not differ significantly between SM and WM eels (Table 3).

**TABLE 2. Biological and morphometric characteristics and percentages of lipid and water in dorsal muscle of wild and stocked migrant silver American Eels captured in the St. Lawrence Estuary in the fall of 2010. Different letters indicate a significant difference among categories of eels (KW $\chi^2$ test). Values are presented as medians (first–third quartiles), minimum, and maximum; $n = $ sample size.**

<table>
<thead>
<tr>
<th>Category of eels</th>
<th>n</th>
<th>TL (mm)</th>
<th>Total mass (g)</th>
<th>Lipid (%)</th>
<th>Water (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WM1</td>
<td>27</td>
<td>1,013 z</td>
<td>2,340 z</td>
<td>16.3</td>
<td>65.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(959–1,087)</td>
<td>(2,137–2,509)</td>
<td>(14.8–18.6)</td>
<td>(63.0–66.4)</td>
</tr>
<tr>
<td>WM2</td>
<td>24</td>
<td>968 y</td>
<td>1,890 y</td>
<td>15.0</td>
<td>66.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(915–979)</td>
<td>(1,576–2,283)</td>
<td>(13.3–16.1)</td>
<td>(64.9–68.7)</td>
</tr>
<tr>
<td>SM</td>
<td>51</td>
<td>651 x</td>
<td>540 x</td>
<td>9.9</td>
<td>70.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(614–679)</td>
<td>(454–614)</td>
<td>(8.7–11.4)</td>
<td>(69.1–72.0)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Results of statistical tests:</th>
</tr>
</thead>
<tbody>
<tr>
<td>KW $\chi^2$</td>
</tr>
<tr>
<td>$P$</td>
</tr>
</tbody>
</table>
TABLE 3. Silvering and histological indices of maturity for different categories of wild and stocked migrant silver American Eels captured in the St. Lawrence River estuary in the fall of 2010. Different letters indicate a significant difference among categories of eels (KW \( \chi^2 \) test). Values are presented as medians (first–third quartiles), minimum, and maximum; \( n \) = sample size.

<table>
<thead>
<tr>
<th>Category of eels</th>
<th>Ocular index</th>
<th>Pectoral fin index</th>
<th>Digestive tract index</th>
<th>Oocyte diameter (mm)</th>
<th>Oocytes with cortical alveoli (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WM1</td>
<td>6.81 z (5.68–7.22)</td>
<td>4.93 z (4.35–5.31)</td>
<td>0.58 y (0.49–0.66)</td>
<td>0.28 z (0.26–0.30)</td>
<td>72.4 (67.5–75.5)</td>
</tr>
<tr>
<td>WM2</td>
<td>6.53 z (6.05–7.11)</td>
<td>4.91 z (4.47–5.28)</td>
<td>0.55 y (0.51–0.64)</td>
<td>0.27 z (0.25–0.29)</td>
<td>73.5 (69.8–80.2)</td>
</tr>
<tr>
<td>SM</td>
<td>5.34 y (4.92–5.94)</td>
<td>4.54 y (4.27–4.88)</td>
<td>0.82 z (0.67–0.98)</td>
<td>0.24 y (0.23–0.26)</td>
<td>72.4 (66.7–74.8)</td>
</tr>
</tbody>
</table>

Results of statistical tests:

KW \( \chi^2 \) 30 9 29 23 3
\( P \) <0.0001 0.01 <0.0001 <0.0001 0.26

Lipid and Water Content

Muscle lipid content was lower and water content was higher in SM eels compared with WM eels (KW test: \( \chi^2 = 66 \) and 60, df = 2, \( P < 0.0001 \); Table 2). As expected, in all categories of American Eels lipid content was strongly and inversely correlated to water content (WM1: adjusted \( r^2 = 0.86, F_{1, 25} = 162, P < 0.0001 \); WM2: adjusted \( r^2 = 0.76, F_{1, 22} = 75, P < 0.0001 \); SM: adjusted \( r^2 = 0.72, F_{1, 49} = 127, P < 0.0001 \)).

Lipid reserves required for migration and reproductive investments for migrating silver eels leaving the St. Lawrence Estuary were calculated (Table 4). Based on these estimates, WM eels would have required from 5.4% to 7.6% lipid for migration alone and from 12.5% to 14.8% for both migration and maturation (\( y \)-values ranges, Figure 2A, B). Lipid content in WM eels captured in the St. Lawrence Estuary ranged from 8.4% to 26.5% (Table 2). All WM eels had enough muscle fat reserves to reach the Sargasso Sea (Figure 2A), but not all had enough for maturation (Figure 2B). According to these calculations, more than half of the WM2 eels and 30% of WM1 eels had less than 10% of their initial lipid stores left after migration and maturation (Figure 3).

In contrast, SM eels would have required from 8.1% to 11.8% lipid for migration alone and from 15.2% to 19.0% for both migration and reproductive investments (\( y \)-values ranges, Table 4).

TABLE 4. Estimated percent lipids required for migration alone and for both migration and maturation in different categories of wild and stocked migrant silver American Eels sampled in the St. Lawrence Estuary during fall 2010. Different letters indicate a significant difference among sites (KW \( \chi^2 \) test). Values are presented as medians (first–third quartiles); \( n \) = number of eels analyzed for lipid content.

<table>
<thead>
<tr>
<th>Category of eels</th>
<th>Lipids required for migration (%)</th>
<th>Lipids required for migration and maturation (%)</th>
<th>Initial lipid reserves remaining after migration and maturation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>WM1</td>
<td>6.2 x (5.8–6.6)</td>
<td>13.3 z (12.9–13.7)</td>
<td>19.2 x (8.8–29)</td>
</tr>
<tr>
<td>WM2</td>
<td>6.5 y (6.4–6.9)</td>
<td>13.6 y (13.5–14.0)</td>
<td>9.0 y (−1.9–14.5)</td>
</tr>
<tr>
<td>SM</td>
<td>9.7 z (9.3–10.2)</td>
<td>16.8 x (16.4–17.4)</td>
<td>−68.2 z (−98.2 to −49.7)</td>
</tr>
</tbody>
</table>

Results of statistical tests:

KW \( \chi^2 \) 78 78 75
\( P \) <0.0001 <0.0001 <0.0001
Figure 2C, D). According to our estimation using muscle lipid only, 47% of the SM eels had enough lipid reserves to complete migration (Figure 2C) and none had the lipid stores to complete both migration and maturation (Figures 2C, D, and 3). Several SM eels with less than 10% of dorsal muscle lipid when captured in the St. Lawrence Estuary had a relatively high digestive tract index (IDT > 1) (12 with high IDT of 51 examined, or 24% [95% CI = 13–37%]; Figure 4). This proportion is significantly lower for WM eels (one with high IDT of 51 examined, or 2% [95% CI = 0.05–10%]; Fisher’s exact test; P = 0.002). As a consequence of their smaller size and of the assumption that swimming speed is directly proportional to body length (see equation 1 above), SM eels would have taken 1.6 times longer to reach the spawning grounds in the Sargasso Sea ($T_{SWIM} = 2,045 \pm 139$ h for SM compared with $1,339 \pm 106$ h for WM, mean ± SD).

**DISCUSSION**

This study and previous studies raise several questions regarding the capacity of a stocking program to increase American Eel spawner abundance and escapement to the Sargasso Sea and enhance recruitment. Using measurements of muscle
adequacy of fat reserves in stocked silver eels

Fat reserves and estimations of individual energetic costs of migration and maturation. SM eels may have greater energetic challenges than WM eels. It appears unlikely that after a period of continental growth of less than 6 years, compared with 20 years for WM eels from the upper St. Lawrence River (Jessop 2010), they would complete their migration successfully, in synchrony with wild fish and be able to reproduce. Although there is a concern about the validity of the assumptions used to estimate energy content, migration time, and costs, (see discussion on adequacy of lipid reserves) this study provides a unique comparison of SM with WM eels during the migratory, silvering stage. These calculations clearly demonstrate that SM eels were less fit for reproduction than were WM eels. Because of their small size SM eels had less muscle fat reserves and higher energetic requirements for migration than did WM eels and would have taken a longer time to arrive at the spawning site because optimal swimming speed is directly related to body length.

Size and Age at Migration

As first observed in 2009 (Verreault et al. 2010) and again in 2011 and 2012, body mass and length of SM eels were markedly lower than those of WM eels. Among the 80,000 silver American Eels caught in the fishery from 2009 to 2012, those originating from stocking operations (n = 541; 649 ± 49 mm [mean ± SD], 470–781 mm [minimum—maximum] for female SM eels, 2009–2012) did not show a significant increase in TL during those years (Verreault, unpublished data). Monitoring the length of SM eels will continue since previous studies on European Eels indicate a progressive increase in mean length at migration of female stocked eels from approximately 590 to 710 mm during the first 10 years after the onset of migration (Holmgren et al. 1997).

It is apparent that a proportion of the American Eels that were stocked maintained a final length or size at migration similar (Jessop 2010) to those reported at their site of origin (New Brunswick and Nova Scotia) despite being transplanted as glass eels to a site where wild American Eels have greater final length at migration. This proportion is unknown but likely not marginal since the catch efficiency of small eels in the commercial fishing weirs is very low. The maximum girth circumference of a 650-mm-long eel is approximately 125 mm, while the squared mesh size of the fishing gears is 25.4 mm, resulting in a girth circumference to mesh perimeter ratio of 1.2:1. In comparison, this ratio is 1.7:1 for 850-mm silvers. Growth rates were 138 ± 9 and 84 ± 8 mm/year for SM eels migrating at age 4 and age 7, respectively, and age at migration was inversely correlated to annual growth (Verreault, unpublished data), as reported previously for WM eels (Jessop 2010). Growth rates were higher and ages at migration were lower in SM eels than they were for WM eels grown in freshwater at their site of origin (range of means for three rivers in Nova Scotia: 23.8–28.3 mm/year, 17.1–19.4 years) or at the site of transplantation (range of means for two studies in SLR/LO: 43.2–47.9 mm/year, 19.7–20.9 years) (Jessop 2010). Growth rates in female silver eels are affected by several environmental factors including temperature, salinity, food availability, density, and crowding and by inherent characteristics such as appetite (Cairns et al. 2009). Côté et al. (2009) demonstrated that origin influences the growth of glass eels raised in the same environment but that come from different locations. Our results suggest that origin influences both length at migration and growth rates. Both the laboratory study conducted by Côté et al. (2009) and our experiment in a natural environment support the hypothesis of regional genetic variation in these life history characteristics. This genetic variation could originate from either nonrandom dispersal of individuals with different growth characteristics or differential survival associated with variation in individual genetic characteristics.
Adequacy of Lipid Reserves

According to our estimation, 49% of the SM eels did not have enough lipid reserves to complete migration and none had enough fat stores to complete both migration and maturation based on muscle fat alone. Thus, based on these estimations, SM eels are unlikely to contribute significantly to recruitment unless they interrupt their migration to replenish their fat reserves; however, there is no record of eels stopping once they reach saltwater during their migration. In the 4–5 years spent in the SLR/LO, SM eels grew more rapidly but did not accumulate as much fat as the WSM eels did over 15–20 years. Migrating SM eels had less lipid reserve (10% compared to 18 ± 2.5%) than did similarly-sized (679 ± 119 mm) but older (20 ± 4 years) wild silver American Eels captured at Petite Trinité River, a tributary of the Quebec north shore flowing into the Gulf of St. Lawrence, at a location about the same distance (3,200 km) from the spawning site as was our sampling site in Kamouraska (Tremblay 2009). A higher lipid content (29.9 ± 3.1%) was found in wild Baltic Sea silver European Eels of similar size (655 ± 90 mm), but they had a longer migration route (6,900 km) (Clevestam et al. 2011).

Tremblay (2009) reported that wild American silver eels leaving for migration from Prince Edward Island in the Gulf of St. Lawrence at 2,850 km from the Sargasso Sea have a mean body length of 693 mm, body mass of 595 g, and percentage of somatic lipids of 17.5%. If these values are entered into our calculations, these eels would have 60% of their lipid reserves left after migration and 19% of their reserves remaining after migration and full maturation. In our study, SM eels captured at 650 km from their growing site had a median body length of 651 mm, body mass of 540 g, and somatic lipids of 9.9%. If they had left from their site of origin in New Brunswick–Nova Scotia, SM eels would have approximately 2,000 km to swim to reach the Sargasso Sea. We estimate that these eels would have, on average, 47% of their lipid reserves left after migration and would not have enough lipid reserves (−25%) to complete both migration and full maturation. Thus, SM eels appear to be less fit for successful migration and reproduction than wild migrants departing from Prince Edward Island. This is likely a consequence of fast growth leading to inadequate lipid reserves at the time when they reach the size at which they migrate, which is at a younger age than wild freshwater American Eels from their site of origin.

The median (first–third quartiles) gonadosomatic index (GSI = 100 · gonad weight / body weight) for WSM1, WSM2, and SM eels were 4.46% (4.30–4.86%), 4.19% (3.92–4.54%), and 3.58% (3.24–3.93%), respectively (C. M. Couillard, unpublished data). The gonad development in SM eels is in the same range as that of similar-sized wild eels from Prince Edward Island (GSI: 3.9 ± 0.5%, mean ± SD; Tremblay 2009). These GSI values are one order of magnitude lower than those reported for European Eels matured artificially by hormonal injection and having a GSI of 28–60% (Palstra 2006). The GSI at full maturity is likely similar for American Eels (Oliveira and Hable 2010). Thus, the majority of the energetic investment in gonad maturation occurs later in migration for both SM and WSM eels.

To our knowledge, this is the first study to compare lipid reserves in SM and WSM American Eels of known origin and that have grown in the same location. Compared with our values, higher muscle lipid content (28.4 ± 4.4%) was reported for stocked European Eels (772 ± 62 mm) of unknown geographic origin tagged in the Schwentine River in northern Germany and recaptured during their migration in the Baltic Sea (Prigge et al. 2013). In Sweden, low fat stores were found in migrant eels from Lake Fardume (dorsal muscle lipid: 6.7 ± 2.97%, mean ± SD) originating from stocked elvers in France (Svedäng and Wickström 1997). Further studies are needed to discriminate between the effects of the environmental conditions at the site of origin or at the site of transfer on the accumulation of fat in stocked American Eels or European Eels.

We calculated that all WSM eels had enough muscle fat reserves to reach the Sargasso Sea. However, more than half of the WSM2 eels and 30% of WSM1 eels would have less than 10% of their initial lipid stores left after migration and reproduction. Wild European Eels with a 5,500-km swimming distance consumed 67% of their energy stores during maturation and simulated migration in a swim tunnel (Palstra and van den Thillart 2010). This is within the range reported for other species of fish that have a semelparous life strategy (Svedäng and Wickström 1997; Cleveast et al. 2011). Using the same calculations and assumptions, Cleveast et al. (2011) estimated that 45% of wild Baltic silver European Eels (see description above) would have less than 10% of their initial muscle lipid stores left after migration and reproduction, a proportion within the same range as our estimates for WSM eels (30–58%). A possible explanation for the European Eel decline is the poor quality of females with reduced fat stores, possibly related to altered habitat, that prevent successful spawning migration (Svedäng and Wickström 1997; Geeraerts and Belpaire 2010; Cleveast et al. 2011). Our results suggest that, as observed for European Eels, the fat reserves of a large proportion of the WSM silver American Eels from the SLR/LO may not provide a sufficient reproductive investment.

An alternative explanation for the relatively high proportion of WSM and SM eels with inadequate lipid reserves is that costs for migration were overestimated. There is a great deal of uncertainty on the amount of energy required for a successful spawning migration in American Eels and European Eels. The estimates of costs of transport and of maturation are derived from laboratory swimming experiments that used a relatively small number of artificially mature wild European Eels (Palstra 2006; Palstra and van den Thillart 2010). These estimates could possibly overestimate energetic needs for migration if wild American Eels make use of currents and adapt their behavior (e.g., schooling or shoaling) to reduce swimming costs (Aarestrup et al. 2009; Burgerhout et al. 2013). The route taken by the St. Lawrence River American Eels to the spawning site is unknown. For this report, we have retained the hypothesis that they take the shortest, most energetically conservative route,
as proposed by COSEWIC (2012) and Tremblay (2009). However, if silver American Eels migrate along the continental shelf path as suggested by Jessop (2010) for larval eels, this would add more than 1,000 km to the swimming distance and consequently increase their energetic needs. The European Eels used for the swimming experiments (mean body length, 730 mm; Palstra 2006) were shorter than W_M eels and longer than S_M eels. This could lead to an overestimation of the swimming costs for W_M eels and underestimation for S_M eels since large eels are expected to be more efficient during swimming than are small individuals (Clevestam et al. 2011). The effect of body length on optimal swimming speed should be further explored in small- and large-sized silver American Eels (Palstra et al. 2008; Quintella et al. 2010).

Another source of uncertainty is that fat content in a subsample of muscle may not be identical to fat content in the whole body. In European Eels, fat content varies among different body parts, in which fat content in the tail area (%) is higher but lower in the head area (%) skin contains 9.7% fat (Tesch 2003). Fat content in the liver, gonad, and gastrointestinal tract is not expected to be greater than 2–3% of body mass considering their relative total mass (6–7%). In our study, fat content was analyzed in the dorsal muscle, between the pectoral fin and the insertion of the dorsal fin. Thus, muscle fat content may be slightly underestimated. If we rerun the calculations with the hypothesis that the individual fat reserves are 20% higher than our estimation, 0% of W_M1, 13% of W_M2, and 96% of S_M eels would have less than 10% of their initial lipid stores left after migration and reproduction. It is also likely that American Eels use carbohydrate and/or protein in addition to lipids as sources of energy, as do European Eels (van Ginneken et al. 2005) and Sockeye Salmon Oncorhynchus nerka (Mommsen 2004).

Further studies are needed on tissue distribution of lipids, swimming energetics for different size American eels, sources of energy available to sustain a long starvation period, and energy-saving tactics during migration. The condition of migrating stocked silver American Eels in the St. Lawrence Estuary should be followed for several years since the first migrants may not be representative of the whole output of migrants. Observations made in fall 2011–2012 (Verreault, unpublished data) indicate that the size difference measured in 2009 (Verreault et al. 2010) and in our 2010 samples between stocked and wild migrants remained quite stable. However, it will take another 5–10 years to determine the size distribution of mature females produced from the 6.8 million glass eels stocked in the SLR/LO and the Richelieu River. The experimental glass eel stocking program stopped in 2008 in the Richelieu River and in 2010 in SLR/LO. Long-term monitoring of this program is still under way and we are only partly through an experiment that may take 15 or more years to complete.

Duration of Migration and Stage of Maturation

As observed in the fall of 2009 (Verreault et al. 2010), the 2010 stocked migrant silver American Eels were captured at the same site in the St. Lawrence Estuary as were wild silver migrants originating from the SLR/LO and Richelieu River. Thus, S_M eels do not seem to be disoriented as reported in some studies on stocked European Eels (Westin 2003; Prigge et al. 2013). Migrant American Eels stocked in the upper part of the St. Lawrence River more than 450 km upstream found their way to the brackish waters of the St. Lawrence Estuary. These findings support Tesch’s (1974) hypothesis that orientation mechanisms are not dependent on previous migration experience as immigrating juveniles and that a combination of geomagnetism and olfactory cues could be the main mechanisms driving orientation in silver eels (Tesch 1974; Tsukamoto 2009).

Successful spawning migration not only requires homing to the natal site but also being able to arrive in time for spawning (Tesch 2003; Prigge et al. 2013). Because their body length is 1.6 times shorter (median: 645 mm in S_M versus 1,007 mm in W_M) than that of W_M eels, it is assumed that S_M eels will take 1.6 times longer (30-d delay) to reach the spawning grounds in the Sargasso Sea as swimming speed is related to body length (Palstra 2006; Palstra et al. 2007). However, the assumed longer time required to reach the spawning grounds could result in asynchronous arrival at the spawning site with American Eels from the same growth habitat in the SLR/LO. Body size at migration increases as distance from the spawning site increases (Jessop 2010), reducing the risk of asynchrony for wild American Eels of different sizes. A 10-d delay in the migration peak of S_M eels compared with W_M eels was observed in 2011 at Kamouraska, 650 km downstream from Lake Ontario (Verreault, unpublished data). This gap is expected to increase as American Eels progress along their 3,650-km migration route to the Sargasso Sea ($T_{SWIM} = 2,045 \pm 139$ h for S_M compared with $1,339 \pm 106$ h for W_M, mean $\pm$ SD, 31-d delay). However, the consequences of a 30-d delay on reproductive success may be minor if most spawning by American Eels occurs during a 75-d period, from mid-February through April, as estimated by McCleave (2008).

Stocked migrants exhibited a less advanced stage of oocyte maturation compared with W_M eels. Because S_M eels are expected to reach the spawning site approximately 1 month later than W_M eels, they would presumably have time to reach full gonad maturation providing they had sufficient fat reserves. Stocked migrants also exhibited a less-advanced stage of silvering as shown by their lower ocular index and higher digestive tract index. Ocular enlargement occurs early in the sequence of sexual maturation (Acou et al. 2005; Durif et al. 2005) and is thought to be a requirement for migration at depth in the ocean. Degeneration of the digestive tract is observed in maturing European Eels and in Pink Salmon O. gorbuscha (McBride et al. 1986; Sorensen and Pankhurst 1988). The progressive degeneration of the digestive tract is considered to be an adaptation to conserve energy during the spawning migration (Sorensen and Pankhurst 1988). In silver American Eels with adequate lipid reserves, it is believed that feeding is not required to meet the energy demands of migration and spawning. Several (24%)
stocked eels with initial fat reserves lower than 10% had a high digestive tract index. It is possible that these American Eels will feed during the course of their migration and gain additional fat reserves, or that the resorption of the digestive tract could also provide energy reserves. It is also possible that some American Eels would interrupt their migration for a year, reverse their silverying process, replenish their fat stores, and then resume their migration once they have adequate fat reserves (Svedäng and Wickström 1997; Westin 2003; Durif et al. 2009).

Over their large geographic range, wild silver American Eels exhibit regionally different characteristics at the time of their departure for migration associated with distance from the Sargasso Sea spawning site (Jessop 2010). Our study indicates that transferring glass eels to sites more distant from the Sargasso Sea than their site of origin (~3,000 km to >4,500 km) can disrupt this ecological gradient, reducing the reproductive fitness of SM eels compared with WM eels from SLR/LO. In European stocking programs, glass eels are frequently transferred from southern locations (e.g., France, Spain, or UK) to northern locations (e.g., Baltic sea) and stocked silver eels also appear to have lower fat reserves compared with wild silver eels (Svedäng and Wickström 1997). Therefore, based on these first results and with a precautionary approach, it is recommended to source and stock individuals at sites where they have similar life strategies. This approach would increase the likelihood of successful spawner escapement and also reduce the risk of pathogen introduction (Taylor 2011). If this option is not available, other management options (e.g., reducing exploitation, providing bypass barriers) should be considered to improve spawner escapement. Our results provide useful information for the development of a recovery plan for the American Eel, and for the application of the American Eel and European Eel recovery plan. There is a need for further scientific studies to demonstrate that silver American Eels originating from stocking are able to contribute to recruitment before recommending large-scale stocking as a recovery measure.

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Effects of Seawalls and Piers on Fish Assemblages and Juvenile Salmon Feeding Behavior

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ARTICLE

Effects of Seawalls and Piers on Fish Assemblages and Juvenile Salmon Feeding Behavior

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Abstract
Shoreline modifications, such as seawall armoring and piers, are ubiquitous along developed waterfronts worldwide, and recent research suggests that their ecological effects are primarily negative. We utilized snorkel surveys to quantify the effects of seawalls and piers on fish in nearshore habitats of an urbanized estuary in Puget Sound, Washington. We observed 17 species of fish and 4 species of crab during April–August 2012 at sites modified by seawalls and piers and at reference beach sites with minimal anthropogenic structures. Species assemblages at modified sites were significantly different from those at reference beaches. At modified sites, fish distribution and assemblage structure varied with proximity to the shade cast by piers; overall fish abundances were reduced under piers, and the greatest abundances were observed at high tides in areas directly adjacent to piers. Juvenile Pacific salmon Oncorhynchus spp. were the dominant fish species, and piers reduced their presence and feeding, indicating that areas under piers provide less-valuable habitat to salmon species. Piers may interrupt movements of juvenile salmon when they use shallow waters along shorelines to migrate from freshwater to marine habitats, as juvenile salmon tend to avoid shade under piers, especially at high tides. Our results show that shoreline modifications can alter species assemblage structure, thus potentially creating novel combinations and abundances of species, and can reduce habitat function for species that utilize these and similar habitats elsewhere.

The aggregation, expansion, and maintenance of residential, commercial, and tourism activities in estuarine and coastal waterfront landscapes have transformed these areas on a global scale (Bulleri and Chapman 2010). Most of these activities are accompanied by shoreline modifications, such as armoring (e.g., seawalls and riprap) and overwater structures (e.g., piers and floating docks) that provide the economically important functions of erosion protection and waterfront access. Waterfront development is likely to continue as human populations grow and locate disproportionately in coastal, urban locations (Grimm et al. 2008) and as climate change and rises in sea level occur (Bulleri and Chapman 2010). Estuaries are especially vulnerable to change, as 22 of the world’s 32 largest cities are located on estuaries (Ross 1995). Despite the widespread use of shoreline modifications along developed waterfronts, ecological effects of the modifications have only recently been studied, and many of the results indicate negative effects on indigenous species (reviewed by Bulleri and Chapman 2010).

Recent research suggests that shoreline armoring drives ecological change. Shoreline armoring, which is the use of hard structures to absorb wave energy and prevent erosion, can alter the physical environment of shallow waters by truncating the intertidal area (Chapman and Bulleri 2003) and hardening the substrate (Airoldi et al. 2005). Armoring can reduce the production and input of terrestrial invertebrates (i.e., fish prey) into aquatic ecosystems (Peterson et al. 2000; Chapman 2003; Cruz Motta et al. 2003; Romanuk and Levings 2003; Moschella et al. 2005; Sobocinski et al. 2010), which may lead to reduced consumption of terrestrial prey by fish (Toft et al. 2007). Introducing novel structures to aquatic habitats can also attract atypical and nonnative organisms (Glasby 1998; Davis et al. 2002; Glasby et al. 2007; Strayer et al. 2012). Most of the research...
investigating the effects of shoreline armoring on fish is recent; such studies have used scuba (Clynick 2006; Clynick et al. 2008), snorkeling (Toft et al. 2007, 2013), enclosure nets (Toft et al. 2007), beach seine (Bilkovic and Roggero 2008), and electrofishing (Strayer et al. 2012), and the resulting data suggest that land development and changes to shoreline structure influence the composition of nearshore fish species. Seawalls, which are vertical slabs of hard, typically featureless surfaces, are a common type of shoreline armoring, but their effects on fish are not well understood (however, see Toft et al. 2013).

Overwater structures, such as piers and floating docks, constitute another type of shoreline modification that causes ecological change by reducing light and introducing pilings to shallow waters. In the Hudson River estuary, a series of studies demonstrated that overwater structures can negatively impact fish: acoustic surveys showed that a large pier reduced pelagic fish abundances (Able et al. 2013); piers changed the composition of invertebrate (fish prey) species, with reduced abundances of larger species (Duffy-Anderson and Able 2001); and cage experiments suggested that shading of habitat by piers caused a reduction in growth opportunities by limiting prey detection and consumption by demersal fishes (Duffy-Anderson and Able 1999, 2001). In Puget Sound, Washington, shallow-water areas that were located directly adjacent to areas shaded by overwater structures were shown to have high densities of fish, whereas pier pilings were often utilized by crabs (Toft et al. 2007), indicating that overwater structures influenced fish and crab distributions.

The objective of our study was to quantify the effect of seawalls and piers on nearshore fish and crab communities in an urbanized estuary (Elliott Bay, Seattle, Washington) by comparing their distribution and species assemblage structure (1) between highly modified sites and reference beaches and (2) among stations within modified sites, with stations being defined based on their proximity to piers. Juvenile Pacific salmon Oncorhynchus spp. were the focus of this study, and our analysis quantified their ability to access and feed in modified nearshore habitats. We were interested in effects on juvenile salmon because they are among the dominant fish species in our study area during the spring and summer months; they have cultural, ecological, and economic significance (discussed in detail by Quinn 2005); they rely on nearshore habitat early in their life history (Simenstad et al. 1982); and the Chinook Salmon O. tshawytscha in our study area are currently listed as threatened under the Endangered Species Act.

Pacific salmon are anadromous species that enter estuarine or marine environments as juveniles, exhibiting a strong initial tendency to stay in shallow waters, which they use for feeding, predator refuge, and salinity acclimatization (Simenstad et al. 1982). In developed areas, this tendency places the juvenile salmon close to shoreline modifications (Toft et al. 2007), including armoring that reduces the production of their invertebrate prey (Sobocinski et al. 2010). Juvenile salmon are active visual predators, capturing individual prey in the water column and from the substrate (Quinn 2005). Laboratory experiments have suggested that light levels affect prey detection by juvenile salmon (Ali 1959), but the effects of shade on salmon have otherwise received little attention.

METHODS

Study system.—Puget Sound is an inland sea with cold temperate waters and salinity above 25 psu in areas that are not directly adjacent to riverine input. Puget Sound experiences mixed semidiurnal tides, including a daily cycle of two approximately equal high-water levels and two unequal low-water levels. Natural beaches in Puget Sound are composed of mixed sand and gravel sediments sustained by coastal bluff erosion (Shipman 2010). Within Puget Sound, the Duwamish River delta and Elliott Bay (Figure 1) are characterized by severe wetland loss and the replacement of bluff-backed beaches with armored shorelines (Simenstad et al. 2011). Elliott Bay is a 21-km² estuarine embayment that is highly urbanized, occurring entirely within the City of Seattle. About 99% of the shoreline is armored by seawalls and riprap, and numerous overwater structures extend into the bay (Simenstad et al. 2011).

Six shallow-water sites within Elliott Bay were monitored (Figure 1). Three of the sites (hereafter, “seawall sites”; S1–S3) were directly adjacent to urban infrastructure and were completely modified by seawalls that effectively removed the intertidal zone. Each seawall site included one large wooden pier (~4.3 m above mean lower low water [MLLW]) that was over 60 m wide and extended over 100 m into the bay. The shorelines

![Figure 1](https://example.com/figure1.png) Locations of sampling sites within Elliott Bay, Washington. Sites included three replicate seawall sites (S1–S3) and three reference beaches (R1–R3).
of three reference beaches (R1–R3) were composed of sloping, heterogeneous sand and cobble that formed an intertidal zone (R2 is described in detail by Toft et al. 2013). Reference beaches were located within city parks where there were no intertidal seawalls or piers.

Physical data.—Tidal height data relative to MLLW was retrieved from Tides and Currents (National Oceanic and Atmospheric Administration; NOAA 2013). For each fish survey, snorkelers measured the position of pier shade relative to overhead pier structure (which varied with the position of the sun and with tidal height), water depth, and horizontal underwater visibility by using a tape measure. Efforts were made to snorkel during conditions of at least 2.5-m underwater visibility; transects that did not meet this requirement were excluded from analysis to minimize the effects of turbidity on fish count efficiency and on the ability to detect the fish’s behavioral responses to observers (Toft et al. 2007, 2013).

Representative light levels were measured relative to the pier at one of the seawall sites (S2) once per month during April–July 2013. A Li-Cor Spherical Underwater Quantum Sensor was used to measure 15-s averages of photosynthetically active radiation (PAR; i.e., 400–700-nm wavelength) above the surface and at underwater depths of 0.0, 0.5, 1.0, 1.5, and 2.0 m. These measurements occurred approximately 1 m away from the seawall in ambient light and under the pier at distances of 3, 15, and 24 m from the pier edge. Measurements occurred during ebbing tides.

Fish and crab observations.—Snorkeling, a visual survey method, was used to monitor fish because (1) it allowed for accurate fish identification and behavioral information (e.g., feeding activity) to be collected (Toft et al. 2007, 2013); (2) it allowed the entire water column to be surveyed, including in areas under piers and close to urban infrastructure, where other sampling methods are impractical; (3) visual surveys do not confound catch efficiency and species composition as occurs in net surveys that sample habitats of different substrate types (Rozas and Minello 1997); and (4) it was well suited for use in observing our focal species, which mostly occupy the middle or upper portion of the water column.

In total, 192 snorkel surveys occurred during April–August 2012, coinciding with the peak of juvenile salmon migration (Toft et al. 2007). Surveys occurred during daylight at each site approximately once per week. An equal number of surveys took place at each site during high and low tides at heights (mean ± SE) of 2.5 ± 0.06 and 0.77 ± 0.07 m MLLW, respectively. For each data collection event, two observers simultaneously swam surface transects that were 3 and 10 m from and parallel to shore (Figure 2). At high tides, the water depths (mean ± SE) along the transects were 2.3 ± 1.0 m (3 m from shore) and 3.6 ± 1.6 m (10 m from shore); at low tides, the depths were 1.4 ± 0.6 and 2.4 ± 0.8 m. Observers swam slowly to minimize behavioral responses in fish and to allow for their vision to adjust to lower-light conditions when surveying shaded areas under piers. Eight observers who were trained in the identification of local fish and crab species participated in the surveys. To standardize data collection and minimize interobserver effects, particular attention was given to instructing observers on the identification of juvenile salmon species and how to estimate large counts of fish. We assumed that each sampling event comprised an independent observation of fish because surveys were separated on average by 1 week, which encompassed several tidal cycles, and they targeted mostly mobile and often migrating species in relatively small sites.

Observers recorded the finest identifiable taxon, group size, and water column position (surface, middle, or bottom) of fish and crabs. For juvenile salmon, observers recorded the presence or absence of feeding activity, which was characterized by conspicuous darting motions. Feeding at the surface or substrate was indicated by individuals accelerating toward and contacting these areas. Feeding in the water column was indicated by individuals changing their orientation and darting toward a presumed prey item in the water. When salmon were not feeding, their movements were horizontal and often unified in a shoal. Juvenile salmon (along with other fish and crabs) were typically observed several meters away from snorkelers and rarely responded to observer presence, but those that accelerated away from observers in a distinct fleeing behavior (Toft et al. 2007) were excluded from behavioral analyses.

Sites were constrained by urban infrastructure, which limited the amount of continuous shoreline that could be surveyed, and we chose to sample the maximum amount of habitat available at each site. Transect lengths at reference beaches were limited by the amount of unarmored beach shoreline at each site and were 75 m (R1 and R3) and 35 m (R2). Transect lengths at seawall sites were constrained by the amount of continuous, unshaded shoreline bounded by piers that were unevenly spaced along the seawall. Seawall site transects were established to measure the effects of one pier on fish distributions while minimizing the effects of the adjacent pier (Figure 2), which resulted in seawall site transect lengths of 63 m at S1, 39 m at S2, and 69 m at S3. The widths of all transects were quantified by horizontal underwater visibility (Toft et al. 2007, 2013).

At seawall sites, the fine-scale positions of fish and crabs along transect lines were recorded by using landmarks along
FIGURE 3. Organization of the data, including the following factors: shoreline type (seawall site versus reference beach; fixed), site (S1, S2, S3, R1, R2, and R3; random, nested within shoreline type), section (pier, corner, or open; fixed), and transect depth (shallow [3 m from shore] or deep [10 m from shore]; fixed). Sample size \( (n) \) indicates the number of surveys that occurred at high tide and low tide, respectively.

the shoreline. Observations along seawall sites were also categorized into three pre-assigned sections (pier, corner, and open) that were defined by their locations relative to the piers. The length of each section constituted one-third of the transect length. The pier section was defined as the area underneath the pier; the corner section was the middle portion of the transect and started at the edge of the pier; and the open section was farthest from the pier and started at the end of the corner section (Figure 2). Open sections at each site were therefore located an equivalent distance from the piers on either side, regardless of the uneven pier spacing along the seawall. Because of the variable position of shade lines, borders of pier and corner sections were defined by the structural presence of piers rather than based on the shade cast by piers; this ensured equal sampling intensity among sections. Surveys always occurred in the same order (open, corner, and pier), which allowed observers to swim directly from a boat to the beginning of the transect with minimal site disturbance. Transects at reference beaches were not delineated into sections because no artificial structures were present in the water column.

Observations of juvenile Chum Salmon *O. keta* and Pink Salmon *O. gorbuscha* were consolidated into the category “Chum/Pink Salmon” because these species were difficult to distinguish underwater and because they overlapped in size and in timing of peak abundances. Juvenile Coho Salmon *O. kisutch*, which look similar to Chinook Salmon when observed during snorkeling and which occasionally shoal with Chinook Salmon, were present in this system but are relatively rare (Toft et al. 2007); therefore, a small percentage of Chinook Salmon observations may have included Coho Salmon.

**Analysis.**—Statistical analysis was conducted in R version 2.15.2 (R Development Core Team 2012) utilizing the BIOSTATS collection of R functions (McGarigal 2011) and the Vegan package (Oksanen et al. 2013). The two main analyses compared observations (1) between seawall sites and reference beaches and (2) among sections within seawall sites (Figure 3). Density data were used for comparisons between seawall sites and reference beaches to standardize data from transects of unequal length. Density data were also used for comparisons of species assemblage structure among sections within seawall sites. Fish density was calculated as fish count/(transect length \( \times \) transect width). Another metric (hereafter referred to as an “encounter”) was defined as an observation of an independently swimming shoal or a single fish; this metric treated all observations equally regardless of shoal size. Thus, for each observation, two types of data were recorded: the total number of fish observed (a number from 1 to 1,000) and the encounter (always counting as one, regardless of shoal size). The encounter metric is useful because shoaling behavior is not well understood in the context of habitat selection, and a large group of fish may not be more indicative of habitat use than a single fish (Able et al. 2013).
Multivariate analysis was conducted in Vegan (Oksanen et al. 2013). Nonmetric multidimensional scaling was used to visualize differences in assemblage structure (1) between seawall sites and reference beaches and (2) among pier, corner, and open sections within seawall sites separately for high- and low-tide data, excluding species that were observed in less than 5% of the surveys. Data from high and low tides were analyzed separately because of an a priori hypothesis that fish distributions among seawall site sections were affected by light levels, which are lowest under piers during high tides that limit penetration of horizontal ambient light. Species with statistically significant loadings on the axes were identified by permutation and visualized by vectors with the function envfit. To aid in interpretation, ellipses containing 1 SD of two-dimensional point spreads around their means were overlaid onto plots by using the function ordiellipse. We tested for differences in species assemblage structure by using the function adonis, which is a permutational multivariate ANOVA (PERMANOVA). The PERMANOVA tests were performed on Bray–Curtis dissimilarity matrices calculated from loge transformed density data, excluding species that were observed in less than 5% of surveys (Bray and Curtis 1957; Anderson 2001; McArdle and Anderson 2001). In comparisons between seawall sites and reference beaches, factors included shoreline type (seawall site or reference beach; fixed), position (3 or 10 m from shore; fixed), site nested within shoreline type (S1, S2, S3, R1, R2, or R3; random), and interactions. In comparisons among pier, corner, and open sections within seawall sites, factors included section (pier, corner, or open; fixed), position (3 or 10 m from shore; fixed), and their interactions; sites (S1, S2, or S3; random) were treated as a blocking factor by constraining the permutations by site (Oksanen et al. 2013). All factors were incorporated into PERMANOVA models, but we only present statistics for the main effects of shoreline or section type.

To test for differences in single-species densities between seawall sites and reference beaches, ANOVA tests were conducted on loge transformed data using the same factors used for the PERMANOVA tests. To test for uneven distribution of fish among sections within seawall sites, a chi-square test was performed on count data separately for high and low tides. Our design ensured that even amounts of area (m²) were sampled among pier, corner, and open sections; therefore, we used the chi-square test to evaluate the null hypotheses that (1) one-third of the total number of fish observed would occur in each section; and (2) one-third of the total number of encounters would occur in each section. The chi-square test was also used to compare feeding versus nonfeeding behavior in juvenile salmon (1) between seawall sites and reference beaches and (2) among pier, corner, and open sections within seawall sites (Toft et al. 2013). When the chi-square test was significant for data with more than two groupings, the data were subdivided to isolate significantly different groupings (Zar 2010). For chi-square analyses of salmon feeding behavior among sections within seawall sites, data were pooled for all salmonid species, including unidentified salmon, to allow for more robust comparisons while separating high- and low-tide data. Salmon feeding behavior at seawall sites was also analyzed by using a binomial test to evaluate the a priori hypothesis that proportions of salmon exhibiting feeding behavior would be lowest in pier sections (probability = 0.333) for each combination of tide and identified salmon species (Zar 2010).

RESULTS

 Approximately 35,000 individuals representing 17 fish species and 4 crab species were observed (Table 1). Juvenile Chum/Pink Salmon (56% of total fish) and Shiner Perch (17% of total fish) were the numerically dominant fish species. Juvenile Chum/Pink Salmon, juvenile Chinook Salmon, Kelp Perch, red rock crabs, Striped Seaperch, Shiner Perch, and Tubesnouts were the most common species and were observed in greater than 5% of surveys. Pacific Sand Lances were rarely observed, but three shoals in the corner sections of seawall sites totaled 3,500 fish. Large predators were rare; the most common of these was the Lingcod (0.006% of total fish). It is important to note that our snorkeling methods were appropriate for observing the common species (those occurring in > 5% of surveys) but were not as effective for observing some of the rarer species (e.g., small demersal fish) listed in Table 1. We provide Table 1 to generally describe the fish and crab community, although our main focus is on the common species.

Juvenile Chinook Salmon and Chum/Pink Salmon were observed at the surface and middle of the water column; Kelp Perch, Shiner Perch, and Striped Seaperch were most often observed in the middle of the water column; and Tubesnouts and red rock crabs were demersal (Table 2). Red rock crabs were not exclusively found at the bottom of the water column because they climbed structures such as pier pilings.

Comparison of Seawall Sites and Reference Beaches

Community assemblage structure.—Ordination of species assemblage structures at high tides showed that red rock crab and Tubesnout species vectors were correlated with seawall site ellipse, whereas Chum/Pink Salmon and Striped Seaperch species vectors were to a lesser degree correlated with reference beach ellipse (Figure 4). Patterns at low tides were less clear; however, Kelp Perch, red rock crab, and Tubesnout species vectors were correlated with the seawall site ellipse, while Chinook Salmon and Chum/Pink Salmon species vectors were slightly more correlated with the reference beach ellipse (Figure 4). The PERMANOVA tests indicated that fish and crab assemblage structures at seawall sites were significantly different than those at reference beaches at high tides (PERMANOVA: F1, 59 = 4.43, P < 0.01) and low tides (F1, 59 = 2.0, P = 0.03).

Fish distribution.—Seawall sites and reference beaches did not significantly differ in densities of Chinook Salmon (ANOVA, high tide: F1, 80 = 3.04, P = 0.09; low tide: F1, 81 = 0.69, P = 0.41; Figure 5) or Chum/Pink Salmon (high tide: F1, 80 = 0.97, P = 0.15; low tide: F1, 81 = 0.01, P = 0.92;
### TABLE 1. Mean (±SE) density of fish and crabs (individuals/1,000 m²) in the pier, corner, and open sections within seawall sites and at reference beaches (beach) at high or low tide in Elliott Bay, Washington.

<table>
<thead>
<tr>
<th>Group or species</th>
<th>High tide</th>
<th>Low tide</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Pier</td>
<td>Corner</td>
<td>Open</td>
<td>Beach</td>
<td>Pier</td>
</tr>
<tr>
<td>Juvenile salmon</td>
<td></td>
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</tr>
<tr>
<td>Chinook Salmon</td>
<td>45.3 ± 39.6</td>
<td>25.6 ± 13.6</td>
<td>23.9 ± 11.6</td>
<td>5.6 ± 2.3</td>
<td>42.2 ± 40.0</td>
</tr>
<tr>
<td>Oncorhynchus tsawatscha</td>
<td></td>
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<tr>
<td>Chum/Pink Salmon O. keta/O. gorbuscha</td>
<td>563.2 ± 454.3</td>
<td>1,460.6 ± 708.2</td>
<td>1,018.5 ± 736.8</td>
<td>328.3 ± 140.6</td>
<td>250.0 ± 188.2</td>
</tr>
<tr>
<td>Unidentified juvenile salmon Oncorhynchus spp.</td>
<td>70.3 ± 66.8</td>
<td>6.5 ± 1363</td>
<td>1.5</td>
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<td>42.2 ± 40.0</td>
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<tr>
<td>Forage fish</td>
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<td>Pacific Sand Lance Ammodytes hexapterus</td>
<td>615.8 ± 488.8</td>
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<td>17.8</td>
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<tr>
<td>Pacific Herring Clupea pallasii</td>
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<td>Surf Smelt Hypomesus pretiosus</td>
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<td>Unidentified forage fish</td>
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<tr>
<td>Surfperches</td>
<td></td>
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<tr>
<td>Kelp Perch Brachyistius frenatus</td>
<td>2.7 ± 2.0</td>
<td>14.5 ± 7.0</td>
<td>1.1 ± 0.8</td>
<td>0.2 ± 0.2</td>
<td>2.0 ± 1.1</td>
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<tr>
<td>Pile Perch Damalichthys vacca</td>
<td>1.2</td>
<td>3.3 ± 2.3</td>
<td>0.7 ± 0.6</td>
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<tr>
<td>Striped Seaperch Embiotoca lateralis</td>
<td>6.1 ± 4.1</td>
<td>4.9 ± 2.6</td>
<td>4.2 ± 2.6</td>
<td>3.4 ± 1.3</td>
<td>5.9 ± 3.1</td>
</tr>
<tr>
<td>Shiner Perch Cymatogaster aggregata</td>
<td>504.3 ± 304.9</td>
<td>225.4 ± 97.7</td>
<td>12.0 ± 5.6</td>
<td>0.9</td>
<td>175.3 ± 167.8</td>
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<tr>
<td>Unidentified perch</td>
<td>0.8</td>
<td>0.2</td>
<td>&lt;0.1</td>
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<tr>
<td>Crabs</td>
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<td>Dungeness crab</td>
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<tr>
<td>Northern kelp crab Pugettia producta</td>
<td>0.2</td>
<td>1.2 ± 0.7</td>
<td>0.3</td>
<td>&lt;0.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Red rock crab Cancer productus</td>
<td>6.5 ± 2.0</td>
<td>4.0 ± 1.4</td>
<td>1.6 ± 0.8</td>
<td>0.6 ± 0.3</td>
<td>0.5</td>
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<tr>
<td>Shore crabs Hemigrapsus spp.</td>
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<td>Demersal fish</td>
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<td>Lingcod Ophiodon elongatus</td>
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<td>Penpoint Gunnel</td>
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<td>Apodichthys flavidus</td>
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<td>Rock Sole Lepidopsetta bilineata</td>
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<td>Sculpins (Cottidae)</td>
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<td>Spotted Ratfish Hydrologus collei</td>
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<tr>
<td>Unidentified gunnels (Pholidae)</td>
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<tr>
<td>Other fish</td>
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<tr>
<td>Pacific Lamprey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Entosphenus tridentatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larval fish</td>
<td>1.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Threespine Stickleback</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gasterosteus aculeatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tubesnout Alloreticutes flavidus</td>
<td>82.3 ± 32.0</td>
<td>90.0 ± 62.8</td>
<td>190.6 ± 167.5</td>
<td>&lt;0.1</td>
<td>51.6 ± 21.6</td>
</tr>
<tr>
<td>Unknown species</td>
<td>36.8 ± 25.3</td>
<td>0.1</td>
<td></td>
<td></td>
<td>0.4</td>
</tr>
</tbody>
</table>
TABLE 2. Depth distribution of common species observed at seawall sites and reference beaches in Elliott Bay. Surface/middle indicates a shoal of fish that included individuals distributed at the surface and middle of the water column.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total encounters</th>
<th>Water column position (% of encounters)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Surface</td>
</tr>
<tr>
<td>Chinook Salmon</td>
<td>81</td>
<td>27.16</td>
</tr>
<tr>
<td>Chum/Pink Salmon</td>
<td>108</td>
<td>60.19</td>
</tr>
<tr>
<td>Kelp Perch</td>
<td>45</td>
<td>6.67</td>
</tr>
<tr>
<td>Red rock crab</td>
<td>66</td>
<td>3.03</td>
</tr>
<tr>
<td>Shiner Perch</td>
<td>101</td>
<td>2.97</td>
</tr>
<tr>
<td>Striped Seaperch</td>
<td>83</td>
<td>0.00</td>
</tr>
<tr>
<td>Tubesnout</td>
<td>77</td>
<td>0.00</td>
</tr>
</tbody>
</table>

FIGURE 4. Nonmetric multidimensional scaling ordination of species assemblage structures, comparing seawall sites (S1–S3) to reference beaches (R1–R3) and comparing pier (P), corner (C), and open (O) sections for high- and low-tide data. Ellipses show 1 SD of two-dimensional point spreads around the mean; P-values refer to results from permutational multivariate ANOVA.
Figure 5). Of the seven species that were observed in over 5% of surveys, only the red rock crab exhibited densities that were significantly different depending on shoreline type, occurring in greater abundance at seawall sites than at reference beaches at high tides (ANOVA: $F_{1, 80} = 12.10, P < 0.01$) and low tides ($F_{1, 81} = 4.40, P = 0.04$).

**Juvenile salmon feeding behavior.**—There was no significant difference in the feeding behavior of juvenile Chinook Salmon between seawall sites and reference beaches at high tides ($\chi^2 = 0.04, df = 1, P = 0.84$) or low tides ($\chi^2 = 0.68, df = 1, P = 0.41$). Feeding behavior of Chum/Pink Salmon was significantly greater at seawall sites than reference beaches at high tides ($\chi^2 = 4.19, df = 1, P = 0.04$) but not at low tides ($\chi^2 = 0.03, df = 1, P = 0.86$).

### Comparison of Sections within Seawall Sites

**Effect of the S2 pier on light.**—Light measurements taken relative to the pier at S2 indicated that this pier caused a substantial decrease in PAR in the air and at the depths occupied by most fish (Table 3). The level of PAR was inversely related to the distance from the pier edge and to water depth.

**Community assemblage structure.**—Ordination of species assemblage structures at high tide showed that corner and open sections had similar species compositions; Chum/Pink Salmon, Shiner Perch, and Tubesnout species vectors were correlated with the ellipses of these sections, whereas the red rock crab species vector was correlated with pier section ellipse (Figure 4).

### Table 3

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Ambient PAR</th>
<th>Distance (m) from pier edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>1.028.2 ± 446.6</td>
<td>3</td>
</tr>
<tr>
<td>0.0 (subsurface)</td>
<td>763.3 ± 424.4</td>
<td>15</td>
</tr>
<tr>
<td>0.5</td>
<td>645.4 ± 384.7</td>
<td>24</td>
</tr>
<tr>
<td>1.0</td>
<td>446 ± 261.5</td>
<td></td>
</tr>
<tr>
<td>1.5</td>
<td>370.1 ± 222.0</td>
<td></td>
</tr>
<tr>
<td>2.0</td>
<td>328.5 ± 189.8</td>
<td></td>
</tr>
</tbody>
</table>
Patterns were less clear for low tides. To a lesser degree than at high tide, Striped Seaperch and red rock crab species vectors were correlated with open and corner section ellipses, the Chum/Pink Salmon species vector was correlated with corner and pier section ellipses, and Tubesnout species vector was correlated with the pier section ellipse (Figure 4). Within seawall sites, species assemblages were significantly different among sections at high tide (PERMANOVA: $F_{2,74} = 1.87, P = 0.02$) but not at low tide ($F_{2,65} = 1.20, P = 0.52$).

**Fish and crab distribution.**—Within seawall sites, fish and crab abundances varied based on proximity to the pier structures (Figure 6) and in relation to the shade cast from piers (Figure 7). Overall fish abundances were lower in pier sections, and fish were consistently observed to be directly adjacent to shade and were less often observed in shaded areas (Figure 7). Overall fish abundances were lower under piers and highest in corner sections during high tides (Figure 6). Differences in fish distribution between tidal stages and among sections were attributable mainly to differences in juvenile salmon distribution. During high tides, total fish counts were over five times greater in corner sections than in pier sections. Chinook Salmon were significantly more abundant in corner sections during high tides.

**FIGURE 7.** Locations of common fish and crab species relative to pier shade (gray rectangles) along linear transects positioned 3 and 10 m from shore in Elliott Bay during high or low tide. Data points are from all sampling days and sites (standardized by transect length) and are proportional in size to the logarithm of fish group size, which ranged from 1 to 1,000 individuals. Darkened points outside of pier shade boundaries indicate observations that occurred under pier structures but not in the shade.
(χ² = 11.7, df = 1, P < 0.01), and Chum/Pink Salmon were significantly less abundant in pier sections (χ² = 1,001, df = 1, P < 0.01) and more abundant in corner sections than in open sections (χ² = 383, df = 1, P < 0.01; Figure 6). The number of Chinook Salmon encounter events was significantly lower in pier sections at high tide (χ² = 6.5, df = 1, P = 0.04); Chum/Pink Salmon encounters showed no patterns among sections at high tide (χ² = 1.0, df = 2, P = 0.60; Figure 6).

Effects of piers on juvenile salmon distributions were different at low tides than at high tides, although overall fish counts remained lowest under piers. During low tides, Chinook Salmon were more abundant in corner sections (χ² = 274, df = 1, P < 0.01) and significantly less abundant in pier sections than in open sections (χ² = 13, df = 1, P < 0.01; Figure 6). Chum/Pink Salmon abundances at low tides were significantly greater in areas under piers than in other sections (χ² = 46, df = 1, P < 0.01) and were greater in corner sections than in open sections (χ² = 5.1, df = 1, P = 0.02; Figure 6). Shoals of Chum/Pink Salmon were also observed farther into shaded areas at low tides than at high tides (Figure 7). Chinook Salmon were never encountered in pier sections at low tide, and encounters were significantly greater in corner and open sections (χ² = 12, df = 1, P < 0.01). Chum/Pink Salmon encounters were not significantly different among sections during low tides (χ² = 1.1, df = 2, P = 0.56; Figure 6).

The distribution of red rock crabs differed from fish distributions. At high tides, abundances were greatest in pier and corner sections (χ² = 6.0, df = 1, P = 0.02; Figure 6). Red rock crabs were less abundant overall at low tides, and distributions were not significantly different among sections (χ² = 2.9, df = 1, P = 0.23). Red rock crabs were rarely seen in groups; total counts and the number of encounter events were equivalent. Unlike other species, red rock crabs were commonly observed to occur several meters away from sunlit areas (Figure 7).

Juvenile salmon feeding behavior.—At high tides, the feeding behavior of juvenile salmon (all species combined) was greater in open and corner sections than in pier sections (χ² = 3.57, df = 1, P = 0.059; Figure 8). Differences in juvenile salmon feeding prevalence among sections at low tides were not significant (χ² = 2.58, df = 2, P = 0.27; Figure 8). However, feeding behavior was consistently lower under piers for each combination of salmon species and tide, excluding Chinook Salmon at low tide because they were never observed in pier sections (binomial test: P = 0.037; Figure 8).

DISCUSSION

Our results demonstrate that the presence of seawalls and piers causes measurable change in the fish assemblages of Elliott
Bay, Washington. The present findings expand on a recent but
geoographically diverse literature, including studies conducted
in Australia (Clynick et al. 2008), Italy (Clynick 2006), Puget
Sound (Toft et al. 2007), and the Hudson River (Strayer et al.
2012). These studies collectively suggest that the fish assem-
bles at many developed waterfronts are different from his-
torical assemblages. There are few natural analogs to featureless,
vertical concrete shorelines or to large shaded areas created
by piers; the effects at the intersection of these two types of
modification are particularly unique. At high tides, corner sec-
tions at seawall sites were inhabited by relatively abundant fish
communities that differed in assemblage structure from those
observed in adjacent areas, especially pier sections, where fish
were rare and crabs were relatively common. This finding is con-
sistent with the hypothesis proposed by Hobbs et al. (2006) that
human-induced changes to the abiotic environment can create
novel ecosystems—those with species combinations and rela-
tive abundances that did not occur historically. We assumed that
fish were distributed relative to the amount of habitat between
adjacent piers, which varied among seawall sites. The fine-scale
positions of fish relative to pier shade (standardized by transect
length) suggest that this is accurate. However, if the fish aggre-
gated next to piers according to their absolute distance rather
than relative distance from the piers, we may have underesti-
imated aggregation effects in the corner sections because these
sections were longer at the larger sites (13 m [S2] versus 21 m
[S1] and 23 m [S3]) and included areas that were farther away
from piers.

Our results from three replicate piers suggest that the piers
exerted negative impacts on fish in Elliott Bay, especially at high
tides. These findings were supported separately by fish count and
fish encounter metrics and by fine-scale fish distributions rela-
tive to shade, all of which showed that most fish species avoided
areas under piers at high tide. When tides were lower and hori-
zontal ambient light penetrated under the piers, fish distribution
patterns became less distinct and species assemblages were not
significantly different, suggesting that habitat use was driven by
the shade cast by the piers rather than resulting from a struc-
tural effect of the piers. Red rock crabs were an exception, as
they were commonly observed on pier pilings. Shaded areas un-
der piers may mimic nighttime conditions, when red rock crabs
become more abundant in intertidal areas and feed by using
chemosensory cues to locate prey (Robles et al. 1989). Mobile
species, such as Shinier Perch and juvenile salmon, tended to
avoid areas that were shaded by piers; in contrast, Tubesnouts,
which are often stationary in the water column, were common
under the edges of piers, including the shaded areas. A plausi-
ble explanation for this result is that fish with high swimming
speeds may avoid shaded areas rather than experience reduced
visual acuity resulting from rapid changes in light intensity (Ali
1959). Kelp Perch, which use bull kelp _Nereocystis luetkeana_
for cover, were rarely observed in the shaded areas where kelp
did not grow, thus indicating that shade also reduces habitat
quality for fish that interact with algae.

Our findings of reduced fish abundances under piers are con-
sistent with those of Able et al. (2013), who found reduced
pelagic fish abundances under a large pier in the Hudson River
estuary, suggesting that these effects occur in other systems.
Unlike the Hudson River estuary study (Able et al. 2013), we
did not find higher predator abundances in areas under piers, but
predators were rare overall at the depths and habitats that we
sampled, and the effects of piers on predators at greater depths
are a potential topic for further investigation in our region. Re-
results of our study and the study by Duffy-Anderson and Able
(1999 and 2001) suggest that piers can also impair the value of
shallow-water habitats by reducing the feeding ability of fish.
Many fish species are primarily visual predators, and a reduction
in light levels may adversely affect the ability of these predators
to detect prey, especially by reducing the backlighting of prey
at the surface.

We recognized the possibility that the use of visual surveys
could result in underestimation of fish counts or encounters in
shaded areas under piers due to low light levels. Our surveys
minimized this risk by targeting fish species that occurred in
close proximity to observers at the surface of the water column,
often in large schools. Observers also swam slowly enough for
their eyesight to adjust to shaded conditions as they entered
areas under the piers. These areas were not completely dark
because the water level was below the piers even during high
tides, and some (although reduced) horizontal ambient light
could penetrate.

Our results contribute to growing evidence that piers impair
the value of nearshore habitat for juvenile salmon. Simenstad
and Cordell (2000) proposed a framework for assessing habitat
by utilizing metrics that address a habitat’s capability to provide
(1) opportunity, (2) capacity, and (3) realized function for juve-
nile salmon. In this scenario, opportunities for salmon to access
habitat and to benefit from the habitat’s capacity can be inferred
by measuring the extent of tidal flooding, the presence of impor-
tant geomorphic features, and the proximity to anthropogenic
stressors (e.g., pier shade). The capacity of the accessible habi-
tat can be evaluated by examining prey availability and water
temperatures, salinities, and other conditions that promote prey
production and refuge from predators. The realized function,
resulting from opportunity and capacity, can be measured through
habitat-specific residence time, feeding, growth, and survival.
In our study, pier shading was an anthropogenic stressor that
reduced the ability of juvenile salmon to access habitat (i.e.,
reduced opportunity) and caused a reduction in feeding under
piers (i.e., a reduction in realized function).

Previous research has shown that shoreline armorng may im-
pair salmon habitat capacity by directly reducing prey produc-
tion (Sobocinski et al. 2010) and altering substrate temperatures
that support prey production (Morley et al. 2012). However, we
did not find reductions in salmon abundance or feeding inten-
sity related to seawall presence, and detection of these effects
may require more intensive sampling than we conducted. We
found that the prevalence of feeding behavior among Chum/Pink
Salmon was significantly higher at seawall sites than at reference beaches during high tides, when their movements under piers were most restricted. Research on the movements and feeding behavior of juvenile salmon in this system has shown that swimming directionality and feeding are related: salmon tend to either (1) swim in a sinuous path and feed or (2) swim directionally and rarely feed (S. M. Heerhartz, University of Washington and J. D. Toft, unpublished data). It is possible that piers interrupt alongshore movements of salmon, causing them to switch from directional movements without feeding to more sinuous movements accompanied by an increase in feeding intensity. Alternatively, salmon in highly modified habitats may compensate for lower-quality prey by feeding more often. The effects of piers and seawalls on juvenile salmon feeding are likely to occur by different mechanisms (e.g., piers impair prey detection, while seawalls impair prey availability), and our visual survey methods may have been more effective at measuring pier effects than seawall effects. Sampling of salmon diets and available prey fields in nearshore habitats that are modified by seawalls would provide a more detailed understanding of how shoreline armoring affects the capacity and realized function of shorelines for juvenile salmon and other fishes.

Results of our study and the study by Toft et al. (2007) indicate that piers could delay the out-migration of juvenile salmon because (1) juveniles stay in shallow waters early in their life history as they migrate from freshwater and estuarine habitats to marine habitats (Toft et al. 2007), (2) piers are common along waterfronts and extend into waters deeper than those used by juvenile salmon early in their life history (Simenstad et al. 2011), and (3) juvenile salmon avoid the shaded areas created by piers and thus do not cross under piers from one lighted area to another but instead aggregate adjacent to the piers. Our observations of Chum/Pink Salmon occurring farther into shaded areas under piers at low tide may also indicate that out-migrating juvenile salmon wait in corner sections until low tides allow a greater amount of light to penetrate the areas under piers. If piers delay the out-migration of juvenile salmon, this may have negative impacts on their survival by retaining the fish in suboptimal habitats, delaying their access to ephemeral prey resources in more natural habitats (Webb 1991, 1992; Cooney et al. 1995), and increasing their vulnerability to predation (Willette et al. 1999). Although our study provides indirect evidence that piers cause migration delays, methods such as mark–recapture, acoustic tagging, and visual observations that follow salmon would permit direct testing of pier effects on salmon movements.

In our study, fish were surveyed along transects at the surface of the water and close to shore. This strategy was effective at quantifying juvenile salmon and several other fish species across a variety of shoreline conditions, but other observation methods could evaluate how seawalls and piers affect additional fish species. For example, surveying fish at greater depths would extend our results to more resident and benthic species. Toft et al. (2007) found that shoreline armoring reduces flatfish densities in Puget Sound; we also found fewer flatfish at seawall sites relative to reference beaches, but we could not fully evaluate seawall effects on flatfishes because they were rarely observed.

The physical transformation of urban waterfronts is largely irreversible, and the prospect of restoration to prehistorical conditions is impractical. Enhancement of the shoreline by applying habitat improvements is often the only option for improving ecological functions (Toft et al. 2013). As land and seascapes are increasingly transformed, a shift in management toward a more practical approach of assessing and enhancing the functional attributes of new ecosystems—rather than investing resources in trying to restore permanently altered systems—may be warranted (Seastedt et al. 2008). One option to mitigate the effects of shading by overwater structures is to incorporate light-penetrating surfaces, such as glass blocks or grating in pier surfaces. For example, in Elliott Bay, juvenile salmon occur within a few meters of shore, and light-penetrating surfaces are presently being installed that could allow for more natural feeding and movement alongshore. Preliminary research on light-penetrating surfaces has shown that they can reduce shade intensity (Gayaldo and Nelson 2006), but larger-scale evaluations and studies in the context of fish habitat have not occurred. Light mitigation is only one of many enhancements that may increase the functions of highly modified nearshore ecosystems (other examples are reviewed by Chapman and Underwood 2011), and development of these enhancements is a promising area for future research.

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Mike Caputo, Beth Sosik, P. Frank Stevick, and Claire Levy of the University of Washington’s Wetland Ecosystem Team performed data collection and assistance in the field. Funding for this research was provided by the Seattle Department of Transportation. S.H.M. was also supported by the National Science Foundation’s Graduate Research Fellowship Program. Charles Simenstad and three anonymous reviewers provided helpful critiques on previous versions of this paper.

REFERENCES


Characterization of River Herring Bycatch in the Northwest Atlantic Midwater Trawl Fisheries

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Characterization of River Herring Bycatch in the Northwest Atlantic Midwater Trawl Fisheries

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Abstract
In the U.S. northwest Atlantic, the incidental catch of river herring (Alewife Alosa pseudoharengus and Blueback Herring A. aestivalis) by midwater trawl vessels targeting Atlantic Herring Clupea harengus and Atlantic Mackerel Scomber scombrus has become a concern for river herring conservation. Reduction of this incidental catch is a focus of fisheries managers, but information about river herring bycatch is limited. To improve the information available to fishery managers, we combined portside and at-sea observations to examine (1) the size of river herring, (2) the concentration of river herring with respect to the target species, and (3) the yearly contribution of different fishery areas to the total catch of river herring. We divided the fishery’s spatial range into four nearshore areas and tested two null hypotheses: (1) length frequency distributions of river herring are similar between areas and between species and (2) bycatch ratios are similar among areas. We also used length frequency distributions and river herring size at maturity to infer and compare maturity status. Results showed interannual, interspecies, and intraspecies differences in bycatch among and within the four nearshore areas. Bycatch in the northern areas was mainly migratory mature or near-mature river herring from mixed origins, whereas bycatch in the southern areas was a mix of juveniles, prespawning adults from nearby areas, and migratory adults. At the levels seen in 2011 and 2012, bycatch in the midwater trawl fishery could not account for the overall decline in river herring. However, a large proportion of river herring caught in the southern areas of the fishery may be juveniles originating from New Jersey to southern New England. To better understand this impact, continued monitoring and studies examining the at-sea population dynamics of river herring are needed.

The incidental catch of river herring (Alewife Alosa pseudoharengus and Blueback Herring A. aestivalis) at sea has become a concern for their conservation (ASMFC 2012). River herring are consumed by a variety of riverine, estuarine, and oceanic fishes, birds, and mammals, and they once supported productive fisheries along the U.S. Atlantic coast (Bigelow and Schroeder 2002). River herring populations are currently considered to be depleted, and river herring were recently evaluated for listing under the Endangered Species Act (ASMFC 2012; NOAA 2013a). The coastwide decline of river herring was likely caused by a combination of past overfishing, spawning habitat loss, pollution, increases in predator populations, environmental factors, and bycatch (Rulifson 1994; ASMFC 2012).

In the U.S. northwest Atlantic Ocean, river herring are incidentally caught in fisheries that target Atlantic Herring Clupea harengus and Atlantic Mackerel Scomber scombrus. Neither Atlantic Herring nor Atlantic Mackerel are considered overfished, and the two species have considerable economic importance, with landings value averaging about US$23 million and $5 million, respectively, in 2008–2011 (NOAA 2012). Atlantic Herring are also the primary bait species used in the U.S. fishery for American lobster Homarus americanus (NEFMC 2013a). The

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increase in landings of Atlantic Herring and Atlantic Mackerel in the 1990s coincided with a shift in gear from purse seines and weirs to midwater trawls, which now account for the majority of landings (MAFMC 2013; NEFMC 2013a). The high-volume nature of both fisheries can result in significant amounts of bycatch that are hard to quantify and classify. This uncertainty has led to concerns about the potential of the Atlantic Herring and Atlantic Mackerel fleet to capture large amounts of river herring at sea (ASMFC 2012; MAFMC 2013; NEFMC 2013a).

Managers have added regulations to address river herring bycatch in the Atlantic Herring and Atlantic Mackerel fisheries; the regulations include closing large areas of the Atlantic Herring fishery or the entire Atlantic Mackerel fishery if river herring catch limits are reached (MAFMC 2013; NEFMC 2013b). These catch limits are based upon past catch of river herring and assume that the biological characteristics and impact of bycatch are the same throughout the entire range of the fishery. However, the habits of river herring at sea suggest that this assumption is false.

Knowledge of the biological characteristics of river herring caught as bycatch is important for efficient and effective management because of the mixing of river herring life stages and populations at sea. Juvenile river herring migrate out of rivers by the late fall or winter of their first year and may spend 2 years in nearshore waters (Fay et al. 1983; Klauda et al. 1991; Limburg 1998). These nearshore areas are also utilized by adult river herring and by the midwater trawl fishery (Neves 1981; Bethoney et al. 2013a). Once the juvenile river herring become migratory, they join the adults in extensive north–south migrations along the eastern coast of North America and the continental shelf. During their ocean migrations, river herring of different natal origins share common migratory routes and feeding grounds (Neves 1981; Rulifson 1984; Rulifson et al. 1987; Stone and Jessop 1992). River herring show a high degree of spawning site fidelity, returning to the same regions (or even the same rivers) to spawn every year (Messieh 1977; Jessop 1994; Palkovacs et al. 2014). Due to these dynamics, the location of river herring bycatch may not be indicative of maturity status or origin.

The size and origin of river herring caught as bycatch from specific areas at sea have been difficult to determine due to the low frequency of large river herring catch events and the low monitoring levels during the times when river herring are encountered (Bethoney et al. 2013b; NEFMC 2013a). Length frequency combined with weight information is available only over broad regions (ASMFC 2012; MAFMC 2013; NEFMC 2013b). Our objective in the present study was to provide fishery managers with more detailed information on the characteristics (species, sizes, maturity, and origin) of river herring in various regions of the fishery and to discuss the implications that differing characteristics may have for bycatch mitigation strategies. To achieve this objective, we divided the spatial range of the fishery into four nearshore areas and Georges Bank (Figure 1). We then tested two null hypotheses: (1) length frequency distributions of river herring are similar between areas and between species; and (2) bycatch ratios are similar among areas. We also used length frequency distributions and information on river herring size at maturity to infer and compare maturity status. Testing the two null hypotheses provided a general characterization of the similarities and differences in river herring bycatch occurring within these areas and helped to clarify the potential impact of bycatch. In a broader context, we provide an example of the complexities that arise—and potential starting points to address these complexities—when trying to develop bycatch mitigation strategies for highly migratory, data-poor species. The present results also improve the general understanding of how river herring congregate at sea.

METHODS

River herring bycatch information was obtained from the Massachusetts Division of Marine Fisheries (MA-DMF) portside sampling program and from the Northeast Fisheries Observer Program (NEFOP). The MA-DMF portside program samples approximately 50% of the midwater trawl landings that occur in Massachusetts waters; 60–85% of all midwater trawl landings of Atlantic Herring occur in Massachusetts (vessel trip reports for 2008–2012; National Marine Fisheries Service, unpublished data). Samplers take systematic subsamples of whole boat offloads as fish are pumped across dewatering boxes into vats or trucks. The proportion of total weight contributed by each species from all subsamples is extrapolated to the weight of the entire trip. Portside samplers collect a representative sample of river herring during offloads and record the FLs (nearest cm) for fish of each species.

The NEFOP samples about 40% of all midwater trawl trips, with about 15% of trips monitored from January to March, when most of the river herring bycatch occurs (NEFMC 2013a). At sea NEFOP samplers gather information by taking subsamples of each tow. Samplers target a total of 10 subsample baskets of unsorted fishes taken in equal intervals from the catch as it is pumped from the net to the hold. The weight of each species within each subsample is recorded, and the species proportions are extrapolated to the weight of the entire tow. The FLs of each species in basket subsamples are recorded to the nearest centimeter (see NEFSC 2010 for further details on NEFOP midwater trawl sampling protocols).

We analyzed data on Alewife and Blueback Herring bycatch in four nearshore areas, along Georges Bank (GB; National Oceanic and Atmospheric Administration [NOAA] statistical areas 522, 525, 561, and 562), and for the overall fishery (Figure 1). The four nearshore areas were (1) waters off northeast New Jersey and Long Island (NJLI; NOAA statistical areas 612, 613, and 615); (2) southern New England (SNE; NOAA statistical areas 537, 539, and 611); (3) east of Cape Cod (CC; NOAA statistical area 521); and (4) the western Gulf of Maine (GoM; NOAA statistical areas 513 and 514). For each area except GB, results were reported for the months that accounted for greater
than 80% of the observed river herring bycatch from 2000 to 2012 (Table 1). These areas and times reflect the known overall spatial and temporal patterns of river herring bycatch in the midwater trawl fishery and allow for inferences to be made based upon the seasonal distributions of river herring (Cieri et al. 2008; Cournane et al. 2013). Portside and at-sea data were pooled for all analyses. For trips that were sampled by both MA-DMF and NEFOP, portside data were used. Previous analyses found no significant difference between co-sampled portside MA-DMF and at-sea NEFOP estimates of river herring bycatch (Cieri et al. 2008; NEFMC 2013c). Other tests confirming the consistency in length frequencies and data quality between MA-DMF

<table>
<thead>
<tr>
<th>Area</th>
<th>Period</th>
<th>Percentage of bycatch</th>
</tr>
</thead>
<tbody>
<tr>
<td>NJLI</td>
<td>Jan–Mar</td>
<td>99</td>
</tr>
<tr>
<td>SNE</td>
<td>Jan–Mar</td>
<td>81</td>
</tr>
<tr>
<td>CC</td>
<td>Dec–Mar</td>
<td>95</td>
</tr>
<tr>
<td>GoM</td>
<td>Oct–Nov</td>
<td>99</td>
</tr>
</tbody>
</table>
sampling and NEFOP sampling have also been conducted (Bethoney 2013).

The length frequency distribution within each sampling area was determined by

\[ X_{A,i} = \frac{W_{A,i}}{w_{A,i}}, \]

where \( X_{A,i} \) is an expansion factor used to relate the total number of fish measured to the total number of fish caught during trip \( i \) in area \( A \); \( W_{A,i} \) is the total weight of species \( s \) caught during trip \( i \) in area \( A \); and \( w_{A,i} \) is the weight of individuals of species \( s \) caught during trip \( i \) in area \( A \) that were measured and weighed (Roman et al. 2011).

The proportion of species \( s \) in area \( A \) and length-class \( l \) (\( P_{A,s,l} \)) was determined as

\[ P_{A,s,l} = \frac{\sum_i X_{A,s,i} \times n_{A,s,l,i}}{\sum_i X_{A,s,i} \times n_{A,s,i}}, \]

where \( n_{A,s,l,i} \) is the number of measured individuals of species \( s \) in length-class \( l \) on trip \( i \) in area \( A \); and \( n_{A,s,i} \) is the number of sampled fish of species \( s \) on trip \( i \) in area \( A \). Sampled trips from 2008 to 2012 were summed, excluding trips in which only a single length-class was observed. If the weights of measured fish were not available, then the number of Alewives or Blueback Herring measured at each length was multiplied by an estimated weight at length by using an Alewife or Blueback Herring weight-at-length table (MA-DMF, unpublished data). Intraspaces length frequency distributions between areas and interspecies distributions within areas were compared using Kolmogorov–Smirnov tests with \( \alpha \) adjusted based on the number of independent samples (trips) taken for each comparison (Siegel and Castellan 1988).

The number of river herring taken as bycatch from each area during 2011 and 2012 was estimated by

\[ \sum_i X_{A,s,i} \times n_{A,s,l,i} \cdot \frac{n_A - n_A}{N_A}, \]

where \( n_A \) is the number of sampled trips and \( N_A \) is the total number of vessel trip reports (reports of catch required by the federal government for every fishing trip) from midwater trawl vessels targeting Atlantic Herring or Atlantic Mackerel in area \( A \).

River herring bycatch estimates for 2011 and 2012 were generated using a ratio estimator (Cochran 1977). Estimates were generated for each sampling area and for all other areas (including the four nearshore areas during the months not listed in Table 1). Grouping catch on GB with the rest of the fishery creates results that are less representative of overall bycatch. On GB, the midwater trawl vessels capture a large portion of their yearly Atlantic Herring quota but almost no river herring (Cieri et al. 2008; Courmane et al. 2013). Therefore, the sum of estimates from all of these areas was used to estimate total bycatch for the fishery. Similar to the standardized bycatch reporting methodology (Wigley et al. 2007, 2009), an Alewife and Blueback Herring bycatch ratio for each area \( (R_A) \) was calculated by

\[ R_A = \frac{\sum_i r_{A,i}}{\sum_i T_{A,i}}, \]

where \( r_{A,i} \) represents the observed river herring landings (Alewife or Blueback Herring) from trip \( i \) in area \( A \); and \( T_{A,i} \) represents the observed target species landings (Atlantic Herring and Atlantic Mackerel) from trip \( i \) in area \( A \). Variance was estimated as

\[ \text{var}(R_A) = \left( \frac{1}{n_A T_A^2} \right) \times \left[ \left( \frac{\sum_i r_{A,i}^2}{n_A T_A^2} \right) + \left( \frac{\sum_i T_{A,i}^2}{n_A T_A^2} \right) - 2 R_A \left( \frac{\sum_i r_{A,i} T_{A,i}}{n_A T_A^2} \right) \right] \times \left( \frac{N_A - n_A}{N_A} \right). \]

Total river herring bycatch for each area \( (B_A) \) was calculated as

\[ B_A = R_A \times L_A, \]

where \( L_A \) is the total target species landings from area \( A \) based on vessel trip report data. The coefficient of variation (CV) for the ratios, which is the same as the CV for the area, was defined as

\[ \text{CV}(R_A) = \frac{\sqrt{\text{var}(R_A)}}{R_A}. \]

The variance for the sum of bycatch in all areas (Sum) was estimated by following the separate ratio method (Wigley et al. 2007):

\[ \text{var}(\text{Sum}) = \sum_A L_A^2 \times \text{var}(R_A). \]

The CV for the yearly sum was calculated as

\[ \text{CV}(\text{Sum}) = \frac{\sqrt{\text{var}(\text{Sum})}}{\sum_A B_A}. \]

Confidence intervals around ratio estimates were compared between areas, between years, and between species by graphing mean estimates with their associated 95% confidence intervals. Although overlapping confidence intervals do not necessarily indicate nonsignificant results, only means with nonoverlapping
Maturity of river herring was inferred from length. River herring size at maturity increases with spawning latitude (Bigelow and Schroeder 2002). The smallest spawning Blueback Herring observed in the St. Johns River, Florida (the southern extent of the species' range), was approximately 17 cm FL (McBride et al. 2010). Although a relatively small number of fish were measured in these runs (<250 fish), examination of length data from river herring spawning runs in Rhode Island, Massachusetts, New Hampshire, and Maine for 2008–2012 also revealed a minimum size of 17 cm FL, with the vast majority of fish exceeding 20 cm FL (Rhode Island Department of Environmental Management, MA-DMF, New Hampshire Fish and Game Department, and Maine Department of Marine Resources, unpublished data). In the lower St. John River, New Brunswick, spawning female Blueback Herring are seldom less than 21 cm FL (Jessop 2001). In the Gaspereau River system, Nova Scotia, spawning female Alewives are rarely less than 24 cm FL (McIntyre et al. 2007). For this study, river herring smaller than 17 cm FL were categorized as “most likely immature.” Alewives larger than 22 cm FL and Blueback Herring larger than 20 cm FL were categorized as “most likely mature.” The maturity of river herring between these lengths was classified as “unknown.” The addition of the “unknown” category makes this approach more conservative than the approach of Stone and Jessop (1992), who used a cut-off of 19 cm FL to distinguish between mature and immature river herring caught at sea.

RESULTS

Significant differences in Alewife length frequency distributions were found between the GoM and SNE (Kolmogorov–Smirnov test: $D_{16, 33} = 0.41$, $P < 0.05$), the GoM and NJLI ($D_{16, 20} = 0.63$, $P < 0.01$), and the CC and NJLI ($D_{16, 20} = 0.67$, $P < 0.01$). Alewives were generally larger in the GoM than in the other nearshore areas, and the highest percentage of Alewives that were most likely mature (just over 35%) was caught in this area (Figure 2; Table 2). The CC area exhibited the smallest Alewife length range of any area, and about 90% of Alewives were within the size range of unknown maturity (Figure 2; Table 2). The CC area also contained the lowest percentage (about 1%) of Alewives that were most likely immature (Table 2). About 30% of Alewives caught in SNE were most likely immature, while 9% were most likely mature. Close to 60% of Alewives caught in NJLI were smaller than 17 cm FL and most likely immature (Figure 2; Table 2); this represented the highest percentage of juvenile Alewives present in any area.

The Alewife bycatch rate significantly differed between areas and between years (Figure 3). Compared with the other areas, bycatch of Alewives in the GoM was minimal during 2011 and 2012 despite about three times as much fishing effort in the GoM during 2011 relative to 2012 (Tables 3, 4). The bycatch rate, weight, and number of Alewives removed from the CC area could only be estimated for 2012 (Tables 3, 4). From 2011 to 2012, the Alewife bycatch rate increased in SNE and decreased in NJLI (Figure 3).

For Blueback Herring, significant differences in the length frequency distributions were only found between the GoM and SNE ($D_{24, 27} = 0.39$, $P < 0.05$). Blueback Herring caught in the GoM area were generally larger than those caught in SNE (Figure 4). The GoM area also contained the highest percentage (about 60%) of Blueback Herring that were most likely mature (Table 2). As was observed for Alewives, the length range of Blueback Herring in the bycatch was smaller in the CC area than in any other area, and over 75% of Blueback Herring in the CC area were classified as being of unknown maturity (Figure 4; Table 2). About 65% of Blueback Herring caught in SNE were of unknown maturity, but the percentage of Blueback Herring that were most likely mature (27%) was higher than the percentage that were most likely immature (9%; Figure 4; Table 2). In NJLI, most of the Blueback Herring caught were larger than 17 cm FL, but this area contained the highest percentage of immature individuals (Table 2).

The bycatch rate of Blueback Herring significantly differed between areas and between years (Figure 3). Blueback Herring bycatch in the GoM decreased from 2011 to 2012, whereas the bycatch rate did not (Tables 3, 4). In contrast to the results for Alewives, the Blueback Herring bycatch rate significantly increased in both SNE and NJLI from 2011 to 2012.

Overall, fishery effort and river herring bycatch increased from 2011 to 2012 (Tables 3, 4). Approximately 30% of all trips and target species catch came from the four nearshore areas in 2011, and almost 40% of all trips and target species catch came from these areas in 2012 (Tables 3, 4). Within the areas, river herring constituted 0.18% of the catch by weight in 2011 and 0.71% of the catch by weight in 2012. Bycatch rates of Alewives and Blueback Herring were much more variable in 2012 than in 2011 (Figure 3). Compared with the other three nearshore areas, the GoM had significantly lower river herring...

<table>
<thead>
<tr>
<th>Maturity status</th>
<th>NJLI (Jan–Mar)</th>
<th>SNE (Jan–Mar)</th>
<th>CC (Dec–Mar)</th>
<th>GoM (Oct–Nov)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alewife</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Immature</td>
<td>59</td>
<td>31</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Uncertain</td>
<td>30</td>
<td>60</td>
<td>93</td>
<td>60</td>
</tr>
<tr>
<td>Mature</td>
<td>11</td>
<td>9</td>
<td>6</td>
<td>36</td>
</tr>
<tr>
<td><strong>Blueback Herring</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Immature</td>
<td>20</td>
<td>9</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Uncertain</td>
<td>40</td>
<td>64</td>
<td>76</td>
<td>39</td>
</tr>
<tr>
<td>Mature</td>
<td>40</td>
<td>27</td>
<td>23</td>
<td>58</td>
</tr>
</tbody>
</table>
TABLE 3. Catch and effort information for midwater trawl vessels targeting Atlantic Herring and Atlantic Mackerel at specific times and areas during 2011 (NJLI = New Jersey and Long Island; SNE = southern New England; CC = east of Cape Cod; GoM = western Gulf of Maine; GB = Georges Bank). The "Other" column includes trips that occurred in the sampling areas during the months not shown in parentheses. Catch weight is presented with the coefficient of variation (CV; %) in parentheses. Asterisks denote numbers of fish that were not within 1 CV of catch estimates when a weight was extrapolated from length frequencies. Blueback Herring numbers with asterisks are probably overestimates, whereas Alewife numbers with asterisks are probably underestimates.

<table>
<thead>
<tr>
<th>Variable</th>
<th>NJLI (Jan–Mar)</th>
<th>SNE (Jan–Mar)</th>
<th>CC (Dec–Mar)</th>
<th>GoM (Oct–Nov)</th>
<th>GB (all months)</th>
<th>Other (see caption)</th>
<th>All areas (all months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target catch</td>
<td>5,047</td>
<td>1,776</td>
<td>327</td>
<td>10,130</td>
<td>32,017</td>
<td>9,871</td>
<td>59,168</td>
</tr>
<tr>
<td>Trips</td>
<td>29</td>
<td>16</td>
<td>2</td>
<td>49</td>
<td>194</td>
<td>66</td>
<td>356</td>
</tr>
<tr>
<td>Sampled trips</td>
<td>21</td>
<td>8</td>
<td>0</td>
<td>21</td>
<td>97</td>
<td>18</td>
<td>165</td>
</tr>
<tr>
<td>Alewife catch weight (metric tons)</td>
<td>14.0 (15)</td>
<td>1.3 (26)</td>
<td>NA</td>
<td>0.9 (26)</td>
<td>0.8 (35)</td>
<td>6.4 (53)</td>
<td>23.4 (17)</td>
</tr>
<tr>
<td>Alewife number</td>
<td>273,257</td>
<td>40,607</td>
<td>NA</td>
<td>2,200*</td>
<td>NA</td>
<td>200,431</td>
<td>516,495</td>
</tr>
<tr>
<td>Blueback Herring catch weight (metric tons)</td>
<td>8.6 (20)</td>
<td>0.1 (57)</td>
<td>NA</td>
<td>5.4 (30)</td>
<td>0</td>
<td>4.8 (52)</td>
<td>19.0 (18)</td>
</tr>
<tr>
<td>Blueback Herring number</td>
<td>359,005*</td>
<td>NA</td>
<td>NA</td>
<td>37,568</td>
<td>0</td>
<td>141,574</td>
<td>538,147</td>
</tr>
</tbody>
</table>

FIGURE 2. Length frequencies of Alewives caught by midwater trawl vessels in the four nearshore areas (GoM = western Gulf of Maine; CC = east of Cape Cod; SNE = southern New England; NJLI = New Jersey and Long Island) from 2008 to 2012.
FIGURE 3. Mean bycatch rates (± 95% confidence interval) for Alewives (upper graph) and Blueback Herring (lower graph) in the four nearshore areas (NJLI = New Jersey and Long Island; SNE = southern New England; CC = east of Cape Cod; GoM = western Gulf of Maine) during 2011 (black symbols) and 2012 (gray symbols). Mean bycatch rates for Alewives in the GoM and for Blueback Herring in SNE were less than 0.01% in 2011. Due to small sample size, no ratio was calculated for the CC area in 2011.

Bycatch Description

River herring that were caught in the GoM appeared to be larger and more mature than river herring that were caught in the other nearshore areas. The length frequencies of river herring bycatch in this area are consistent with those of spawning runs throughout the U.S. range of river herring (McBride et al. 2010; ASMFC 2012), and they lack the presence of the larger mature fish that are more commonly found in the Canadian portion of the species’ range (Jessop 2001; McIntyre et al. 2007). However, based on river herring life history, the Alewives and Blueback Herring observed in this area most likely consist of mature fish from mixed U.S. stocks that are migrating south to wintering grounds rather than juveniles from northern stocks. In the late summer or early fall, river herring begin to leave their summer feeding grounds in the Bay of Fundy and migrate to wintering areas in SNE and the mid-Atlantic (Neves 1981; Rulifson 1984; Rulifson et al. 1987; Stone and Jessop 1992). This timing would result in river herring passage through the GoM at the same time that midwater trawl vessels are active in the area.

The results from the CC area are unclear, but based on migratory and life history patterns the river herring caught in the CC area may also be mostly migratory. Although length samples in the CC area were from trips taken throughout the time range examined, the Alewife length frequency was derived from 10 trips and the Blueback Herring length frequency was derived from six trips; in all other areas, at least 19 trips were used to create length frequencies. The smaller sample sizes for the CC area may explain (1) the truncated range of length frequencies and (2) the statistical similarity in length frequency distributions between the CC area and most other areas despite this truncated range. However, there may be a biological explanation for this distribution. The fishery within the CC area is concentrated at depths between 50 and 100 m, which exceed the depths at which small, nonmigratory, age-2 or younger river herring are expected to be found, thereby explaining their absence from length frequencies (Bigelow and Schroeder 2002). At some point prior to their first spawning event, immature river herring join the older fish as they undergo north–south migrations. Forage fishes such as river herring school with fish of similar size (Fréon and Munday 1999; Krause et al. 2000), and large-scale migrations may be a learned behavior (McKeown 1984). Thus, it is plausible that when migrating for the first time, juveniles school with the smaller migrating fish. Like the closely related American Shad _Alosa sapidissima_, the movement of river herring from summer feeding grounds to wintering sites may be triggered by environmental cues (Leggett and Whitney 1972; Dadswell et al. 1987; Stone and Jessop 1992). If all size-classes of river herring begin their migrations based on the same cues, then schools of
TABLE 4. Catch and effort information for midwater trawl vessels targeting Atlantic Herring and Atlantic Mackerel at specific times and areas during 2012 (see Table 3 for definition of area codes). The “Other” column includes trips that occurred in the sampling areas during the months not shown in parentheses. Catch weight is presented with the coefficient of variation (CV; %) in parentheses. Asterisks denote numbers of fish that were not within 1 CV of catch estimates when a weight was extrapolated from length frequencies. Blueback Herring numbers with asterisks are probably overestimates, whereas Alewife numbers with asterisks are probably underestimates.

<table>
<thead>
<tr>
<th>Variable</th>
<th>NJLI (Jan–Mar)</th>
<th>SNE (Jan–Mar)</th>
<th>CC (Dec–Mar)</th>
<th>GoM (Oct–Nov)</th>
<th>GB (All months)</th>
<th>Other (see caption)</th>
<th>All areas (all months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target catch</td>
<td>4,856</td>
<td>11,662</td>
<td>4,027</td>
<td>3,157</td>
<td>29,538</td>
<td>9,314</td>
<td>62,554</td>
</tr>
<tr>
<td>Trips</td>
<td>30</td>
<td>65</td>
<td>19</td>
<td>16</td>
<td>179</td>
<td>51</td>
<td>360</td>
</tr>
<tr>
<td>Sampled trips</td>
<td>13</td>
<td>28</td>
<td>10</td>
<td>7</td>
<td>134</td>
<td>34</td>
<td>226</td>
</tr>
<tr>
<td>Alewife catch (metric tons)</td>
<td>2.4 (29)</td>
<td>24.6 (17)</td>
<td>17.6 (59)</td>
<td>0.4 (57)</td>
<td>0.2 (20)</td>
<td>0</td>
<td>45.3 (25)</td>
</tr>
<tr>
<td>Alewife number</td>
<td>12,162</td>
<td>304,800</td>
<td>184,707</td>
<td>NA</td>
<td>393*</td>
<td>0</td>
<td>502,062</td>
</tr>
<tr>
<td>Blueback Herring catch (metric tons)</td>
<td>56.0 (45)</td>
<td>43.6 (21)</td>
<td>22.4 (55)</td>
<td>0.8 (59)</td>
<td>0</td>
<td>0</td>
<td>122.8 (27)</td>
</tr>
<tr>
<td>Blueback Herring number</td>
<td>613,009</td>
<td>792,130*</td>
<td>150,204</td>
<td>11,087</td>
<td>0</td>
<td>0</td>
<td>1,556,430</td>
</tr>
</tbody>
</table>

larger fish would reach the wintering grounds first (Weihs 1987; Jobling 1995a). Larger river herring may pass through the CC area prior to December, resulting in the fishery catch of only the smaller, mixed-maturity schools. The intraspecies size distributions in SNE and NJLI were similar, suggesting that these areas contain a complex mix of juveniles, prespawning adults from nearby rivers, and migratory adults. In both areas, fishing effort was concentrated at depths

![FIGURE 4. Length frequencies of Blueback Herring caught by midwater trawl vessels in the four nearshore areas (GoM = western Gulf of Maine; CC = east of Cape Cod; SNE = southern New England; NJLI = New Jersey and Long Island) from 2008 to 2012.](image-url)
less than 50 m, leading to overlap with immature and adult river herring (Neves 1981; Fay et al. 1983; Bethoney et al. 2013a). The presence of mature river herring, especially during March, could indicate the capture of prespawning fish of local origin or river herring moving along the coast toward northern spawning areas. Recent spawning runs of Blueback Herring in Rhode Island and Connecticut have been extremely small in comparison with Alewife run sizes (ASMFC 2012); this difference suggests that Blueback Herring caught in SNE are more likely to be migratory than Alewives.

The NJLI area was the only area in which the size distributions of Alewives and Blueback Herring were significantly different. The difference may be due to interannual shifts in the location of fishing effort within NJLI and river herring wintering sites. During the winter, adult Alewives are located in deeper waters than adult Blueback Herring (Neves 1981; Bethoney et al. 2013a). However, juveniles of both species co-occur in nearshore areas (Fay et al. 1983; Klauda et al. 1991; Limburg 1998). Fishing effort in the NJLI area is concentrated at depths shallower than 50 m, which therefore may explain the overall lower proportion of larger Alewives. The shift from nearly equal bycatch of Alewives and Blueback Herring in 2011 to predominantly Blueback Herring bycatch in 2012 supports this explanation. In 2011, most of the bycatch occurred off the northeastern coast of New Jersey around the Hudson Canyon (NOAA statistical area 612; Figure 1). This area is known habitat for immature river herring from the Hudson River and nearby rivers (Fay et al. 1983; Limburg 1998). In contrast, most of the bycatch in 2012 occurred in NOAA statistical area 613 (Figure 1) from nearshore Long Island to depths of 50 m, which has been identified as Blueback Herring wintering grounds (Neves 1981; Bethoney et al. 2013a). Thus, in 2011, juveniles of both species were caught in the Hudson Canyon, while in 2012 the midwater trawl vessels primarily caught larger Blueback Herring.

Bycatch Implications and Mitigation Strategies

Despite the uncertainties surrounding the coastwide impact of river herring bycatch, strategies for bycatch mitigation should be consistent with the differing impacts of bycatch in different areas of the fishery. Limits based only upon historical bycatch, which have been implemented in the Atlantic Mackerel and Atlantic Herring fisheries, do not recognize the potential varying importance of these areas to the midwater trawl fleet. Action to limit the amount of river herring taken via a fleet communication system coupled with environmental data has begun in the GoM, with promising results (Bethoney 2012). The lower bycatch rate in the GoM than in other areas during 2011 and 2012 differs from patterns observed from 2005 to 2009 (Cieri et al. 2008; Courmame et al. 2013). In early January 2013, midwater trawl vessels were alerted of high river herring bycatch occurring within the CC area. Vessels avoided this area for 1 week, and no further high-bycatch events were observed (SMAST 2013).

The larger proportion of river herring in the immature size range within SNE and NJLI than within the GoM indicates a greater potential for bycatch in these areas to affect a smaller subset of nearby rivers and year-classes. In populations with small spawning stocks, strong year-classes can lead to substantial increases in overall population size (Jobling 1995b). Fewer year-classes are likely represented in juvenile aggregations. Furthermore, anadromy may have evolved due to improved fitness through increased survival of early life history stages (Dodson 1997). Thus, a reduction in juvenile bycatch mortality may be most beneficial to river herring populations. However, many factors can determine year-class strength before juvenile river herring can be caught as bycatch (Gibson and Myers 2003; Gahagan et al. 2010; ASMFC 2012). Although the magnitude of river herring removals is notable in comparison with estimated run sizes for several rivers adjacent to the SNE and NJLI areas, an evaluation of these removals is impossible given the current method of river herring stock assessment and the resolution of the information collected (ASMFC 2012).

Regulations that limit the amount of river herring taken in the SNE and NJLI areas may be justified given (1) the depleted state of river herring runs in northern mid-Atlantic and SNE rivers and (2) our conclusion that bycatch in SNE and NJLI likely comprises a considerable percentage of less-migratory juveniles (ASMFC 2012). Given the uncertainties surrounding the impact of bycatch on local populations and the seasonal importance of these areas to the midwater trawl fishery, closure of the SNE and NJLI areas would be unjustified. Static, smaller-scale closures would also be problematic due to the interannual variability in bycatch patterns within these areas (Bethoney et al. 2013b). Similarly, the development of intra-annual patterns that can be exploited via a fleet communication system varies from year to year (Bethoney et al. 2013b; SMAST 2013). Thus, a biologically based limit on the amount of river herring taken in
SNE and NJLI may be the best approach. To achieve this, river herring that are caught at sea must be linked to their populations of origin, possibly through genetic (Palkovacs et al. 2014) or morphometric (Rulifson 1984) analysis. At-sea removals could then be linked to index river mortality rates, and limits could be set based on bycatch amounts that would cause notable declines in the run sizes of index rivers.

At the levels seen in 2011 and 2012, bycatch in the midwater trawl fishery cannot account for the overall decline in river herring. For example, in 2011, the number of river herring estimated to have passed the Benton River fishway, Maine (ASMFC 2012), was similar to the number we estimated as taken by midwater trawl vessels in 2011 and 2012 combined. Furthermore, a consistent decline in the oceanic biomass of river herring has been documented since 1976, long before the establishment of the current midwater trawl fishery (i.e., in the 1990s; ASMFC 2012). A comprehensive review of rangewide threats to river herring (NOAA 2013a) identified dams and other barriers as the most significant threat to river herring populations, while water quality, climate change, predation, water withdrawal, dredging, and several other threats were also identified in addition to bycatch. The midwater trawl fishery is not the only fishery in which river herring are incidentally caught (Wigley et al. 2009). Bycatch in the midwater trawl fishery is highly variable from year to year, and the greatest potential impact on river herring appears to be for rivers from New Jersey to SNE. To better understand this impact, continued monitoring and studies examining the at-sea population dynamics of river herring are needed. Small improvements to existing monitoring programs, such as prioritization of length frequencies and further coordination among the NEFOP, MA-DMF, and other state agencies, will also allow for improvements (e.g., creation of intra-annual length frequencies and a reduction in CVs for weight estimates).

Basic biological measurements of bycatch species in conjunction with life history knowledge can greatly aid in the development of bycatch mitigation strategies. The composition of fish assemblages, especially those that are highly migratory, can differ over the range of a fishery. False assumptions about the similarity in bycatch among different areas can lead to ineffective strategies, while identifying where the impact of bycatch may be the greatest and focusing mitigation on these areas can increase the benefit to bycatch species and minimize the impact on the fishery. In areas characterized by great uncertainty, collaboration with fishery participants is an effective way to increase available data and potentially reduce bycatch (Roman et al. 2011; Bethoney et al. 2013b; O’Keefe et al. 2014).

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Use of an Ecosystem-Based Model to Evaluate Alternative Conservation Strategies for Juvenile Chinook Salmon in a Headwater Stream

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ARTICLE

Use of an Ecosystem-Based Model to Evaluate Alternative Conservation Strategies for Juvenile Chinook Salmon in a Headwater Stream

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Abstract
Declining abundance of Chinook Salmon Oncorhynchus tshawytscha across the Pacific Northwest is an issue of great concern ecologically, culturally, and economically. Growth during the first summer is vitally important for juvenile Chinook Salmon, as it influences not only life history decisions (to smolt or not to smolt) but also subsequent river and ocean survival. Using Ecopath with Ecosim, we developed a food web model for a representative stream in the Salmon River basin, Idaho, to evaluate potential species-specific and food web effects of three management strategies: (1) adding salmon carcasses or carcass analogs to promote primary production and detrital availability that were lost due to declining salmon returns; (2) removal of nonnative Brook Trout Salvelinus fontinalis, which are competitors with and predators on juvenile Chinook Salmon; and (3) stocking hatchery Chinook Salmon into streams to supplement wild production. Overall, juvenile Chinook Salmon responded strongly to increases in basal resources. Removal of Brook Trout had little effect on potential production for juvenile Chinook Salmon, but the responses of sculpins Cottus spp. were strong, primarily due to the sculpins' high degree of dietary overlap with and predation by Brook Trout. Supplementation with hatchery-origin juveniles depressed the production of wild juvenile Chinook Salmon, especially at the densities commonly applied to streams in this region. Our results suggest that efforts to enhance basal resources are likely to be the most effective in promoting the production of juvenile Chinook Salmon and nearly all food web groups considered in our model system. Removal of nonnative Brook Trout is unlikely to substantially affect salmon but could have a disproportionately large effect on nongame species, which are generally overlooked in single-species management approaches.

The conservation of threatened and endangered populations of Pacific salmon Oncorhynchus spp. is a well-established example of federally mandated single-species management for which an increasingly broad ecosystem perspective has been advocated (Naiman et al. 2002; Independent Scientific Advisory Board 2011). This broader ecosystem perspective and the implementation of specific ecosystem management techniques require an understanding of the ecological framework in which a species functions and the complex suite of direct and indirect interactions among organisms (Boersma et al. 2001). Ecosystem modeling has become an important tool in exploring these connections and in developing and testing alternative management and conservation strategies. Modeling exercises can reveal tradeoffs that improve conditions both for target species and for the whole food web (Christensen et al. 1996). This is particularly relevant for work with threatened and endangered species, where the opportunities to field test multiple alternative management options or ecosystem manipulations are limited.

Wild populations of Chinook Salmon O. tshawytscha have declined across the Pacific Northwest, spurring a great deal of interest in the factors that promote (or inhibit) production of juvenile Chinook Salmon in rearing streams (Kareiva et al. 2000).

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The growth and survival of juvenile salmon in freshwater are affected by a number of ecological factors. In the present study, we focused on three areas of particular concern with regard to wild Chinook Salmon survival and production in headwaters of the interior Columbia River basin: (1) declining numbers of returning adults, leading to the loss of nutrient subsidies provided by the decay of spawner carcasses (Stockner 2003); (2) species invasion—specifically the introduction of Brook Trout Salvemius fontinalis (Sanderson et al. 2009a; Macneale et al. 2010); and (3) stocking of hatchery-origin juveniles into systems that contain wild populations, thus impacting resource availability for target and nontarget wild fishes (Levin et al. 2001; Weber and Fausch 2005).

These three factors reflect processes by which the production of juvenile Chinook Salmon can be affected: bottom-up resource availability, top-down predator effects, and direct and indirect competition. First, declines in adult salmon abundance lead to a loss of nutrient and organic matter subsidies in these oligotrophic stream environments, which may result in reduced juvenile salmon production through several pathways that are mediated by the stream food web (Wipfli and Baxter 2010). Carcasses of postspawn adult salmon provide a direct detrital subsidy to invertebrates and fish, and the inorganic nutrients that are released during the decomposition of the carcasses can promote periphyton growth, thereby indirectly increasing secondary production (Bilby et al. 1998; Kiernan et al. 2010). Second, in many of these same systems, invasive piscivores are having profound impacts on native salmonids (Eby et al. 2006; Sanderson et al. 2009a). In headwater streams of western North America, the most pervasive invader is the Brook Trout (Dunham et al. 2002; Peterson et al. 2008), which both preys upon and competes with native salmonids (Dunham et al. 2002; Peterson et al. 2004). Finally, juvenile salmon of hatchery origin are an additional source of resource competition in many nursery streams. Fish that are stocked as parr often remain in or near the area where they were released (Peery and Bjornn 2000), which can lead to direct competition among wild and hatchery-origin fish throughout the critical growth period in summer. A number of studies have documented declines in native salmonid abundance when hatchery-origin fish are stocked into systems with wild populations (Nickelson 2003; Weber and Fausch 2005).

Food web models have become important tools for exploring the effects of management actions aimed at conservation of species that are known to experience important bottom-up, top-down, and competitive relationships (Christensen et al. 1996). In application to streams, food web models have been used to evaluate functional redundancy, bottom-up versus top-down controls, and the impacts of invasive species (McIntyre et al. 2007; Saito et al. 2007). For lake and ocean ecosystems, Ecopath with Ecosim (EwE) software (Christensen and Walters 2004) is a well-established semiquantitative ecosystem/food web modeling program based on a mass-balance framework for energy flow through the system. The EwE program is a particularly valuable tool for evaluating how changes in the abundances of species or groups of species directly and indirectly affect other groups. For example, EwE models have been used to estimate the extent of bottom-up control in aquatic food webs, effects of top predators on lower trophic levels, communitywide impacts of fishery bycatch, and ecosystem-scale impacts of fishery management practices (reviewed by Christensen and Walters 2011). The EwE program has been applied to streams in only a few cases, but the work by Meyer and Poepperl (2004) clearly demonstrated that balanced and informative Ecopath models can be created for small stream ecosystems and that the common practice of integrating empirical data with parameter borrowing (Christensen and Walters 2004) to fill out models can be applied.

We created an EwE model for a typical tributary of the Snake River, Idaho, in which juvenile Chinook Salmon occur sympatriically with nonnative Brook Trout. We simulated and monitored food web responses to three management actions that were designed to address the three focus areas of concern noted above for juvenile Chinook Salmon:

1. Increase basal resources via salmon carcass and carcass analog additions;
2. Reduce or remove a nonnative competitor/predator (Brook Trout); and
3. Increase competition by stocking hatchery-origin juvenile Chinook Salmon into the stream with the existing population of wild Chinook Salmon.

METHODS

Study Site

The stream from which most of our data are derived, the South Fork of the Salmon River, Idaho, is an important Chinook Salmon spawning and nursery stream that also contains a self-sustaining population of wild Brook Trout in the main stem and associated tributaries (Adams et al. 2002). We created our model by using fish abundance, invertebrate abundance, and diet data from this fourth-order stream in the Snake River basin, with salmon abundances, nonnative trout abundances, and habitat in the middle range of those observed for Chinook Salmon rearing streams in this region (Achord et al. 2007; Sanderson et al. 2009b). Typical Chinook Salmon nursery streams in the region are alluvial, with gradients ranging from about 1% to 5% and with mixed riparian vegetation consisting of grasses, woody shrubs, and conifers. In mid-summer, fish communities are dominated by juvenile Chinook Salmon (Macneale et al. 2010), in particular the evolutionarily significant unit of spring/summer (or “stream-type”) Snake River basin Chinook Salmon. The majority of juvenile salmon rear over the summer and migrate out of the headwaters by mid-October; some overwinter in the system, but their numbers are substantially reduced and the relative dominance of resident fish species increases. Our study focused on food web dynamics during the summer months, when juvenile salmon dominate; this is the period for which we have well-quantified empirical data on fish and invertebrate
We assumed that nutrient and biomass fluxes into the study area generally equaled fluxes and export out of the study area; this assumption is consistent with other applications of EwE to streams (Meyer and Poepperl 2004). Food web groups and final parameter values are reported in Table 1, and initial diet compositions are provided in Table 2. Details on model balancing, parameter estimation, and diets are provided in Supplement A.

Once the initial Ecopath model was balanced, we ran the Ecosim portion of the model to compare the responses of juvenile Chinook Salmon and other groups in the food web to our three management alternatives. In the Ecosim model, biomasses of all functional groups are dynamic and represented by differential equations such that the trophic linkages between groups will permeate throughout the food web by direct and indirect pathways (Christensen and Walters 2004). The Ecosim equation for each group i is

\[
\frac{dB_i}{dt} = g_i \cdot \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i,
\]

where \(g_i\) = growth efficiency; \(\sum_j C_{ji}\) = rate of consumption of all prey j by group i; \(\sum_j C_{ij}\) = rate of consumption of group i by all predators j; \(I_i\) = immigration rate; \(M_i\) = mortality not attributable to other model groups; \(F_i\) = fishing mortality rate; \(e_i\) = emigration rate; and \(B_i\) = biomass. In our models, all \(I_i\) and \(e_i\) are equal to 0. The C terms are density dependent in that consumer diets will vary from their initial values as a function of changing prey densities (Christensen and Walters 2004). Within Ecosim, parameters of individual groups can be perturbed, and such changes will reverberate through the food web via direct and indirect trophic interactions.

For each of the management options explored below, we applied a continuous perturbation to one or more functional groups as outlined below, and then we ran model simulations through for 20 “years” (i.e., annual time steps for 20 model iterations). For example, for a 10% increase in the primary...
TABLE 1. Input parameters for the Ecopath model, including the production : biomass ratio (P/B); consumption : biomass ratio (Q/B); ecotrophic efficiency (EE); and production : consumption ratio (P/Q). Fish groups include Brook Trout less than 150 mm (BKT < 150); Brook Trout greater than 150 mm (BKT > 150); Bull Trout less than 150 mm (BLT < 150); Bull Trout greater than 150 mm (BLT > 150); juvenile Chinook Salmon less than 150 mm (CH < 150); Rainbow Trout/steelhead greater than 150 mm (RBT > 150); Cutthroat Trout (CT; all sizes); sculpins (SCLPN; all sizes); and whitefishes Prosopium spp. (WHTFH; all sizes).

<table>
<thead>
<tr>
<th>Group name</th>
<th>Trophic level</th>
<th>Biomass (g/m²)</th>
<th>P/B</th>
<th>Q/B</th>
<th>EE</th>
<th>P/Q</th>
<th>Detritus import (g·m⁻²·year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periphyton</td>
<td>1.00</td>
<td>1.287</td>
<td>83.91</td>
<td>64.49</td>
<td>0.09</td>
<td>0.09</td>
<td>0.24</td>
</tr>
<tr>
<td>Macrophytes</td>
<td>1.00</td>
<td>0.893</td>
<td>7.39</td>
<td>83.91</td>
<td>0.24</td>
<td>0.24</td>
<td></td>
</tr>
<tr>
<td>Microbes</td>
<td>2.00</td>
<td>8.944</td>
<td>15.48</td>
<td>15.48</td>
<td>0.04</td>
<td>0.04</td>
<td>0.24</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>2.13</td>
<td>0.272</td>
<td>3.72</td>
<td>46.47</td>
<td>0.86</td>
<td>0.08</td>
<td></td>
</tr>
<tr>
<td>Plecoptera</td>
<td>3.03</td>
<td>0.089</td>
<td>2.99</td>
<td>16.64</td>
<td>0.46</td>
<td>0.18</td>
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</tr>
<tr>
<td>Trichoptera</td>
<td>2.13</td>
<td>0.130</td>
<td>2.28</td>
<td>19.00</td>
<td>0.95</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Chironomidae</td>
<td>2.27</td>
<td>0.100</td>
<td>12.50</td>
<td>96.15</td>
<td>0.98</td>
<td>0.13</td>
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<td>Coleoptera</td>
<td>2.28</td>
<td>0.148</td>
<td>3.50</td>
<td>17.50</td>
<td>0.44</td>
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<tr>
<td>Noninsect aquatics</td>
<td>2.69</td>
<td>0.166</td>
<td>3.40</td>
<td>21.26</td>
<td>0.93</td>
<td>0.16</td>
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<tr>
<td>Other Diptera</td>
<td>2.11</td>
<td>0.221</td>
<td>8.83</td>
<td>73.56</td>
<td>0.71</td>
<td>0.12</td>
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<tr>
<td>BKT &lt; 150</td>
<td>3.28</td>
<td>0.009</td>
<td>0.86</td>
<td>3.45</td>
<td>0.75</td>
<td>0.25</td>
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<td>BKT &gt; 150</td>
<td>3.96</td>
<td>0.008</td>
<td>0.37</td>
<td>1.84</td>
<td>0.00</td>
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</tr>
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<td>BLT &lt; 150</td>
<td>3.26</td>
<td>0.002</td>
<td>0.86</td>
<td>3.45</td>
<td>0.00</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>BLT &gt; 150</td>
<td>3.90</td>
<td>0.014</td>
<td>0.37</td>
<td>1.84</td>
<td>0.00</td>
<td>0.20</td>
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</tr>
<tr>
<td>CH &lt; 150</td>
<td>3.23</td>
<td>0.109</td>
<td>1.45</td>
<td>5.82</td>
<td>0.05</td>
<td>0.25</td>
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</tr>
<tr>
<td>RBT &lt; 150</td>
<td>3.20</td>
<td>0.038</td>
<td>1.26</td>
<td>5.05</td>
<td>0.01</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>RBT &gt; 150</td>
<td>3.20</td>
<td>0.021</td>
<td>0.55</td>
<td>2.75</td>
<td>0.48</td>
<td>0.20</td>
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</tr>
<tr>
<td>CT</td>
<td>3.14</td>
<td>0.032</td>
<td>1.26</td>
<td>5.05</td>
<td>0.00</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>SCLPN</td>
<td>3.35</td>
<td>0.010</td>
<td>1.44</td>
<td>5.74</td>
<td>0.80</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>WHTFH</td>
<td>3.33</td>
<td>0.032</td>
<td>0.41</td>
<td>4.14</td>
<td>0.00</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>Detritus</td>
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<td>82.760</td>
<td>99.99</td>
<td>375</td>
<td>0.99</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>

The production rate, we increased the primary production rate by 10% above the initial Ecopath model level and maintained production at 10% above initial throughout the next 20 iterations of the model. In response to perturbations, functional groups increased or decreased in biomass, depending on the magnitude of the perturbation and the strength of the direct and indirect food web pathways that linked them to the perturbed group(s). For example, groups (e.g., Ephemeroptera and Coleoptera) that feed to the greatest degree on periphyton should respond strongly to increased periphyton at first; however, as the biomass of these groups increases, their predators should respond positively, thereby tempering their final relative biomass response. The strength of the EwE model is that it accounts not only for these individual predator–prey dynamics but also for how potential increases in predator biomass due to greater food resources in one group (e.g., Ephemeroptera) may influence predation pressure in another group that would not have necessarily benefited to the same degree from increasing periphyton (e.g., non-insect aquatic taxa). Eventually, the model reaches a new equilibrium, reflecting a new balance in the system among all model groups. The model generally reached this new steady state after about 15 annual iterations in our analysis.

Management Scenarios

Increase basal resources (periphyton and detritus).—We used the forcing function option in Ecosim to evaluate five levels of increased periphyton P/B: 2, 5, 10, 25, and 100% increases. The small increases reflect a range of potential changes in production associated with greater nutrient availability after the addition of adult salmon carcasses or carcass analogs. The larger increases were applied to evaluate a broader range of food web responses, but these higher values are clearly possible; Sanderson et al. (2009b) documented order-of-magnitude increases in periphyton standing stocks on nutrient-diffusing substrate with added nitrogen and phosphorus in salmon rearing streams within the Salmon River basin, Idaho.

Salmon carcasses not only provide nutrients that can promote primary production but also detritus that is consumed directly. A simple increase in detrital availability would not necessarily reflect the highly labile nature of this food source, so rather than increase the baseline detrital B, we instead increased the vulnerability (sensu Christensen and Walters 2004) of detritus to its consumers by 2, 5, 10, 25, 50, and 100%. This is not a direct proxy for carcass inputs, but it is functionally similar, as it represents greater access to the detritus pool. Many invertebrate species have been shown to feed on salmon
TABLE 2. Diets used in the Ecopath model. Values represent the proportion of the predator’s diet that consists of the prey item listed in the first column. Fish groups are defined in Table 1.

<table>
<thead>
<tr>
<th>Prey/diet item</th>
<th>Microbes</th>
<th>Ephemeroptera</th>
<th>Plecoptera</th>
<th>Trichoptera</th>
<th>Chironomidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periphyton</td>
<td>0</td>
<td>0.308</td>
<td>0.02</td>
<td>0.188</td>
<td>0.122</td>
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<td>0.011</td>
<td>0.01</td>
<td>0.075</td>
<td>0.039</td>
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<td>0.003</td>
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<td>0.001</td>
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<td>Trichoptera</td>
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<td>0.05</td>
<td>0.001</td>
<td>0</td>
</tr>
<tr>
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<td>0.006</td>
<td>0.22</td>
<td>0.004</td>
<td>0.01</td>
</tr>
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<td>0.01</td>
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<tr>
<td>BKT &gt; 150</td>
<td>0</td>
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<tr>
<td>BLT &gt; 150</td>
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carcasses, so we ensured that all invertebrate groups had detritus as a component of their diets (Table 2). Microbes consumed 100% detritus; Trichoptera, Chironomidae, and other Diptera were the macroinvertebrate groups that were most heavily reliant on detritus. None of the fish groups consumed detritus directly.

Reduce or remove a nonnative competitor/predator.—The relative influence of Brook Trout was evaluated by altering Brook Trout \( B \). We reduced Brook Trout \( B \) (in both size-classes) by applying four different levels of fishing mortality (\( F \); equation 2): 5, 25, 50, and 100%. These mortality rates represent the degree of instantaneous mortality at the start of each model iteration. As with the increases in basal resources, the larger \( F \)-values were included to evaluate potential end-member responses. We calculated the final biomass responses of juvenile Chinook Salmon and other food web groups relative to their initial status and then compared relative responses within and among scenarios.

Increase competition by stocking hatchery-origin juvenile Chinook Salmon.—To assess the impacts of stocking juvenile hatchery-origin Chinook Salmon into this system, we included an additional group (hereafter, “stocked CH0”) in the model. For this analysis, we created a separate model that encompassed all of the original groups and original values from the original balanced model (including EE values) along with the stocked CH0 group. Simulated CH0 stocking densities ranged from 0.02 to 2.0 g dry weight (DW)/m\(^2\). The summer \( B \) of wild juvenile Chinook Salmon in the focal stream from which all biomass data were collected was 0.11 g DW/m\(^2\). The density of hatchery-origin juvenile Chinook Salmon is rarely quantified per unit area since the fish disperse after release, but the range of stocking values assessed in our analysis encompassed the range of densities occurring after poststocking dispersal, as observed in Snake River tributaries by Peery and Bjornn (2000). Although hatchery-origin fish do not necessarily grow at exactly the same rate or feed on exactly the same diet items as wild fish, for the purposes of this analysis, we assumed that EwE parameters for CH0 were the same as those for wild fish. With inputs that included EE values, the initial Ecopath model accounted for imbalance through biomass accumulation or loss (i.e., the BA term in equation 1). We then ran Ecosim for 20 iterations and evaluated the final responses of juvenile Chinook Salmon and other food web groups to densities of stocked CH0.

Analysis

We focus our present analysis on a comparison of the final relative change in \( B \) within and among model scenarios for each taxonomic group at the end of the model runs. We focus only on
the relative change to allow for greater internal consistency in comparing the influence of the three management options on the same original Ecopath model. We used a linear regression model to assess the final relative change in $B$ as a function of trophic position for each group under each of the four basic scenarios (increased periphyton, increased detritus, Brook Trout removal, and CH0 stocking at a density equal to the wild population). For these regressions, we used an $\alpha$ value of 0.05 as the criterion for significance.

RESULTS

Increase Basal Resources (Periphyton and Detritus)

Increased primary production and greater access to labile detritus led to increases in relative $B$ for most groups by the end of the model run. Increases in primary production led to the largest increases in relative $B$ of juvenile Chinook Salmon among the individual manipulation scenarios (Figure 1). A 5% increase in periphyton production led to a 6% increase in juvenile Chinook Salmon $B$ in our modeled food web. With a 10% increase in periphyton production, juvenile Chinook Salmon $B$ increased by 12%; with more substantial increases in primary productivity (25% and 50%), juvenile Chinook Salmon $B$ increased linearly by 29% and 60%, respectively (Figure 2). There were also notable increases in $B$ for nearly all other groups, especially the fish groups (Table SB.1 in Supplement B online).

Increases in detrital vulnerability led to notable increases in juvenile Chinook Salmon $B$; however, the responses were not as strong for increased detrital vulnerability as they were for increased periphyton production (Figure 2; Table SB.1). When periphyton production and detrital vulnerability were both increased, final relative changes in $B$ for the food web groups were, as expected, larger than those observed for either scenario alone. For example, a scenario involving a 25% increase in periphyton production and a 5% increase in detrital vulnerability yielded slightly more than a 31% increase in relative $B$ of juvenile Chinook Salmon (Table SB.1).

The relative change in final $B$ caused by increasing basal resources was greater for higher trophic levels. The responses in final relative $B$ to increased periphyton production across groups were significantly related to trophic position ($P = 0.004$, $r^2 = 0.35$; Figure 3A); relative $B$ responses to increased detrital availability were also significantly related to trophic position ($P < 0.001$, $r^2 = 0.75$; Figure 3B). As expected, invertebrate groups with larger periphyton components in their diets, such as Ephemeroptera and Coleoptera, experienced substantial increases in relative $B$ early in the model progression; however, as predator $B$ subsequently increased, the relative $B$ of these grazer...
taxa and other invertebrate prey groups declined, although the responses still generally remained positive (Figure 3A).

Reduce or Remove a Nonnative Competitor/Predator

Despite some dietary overlap and a predator–prey interaction between Brook Trout and juvenile Chinook Salmon, Brook Trout removal had a limited influence on juvenile Chinook Salmon in our model (Figure 1). The B of juvenile Chinook Salmon increased by only 3.4% after the complete removal of Brook Trout. A comparable increase in B could be achieved with only about a 3% increase in periphyton production (Figure 2). The majority of the food web groups were minimally affected by 100% Brook Trout removal, and responses were not well associated with trophic position or broad taxonomic groupings (Figures 1, 3).

Although the influence of Brook Trout removal was limited for most invertebrate groups and for juvenile Chinook Salmon in summer, Brook Trout removal did influence sculpins and, to a lesser degree, other trout species. Complete Brook Trout removal led to a 51% increase in the B of sculpins, a 22% increase in the B of Rainbow Trout/steelhead larger than 150 mm, and a 16% increase in the B of Bull Trout larger than 150 mm. In contrast to the limited amount of primary production that was needed to attain a juvenile Chinook Salmon response equivalent to that from Brook Trout removal, the model comparison suggested that an appreciable increase in periphyton production (65%) was required to generate an increase in sculpin B comparable to the response obtained via Brook Trout removal (Figure 2). Unlike responses to increased basal resources, the responses of sculpins to decreases in Brook Trout B were non-linear. Slight reductions in Brook Trout B led to relatively substantial increases in sculpin B (Figure 2C).

Increase Competition by Stocking Hatchery-Origin Juvenile Chinook Salmon

The addition of hatchery-origin juvenile Chinook Salmon in this model yielded declines in wild juvenile Chinook Salmon abundance. When CH0 stocking density was equal to resident wild population abundance during summer (~0.11 g DW/m²), the relative B of wild Chinook Salmon declined by about 7% (Figure 2D). However, densities of stocked fish are generally much higher than this, especially immediately after the stocking event (Peery and Bjornn 2000). At higher stocking densities, the impacts of CH0 on wild Chinook Salmon and on other native fishes were more severe. For example, at a CH0 stocking density of 0.5 g DW/m² (nearly five times the density of wild juvenile Chinook Salmon in this study), juvenile Chinook Salmon B declined by 34% and Cutthroat Trout B declined by 40% (Figure 2D). The degree of impacts from stocked CH0 was also significantly related to trophic position, with higher trophic levels generally declining the most (P < 0.001, r² = 0.60; Figure 3D).
**FIGURE 1.** Model output of the food web responses to four scenarios, with the juvenile Chinook Salmon response highlighted in bold: (A) 25% increase in periphyton primary production; (B) 25% increase in detrital vulnerability, reflecting anticipated increases in labile carbon in detritus with the addition of salmon carcasses; (C) 100% removal of Brook Trout from the study reach; and (D) stocking of hatchery-origin juvenile Chinook Salmon (CH0) at a density of 0.5 g dry weight (DW)/m².

**DISCUSSION**

Our model indicates that basal resource availability has a much stronger influence on juvenile Chinook Salmon production potential than Brook Trout presence or CH0 stocking in typical nursery streams in the Salmon River basin. This supports the contention that even minor declines in primary production and detritus associated with decreasing salmon populations and postspawn carcass inputs could influence summer production of juvenile Chinook Salmon in this region (Naiman et al. 2002; Stockner 2003). Brook Trout removal had a substantial influence on native sculpins in the model, but otherwise the overall food web impacts appeared to be limited relative to the...
impacts exerted by changes in basal resource availability and juvenile Chinook Salmon densities in summer. Stocking of CH0 diminished the capacity of the system to support wild juvenile Chinook Salmon, particularly at higher densities.

Responses to Increased Basal Resources

Results from our model suggest strong bottom-up controls on secondary production in this stream. In particular, increased periphyton production yielded much larger increases in secondary production than did increases in detritus availability for consumers. Although streams are a well-established example of allochthonously subsidized ecosystems (Fisher and Likens 1972; Wallace et al. 1997), studies from forested streams have demonstrated that processes which increase primary production, such as increased light due to forest management, lead to substantial increases in secondary production above and beyond levels associated with pretreatment conditions, when allochthonous material input dominated the base of the food web (Kiffney et al. 2003). The relatively limited response to increased detritus vulnerability is likely due in part to limitations in the model and our inability to account for carbon lability. We increased detritus vulnerability to detrital consumers, but it is unclear how much an increase in carcasses affects the entire detrital pool. We addressed this in the current study by presenting a range of potential changes. The specific magnitude of the response remains uncertain and clearly warrants further research.

The magnitude of salmon carcass inputs or other anthropogenic nutrient inputs (intended or unintended) that is required to yield a measurable increase in primary productivity will depend upon the underlying conditions of the system and how nutrients (and carcasses, specifically) are added (Janetski et al. 2009). Overall, though, our results suggest that efforts to
mitigate cultural oligotrophication are warranted, assuming that salmon carcass or carcass analog additions are large enough to actually promote periphyton production. If greater carcass abundances occur naturally through increased spawner densities, the periphyton response may depend upon substrate mobility. Some studies have found clear positive associations between spawning salmon and stream periphyton (e.g., Johnston et al. 2004; Chaloner et al. 2007), whereas other studies have found that spawning activities that disrupt substrates across a large area can lead to decreases in periphyton standing stocks (Verspoor et al. 2010) or have indicated that food itself is not likely to be limiting salmon abundance (Bellmore et al. 2012). The presence of actively spawning salmon also substantially increases direct carbon subsidies above and beyond carcass additions alone through dislodged eggs, a factor that is not accounted for in our model. The addition of salmon carcasses or carcass analogs alone—without associated substrate modification from spawning—often yields increases in primary production and secondary production (Wipfli et al. 2004), but a positive response is not guaranteed (Ambrose et al. 2004; Harvey and Wilzbach 2010). Ultimately, increasing periphyton production can be effective, but background conditions of the system will influence the effectiveness of these additions (Ambrose et al. 2004; Bellmore et al. 2012); furthermore, it should be noted that other factors (e.g., disease introduction) warrant consideration before additions are unilaterally applied (Compton et al. 2006).

The Impacts of Brook Trout Invasion

Our analysis suggested that the impacts of Brook Trout invasion in these systems are confined to relatively few species. This was surprising given that the impacts of nonnative species in other systems have been shown to be widespread, with direct effects on competitors and prey species and indirect effects that radiate through the food web (Pringle et al. 2007). In aquatic environments, fish invasions have been particularly striking in their direct and cascading influences on the invaded ecosystems (Vander Zanden et al. 1999; Baxter et al. 2004). The invasion of a novel predator into aquatic ecosystems has been shown to dramatically impact native prey species and can produce shifts in the diet and behavior of native predators (Vander Zanden et al. 1999; Lepak et al. 2006). Invasion by a nonnative trout species
can affect not only native salmonids but also native invertebrate communities, with implications for terrestrial biota that feed on insects emerging from the stream (Baxter et al. 2004). We observed a clear impact of Brook Trout on a few native fish species in our analysis, but the overall food web impacts within the stream appeared to be relatively limited.

The limited responses to Brook Trout removal were somewhat unexpected, but competitive interaction, degrees of predation, and diet overlap among salmonids can also vary regionally and with the size and complexity of the fish and invertebrate communities (Sanderson et al. 2009a). For example, Dunham et al. (2000) found substantial diet overlap between Brook Trout and Lahontan Cutthroat Trout *O. clarkii henshawi* in southeastern Oregon and northern Nevada, but similar studies in other regions found limited diet overlap and instead attributed Brook Trout invasion success to differential recruitment (McGrath and Lewis 2007). In most cases, predation is not thought to be the dominant factor leading to Brook Trout displacement of native salmonids (Dunham et al. 2002); however, it has been noted as a probable impact in some cases (McHugh et al. 2008). We did include juvenile Chinook Salmon in the diet of Brook Trout for our model, but (in mid-summer at least) the *B* of predatory Brook Trout and the levels of predation were insufficient to severely impact juvenile Chinook Salmon *B*. We acknowledge that a focus on summer processes could underestimate Brook Trout predation on young-of-the-year salmon in spring. Given the lack of a strong whole-food-web effect of Brook Trout removal during summer in the current model analysis as well as the limited diet overlap documented by Macneale et al. (2010), we hypothesize that for the summer period, Brook Trout impacts on native salmonids are likely to be a result of larger Brook Trout excluding other fish from preferred habitats rather than a result of direct predation or competition for food resources. This would be consistent with work by McGrath and Lewis (2007) in the interior western USA; those authors found that competition for space at bottlenecks in life history strategies between Brook Trout and native Greenback Cutthroat Trout *O. clarkii stomias* had the greatest impact on the native species. The stream evaluated here is somewhat larger than those assessed by McGrath and Lewis (2007), but habitat availability and competition for habitat are clearly key considerations. Competition for space is difficult to simulate in Ecosim; one way of doing so is the use of “mediation functions” (Espinosa-Romero et al. 2011), wherein the ability of a group (e.g., juvenile Chinook Salmon) to forage on prey (e.g., invertebrates in preferred stream habitat) is made to be functionally dependent upon the abundance of a mediating group (in this case, Brook Trout). The challenge in using mediation functions is identifying reasonable functional shapes (e.g., linear, hyperbolic, or sigmoid) and response magnitudes, which must be determined through careful experimentation. We did not apply such functions here because they would have been largely speculative in the absence of experimental data.

### Hatchery/Stocking Influence

As expected, the stocking of CH0 at high densities significantly impacted all fish groups and most invertebrate groups in the system. For the period shortly after stocking, when densities are particularly high, impacts on the local food web are likely to be especially strong. As the CH0 disperse, their densities do decline, but the densities remain elevated for the duration of the summer, at least within 5 km of the stocking areas (Peery and Bjornn 2000). Our model results suggest that the presence of stocked CH0 even at low densities has the potential to influence wild Chinook Salmon populations. To avoid this competition, CH0 are often held until the smolt life stage so that they emigrate early, thereby reducing their influence on local wild populations.

When fish are stocked into a stream, their realized densities can be difficult to calculate; we therefore evaluated a range of potential CH0 densities in our analysis. This range of densities encompassed those estimated in an experiment quantifying the densities of stocked hatchery-origin juvenile (parr) Chinook Salmon in four Snake River tributaries over the course of a summer (Peery and Bjornn 2000). In that study, fish were stocked at a single period in time but under two different regimes: single-point stocking versus stocking at multiple points along 5–6-km reaches. At 12 weeks poststocking, estimated biomass densities in the study reaches proximate to the initial stocking sites declined from early maxima of as much as 1.14 g DW/m² but remained between 2.0 and 4.5 times the 0.11-g DW/m² biomass density of wild Chinook Salmon in our study stream (0.22 g DW/m² for the dispersed stocking and 0.48 g DW/m² for the single-point stocking). Actual fish additions ranged from 12,000 juvenile Chinook Salmon parr in a 7-m-wide stream to 80,000 parr in a 12-m-wide stream; the biomass density (g DW/m²) estimates are based on a mean parr mass of 5 g and DW equal to 20% of wet weight (Trudel et al. 2005). The range of stocking values assessed in our analysis covered the likely range of potential realized densities of stocked CH0, depending upon how far the area of interest is from a specific stocking location.

Management for salmon systems like the Salmon River and the Snake River rarely includes a single action. Although stocking is widespread in many Snake River basin streams, salmon carcass or carcass analog additions are also widespread, and these management options can occur concurrently. The importance of the interactions among management options is highlighted in Pearsons’ (2008) paper, stressing the need to consider multiple interacting factors in salmon management—specifically the stocking of hatchery fish into systems that support wild populations. While the scenario comparisons described here suggest that salmon carcass additions have the potential to mitigate the negative impacts of stocking CH0 into a stream with wild juvenile Chinook Salmon in summer, we stress that this sort of speculation based on the results presented here should be considered with great caution. Given the limitations of our data, our results are a reasonable first step in hypothesis generation for future research on such interacting effects, but
greater empirical data on year-round diet and biomass will be needed to more effectively flesh out concurrent management options.

Mixed Trophic Impacts and Model Caveats

We used the mixed trophic impact output (Table SB.2) from the Ecosim analysis to conduct a preliminary exploration of model sensitivity. This output is a matrix of each group’s impact on each of the other groups. The mixed trophic impact analysis is similar to an “ordinary sensitivity analysis” (Majkowski 1982; Libralato et al. 2006). Overall, the mixed trophic impact output suggested a fairly balanced food web, with no single group having a disproportionate influence across all other groups. In our model, the strongest positive effect of one group on another was for Bull Trout and Trichoptera. This is somewhat counterintuitive since trichopterans are part of the Bull Trout’s diet, but Bull Trout also prey upon and compete with a number of other fish species that also eat trichopterans. Therefore, in this analysis, once all food web interactions were accounted for, Bull Trout provided a net benefit for Trichoptera. The strongest negative relationship between two groups was the impact of juvenile Rainbow Trout/steelhead on sculpins (value = −0.771). For juvenile Chinook Salmon, all values in the mixed trophic impact analysis were between −0.2 and +0.3, indicating that no single group had disproportionate leverage on the juvenile Chinook Salmon responses evaluated here.

Because the literature on Brook Trout interactions with native salmonids suggests that predation can vary widely (Dunham et al. 2000; 2002), we also conducted a preliminary exploration of Brook Trout diet effects—specifically, the influence of changes in the amount of Brook Trout predation on juvenile Chinook Salmon in the balanced model and with Brook Trout removal. For larger Brook Trout, switching the diet proportion consisting of sculpins (0.25) with the diet proportion consisting of juvenile Chinook Salmon (0.123) yielded a balanced model, and there did not appear to be a strong response to the dietary shift. In the Ecosim model with Brook Trout removal, sculpins still responded much more strongly than juvenile Chinook Salmon. We then elevated the proportion of juvenile Chinook Salmon in the diets of larger Brook Trout to 0.4 and decreased the other diet components proportionally. When Brook Trout were then removed, juvenile Chinook Salmon responses were more pronounced, but in the end the impacts of Brook Trout removal were still more pronounced for sculpins than for juvenile Chinook Salmon (see Tables SB.3 and SB.4 for model run results on juvenile Chinook Salmon under the initial and modified Brook Trout diets).

An additional caveat in the interpretation of the present results is the seasonal nature of the empirical data used (including B estimates and diet data). By focusing only on the summer diet, the model can miss key periods when consumers exhibit highly specialized diets. As noted above, while Ecosim allows for shifts in the proportion of existing prey, predators cannot exploit a novel food resource in the model. For example, sculpins are important salmon egg predators when adult salmon are spawning, and Brook Trout may also eat salmon eggs (Levin et al. 2002). Omission of these relationships (if they are important) eliminates potential pathways and feedbacks from the model.

Overall, we remained internally consistent in this analysis and focused on a comparison of relative responses to various management options within the same model framework. In thinking beyond the specific scenario comparisons, our results do provide the foundation for hypothesis development and future experimental work on the interaction among biota in the systems. The influence of nonnative Brook Trout on native sculpins was particularly striking in this respect. Sculpins are often overlooked in salmon carcass studies since they are not target species for fish management and since they are difficult to capture and efficiently deplete in multiple-pass electrofishing surveys. Because sculpins are hard to see, are hard to quantify, and carry no recreational value, they have received limited consideration in studies evaluating the impacts of nonnative Brook Trout and the loss of anadromous salmon. We hypothesize that some of the most severe impacts of Brook Trout invasion may be on native sculpin populations rather than on native salmonids.

Limitations in our ability to account for labile carbon from salmon carcasses and eggs likely weighted our results more heavily toward autotrophic pathways in a hypothetical carcass addition scenario. Although changing carbon susceptibility was worked in a general sense to address the addition of labile carbon, future development of this model will include greater accountability for potentially labile allochthonous carbon from carcasses and eggs. In regard to autotrophic responses, the characteristics of a specific stream are a key consideration in evaluating autotrophic responses to nutrient supplementation from salmon carcass analogs or direct addition (Janetski et al. 2009). For this reason, we evaluated the food web responses in our model across a wide range of changes in primary production.

Conclusions

The model applied here suggests that juvenile Chinook Salmon production in a low-gradient, mid-order stream of central Idaho is dominated by bottom-up food web processes relative to the influences of a nonnative competitor/predator or stocked conspecifics (Figure SB.1 in Supplement B). Responses to increases in the availability of basal resources in summer were widespread and were significantly related to trophic position. In contrast, Brook Trout trophic effects in the model were confined largely to sculpins, which filled known niches in the food web. Our results suggest that conservation efforts focusing only on juvenile Chinook Salmon should direct efforts toward projects that increase labile carbon and promote primary production, especially if those systems receive a high density of stocked CH0 in addition to the wild population. If, however, one takes a whole-ecosystem perspective that incorporates impacts on other fish species (especially native sculpins) and the invertebrate community or if behavioral interactions (e.g., space competition with native salmonids) prove significant, then
Brook Trout removal should be considered in addition to efforts that increase basal resources.

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Genetic Diversity and Population Structure of Spring Chinook Salmon from the Upper Willamette River, Oregon

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Genetic Diversity and Population Structure of Spring Chinook Salmon from the Upper Willamette River, Oregon

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Abstract
Effective management of Pacific salmon requires an accurate understanding of both population genetic diversity and structure. Spring Chinook Salmon Oncorhynchus tshawytscha from the upper Willamette River (UWR), Oregon, are listed as threatened under the U.S. Endangered Species Act, and although this evolutionarily significant unit is recognized to be distinct from other Columbia River stocks, genetic relationships among its constituent hatchery and wild populations remain obscure. We used genotypic data from 13 microsatellite loci to test whether hatchery populations of UWR spring Chinook Salmon are most similar to wild populations within the same subbasin, or whether hatchery populations from different subbasins are more similar to each other than to local wild populations. We also tested for differences between the genetic diversities of hatchery and wild populations, as measured through heterozygosity and allelic richness. Our results suggest that populations are weakly structured among subbasins and, in all cases, hatchery populations are genetically most similar to local wild populations. We also found heterozygosity to be higher ($P = 0.009$) in hatchery populations (median, 81.5%) than in wild populations (median, 75.2%), but observed no significant difference with respect to allelic richness ($P = 0.406$). We conclude that hatchery-origin UWR spring Chinook Salmon represent genetically appropriate founder populations for ongoing reintroduction programs and recommend that the conservation and recovery of this stock proceed through management actions developed specifically for each subbasin. We further recommend that current restrictions on hatchery stock transfers among UWR subbasins be continued to preserve extant population genetic structure.

For several decades, fisheries managers have used genetic data to gain insight to the population structure of Pacific salmon species (Oncorhynchus spp.). Genetic information has been used to delineate evolutionarily significant units (ESUs) and develop recovery plans for threatened and endangered species. Although ESU-level information may address broad-scale management questions, important genetic diversity can be structured at finer spatial scales (see Banks et al. 2000; Myers et al. 2006; Neville et al. 2007). An understanding of such fine-scale structure is important because human activities, such as habitat alterations and hatchery operations, can potentially impact the genetic and life history diversity that lends resilience to salmon populations (Eldridge et al. 2009).

The Willamette River is the second largest tributary of the Columbia River in terms of average discharge and is contained entirely within the state of Oregon. The upper Willamette River (UWR) basin is defined, in part, by the 12-m-high basalt shelf at Willamette Falls (Figure 1) that, before construction of a fish ladder in 1882, was only traversable by salmon during high flows of late winter and spring (Myers et al. 2006). Although Willamette Falls historically excluded fall-run Chinook Salmon O. tshawytscha from the upper basin, spring Chinook Salmon are native to the UWR, but have declined in numbers to a fraction of their historical, natural abundance. Accordingly, UWR spring Chinook Salmon were listed as threatened under the U.S. Endangered Species Act in 1999, and this status was reaffirmed in 2005 and 2010 (Ford 2011). Diverse factors have contributed to the decline of UWR spring Chinook Salmon (NMFS 2008). Foremost among these, the construction and continued operation of flood-control and hydroelectric dams on all major UWR...
FIGURE 1. The Willamette River basin and collection sites for clipped (hatchery origin) Chinook Salmon tissue samples. Samples were collected from unclipped fish throughout the labeled tributaries.
tributaries (Figure 1) has impeded adult and juvenile migrations and altered the flow, temperature, and other qualities (i.e., substrate, depth, total dissolved gases) of critically important riverine habitats (NMFS 2008). To mitigate for these negative impacts on native fish and fisheries, five state-operated hatcheries produce UWR spring Chinook Salmon for harvest and reintroduction programs. However, introgression from hatchery-produced salmon may pose serious genetic risks to the recovery of natural populations (Waples 1991; Levin et al. 2001; Araki et al. 2008), especially if hatchery populations are genetically less diverse than or significantly diverged from local wild populations (Ryman and Laikre 1991; Basket and Waples 2012). This potential risk is of particular concern to the management of UWR spring Chinook Salmon because large numbers of adult hatchery fish are released above UWR dams to expand the species’ spawning distribution into otherwise vacant or underutilized habitats.

In their review of historical population structure, Myers et al. (2006) identified seven historically independent populations of UWR spring Chinook Salmon native to the Clackamas, Molalla, North Santiam, South Santiam, Calapooia, McKenzie, and Middle Fork Willamette rivers. Clackamas River spring Chinook Salmon are included in the UWR spring Chinook Salmon ESU, even though the Clackamas and Willamette rivers join below the geographic boundary of the upper basin (Willamette Falls, Figure 1). Collectively, UWR spring Chinook Salmon are among the most genetically distinct of Columbia River Chinook Salmon (Waples et al. 2004; Narum et al. 2010; Moran et al. 2013). However, hatchery stock transfers, which were common prior to 1997 (Kostow 1995), may have weakened or eliminated genetic structure among spring Chinook Salmon populations within the basin. Myers et al. (2006) provided evidence of some genetic structure for UWR populations, though those authors acknowledged that their results may have been compromised by the inclusion of juvenile samples, which can produce skewed patterns of population structure due to overrepresentation of some family groups, i.e., the Allendorf–Phelps effect (Allendorf and Phelps 1981; Waples 1998). Indeed, their findings suggested that some hatchery populations were more closely related to wild spring Chinook Salmon from distant subbasins than to their neighboring wild population. However, it is unclear whether their results reflected actual relationships among UWR spring Chinook Salmon populations or if the Allendorf–Phelps effect masked true population structure.

In this study, we use the UWR spring Chinook Salmon population designations identified by Myers et al. (2006) and data from adult fish characterized at 13 standardized microsatellite loci (Seeb et al. 2007) to determine whether (1) UWR hatchery spring Chinook Salmon are most closely related to local wild populations and (2) UWR hatchery spring Chinook Salmon are genetically less diverse than wild populations, as measured through heterozygosity and allelic richness.

METHODS
Sample collections and microsatellite genotyping.—From June to October 2011 we collected otolith and fin tissue samples from carcasses of unclipped (adipose fin), presumably wild-origin, adult spring Chinook Salmon from the Clackamas, North Santiam, South Santiam, Molalla, McKenzie, and Middle Fork Willamette rivers (Figure 1). Since 1997, all spring Chinook Salmon from UWR hatcheries have been adipose fin-clipped to allow for selective harvest of hatchery-produced fish. These fish are also passively marked with programmed temperature oscillations that produce recognizable otolith banding (Volk et al. 1999). We examined otoliths from all unclipped Chinook Salmon sampled for this study to confirm wild-origin status. During the same year, we also collected fin tissue samples from adult hatchery-origin spring Chinook Salmon at the Clackamas, Marion Forks (North Santiam), South Santiam, McKenzie, and Willamette hatcheries. We also included samples from spring Chinook Salmon from the Catherine Creek Hatchery in our analyses. This geographically distant population from the Grande Ronde River of the upper Columbia River basin served as the outgroup of our study to provide broader context to genetic distance estimates for UWR spring Chinook Salmon populations. Fall Chinook Salmon are rare or absent from most UWR tributaries and typically spawn later than spring Chinook Salmon, and thus, experienced surveyors made visual assessments to avoid including fall Chinook Salmon among samples. All tissue samples were stored in labeled vials containing 95% ethanol.

We used the protocol of Ivanova et al. (2006) to isolate whole genomic DNA from Chinook Salmon tissue samples. We used touchdown PCR (Korbie and Mattick 2008) with fluorescently labeled primers to amplify 13 microsatellite markers: Ots208, Ots213, Ots9, Ots211, Ogo4, OtsG474, Ssa408, Ogo3, Ots3, Ots212, Oki100, Ots201, Oki100, Ots201, and Omm1080. Primer sequences for these markers are provided by references in Seeb et al. (2007), and reaction conditions are available from the authors upon request. All PCR products were separated and visualized on an ABI 3730XL DNA Analyzer (Applied Biosystems) and scored by size against a 500-bp standard with GeneMapper software (Applied Biosystems).

Analyses.—To reduce genotyping error effects from low quality DNA samples (Pompanon et al. 2005), we excluded all samples that amplified at fewer than 7 of 13 microsatellite loci from our analyses. We used the program GENETIX (Belkhir et al. 2004) to produce estimates of observed heterozygosity (\( H_o \)) and expected heterozygosity (\( H_e \)) for all study populations. We used a Kruskal–Wallis ANOVA on ranks to test for basin-wide difference between observed heterozygosities of hatchery and wild populations, and we used a Friedman rank sum test to compare \( H_e \) values for hatchery and wild population pairs within subbasins. We used the program GENEPOP to perform Hardy–Weinberg equilibrium (HWE) exact tests (Haldane 1954) and score (a.k.a. \( U \)) tests (Raymond and Rousset 1995;
Rousset 2007) to detect locus-specific heterozygosity excesses or deficits within each population. We also used GENEPOP to perform exact tests for linkage disequilibrium (LD) between all locus pairs within each population. We controlled the false discovery rate (FDR) of multiple tests according to the methods of Benjamini and Hochberg (1995; also see Narum 2006) and used a maximum (unadjusted) critical value of \( \alpha = 0.05 \) to assess significance.

Using our microsatellite data and the program GENETIX, we estimated \( F_{ST} \) (\( \theta \); Weir and Cockerham 1984) for all pairs of populations with \( n > 30 \), then evaluated significance of each \( F_{ST} \) value with a permutation test (1,000 iterations, FDR-adjusted \( \alpha \) from 0.001 to 0.050). We used the program FSTAT (Goudet 1995) to estimate allelic richness for all loci in each population, then calculated mean allelic richness across loci for each population and tested for difference between mean allelic richness of hatchery and wild populations with a Student’s \( t \)-test.

We used the maximum likelihood program CONTML from the PHYLIP version 3.69 software package (Felsenstein 2009; see also Felsenstein 2004:391–414) to infer relationships among all spring Chinook Salmon populations with \( n > 30 \). We visualized the resulting dendrogram with the program TREEVIEW (Page 1996). To assess node confidence, we bootstrapped the allele frequency data (1,000 resamples) with the program SEQBOOT (Felsenstein 2009), inferred dendrograms as before (for all 1,000 data sets), constructed a consensus tree with the program CONSENSE (Felsenstein 2009), then examined bootstrap values for each node. The resulting bootstrapped tree provides statistical support for a graphical representation of genetic distance relationships among hatchery and wild spring Chinook Salmon populations from the UWR and Catherine Creek Hatchery.

**RESULTS**

We collected 1,797 tissue samples from unclipped spring Chinook Salmon from tributaries of the Willamette River. Of these, 1,506 lacked otolith thermal marks and were classified as wild spring Chinook Salmon. Samples included spring Chinook Salmon from multiple age-classes. Although we surveyed the Calapooia River on multiple occasions, no carcasses were encountered nor were any samples collected from this subbasin. We subjected 391 of the wild-origin samples, representing six hatchery.ry samples, which we collected from carcasses in various states of decomposition.

**Heterozygosity**

Across all UWR subbasins, the median of observed heterozygositites was significantly higher (Kruskal–Wallis ANOVA on ranks: \( H = 6.818, df = 1, P = 0.009 \)) in hatchery populations (median, 81.5%) than in wild populations (median, 75.2%). Similarly, hatchery populations presented higher heterozygositites than did wild populations within subbasin pairs (Friedman rank sum test: \( \chi^2 = 5, df = 1, P = 0.025 \); Table 1). Exact test results indicated that all populations, except the Catherine Creek Hatchery (\( P = 0.2303 \)) and Molalla wild (\( P = 0.9103 \)) populations, were not in HWE (\( P < 0.0001 \)). Subsequent score (\( U \)) tests revealed that this result was largely driven by lower than expected heterozygosities at two loci: Omm1080 and Ots213. That is, all populations except the Catherine Creek Hatchery population and the small collections of wild fish from the Molalla and Middle Fork Willamette rivers showed significant evidence for heterozygote deficits (\( P < 0.0006 \)) at one or both of these loci. Although no clear pattern was evident for HWE between hatchery and wild populations, the number of locus pairs in LD was consistently higher in hatchery populations than in wild populations.

**Pairwise \( F_{ST} \)**

Among UWR populations upstream from Willamette Falls pairwise \( F_{ST} \) values ranged from 0 to 0.009 (Table 2). Populations from above Willamette Falls were more diverged from the Clackamas River hatchery population (\( F_{ST} = 0.009–0.013 \)) than from the Clackamas River wild population (\( F_{ST} = 0.001–0.005 \)). Pairwise \( F_{ST} \) values between the Catherine Creek hatchery population and UWR populations were generally an order of magnitude greater than that observed among UWR populations (Table 2). Wild spring Chinook Salmon from the Molalla and Middle Fork Willamette rivers were not included in this analysis due to small sample sizes (Table 1).

We found that \( F_{ST} \) values were not significantly different from zero for hatchery and wild population pairs within UWR subbasins above Willamette Falls (North Santiam, \( P = 0.047 \); South Santiam, \( P = 0.535 \); McKenzie, \( P = 0.317 \)). With a single exception, both hatchery and wild populations from all UWR subbasins were significantly diverged from hatchery and wild populations from other subbasins. Interestingly, analysis of pairwise \( F_{ST} \) values suggested that neither hatchery nor wild spring Chinook Salmon from the South Santiam River were significantly diverged from wild Clackamas River spring Chinook Salmon.

**Allelic Richness**

Although per locus allele counts varied considerably among populations, we observed similar levels of allelic richness among populations when sample sizes were normalized by
CHINOOK SALMON POPULATION STRUCTURE

TABLE 1. Collection location, origin, and number of spring Chinook Salmon samples analyzed from the Willamette River and Catherine Creek Hatchery (Grande Ronde River), 2011. Samples were characterized at 13 microsatellite loci to estimate each population’s expected heterozygosity (\(H_e\)), observed heterozygosity (\(H_o\)), mean allelic richness (AR; normalized for \(n = 22\) per population), and the number of loci not in Hardy–Weinberg equilibrium (HWE) and in linkage disequilibrium (LD).

<table>
<thead>
<tr>
<th>Collection location</th>
<th>Origin</th>
<th>Number of samples</th>
<th>(H_e)</th>
<th>(H_o)</th>
<th>AR</th>
<th>HWE</th>
<th>LD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catherine Creek</td>
<td>Hatchery</td>
<td>33</td>
<td>0.744</td>
<td>0.735</td>
<td>11.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Clackamas</td>
<td>Hatchery</td>
<td>80</td>
<td>0.806</td>
<td>0.815</td>
<td>11.8</td>
<td>4</td>
<td>38</td>
</tr>
<tr>
<td>North Santiam</td>
<td>Hatchery</td>
<td>95</td>
<td>0.819</td>
<td>0.820</td>
<td>12.2</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>South Santiam</td>
<td>Hatchery</td>
<td>94</td>
<td>0.814</td>
<td>0.813</td>
<td>12.3</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>McKenzie</td>
<td>Hatchery</td>
<td>95</td>
<td>0.821</td>
<td>0.805</td>
<td>12.1</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>Middle Fork Willamette</td>
<td>Hatchery</td>
<td>144</td>
<td>0.819</td>
<td>0.818</td>
<td>12.0</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>Clackamas</td>
<td>Wild</td>
<td>51</td>
<td>0.828</td>
<td>0.752</td>
<td>13.2</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Molalla</td>
<td>Wild</td>
<td>8</td>
<td>0.753</td>
<td>0.823</td>
<td>11.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>North Santiam</td>
<td>Wild</td>
<td>72</td>
<td>0.796</td>
<td>0.777</td>
<td>11.9</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>South Santiam</td>
<td>Wild</td>
<td>62</td>
<td>0.808</td>
<td>0.746</td>
<td>12.1</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>McKenzie</td>
<td>Wild</td>
<td>67</td>
<td>0.824</td>
<td>0.788</td>
<td>12.1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Middle Fork Willamette</td>
<td>Wild</td>
<td>12</td>
<td>0.706</td>
<td>0.620</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

rarefaction to a minimum 22 diploid individuals. Among Willamette River populations, wild fish from the Clackamas River presented the highest allelic richness, and wild fish from the North Santiam River presented the lowest allelic richness (Table 1). The Catherine Creek Hatchery population presented the lowest allelic richness (11.8) of any population examined. Overall, we found no significant difference for allelic richness between hatchery and wild spring Chinook Salmon from the upper Willamette River (\(t = -0.884, df = 7, P = 0.406\)), though power to reject the null hypothesis for this test was very low (\(\beta = 0.05\)). Assumptions of normality (Shapiro–Wilk test: \(P = 0.119\)) and equal variance (\(P = 0.595\)) for this test were met.

Genetic Structure among Populations

We inferred a maximum likelihood tree for Willamette River and Catherine Creek Hatchery spring Chinook Salmon from our genotypic data. This dendrogram (Figure 2) suggests that within the Willamette River, spring Chinook Salmon hatchery populations are genetically most similar to local wild populations from the same subbasin. In most cases, these subbasin level hatchery–wild pairings received bootstrap support approaching or exceeding 70%. An exception to this pattern involved the hatchery and wild populations from the South Santiam River and hatchery fish collected from the Middle Fork Willamette River. These putative populations formed a polytomy with insignificant

TABLE 2. Pairwise \(F_{ST}\) values (\(\theta; \text{Weir and Cockerham 1984}\)) among hatchery- (H) and wild-origin (W) spring Chinook Salmon populations from the Willamette River and Catherine Creek Hatchery (Grande Ronde River) estimated from genotypic data for 13 microsatellite loci. Values not significantly different from zero (false discovery rate-adjusted \(\alpha\) from 0.001 to 0.050) are indicated in bold italic text.

<table>
<thead>
<tr>
<th>Source</th>
<th>Clackamas H</th>
<th>Clackamas W</th>
<th>Willamette H</th>
<th>McKenzie H</th>
<th>McKenzie W</th>
<th>North Santiam H</th>
<th>North Santiam W</th>
<th>South Santiam H</th>
<th>South Santiam W</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catherine H</td>
<td>0.111</td>
<td>0.106</td>
<td>0.106</td>
<td>0.107</td>
<td>0.102</td>
<td>0.100</td>
<td>0.110</td>
<td>0.099</td>
<td>0.104</td>
</tr>
<tr>
<td>Clackamas H</td>
<td>0.007</td>
<td>0.012</td>
<td>0.013</td>
<td>0.013</td>
<td>0.013</td>
<td>0.010</td>
<td>0.012</td>
<td>0.010</td>
<td>0.009</td>
</tr>
<tr>
<td>Clackamas W</td>
<td>0.004</td>
<td>0.003</td>
<td>0.003</td>
<td>0.004</td>
<td>0.005</td>
<td>0.003</td>
<td>0.004</td>
<td>0.003</td>
<td>0.003</td>
</tr>
<tr>
<td>Willamette H</td>
<td>0.007</td>
<td>0.006</td>
<td>0.006</td>
<td>0.008</td>
<td>0.009</td>
<td>0.004</td>
<td>0.005</td>
<td>0.004</td>
<td>0.003</td>
</tr>
<tr>
<td>McKenzie H</td>
<td>0.000</td>
<td>0.000</td>
<td>0.003</td>
<td>0.006</td>
<td>0.006</td>
<td>0.004</td>
<td>0.003</td>
<td>0.004</td>
<td>0.003</td>
</tr>
<tr>
<td>McKenzie W</td>
<td>0.000</td>
<td>0.004</td>
<td>0.006</td>
<td>0.006</td>
<td>0.004</td>
<td>0.005</td>
<td>0.006</td>
<td>0.004</td>
<td>0.005</td>
</tr>
<tr>
<td>North Santiam H</td>
<td>0.002</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
<td>0.004</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
<td>0.005</td>
</tr>
<tr>
<td>North Santiam W</td>
<td>0.005</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
<td>0.004</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
<td>0.005</td>
</tr>
<tr>
<td>South Santiam H</td>
<td>0.000</td>
<td>0.005</td>
<td>0.005</td>
<td>0.006</td>
<td>0.004</td>
<td>0.005</td>
<td>0.006</td>
<td>0.005</td>
<td>0.005</td>
</tr>
</tbody>
</table>
internal branch lengths (95% CI) and <50% bootstrap support of branch nodes. Bootstrap support between Catherine Creek and UWR populations was 100%.

**DISCUSSION**

**Heterozygosity and Allelic Richness**

Genetic diversity is fundamental to the short-term resilience and long-term adaptive potential of salmon populations (Waples et al. 1990; Allendorf 2005). Both heterozygosity and allelic richness are important components of genetic diversity that can be directly compared among populations. We found that mean heterozygosities of Willamette River spring Chinook Salmon populations ranged from 62% to 82%. Our estimates of observed heterozygosity for hatchery populations from the North Santiam and McKenzie rivers (Table 1) differed by less than 1% from those previously reported by Narum et al. (2010), placing these populations among the top 5 of 37 Columbia River spring Chinook Salmon populations described by those authors. We also found that within subbasins of the Willamette River, hatchery populations presented higher heterozygosities than did local wild populations. The large size of UWR spring Chinook Salmon hatchery populations has likely served to maintain heterozygosities above levels found in the typically smaller wild populations, which may experience stronger effects from random genetic drift.

Nearly all UWR spring Chinook Salmon populations presented some evidence for departures from HWE expectations, and there were heterozygote deficits at *Omm1080* or *Ots213* in all but one population. Most populations also presented some evidence of linkage disequilibrium (Table 1), though loci in LD were not consistent across populations. It is not surprising that allele frequencies deviated from HWE expectations at some loci, as our data violated several assumptions required for HWE. Specifically, the assumption of nonoverlapping generations is violated by inclusion of multiple age-classes among samples. Moreover, migration among populations may contribute to departures from HWE. Although HWE departures can also result from genotyping errors, replicate PCR and electrophoretic analyses for a subset of samples suggested allele assignment error rates of <1%. The higher frequencies of LD in hatchery populations may, however, result from monogamous hatchery spawnings that likely produce a greater proportion of full siblings and apparent family structure among adult returns than...
found in wild populations, which are commonly characterized by polygamous mating systems (Bentzen et al. 2001).

Although hatchery populations consistently presented higher heterozygosities than wild populations, we found no clear pattern for allelic richness. However, the Clackamas River wild population did present a slightly higher mean allelic richness than other populations, perhaps as a result of admixture generated by inadvertent sampling of a small number of fall or hybridized Chinook Salmon in this subbasin. This hypothesis is consistent with the relatively high number of loci not in HWE for wild Clackamas River spring Chinook Salmon (Table 1), but it cannot be tested with our current data set.

Genetic Divergence ($F_{ST}$)

In contrast with the findings of Myers et al. (2006), our pairwise $F_{ST}$ estimates suggest that, in the upper Willamette River, hatchery-origin spring Chinook Salmon are genetically most similar to local, wild fish. In most cases, $F_{ST}$ values between local hatchery and wild populations were not significantly different from zero, which reflected no measurable genetic differentiation. By identifying wild-origin fish as only those that lacked adipose fin and otolith marks, our methodology maximized the chance of detecting genetic differences between hatchery and wild fish, should they exist.

The observed similarity between hatchery and wild UWR spring Chinook Salmon is undoubtedly driven by several factors. Although a composite “Willamette stock” of spring Chinook Salmon was used for many years at UWR hatcheries, current hatchery broodstocks were founded either entirely or partially from local, wild spring Chinook Salmon in the mid-1990s or earlier (see Johnson and Friesen 2010 for a review of UWR hatchery broodstock histories). Since that time, ongoing migration between hatchery and local wild populations has continued through natural production by stray hatchery fish and integration of wild fish into hatchery broodstocks. The proportion of hatchery-origin Chinook Salmon (PHOS) on UWR spawning grounds has varied among years and locations. From 2002 to 2010, 4% to 69% of spawners encountered below Dexter Dam on the Middle Fork Willamette River were of hatchery origin (Cannon et al. 2011). During the same period, PHOS ranged from 4% to 73% on the North Santiam River (Cannon et al. 2011). Similarly, the proportion of wild (or natural-origin) fish integrated into hatchery broodstocks (PNOB) has varied among facilities and years (Cannon et al. 2011); from 2002 to 2010, PNOB ranged from 0.3% to 10.1% at the Middle Fork Willamette Hatchery and from 0.3% to 36.2% at Marion Forks Hatchery (North Santiam River). Overall, PHOS tended to exceed PNOB in most UWR subbasins with hatchery facilities. Current marking and annual monitoring programs now provide estimates for these migration parameters, though comparable estimates are not available before the 1997 brood year when otolith thermal marking first began at UWR hatcheries (Johnson and Friesen 2010).

Although most pairwise $F_{ST}$ estimates were statistically significant among populations from different UWR subbasins (Table 2), they were generally lower than values reported for spring Chinook Salmon populations from the Snake ($F_{ST} = 0.017–0.045$; Narum and Stephenson 2007), Klamath ($F_{ST} = 0.011–0.024$; Kinziger et al. 2008), and California’s Central Valley rivers ($F_{ST} = 0.005–0.026$; Garza et al. 2008) as characterized with the same genetic markers used in our study. Pairwise $F_{ST}$ values between the Clackamas Hatchery population and other UWR populations were higher than those among most UWR populations, though $F_{ST}$ values between the Clackamas River wild population and populations from the South Santiam River were insignificant. Straying of South Santiam Hatchery spring Chinook Salmon into the Clackamas River wild population does not provide a likely explanation for this result, because, from the near 1.8 million coded-wire-tagged Chinook Salmon released from the South Santiam Hatchery from 1995 to 2010, only 11 of the 5,244 fish recovered as adults were recorded in the Clackamas River (unpublished data from the Regional Mark Information System; http://www.rmpc.org/). Stray rates among wild UWR spring Chinook Salmon populations remain unknown.

Genetic Structure among Populations

The maximum likelihood tree of Willamette River spring Chinook Salmon further revealed similarities between hatchery and wild populations within subbasins, because local hatchery and wild populations formed branch pairs in all possible cases. Our findings indicate that Willamette River spring Chinook Salmon populations are weakly structured at the subbasin level, and little or no genetic variance is explained by hatchery or wild origin within subbasins. As speculated by Myers et al. (2006), the population structure previously reported within this ESU was likely influenced by the inclusion of closely related individuals among juvenile samples. Unless relatedness is accounted for, data from juvenile samples can easily inflate population divergence estimates and distort genetic relationships (see Allendorf and Phelps 1981). We believe that our results, derived from analyses of adult UWR spring Chinook Salmon, provide an accurate depiction of contemporary UWR spring Chinook Salmon population structure; it is characterized by weak but significant structure among subbasins and no significant divergence between hatchery and wild populations within subbasins.

Management Implications

The weak but significant genetic structure we observed among populations from different subbasins suggests that conservation and recovery efforts for UWR spring Chinook Salmon should be implemented through subbasin-specific management actions, as identified by ODFW et al. (2011). Current restrictions on stock transfers among UWR spring Chinook Salmon populations should further preserve and possibly strengthen genetic
structure among populations from different subbasins, thereby promoting adaptation to local conditions.

The relatively high heterozygosities of UWR hatchery spring Chinook Salmon and similarities between hatchery and wild populations within subbasins suggest that hatchery-origin spring Chinook Salmon represent genetically appropriate founders for local reintroduction programs. Anderson et al. (2013) concluded that hatchery spring Chinook Salmon can provide demographic benefits to reintroduction programs, and their use for this purpose in the UWR basin has been recommended by NMFS (2008). However, as dam passage for adult and juvenile salmon is improved and determined to be adequate for above-dam population viability, short-term demographic benefits from hatchery fish should be carefully weighed against potential threats that these fish may pose to the evolution, productivity, and long-term viability of recipient populations. Moreover, near-term UWR monitoring and research efforts should aim to identify negative ecological effects that hatchery spring Chinook Salmon might have on wild populations.

Our most relevant finding to conservation and recovery efforts for UWR spring Chinook Salmon may be that, despite rigorous sampling, we identified only 25 naturally produced fish returning to the Middle Fork Willamette River at or below Dexter Dam (of which only 12 were used in the analysis due to poor sample quality). According to reports by Hutchinson et al. (1966) and Thompson et al. (1966; also see McElhany et al. 2007), this subbasin once ranked among the most productive UWR tributaries for wild spring Chinook Salmon, before the construction of Lookout Point and Dexter dams (Figure 1) isolated 345 km of high quality spawning and rearing habitat (Cramer et al. 1996). Extensive annual releases (hundreds to thousands) of adult hatchery-origin spring Chinook Salmon above these dams in every year of the last decade (Johnson and Friesen 2010) have consistently failed to result in wild adult returns despite apparently substantial natural production of juveniles (Monzyk et al. 2013; Romer et al. 2013). Keefer et al. (2012) reported high juvenile mortality rates (35–70%) during passage at Middle Fork Willamette dams and Monzyk et al. (2013) documented predation on juvenile Chinook Salmon by resident fishes within the reservoirs. Consistent with the findings of those authors our results suggest that significant improvements to juvenile passage are needed to recover wild spring Chinook Salmon in this UWR subbasin.

Plans for a path toward recovery may be drafted from lessons learned from the Fall Creek tributary of the Middle Fork Willamette River, where a wild population of spring Chinook Salmon, founded by hatchery-origin fish, has begun to expand in apparent response to dam operations that promote juvenile passage (USACE 2013). These results underscore both the potential of hatchery-origin fish for local reintroduction programs and the fundamental role that improved dam passage must play to secure the long-term viability of spring Chinook Salmon in the upper Willamette River.

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Physiological Stress Responses to Prolonged Exposure to MS-222 and Surgical Implantation in Juvenile Chinook Salmon

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Physiological Stress Responses to Prolonged Exposure to MS-222 and Surgical Implantation in Juvenile Chinook Salmon

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Abstract
This study simulated large-scale monitoring program operations to evaluate the responses of age-1 Chinook Salmon Oncorhynchus tshawytscha to tricaine methanesulfonate (MS-222; 80 mg/L) exposure and intracoelomic acoustic microtransmitter implantation. The MS-222 exposure effects and appropriate exposure times for juvenile Chinook Salmon undergoing intracoelomic implantation were determined using blood analytes (Na⁺, K⁺, Ca²⁺), blood pH, plasma cortisol, and survival immediately following anesthetic exposure (3, 6, 9, and 12 min on day 0) and over a recovery period (days 1, 7, and 14). In addition, effects were examined in surgically implanted and nonimplanted fish (but exposed to MS-222 for 3 min) over a 14-d recovery period. Regardless of anesthetic exposure time, there were no mortalities during exposure on day 0 or over the recovery period. On day 0, MS-222 exposure treatments of 9 and 12 min resulted in significantly higher Na⁺ and Ca²⁺ and lower K⁺, indicating a reduced ability to maintain osmotic balance; however, MS-222 effectively dampened the cortisol release following surgical implantation and anesthetic exposure. Cortisol concentration was significantly higher in surgically implanted fish than in those not surgically implanted over the recovery period. Given these results, we recommend MS-222 exposure (80 mg/L) times of 6 min or less for compliance programs and studies involving age-1 Chinook Salmon. In addition, we recommend for other monitoring programs, regardless of species, that maximum MS-222 exposure times are implemented to minimize stress and surgical effect and that exposure times are specific to a species’ life stage to prevent overexposure and long-term effects. Furthermore, the knowledge of effects and the development of maximum exposure times are beneficial for hatchery programs, fish barging or transportation programs, and most studies in which fish behavior and physiological responses would need to be dampened using MS-222 without adverse side effects.

Acoustic telemetry is utilized routinely to monitor habitat use, behavior, and survival of juvenile salmonids (Clemens et al. 2009; Cooke et al. 2011; Skalski et al. 2013). Telemetry technology requires the attachment of an acoustic transmitter to a fish, commonly through surgical intracoelomic implantation (Bridger and Booth 2003; Makiguchi and Ueda 2009; Cooke et al. 2011). This invasive procedure can affect the physiology and behavior of the fish, consequently violating telemetry and

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survival model assumptions (i.e., tagged fish are representative of untagged fish migrating in the river; neither the presence of the tag nor the implantation process affects survival, behavior, or physiology of the fish) (Pevcn et al. 2005; Thiem et al. 2011). While some studies have concluded minimal to no effects from tag presence or the implantation process (Caputo et al. 2009; Chittenden et al. 2009; Ammann et al. 2013), others have found negative effects, such as increased mortality and cortisol levels or reduced growth rates (Jepsen et al. 2001; Lacroix et al. 2004; Welch et al. 2007; Carlsson et al. 2012; Lee et al. 2013). In addition, growth, swimming performance, predator avoidance, and overall survival may be hindered from the surgical implantation process or the increased weight from the implanted tags (Adams et al. 1998; Chittenden et al. 2009; Carlsson et al. 2012). Few studies, though, have examined the effects from the tag and implantation process in conjunction with anesthetic exposure, which is crucial for validating study assumptions and results, especially for large-scale monitoring programs for which anesthetic exposure times are variable for batch-anesthetized fish and can extend beyond Stage 4 induction (loss of equilibrium; Summerfelt and Smith 1990). Regardless of outcome, studies of the effects from tags and implantation processes test model assumptions and improve our understanding of potential performance effects on study fish, which is critical for legally mandated compliance studies.

The stress associated with the surgical implantation process is variable due to factors like species, life stage, fish size, fish health, and transmitter dimensions and weight (Lacroix et al. 2004; Chittenden et al. 2009; Woodley et al. 2011; Ammann et al. 2013). Intracoelomic surgical implantation requires several steps, including the cutting of tissue, insertion of an acoustic transmitter and, in some studies, a passive integrated transponder, and closing the incision (Wagner et al. 2011; Woodley et al. 2011). The implanted device(s) may affect the ability of the fish to completely fill its swim bladder or gastrointestinal system, subsequently affecting buoyancy, ability to navigate, and ultimately growth (Perry et al. 2001; Welch et al. 2007; Larsen et al. 2013). Besides the physical tissue damage and tag burden, the surgical implantation process disrupts the mucus coat and subsequently increases skin permeability and the potential for osmotic imbalance (Shepard 1994; Zydlewski et al. 2010). Poorly opposed incised tissue or insufficient suture tension to close the incision allows for fluid exchange between the coelomic cavity of the fish and the environment (Wagner et al. 2000; Fontenot and Neiffer 2004), resulting in osmotic imbalances similar to that of fish with descaling issues (Zydlewski et al. 2010). To minimize stress and unintentional physical damage during surgical implantation, fish are often anesthetized for surgical procedures using tricaine methanesulfonate (MS-222).

Of the many available anesthetics, MS-222 is the most commonly used chemical anesthetic for fisheries and aquaculture research because the U.S. Food and Drug Administration and the European Union approved its use for food fish (Carter et al. 2011). It elicits an anesthetic state by depressing the central and peripheral nervous systems (Ferreira et al. 1984; Butterworth and Strichartz 1990; Summerfelt and Smith 1990), but the full biochemical process and implications of the effects are not fully understood in fish (Ueta et al. 2007). Unfortunately, MS-222 can act as a stressor during induction and throughout the exposure period. For example, the depression of the central nervous system results in bradycardia, which in turn leads to a decrease of oxygen uptake and a decrease of carbon dioxide excretion causing hypoxemia and concomitantly localized acidosis (Houston et al. 1971; Iwama et al. 1989; Ross and Ross 2008). Also, MS-222 can alter hematological parameters, such as hematocrit and pH and concentrations of glucose, lactate, corticosteroids (e.g., cortisol), amino acids, and electrolytes (e.g., Na+, K+, Ca2+) (Reinitz and Rix 1977; Cho and Heath 2000; Congleton 2006). As stress responses redirect energy away from other physiological processes to meet the metabolic demands of the response, a fish’s behavior and ability to perform may be altered, violating telemetry and survival model assumptions. Physiological responses to MS-222 are highly variable between species and life stages (Carter et al. 2011); thus, it is important to understand the correct administration of MS-222 for a particular species and life stage.

Manufacturer guidelines for MS-222 suggest a maximum tolerated exposure length of 4–12 min (with induction occurring in less than 2–4 min) to MS-222 (80–135 mg/L) for species in the Salmonidae family when held at water temperatures between 7°C and 17°C (Argent Chemical Laboratories 2011), which is largely based on the LC50 (the concentration that is lethal to 50% of the test fish over the first 96 h). Fish should be exposed to the anesthetic for as short of a time as possible; however, the large time frame for safe exposure (i.e., 4–12 min) allows for variability between studies and individual fish, and, consequently, variability in exposure concentration and time may affect a fish’s physiology or performance. During large-scale (e.g., basinwide) monitoring and compliance monitoring programs, like those occurring in the Columbia River basin to evaluate salmonid hydropower facility passage, passage routes, and survival, upwards of 25,000 fish are surgically implanted in an 11-week period (Skalski et al. 2013). These compliance studies document whether a Federal action is likely to jeopardize the continued existence of a species listed under the Endangered Species Act or result in the destruction or adverse modification of the species’ critical habitat. Given the large number of fish handled and implanted with acoustic transmitters, the process must be well documented, controlled, and legally defendable. The surgical implantation process involves batch anesthetization (i.e., several fish at once) in a knockdown dose of MS-222 (80 mg/L); fish are then individually placed in a vessel containing knockdown MS-222; assigned tags, fish condition, weight, and length are noted; fish are photographed and then transported to a surgeon for implantation (Axel et al. 2011). After anesthetic induction, this process ranges from 1 to 4 min (Axel et al. 2011) due to the number of steps and data acquisition programs. Lastly, depending on the surgeon’s experience,
the surgery can take another 1.5–4 min (total process ranging from 4 to 12 min). As indicated, anesthetic exposures and intracoelomic implantation, singularly, can result in stress responses and when coupled may further alter physiology and behavior responses and, consequently, fish survival. Thus, the determination of optimal exposure times specific to surgical implantation would help to inform managers and better address telemetry study assumptions.

Understanding the stress responses from extended exposure to MS-222 and surgical implantation can provide better guidelines as to the length of time that fish can be exposed to the anesthetic to minimize effects on physiological performance or survival. In this study, physiological effects of MS-222 exposure were evaluated immediately following surgical implantation in age-1 Chinook Salmon Oncorhynchus tshawytscha exposed to MS-222 (80 mg/L) for varying times (3, 6, 9, and 12 min) to estimate optimal exposure durations. Additionally, surgical and anesthetic effects on physiology were evaluated during the recovery period (days 1, 7, and 14). Whole blood analyte concentrations (Na\(^+\), K\(^+\), and Ca\(^{2+}\)), whole blood pH, plasma cortisol, and mortality were measured to evaluate primary, secondary, and tertiary stress responses (Barton 2002).

**METHODS**

**Fish acquisition.**—Age-1 Chinook Salmon (body mass = 41.1 ± 9.5 g [mean ± SD]; fork length = 150.0 ± 9.8 mm) were reared at Pacific Northwest National Laboratory Aquatic Research Laboratory facilities (Richland, Washington) from eyed eggs. Fish were housed in 890-L circular fiberglass tanks supplied with aerated well water (15°C) and held on a 12 h light : 12 h dark cycle. Prior to and throughout the experiment, fish were fed BioDiet pellets (Bio-Oregon, Longview, Washington) daily at a rate of 1.3% of the mean body mass. Food was restricted 24 h before the start of the experiment and before postexposure sampling to reduce the strain during anesthetic exposure; however, the fish were not in a state of fasting or starvation and this should not have affected the data collected on day 0. All activities were conducted in accordance with guidelines set by the Institutional Animal Care and Use Committee, a U.S. self-regulating committee (IACUC 2010-08).

**Experimental design.**—The treatments consisted of fish exposed to surgical implantation (herein referred to as “SI”) and one of four MS-222 exposure treatments of 3, 6, 9, or 12 min and then further assigned to one of four postexposure sampling days: 0, 1, 7, or 14. Due to the inherent individual variability of induction time for a fish to reach Stage 4 (approximately 2–4 min; Summerfelt and Smith 1990), the actual mean ± SE time per treatment on day 0 was as follows: 3.5 ± 0.13 min (3 min), 6.5 ± 0.11 min (6 min), 8.8 ± 0.10 min (9 min), and 12.0 ± 0.11 min (12 min). A nonimplanted treatment group (surgical control, herein referred to as “SC”) consisted of fish that were exposed to MS-222 until the loss of equilibrium (3.5 ± 0.13 min). The final sample sizes for each MS-222 exposure treatment and sampling day (day 0, 1, 7, or 14) varied by sample type. Survival samples sizes (given in order of days 0, 1, 7, and 14) were as follows: surgical control (n = not applicable [NA], 5, 5, 5), 3 min (n = 10, 10, 10, 10), 6 min (n = 10, 9, 10, 9), 9 min (n = 10, 10, 10, 9), and 12 min (n = 9, 10, 10, 10); blood analyte sample sizes were as follows: surgical control (n = NA, 4, 3, 4), 3 min (n = 8, 4, 4, 4), 6 min (n = 15, 15, 12, 8), 9 min (n = 11, 13, 6, 5), and 12 min (n = 8, 5, 6, 2); and lastly plasma cortisol sample sizes were as follows: surgical control (n = NA, 5, 5, 6), 3 min (n = 7, 10, 12, 9), 6 min (n = 20, 15, 18, 13), 9 min (n = 12, 14, 10, 15), and 12 min (n = 8, 6, 9, 7).

**Anesthetic treatment and surgical implantation.**—Pretreatment handling was similar across treatments. Simulating large-scale field operations, fish were netted and immediately transferred to an aerated anesthetic bath containing MS-222 (80 mg/L) buffered with NaHCO\(_3\) (80 mg/L) for their allotted time (i.e., 3, 6, 9, or 12 min). All fish, anesthetized to Stage 4 anesthesia, were immediately weighed, measured, and photographed to document gross observable fish condition. The SC fish were placed in fresh aerated water to recover to equilibrium. The SI fish were given a maintenance dose of anesthetic (40 mg/L) during surgical implantation (typically 2–3 min). A 5–7-mm incision was made (Micro-Unitome knife, 3-mm blade; Becton Dickinson and Company, Franklin Lakes, New Jersey) along the linea alba between the pectoral fins and pelvic girdle. A Juvenile Salmon Acoustic Telemetry System acoustic microtransmitter (12 mm long, 5.2 mm wide, 3.8 mm high, and a mass of 0.43 g in air; Advance Telemetry Systems, Isanti, Minnesota) and a passive integrated transponder (Model HPT 12; 12.5 mm long, 2.1 mm wide, and a mass of 0.1 g in air; Destron Technologies, St. Paul, Minnesota) were inserted into the coelomic cavity, and the incision was closed with two simple interrupted sutures using 5-0 Monocryl sutures and a 2 × 2 × 2 × 2 wrap knot pattern. Immediately following surgery, day-0 SI fish were sampled and euthanized with an overdose of MS-222 (250 mg/L), while the remainder of the SI fish recovered in fresh aerated water until equilibrium was reached. The SC and SI fish were assigned to one of three holding tanks based on posttreatment sampling day (day 1, 7, or 14), with each exposure time equally represented in each tank.

**Blood sampling and physiological measurements.**—Blood samples (0.4 mL) were collected from the caudal vein into syringes containing lyophilized sodium heparin, then dispensed into a polypropylene centrifuge tube and held (estimated 5 min) on ice until analysis. An EasyLyte analyzer (Medica Corporation, Bedford, Massachusetts) with internal calibration and temperature adjustment was used to measure blood Na\(^+\), K\(^+\), Ca\(^{2+}\), and pH levels. A single-point external standard verification was used for Na\(^+\), K\(^+\), and Ca\(^{2+}\), and a three-point external standard verification was used for pH. Quality assurance and quality control measures were applied before sampling and throughout the sampling day (every 5th sample or every 30 min). Blood samples were centrifuged at 3,000 g for 10 min.
at 4°C, and the plasma was collected and stored at −80°C for subsequent cortisol analyses.

Plasma cortisol concentrations were determined by competitive plasma cortisol expression enzyme immunoassay following the manufacturer’s protocol (Cayman Chemical Company, Ann Arbor, Michigan). Plasma samples were not purified prior to cortisol analysis as preliminary tests indicated there was little to no interference from contaminants; however, samples that were clotted were removed from analyses. Prior to analysis, plasma samples were diluted 100 fold using enzyme immunoassay buffer, determined by preliminary tests. Plasma samples reading > 80% bound cortisol were diluted 150 fold and retested. Samples were analyzed in triplicate (BioTek PowerWave HT, BioTek Inc.; set at 405 nm) and randomized between plates to minimize interassay variation.

Statistical analyses.—In all analyses, the parametric assumptions of normality and homogeneity of variance were tested. All analyses were conducted at α = 0.05 using JMP statistical software (Version 10.0; Cary, North Carolina). Length and weight were regressed to ensure that they would not be confounding factors when comparing responses between days. There were no significant differences in fish weight among day treatments (all \( P \geq 0.286 \)), allowing the fish to be pooled for the subsequent analyses. A one-way analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) post hoc analysis tested for differences in physiological stress response variables (Na\(^+\), Ca\(^{2+}\), K\(^+\), pH, and cortisol) for each MS-222 time exposure (i.e., 3-, 6-, 9-, and 12-min treatments) on day 0 to determine the physiological effects of MS-222 exposure on SI fish. A two-way ANOVA followed by Tukey’s HSD test was to examine the physiological stress responses between SC and 3-min-treatment SI fish and across days (days 1, 7, and 14). Lastly, differences in physiological stress responses between MS-222 time exposure treatments (i.e., 3, 6, 9, and 12 min) and across days (days 1, 7, and 14) were examined using a two-way ANOVA followed by Tukey’s HSD.

RESULTS

Physiological Responses to MS-222 Exposure, Day 0

Physiological stress responses were compared between MS-222 exposure treatments (3, 6, 9, and 12 min) immediately following surgical implantation to determine how MS-222 alters the physiology and to estimate an appropriate anesthetic time exposure limit for surgically implanted juvenile Chinook Salmon (Figure 1). The levels of Na\(^+\) (ANOVA: \( F_{3, 36} = 31.93, P < 0.0001 \)) and Ca\(^{2+}\) (ANOVA: \( F_{3, 36} = 10.57, P < 0.0001 \)) were significantly higher in the 9-min and 12-min treatments than in the 3-min and 6-min treatments (all \( P < 0.005 \)). Inversely, K\(^+\) (ANOVA: \( F_{3, 36} = 14.72, P < 0.0001 \)) was significantly lower in the 9-min and 12-min treatments than in the 3-min and 6-min treatments (all \( P < 0.005 \)). There was no significant difference between MS-222 exposure treatments for pH (ANOVA: \( F_{3, 36} = 2.77, P = 0.0554 \)) or cortisol (ANOVA: \( F_{3, 43} = 0.63, P = 0.60 \)).

Effects of Surgical Implantation over Recovery Period

Stress responses were compared between SC and SI fish across days 1, 7, and 14 to determine if surgical implantation affected stress responses (Figure 2). There was not a significant interaction or main effect between SC and SI fish or across days for Na\(^+\), Ca\(^{2+}\), and pH (all \( P > 0.05 \); Table 1). The level of Ca\(^{2+}\) significantly varied over time (\( P < 0.0001 \)) but not by treatment (Table 1). Post hoc analysis indicated Ca\(^{2+}\) was significantly lower on days 7 and 14 than on day 1 (all \( P < 0.05 \)). Cortisol levels significantly varied over the recovery period (\( P = 0.0075 \)) and were significantly higher in the SI treatment than in the SC treatment (\( P = 0.0035 \); Table 1). Post hoc analyses indicated that cortisol was significantly higher on day 14 than on days 1 and 7 (all \( P < 0.05 \)), and cortisol levels were similar between days 1 and 7 (\( P > 0.05 \)).

Effects of MS-222 Exposure over Recovery Period

Stress responses were compared between MS-222 time exposure treatments (3, 6, 9, and 12 min) to determine how anesthetic exposure affects fish on the day of release and thereafter (Figure 3). There were no significant interactions (all \( P > 0.05 \); Table 2) between exposure treatments and days for Na\(^+\) and pH. The values of K\(^+\) (\( P = 0.0035 \)) and Ca\(^{2+}\) (\( P < 0.0001 \))

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Table 1. Two-way ANOVA results for stress response comparisons between age-1 Chinook Salmon exposed to MS-222 but with no surgical implantation and surgically implanted fish (exposed to MS-222 for 3 min) over the recovery period (days 1, 7, and 14); SS = sum of squares.

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Na(^+)</td>
<td>Treatment</td>
<td>1</td>
<td>197.30</td>
<td>0.79</td>
</tr>
<tr>
<td>Day</td>
<td>2</td>
<td>1,310.57</td>
<td>2.64</td>
<td>0.383</td>
</tr>
<tr>
<td>Treatment × day</td>
<td>2</td>
<td>281.93</td>
<td>0.57</td>
<td>0.576</td>
</tr>
<tr>
<td>Ca(^{2+})</td>
<td>Treatment</td>
<td>1</td>
<td>0.03</td>
<td>0.33</td>
</tr>
<tr>
<td>Day</td>
<td>2</td>
<td>10.45</td>
<td>63.66</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Treatment × day</td>
<td>2</td>
<td>0.03</td>
<td>0.21</td>
<td>0.81</td>
</tr>
<tr>
<td>K(^+)</td>
<td>Treatment</td>
<td>1</td>
<td>1.48</td>
<td>0.80</td>
</tr>
<tr>
<td>Day</td>
<td>2</td>
<td>3.99</td>
<td>1.08</td>
<td>0.36</td>
</tr>
<tr>
<td>Treatment × day</td>
<td>2</td>
<td>0.72</td>
<td>1.84</td>
<td>0.82</td>
</tr>
<tr>
<td>pH</td>
<td>Treatment</td>
<td>1</td>
<td>0.00042</td>
<td>0.35</td>
</tr>
<tr>
<td>Day</td>
<td>2</td>
<td>0.0077</td>
<td>3.24</td>
<td>0.06</td>
</tr>
<tr>
<td>Treatment × day</td>
<td>2</td>
<td>0.0019</td>
<td>0.79</td>
<td>0.47</td>
</tr>
<tr>
<td>Cortisol</td>
<td>Treatment</td>
<td>1</td>
<td>14,945.32</td>
<td>9.60</td>
</tr>
<tr>
<td>Day</td>
<td>2</td>
<td>17,280.80</td>
<td>5.55</td>
<td>0.0075</td>
</tr>
<tr>
<td>Treatment × day</td>
<td>2</td>
<td>1,440.71</td>
<td>0.46</td>
<td>0.63</td>
</tr>
</tbody>
</table>
FIGURE 1. Mean (error bars indicate SE) whole blood analyte (Na\(^+\), K\(^+\), Ca\(^{2+}\)) concentrations, pH, and plasma cortisol concentrations in age-1 Chinook Salmon immediately following intracoelomic implantation for four MS-222 time exposures: 3, 6, 9, and 12 min. Time exposures were binned every 3 min due to the variability in Stage 4 induction times. Different letters indicate significant differences between MS-222 time exposure bins.
FIGURE 2. Mean (error bars indicate SE) whole blood analyte (Na\(^{+}\), K\(^{+}\), Ca\(^{2+}\)) concentrations, pH, and plasma cortisol concentrations in age-1 Chinook Salmon exposed to MS-222 but with no surgical implantation (SC; solid circles) and fish that underwent surgical implantation (SI; 3-min MS-222 treatment; open circles) over the recovery period (days 1, 7, and 14). Fish were exposed to MS-222 until Stage 4 induction. Asterisks indicate significant differences between SC and SI fish, and different uppercase letters indicate significant differences between observation days.
FIGURE 3. Mean (error bars indicate SE) whole blood analyte (Na\(^{+}\), K\(^{+}\), Ca\(^{2+}\)) concentrations, pH, and plasma cortisol concentrations over time (days 1, 7, and 14) in age-1 Chinook Salmon that underwent surgical implantation and were exposed to MS-222 for 3, 6, 9, or 12 min. Different uppercase letters indicate significant differences between observation days.
**DISCUSSION**

Although intracoelomic implantation is invasive, anesthetics, such as MS-222, are routinely used to immobilize the fish and reduce stress; however, anesthetics can also act as stressors (Carter et al. 2011). Understanding how the physiological condition (i.e., blood analytes, pH, and cortisol) of the fish is affected by surgical implantation and exposure to MS-222 is essential in validating the assumptions associated with telemetry studies (Peven et al. 2005) and setting proper anesthetic exposure guidelines (Axel et al. 2011). This study found that the 9- and 12-min MS-222 exposures resulted in significant physiological responses for surgically implanted juvenile Chinook Salmon, but the responses did not persist through the recovery period. Additionally, fish exposed to surgical implantation had significantly greater cortisol levels than the SC fish during the recovery period.

Comparisons of analyte concentrations between MS-222 time exposure treatments immediately following surgical implantation (day 0) indicated that Na\(^+\) and Ca\(^{2+}\) significantly increased and K\(^+\) significantly decreased following the 9- and 12-min exposure treatments. While the mechanism of MS-222 is not fully understood, it is known that MS-222 acts as a general anesthetic and it is thought to be effective at blocking nerve conduction by inhibiting voltage-sensitive Na\(^+\) channels of the central and peripheral nervous systems (Neumcke et al. 1981; Arnold et al. 2002; Ueta et al. 2007). Thus, extracellular Na\(^+\) and Ca\(^{2+}\) were expected to increase and K\(^+\) was expected to decrease in fish exposed to MS-222 (Sladky et al. 2001). Although MS-222 guidelines suggest that salmonids can safely remain in MS-222 (80–135 mg/L) for up to 12 min (Argent Chemical Laboratories 2011), significant blood chemistry alterations occurred in surgically implanted juvenile Chinook Salmon when exposed to MS-222 for 9 min or longer.

Regardless of surgical treatment or MS-222 time exposure, blood analyte concentrations and pH patterns were similar over the recovery period. There were no significant differences in blood analyte concentrations or pH patterns over the recovery period between SC and SI fish (3-min exposure) or between MS-222 time exposure treatments. Similar analyte and pH results between SC and SI fish suggests that the incisions were properly closed and, accordingly, the internal milieu of the fish was not compromised by the exchange of fluids with the external environment (Fontenot and Neiffer 2004). When examining analyte concentrations and pH across the recovery period for SC and SI fish, analytes were more variable on day 1 than on days 7 and 14; however, significant results were seen for K\(^+\) and Ca\(^{2+}\). The level of K\(^+\) was significantly lower on day 7 than on days 1 and 14, and Ca\(^{2+}\) was significantly higher on day 1 than on days 7 and 14. Analyte and pH patterns suggest that SC and SI fish were still in recovery on day 1 but had recovered from surgical and anesthetic stress by day 7. A similar trend was observed in Rainbow Trout Oncorhynchus mykiss that regained acid–base balance by 24–48 h postsurgery (Iwama et al. 1987).

Besides altering extracellular hematological components, immobilizing doses of MS-222 and surgical implantation have been demonstrated to alter cortisol levels (Iwama et al. 1989; Mommsen et al. 1999; Jepsen et al. 2001). In the present study, immediately following surgical implantation (day 0) there was a nonsignificant increase in cortisol levels as MS-222 exposure time increased, which may have a potential biological significance. The observed cortisol increase indicates that there was allocation of metabolic energy towards a stress response, which may have translated into reduced secondary effects (e.g., immune system functioning) or short-term tertiary effects (e.g., swimming performance), yet likely not profound enough to affect long-term growth and survival (Mommsen et al. 1999; Barton 2002; Portz et al. 2006).

While basal cortisol levels are variable in fish (2–42 ng/mL; Gamperl et al. 1994), cortisol begins to increase quickly in the blood as demonstrated in Coho Salmon _O. kisutch_.

**TABLE 2.** Two-way ANOVA results for stress response comparisons between MS-222 time exposure treatments (3, 6, 9, and 12 min) for surgically implanted age-1 Chinook Salmon over the recovery period (days 1, 7, and 14); SS = sum of squares.

<table>
<thead>
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<th>Variable</th>
<th>df</th>
<th>SS</th>
<th>F</th>
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</thead>
<tbody>
<tr>
<td>Na(^+)</td>
<td>Treatment</td>
<td>3</td>
<td>953.37</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>2</td>
<td>1,283.49</td>
<td>1.74</td>
</tr>
<tr>
<td></td>
<td>Treatment × day</td>
<td>6</td>
<td>1,023.95</td>
<td>0.46</td>
</tr>
<tr>
<td>Ca(^{2+})</td>
<td>Treatment</td>
<td>3</td>
<td>0.15</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>2</td>
<td>24.00</td>
<td>98.69</td>
</tr>
<tr>
<td></td>
<td>Treatment × day</td>
<td>6</td>
<td>0.34</td>
<td>0.47</td>
</tr>
<tr>
<td>K(^+)</td>
<td>Treatment</td>
<td>3</td>
<td>8.49</td>
<td>1.76</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>2</td>
<td>19.63</td>
<td>6.09</td>
</tr>
<tr>
<td></td>
<td>Treatment × day</td>
<td>6</td>
<td>9.32</td>
<td>0.96</td>
</tr>
<tr>
<td>pH</td>
<td>Treatment</td>
<td>3</td>
<td>0.009</td>
<td>2.07</td>
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<tr>
<td></td>
<td>Day</td>
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<td>0.010</td>
<td>3.59</td>
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<tr>
<td></td>
<td>Treatment × day</td>
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<td>6.32</td>
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<tr>
<td>Cortisol</td>
<td>Treatment</td>
<td>3</td>
<td>3,553.84</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>2</td>
<td>34,033.18</td>
<td>9.87</td>
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<tr>
<td></td>
<td>Treatment × day</td>
<td>6</td>
<td>17,565.11</td>
<td>1.70</td>
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</table>
following 8 min of confinement stress (Sumpter et al. 1986). Similar to the results seen in this study, Wedemeyer (1970) did not detect a cortisol response for Rainbow Trout following 12 min of MS-222 exposure at a similar concentration (i.e., loss of equilibrium in 3–5 min). In addition, MS-222 doses of 100 mg/L have been shown to be effective at mitigating the cortisol response throughout induction (Iwama et al. 1989); however, at doses of 50 mg/L the cortisol response is delayed, as seen in juvenile Chinook Salmon undergoing gastric tag implantation (Jepsen et al. 2001). While there was not an immediate significant increase in cortisol in this study, it is undeterminable if the response was delayed or completely dampened, as the elevated response seen during the recovery period may be a response to healing or smoltification and not to the surgical process.

Though there was no significant cortisol response observed immediately following surgical implantation and extended MS-222 exposure, cortisol was significantly elevated by day 14 for all fish exposed to MS-222. Across all recovery days, cortisol was significantly reduced for SC fish, suggesting that surgical implantation amplifies stress responses, which are still present 14 d after implantation. Conversely, cortisol levels for surgically implanted Chinook Salmon smolts (fork length = 170–200 mm) returned to normal by 7 d after implantation (Jepsen et al. 2001). Given that cortisol levels for both the SC and SI treatments (all time exposure treatments) significantly increased from day 1 to day 14, the increase may not be solely attributed to MS-222 exposure or surgical implantation but could also be a result of holding stress and other health-related issues, such as disease (Portz et al. 2006), although disease symptoms were not noted. While fish in this study demonstrated primary and secondary stress responses as a result of MS-222 exposure and intracoelomic surgical implantation, stress did not lead to mortality (tertiary response).

In our study, prolonged anesthetic exposures coupled with intracoelomic surgical implantation did not yield mortalities; however, field studies have indicated mortalities 24 h after surgical implantation (Woodley et al. 2011; Skalski et al. 2013). Based on the manufacturer’s recommendations, there is an indication that there is a relationship between mortality and prolonged MS-222 exposure; however, time exposures in this study were within the safe operating guidelines (Argent Chemical Laboratories 2011). Also, MS-222 (100 mg/L) was reported to be lethal to juvenile Chinook Salmon following a 30-min exposure (Strange and Schreck 1978), and Rainbow Trout fingerlings demonstrated 80% mortality following a 15-min exposure at a concentration of 80 mg/L (Gilderhus and Marking 1987). Although stress associated with anesthetic exposure and surgical implantation was not lethal in this study, this may not be the case for salmonids undergoing smoltification or other stressful conditions as seen in field studies.

In summary, the 9- and 12-min MS-222 (80 mg/L) exposures resulted in significant osmotic imbalances immediately following surgical implantation. While MS-222 appeared to be effective at dampening the cortisol response immediately following surgery, there was a nonsignificant increase in cortisol as MS-222 exposure time increased, which may be of biological significance. Despite the effectiveness of MS-222 immediately following implantation, surgical implantation significantly affects the physiology of a fish for up to 14 d after surgery, as seen with increased cortisol. Additionally, although not significant, the increased variability in blood analytes suggests that fish are still recovering on day 1 postsurgery, at which time surgically implanted fish are usually released in river for survival studies. As more and more studies utilize acoustic technology to guide mitigation decisions, additional research needs to be conducted to better determine the effects of the surgical process on salmonids and to better determine when fish should be released in river to more accurately represent untagged in-river fish. Studies like this are important for understanding how the surgical process and associated handling procedures can affect the “normal” physiological state of the fish and thus the behavioral and physiological changes that can be expected after the fish are released.

ACKNOWLEDGMENTS

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REFERENCES


