A Prototype Splitter Apparatus for Dividing Large Catches of Small Fish

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A Prototype Splitter Apparatus for Dividing Large Catches of Small Fish

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Abstract
Due to financial and time constraints, it is often necessary in fisheries studies to divide large samples of fish and estimate total catch from the subsample. The subsampling procedure may involve potential human biases or may be difficult to perform in rough conditions. We present a prototype gravity-fed splitter apparatus for dividing large samples of small fish (30–100 mm TL). The apparatus features a tapered hopper with a sliding and removable shutter. The apparatus provides a comparatively stable platform for objectively obtaining subsamples, and it can be modified to accommodate different sizes of fish and different sample volumes. The apparatus is easy to build, inexpensive, and convenient to use in the field. To illustrate the performance of the apparatus, we divided three samples (total \( N = 2,000 \) fish) composed of four fish species. Our results indicated no significant bias in estimating either the number or proportion of each species from the subsample. Use of this apparatus or a similar apparatus can help to standardize subsampling procedures in large surveys of fish. The apparatus could be used for other applications that require dividing a large amount of material into one or more smaller subsamples.

Due to time or budgetary constraints, it is often necessary in biological surveys to divide large volumes of material or large numbers of organisms collected during a sampling event and to estimate abundances based on the subsample. For any such procedure to be effective, the portion that is to be assessed (i.e., the subsample) must be representative of the entire sample. Many of the problems associated with obtaining a subsample can be avoided with the use of an appropriate “splitter” apparatus, which eliminates, among other factors, human biases (Winner and McMichael 1997). For aquatic systems, several splitter devices have been developed to (1) subdivide volumes of water for the estimation of plankton (Cushing 1961; Hopkins 1962), nekton (Hightower et al. 1976), and fish (Winner and McMichael 1997) abundances; and (2) subdivide volumes of substrate to estimate benthic macroinvertebrate abundances (e.g., Hickley 1975). However, we were not able to find any published description of devices for dividing large catches of fish that have been removed from the water.

In large catches of fish from trawl tows and seines, large-sized and rare species are typically removed before the subsample is taken and are assessed separately (e.g., O’Gorman et al. 2000). One common method of obtaining subsamples involves mixing the fish in a large box or tub and then, based on visual inspection, removing a volume of fish that can be counted in a timely fashion. For example, O’Gorman et al. (2000) took “random” shovelfuls of fish as the catch was being shoveled off the deck. Alternatively, the sample can be divided one or more times. The division process can be accomplished in several ways, such as by pouring the catch directly over the junction of two adjacent tubs (C. Madenjian, U.S. Geological Survey [USGS], personal communication). A longitudinally split piece of polyvinyl chloride pipe is sometimes placed over the junction to prevent fish from accumulating in the seam between the tubs. After each “split,” researchers determine at random (e.g., by flipping a coin) which portion is to be designated as the subsample (or divided again). In many published studies (e.g., Bacheler et al. 2011), however, the method of obtaining the subsample is not mentioned. Typically, the total number of individuals of each species in the total sample is estimated by multiplying the number of fish in the subsample by the ratio of the mass (or volume) of the total sample to the mass (or volume) of the subsample. Removal of a “random” volume by eye, including the method described by O’Gorman et al. (2000), has the potential for bias by the person obtaining the subsample (Winner and McMichael 1997). For example, the scientist may tend to over-represent large or colorful fish in the subsample when manually scooping fish from tubs or off the deck, either by hand or with a tool. Dividing the catch by pouring it over adjacent tubs can be cumbersome and is difficult to perform with precision in rough conditions.

In large-scale fish surveys (e.g., in the Laurentian Great Lakes), cooperating agencies perform trawl tows for annual...
lakewide or regionwide stock assessments (e.g., FTG 2011). Subsamples from these tows are often taken to estimate total catch. However, the subsampling procedure often varies among agencies and even among field crews (M. Stapanian, personal observation; J. Schaeffer, USGS, Ann Arbor, Michigan, personal communication). Therefore, a more standardized methodology for obtaining subsamples is desirable and could make these stock assessments more rigorous.

We present a prototype gravity-fed splitter apparatus for dividing large samples of small fish (30–100 mm TL). The apparatus features a hopper that has a removable shutter, which allows the sample to be divided at the researcher’s convenience. Our goal is to present an apparatus that is inexpensive, is easy to build, and provides an objective and convenient method for obtaining subsamples. We also provide an example of the performance of the apparatus by using a sample containing four species and a known number of fish.

METHODS

Apparatus description.—Our prototype was built with white pine (1.9 cm [0.75 in] thick) and outdoor-grade plywood (Figure 1; Table 1). The main components are the hopper, removable shutter, splitter surfaces, guides, and support members. The dimensions of our apparatus were selected to accommodate the range of fish sizes that are typically caught in bottom trawl surveys of western Lake Erie during autumn (Stapanian et al. 2007, 2009; Kocovsky et al. 2011).

The hopper is centered directly above the apex of the splitter surfaces. The front (Figure 1, A) and back (Figure 1, B) of the hopper are wider at the top than at the bottom, which effectively funnels the fish toward the apex of the splitter surfaces. These features ensure that when the apparatus is properly used, volumes of fish are divided into two nearly equal portions as they fall out of the hopper. The sides of the hopper (Figure 1, C) are joined with wood screws to the front and back. To enable the shutter (Figure 1, D) to slide in and out, the front of the hopper is cut about 1.5 cm shorter at the bottom than the back and sides of the hopper. The shutter fits into a 1.77-cm-wide × 0.64-cm-deep dado groove that is cut about 0.6 cm from the bottom of the sides and back of the hopper. The shutter slides within the dado and between the front vertical supports (Figure 1, E). When the shutter is fully inserted, it protrudes approximately 10 cm out from the front of the hopper. The guides (Figure 1, F) help to channel the fish down the splitter surfaces (Figure 1, G). The guides are attached to the splitter surfaces by wood screws. The top edges of the two splitter surfaces are cut at a 12.5° angle and are joined with epoxy glue to form an apex. The frame of the apparatus consists of vertical (Figure 1, E and H) and horizontal (Figure 1, I and J) supports that join the hopper to the splitter surfaces. These components are attached to the hopper with wood screws. All screws are countersunk. All surfaces of the apparatus are finished with three coats of an outdoor-grade polyurethane varnish. Finally, all surfaces that come into contact with the fish are coated with a layer of wax.

Recommended field procedure.—When in use, the apparatus straddles two tubs or fish boxes, with the bottom edge of each splitter surface resting in one of the tubs. The shutter is fully inserted. Fish are then poured into the hopper and arranged so that the volume is level at the top. At the researcher’s convenience, the shutter is removed by sliding it out completely. The fish then fall out of the hopper, and the sample is divided into two nearly equal portions. The researcher then determines at random (e.g., flips a coin) which portion is to be either counted or divided again. If the sample is to be divided further, we recommend the following sequence. First, fully re-insert the shutter. Second, mix the portion to be divided again, pour it into the hopper, and arrange as before. The subsample or portion to be
divided yet again will fall into the same tub as before, which is now empty of fish. Third, pull out the shutter. Repeat the procedure as needed. The deck is kept orderly with this procedure because the fish that are not to be counted are always in one tub, whereas the subsample (or portion to be divided further) always falls into the other (empty) tub. Finally, the subsample and remaining portion are weighed separately and the fish in the subsample are counted.

**Example of apparatus performance.**—We used the apparatus to divide a known number of individuals \((N = 2,000)\) representing four fish species that are commonly caught in bottom trawl tows in western Lake Erie: age-0 emerald shiners *Notropis atherinoides* (60% of total sample; \(n = 1,200\)), age-0 white perch *Morone americana* (25%; \(n = 500\)), trout-perch *Percopsis omiscomaycus* (10%; \(n = 200\)), and round goby *Neogobius melanostomus* (5%; \(n = 100\)). The hopper was approximately half-full with the 2,000 fish used in this example. For convenience, we combined age-classes of trout-perch and round goby. The trout-perch included a mixture of yearlings and older fish (50%) and age-0 fish (50%). The round goby were also of mixed age, but all were between 70 and 110 mm TL. Age was estimated from growth schedules for these species in western Lake Erie (C. Knight, Ohio Department of Natural Resources, Fairport, personal communication).

Due to time and budgetary constraints, the experiment was performed in the laboratory. A goal was to test the apparatus first in the laboratory so that we could have confidence in its performance (and not waste valuable time estimating error) in the field. All fish had been captured in bottom trawl tows that were conducted in western Lake Erie during autumn 2010. The fish were frozen shortly after capture and were thawed prior to the experiment. Three replicates were performed. In each replicate, the entire sample was thoroughly mixed and then placed into the hopper with the shutter fully inserted. The fish were arranged so that the sample visually appeared to be level with respect to the top of the hopper. The shutter was then removed, and the fish were subsequently divided into approximately equal portions on the two sides. The mass of each portion was measured. By a flip of a coin, one of the portions (the subsample) was selected for assessment. The number of individuals of each species in the subsample was then counted, and the proportion of the subsample comprising each species was calculated. For a given species, we calculated the predicted number of fish in the total sample based on the ratio of the total sample mass to the subsample mass. More formally, for the \(i\)th species in subsample \(j\), the predicted number \((n_i)\) for the total sample was calculated as

\[
 n_i = n_{ij}(m_j + m_k)/m_j, \tag{1}
\]

where \(n_{ij}\) = number of individuals of species \(i\) that were counted in subsample \(j\); \(m_j\) = mass of fish in the subsample; and \(m_k\) = mass of fish in the uncounted portion of the sample.

For each species, we then calculated the proportion error of the predicted value by comparing it with the known number of individuals in the total sample as

\[
 EN_i = (n_i - N_i)/N_i, \tag{2}
\]

where \(N_i\) = the known number of individuals of species \(i\) that were present in the total sample. We also calculated the error in the proportion of the subsample comprised by each species in comparison with the species’ known proportion in the total sample as

\[
 EP_i = [n_{ij}/(\text{total number of fish counted in the subsample})] - P_i, \tag{3}
\]

where \(P_i\) = the known proportion of species \(i\) in the total sample. Negative values of \(EN_i\) and \(EP_i\) indicated underestimates, whereas positive values indicated overestimates. Finally, we calculated 95% CIs for \(EN_i\) and \(EP_i\).
FIGURE 2. Means (±95% CI) of errors in estimating total number of individuals (upper panel) and proportions (lower panel) of four fish species from three replicates of single-split subsamples (each total sample = 2,000 fish) obtained by use of the prototype splitter apparatus. For each species (es = emerald shiner; wp = white perch; tp = trout-perch; rg = round goby), the number above the CI indicates the true value.

RESULTS

The means of $\text{EN}_i$ ranged from $-0.109$ (emerald shiner) to $-0.004$ (trout-perch; Figure 2). Means of $\text{EN}_i$ for trout-perch and round goby were $-0.022$ and $-0.030$, respectively. Thus, for three of the four species, the absolute value of the average error for estimating the number of individuals was less than or equal to 3%. Although all mean values of $\text{EN}_i$ were negative, suggesting underestimation of the number of individuals, the means were not significantly different from zero, as evidenced by the 95% CIs. This result indicated that there were no significant biases in estimating the number of individuals for any of the four species.

The means of $\text{EP}_i$ ranged from $-0.011$ (emerald shiner) to $0.01$ (trout-perch; Figure 2). Therefore, the absolute values of the average errors in estimating proportions of each species were less than or equal to 1.1%. The 95% CIs for mean $\text{EP}_i$ overlapped zero for all species, indicating no significant biases in estimating the proportion of each species from the subsample.

DISCUSSION

Overall, the splitter apparatus performed well in our experiment, as evidenced by the low average absolute values of $\text{EP}_i$ ($\leq 1.1\%$) for all four species and $\text{EN}_i$ ($\leq 3\%$) for three species. None of the mean errors was significantly different from zero. However, the somewhat larger errors in estimating numbers were expected. There were major two sources of error for estimating number: (1) in the count, which was dependent on how homogeneously the sample was mixed, and (2) in the ratio of the total sample mass to the subsample mass. In contrast, the count constituted the only major source of error in estimating proportions. The ratio of masses was influenced by several factors, including evaporation and distribution of the water in the sample. As shown below, these problems are not inherent in the apparatus but instead are due to the methods with which total numbers were calculated and to the characteristics of the species used in the example.

Although not significantly different from zero, the average $\text{EN}_i$ for emerald shiners was more than three times greater than the average values for the other species considered. Based on average mass at age for the species used in our example, which were captured in western Lake Erie during fall (P. Kocovsky, USGS, Sandusky, Ohio, personal communication), emerald shiners (1.63 g) comprised only about 27% of the total biomass of the sample but 60% of the total number of fish. In contrast, white perch (6.86 g) accounted for 25% of the total number of fish but about 48% of the total mass. Trout-perch (5.38 g) and round goby (6.93 g) accounted for about 15% and 10%, respectively, of the total mass. Therefore, the estimated proportion of total mass for the emerald shiner was less than half of this species’ proportion of the total number of fish, whereas the proportions of the total mass for white perch and round goby were about twice their respective proportions of the total number of fish. This factor, combined with the tendency of emerald shiners to adhere to other fish in the sample, suggests that emerald shiners did not mix as uniformly in the total sample volume as the other species. To reduce adherence, we recommend that samples containing emerald shiners or species with similar characteristics be thoroughly rinsed before the samples are divided. Our results also indicate that researchers should exercise caution when estimating numbers of fish from subsamples by using the ratio of mass, particularly when there are large differences in the relative proportions of mass and number among the species in the sample.

The hopper of our apparatus is able to accommodate multispecies samples of approximately 4,000 fish at one time for fish with an average TL of 30–100 mm. The standing height of the apparatus (89 cm) is such that pouring 11.4-L (3-gal) buckets of fish into the hopper is reasonably comfortable for
an average-sized adult human. As mentioned, the dimensions of our apparatus reflect the fish lengths and catch sizes that are commonly encountered in USGS bottom trawl samples in western Lake Erie. However, the apparatus can be modified to accommodate a wide variety of sample characteristics and field conditions. In particular, the dimensions of the hopper can be modified to accommodate the expected catch size and fish body size. We recommend that the distance between the bottom of the hopper and the apex of the splitter surfaces be greater than the average expected TL of the largest species in the hopper. These restrictions ensure that as the fish fall out of the hopper, they flow freely over the splitter surfaces and into the tubs.

The efficacy of any subsampling procedure relies on the characteristics of the sample and how uniformly the sample is mixed before the subsample is obtained. The catch in each bottom trawl sample has its own unique characteristics. For example, we have found that very small fish accumulate at the bottom of tubs and boxes shortly after the cod end of a trawl is emptied therein (M. Stapanian, personal observation; O. Gorman, USGS, Ashland, Wisconsin, personal communication). Furthermore, we have found that some species (e.g., emerald shiner) that are caught during our bottom trawl surveys tend to adhere to other fish, making them more difficult to assess. We submit that these problems are inherent in the characteristics of the samples but not the apparatus. As mentioned, to reduce these effects we recommend rinsing and mixing the sample thoroughly before putting it into the hopper. The hopper in our apparatus is narrower at the bottom, which should reduce potential biases due to uneven distribution of fish from the top to the bottom of the sample.

Our example indicates that the apparatus yields precise results overall. We used fairly small samples of thawed fish (N = 2,000), and we divided the sample only once. Although each sample collected in the field has unique characteristics (e.g., species composition and size structure), our results should reflect those expected from our bottom trawl tows. In practice, a sample can be divided into whichever fraction is practical to assess. Researchers should exercise caution when determining how many times to divide the sample. Although smaller subsamples can be examined more quickly, the errors in estimating total numbers and proportions in a sample containing several species typically increase with smaller subsamples—a function of the binomial expansion.

Our apparatus is not limited to obtaining subsamples of fish. The apparatus could also be used for any other research or industrial application that requires dividing a large amount of material into one or more smaller subsamples. For example, the apparatus can be used to obtain subsamples of large amounts of grain to determine the extent of crop damage due to insects or can be used in industrial processes for quality assurance or quality control. In previous experiments (M. Stapanian, unpublished data), the apparatus divided samples of comparatively homogeneous materials (e.g., charcoal briquettes) and consistently provided subsamples that estimated the total number with less than 2% error.

Our prototype splitter apparatus was made of wood and outdoor-grade plywood, required approximately 3 h for construction by an experienced woodworker, and cost approximately US$30 in materials. Marine-grade plywood, although more expensive than outdoor-grade plywood, is recommended for marine and estuarine use. However, the apparatus can easily be constructed of aluminum or stainless steel, which would probably better withstand heavy, prolonged use. If wood is used, we recommend sealing all seams with a waterproof caulk and using wood screws made of either stainless steel or brass.

Our goal was to present this apparatus as an objective and convenient method for obtaining subsamples of catches. The questions of when and how much to subsample and how much error is acceptable may be species specific; further study to explore these issues is recommended, and our apparatus may represent an objective field tool for addressing these questions. As mentioned, the subsampling procedure in regionwide, interagency stock assessments often varies among agencies and even among field crews (M. Stapanian, personal observation; J. Schaeffer, USGS, personal communication). Use of this apparatus or a similar apparatus in large-scale fish surveys would provide a more standard methodology and may in turn increase the rigor of stock assessments.

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Largemouth Bass Predation Effect on Stocked Walleye Survival in Illinois Impoundments


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ARTICLE

Largemouth Bass Predation Effect on Stocked Walleye Survival in Illinois Impoundments

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Abstract
Survival of stocked fish can be mediated by biotic factors such as size and species, predators, and prey, and abiotic influences such as temperature and habitat. Walleyes Sander vitreus are numerically among the most stocked fish in the USA, yet stocking success of this species is highly variable. We examined the effects of predation by largemouth bass Micropterus salmoides on walleyes across 77 stocking events in 10 Illinois impoundments. Predation mortality was assessed by examining diets of largemouth bass for up to 21 d post walleye stocking. Of 8,591 largemouth bass diets examined, 2.0% contained walleye, corresponding to 4.3% walleye mortality attributable to largemouth bass predation. Largemouth bass predation was greatest within 24 h of stocking, and no predation was observed after 14 d. Predation mortality and fall CPUE of walleyes were related to largemouth bass density; however, we found no relationship between predation mortality and fall CPUE of walleyes. Our results suggest that predation by largemouth bass, a widespread and abundant predator, has a negligible effect on walleye stocking success in Illinois impoundments.

Stocking is an important management tool for maintaining recreational fisheries and for replenishing declining populations of native species. For instance, over 109 walleye Sander vitreus were stocked into 34 U.S. states in 2004 (Halverson 2008), including 25 million walleye stocked into Illinois lakes by the Illinois Department of Natural Resources (unpublished data). Hatchery production is an expensive process, and depending on species, stocking size, and stocking environment, stocking small fish allowed to grow to harvestable size in the wild, or stocking larger fish that have been reared longer in captivity may maximize the tradeoff between relative survival and production cost (Santucci and Wahl 1993; Santucci et al. 1994; Brooks et al. 2002). Species-specific and lake-specific information on relative poststocking survival is therefore needed to inform stocking and management decisions.

Many factors can influence survival of stocked fish, including population structure of both prey and predators. Density and size of prey can affect growth and survival of stocked fish (Carline

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et al. 1986; Wahl et al. 1995; Kolar et al. 2003; Hoxmeier et al. 2004; Fayram et al. 2005; Hoxmeier et al. 2006). When fish are initially stocked into a system, they may become easy prey for predators due to disorientation and stress. Most hatcheries rear fish in plain concrete tanks or ponds, although fish reared in enriched tanks may have higher poststocking feeding and survival rates (Salvanes and Braithwaite 2006; Strand et al. 2010). Moreover, fish are often stocked at one location in a lake (e.g., a boat ramp) and may have limited dispersal from this site, thus potentially creating artificially high densities of naïve prey and increasing predator feeding efficiency (Parsons and Pereira 1997; Buckmeier and Betsill 2002). Stocked fish may therefore be more vulnerable to predation than natural populations, with highest predation effects within 30 d of stocking (Carlne et al. 1986; Wahl and Stein 1989).

Predation on stocked fish is highly variable and may depend on the species and size of fish stocked, as well as predator community composition and size structure (Fayram et al. 2005; Hoxmeier et al. 2006). Spiny-rayed fishes are less vulnerable to predation than soft-rayed species (Wahl 1995; Einfalt and Wahl 1997; Sass et al. 2006). Species such as walleye (Laarman 1978; Santucci and Wahl 1993; Wahl 1995; Fayram et al. 2005), saugeye (sauger S. canadensis × walleye; Stahl et al. 1996), and largemouth bass Micropterus salmoides (Miranda and Hubbard 1994; Diana and Wahl 2009) thus have lower predation mortality than esocids (Carlne et al. 1986; Wahl and Stein 1989; Wahl 1995) and salmonids (Cartwright et al. 1998; Hyvärinen and Vehanen 2004). Likewise, larger size at stocking has generally been linked to higher survival for a number of species (e.g., Laarman 1978; Santucci et al. 1994; Fayram et al. 2005; Diana and Wahl 2009), although some studies of walleye have found that environmental and biological conditions of stocked lakes can be more important than size at stocking (Laarman 1978; Hoxmeier et al. 2006). Size-selective mortality is linked to effective predator density (i.e., the number of potential predators capable of consuming the prey; Carlne et al. 1986). Hence, larger size at stocking can reduce the effective predator density and, thus, predation pressure, even while total predator density remains constant.

The relative importance of predation mortality in mediating walleye stocking success is not well understood. While numerous studies have examined predation mortality in other species, including some with walleye, with few exceptions most have drawn conclusions from five or fewer lakes sampled over short periods (1–2 years). A notable exception was a study of walleye stocking in multiple lakes across 11 years in Wisconsin that found survival of stocked walleyes to be inversely correlated with largemouth bass abundance (Fayram et al. 2005). Our objectives were to determine whether predation by largemouth bass (1) affected walleye survival and stocking success across a number of stocking events, and (2) was mediated by walleye size-at-stocking. We hypothesized that although largemouth bass would not comprise a major source of walleye mortality, walleye mortality would be positively correlated with predator density. We also expected that largemouth bass would prey more heavily on smaller sizes of stocked fish.

**METHODS**

Walleyes were stocked into 10 Illinois impoundments ranging in surface area from 6 to 379 ha, for a total of 77 stocking events from 1991 to 1997 (Table 1). Impoundments varied in

<table>
<thead>
<tr>
<th>Reservoir (ha)</th>
<th>Stocking size (mm)</th>
<th>Stocking events (N)</th>
<th>Stocking density (N/ha)</th>
<th>Walleye CPUE (N/h)</th>
<th>Largemouth bass density (N/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bloomington (250)</td>
<td>34–53</td>
<td>7</td>
<td>10–102</td>
<td>0.3–22.9</td>
<td>7–16</td>
</tr>
<tr>
<td>East Fork (379)</td>
<td>43–50</td>
<td>3</td>
<td>99–124</td>
<td>0.3–21.4</td>
<td>6–25</td>
</tr>
<tr>
<td>George (68)</td>
<td>36–53</td>
<td>4</td>
<td>98–123</td>
<td>0.04–3.0</td>
<td>7–17</td>
</tr>
<tr>
<td>Le Aqua Na (16)</td>
<td>39–47</td>
<td>6</td>
<td>39–109</td>
<td>0.4–8.2</td>
<td>7–33</td>
</tr>
<tr>
<td>Pierce (66)</td>
<td>87–117</td>
<td>7</td>
<td>62–91</td>
<td>0.0–15.2</td>
<td>7–33</td>
</tr>
<tr>
<td>Randolph Co. (26)</td>
<td>34–55</td>
<td>10</td>
<td>49–127</td>
<td>0.9–62.5</td>
<td>2–26</td>
</tr>
<tr>
<td>Ridge (6)</td>
<td>38–50</td>
<td>5</td>
<td>100</td>
<td>0.0–1.7</td>
<td>23–356</td>
</tr>
<tr>
<td>Sam Dale (78)</td>
<td>96–118</td>
<td>5</td>
<td>62–117</td>
<td>0.0–0.3</td>
<td>23–356</td>
</tr>
<tr>
<td>Sara (237)</td>
<td>34–37</td>
<td>2</td>
<td>117–125</td>
<td>0.0–6.1</td>
<td>69–158</td>
</tr>
<tr>
<td>Sterling (53)</td>
<td>93–106</td>
<td>5</td>
<td>51–90</td>
<td>1.6–18.3</td>
<td>2–8</td>
</tr>
</tbody>
</table>

**TABLE 1.** Summary of walleye stocking (May–August 1991–1997) in 10 Illinois reservoirs. Walleyes were stocked as small fingerlings (45 mm TL) at a target density of 90/ha or as large fingerlings (100 mm TL) at 65/ha. Largemouth bass density was limited to the number (N) large enough to consume the stocked walleyes.
productivity (although all were eutrophic) and predator densities (see Hoxmeier et al. 2006). Largemouth bass, a known predator of juvenile walleye (Santucci and Wahl 1993; Fayram et al. 2005; Hoxmeier et al. 2006), were the most abundant piscivore across all study lakes (density range, 1–356 /ha). Other predators present in the impoundments included channel catfish Ictalurus punctatus, white bass Morone chrysops, and adult walleyes. Prey fish communities were predominately by bluegill Lepomis macrochirus and gizzard shad Dorosoma cepedianum (Hoxmeier et al. 2006). No natural reproduction of walleyes was known to occur in study impoundments. Densities and composition of aquatic vegetation communities were variable across impoundments and years, but consisted primarily of pondweed Potomogon spp., coontail Ceratophyllum demersum, water milfoil Myriophyllum spp., and naiad Najas spp.

Walleyes were obtained from the Jake Wolf Memorial Fish Hatchery (Manito, Illinois) and the LaSalle Fish Hatchery (Marseilles, Illinois). Fish were stocked as small (mean total length [TL] = 44.8 mm; 57 stocking events, May–June) or large (mean = 100.3 mm TL; 20 stocking events, July–August) fingerlings. Small fingerlings were marked by immersion in 500 mg/L oxytetracycline (OTC) for 6 h prior to stocking (Brooks et al. 1994). Large walleyes were marked by clipping either the right or left pelvic fin in alternating years. Clipping occurred at the hatchery 2–7 d prior to stocking; fish were held for recovery in raceways and to account for any handling mortality. Fish were transported to impoundments in oxygenated hauling tanks, acclimated to impoundment temperatures by transferring impoundment water into the hauling tanks until temperatures were equalized (Clapp et al. 1997), and stocked at one nearshore location, typically at the boat ramp. We measured 50 individuals (TL; mm) for each stocking event. Target stocking densities were 90 small walleyes/ha or 65 large walleyes/ha, but this varied with fish availability in some instances (Table 1).

Predation on walleyes by largemouth bass was assessed by examining diets of largemouth bass diets that were captured during nighttime shoreline electrofishing of the entire impoundment perimeter on the day of stocking and at 1, 2, 3, 5, 7, 10, 14, and 21 d poststocking. The number of stomachs sampled was standardized by sampling effort, which is related to predator density. Gastric lavage (Foster 1977) was used to recover dietary items from each largemouth bass, and all prey items caught were measured, weighed, and examined for fin clips indicating prior capture; fins were clipped if no prior clip was present. We used Schnabel population estimates to determine the population density of largemouth bass in each impoundment. Estimates of walleye mortality due to largemouth bass predation were estimated by

\[ Y_i = \sum_{j=1}^{d} \frac{a_j}{b_j} x_i \]

where \(a\) is the number of walleyes recovered from \(b\) largemouth bass stomachs during sample \(j\), \(x\) is the estimated effective population of largemouth bass of the size (TL) capable of consuming each size-class of walleye (1.75 times prey TL; Santucci and Wahl 1993; Wahl 1995), and \(d\) is the number of days poststocking (Carlne et al. 1986; Wahl and Stein 1989). Estimates of walleye mortality due to largemouth bass predation between stocking dates were calculated using linear interpolation.

Electrofishing surveys are commonly used for walleye population estimates (Fayram et al. 2005; Hoxmeier et al. 2006); survival of stocked walleyes was therefore also estimated using nighttime shoreline electrofishing surveys conducted every 2 weeks during the fall (September–November). All walleyes caught were measured, weighed, examined for the presence of fin clips, and subsampled (frozen) for later examination of OTC marks. Otoliths were later removed and examined for OTC marks in the laboratory, using a compound microscope with a 100-W ultraviolet light source, a 450–490-nm excitation filter and 515-nm barrier filter, and a 510-nm dichroic mirror. Due to an insufficient number of walleye recaptures at many impoundments, we were unable to use Schnabel population estimates for comparisons among stocking events, so CPUE (number/h of electrofishing) was used instead, which has been shown to be highly correlated to number of walleye/ha (Hoxmeier et al. 2006).

We examined differences in predation mortality in four impoundments that were stocked over 2–6 years with both small and large fingerlings (Table 1). We tested for differences using a mixed-effects-model likelihood-ratio test (LRT) in the lme4 package (Bates et al. 2011) implemented in R 2.14 (R Development Core Team 2008) to account for temporal and spatial pseudoreplication. Percent predation mortality was the response variable, years and impoundments were random variables, and stocking size was the fixed variable. Relationships between largemouth bass density and fall walleye CPUE and walleye predation mortality and fall walleye CPUE were tested using a two-dimensional Kolmogorov–Smirnoff test (2DKS), implemented
FIGURE 1. Mean number (±SE) of walleyes recovered from largemouth bass stomachs following 77 stocking events across 10 reservoirs and 7 years in Illinois. Numbers of largemouth bass stomachs examined are in parentheses.

using big2dks software (Garvey et al. 1998). The 2DKS test detects patterns in bivariate data, where $DBKS$ is the maximum difference between the observed and expected proportions and $P < 0.05$ indicates that the distribution is nonrandom.

RESULTS
Approximately 500,000 small and 33,000 large walleye fingerlings were stocked into the 10 impoundments during the 7-year study. We sampled the diets of 8,591 largemouth bass stomachs. The mean number of diets per stocking event was 110.7 (SD, 94.6), and we recovered 132 of the small and 42 of the large stocked walleyes. Overall, 2.0% of largemouth bass stomachs contained walleye, and total mortality of stocked walleyes due to largemouth bass predation was 4.3%. We did not detect largemouth bass predation on walleyes in 42 (54.5%) stockings. Predation on walleyes by largemouth bass was greatest on the day of stocking: 0.046 walleyes/stomach and 3.9% of the stomachs examined contained one or more walleyes (Figure 1). Predation declined exponentially over the next 21 d, with the next highest predation rates occurring on day 1 (when 1.3% of largemouth bass stomachs contained walleyes) and day 3 (when 1.8% did). By 14 d poststocking we detected no predation by largemouth bass on walleye (Figure 1).

In impoundments stocked with both small and large fingerlings, mean (SD) estimated mortality of small walleyes was 6.2% (23.4) and ranged from 0% to 100%, the majority being less than 19% (Figure 2). Mean (SD) mortality due to predation of large walleyes was 7.6% (15.6), and ranged from 0.0% to 56.9%. There were no differences between mortality due to largemouth bass predation between small and large walleyes stocked into the same impoundments (LRT = 0.043, $P = 0.84$).

Despite low largemouth bass predation on stocked walleyes, largemouth bass density was related to walleye predation mortality (2DKS, $X = 1.59, Y = 0.48, DBKS = 0.16, P = 0.0002$; Figure 2a). Although many stocking events resulted in no survival of stocked walleyes to the fall (mean [SD] survival = 2.6% [6.0]; mean CPUE = 5.5 [9.8]), the 2DKS test detected a nonran-

FIGURE 2a (a) Largemouth bass predation mortality on stocked walleyes, (b) fall CPUE for stocked walleyes as functions of largemouth bass effective predator densities, and (c) fall walleye CPUE as a function of walleye mortality due to largemouth bass predation. Polynomial best fits are represented by solid lines. Values producing $DBKS$ (two-dimensional Kolmogorov–Smirnoff test) are represented by solid diamonds.

DISCUSSION
Largemouth bass predation on walleye fingerlings was highest immediately after stocking, and we detected no predation mortality after 14 d. Timing of predation is consistent with an earlier study that found 76% of walleyes eaten by largemouth bass in Ridge Lake, Illinois, were consumed within 48 h (Santucci and Wahl 1993). Predation losses of saugeyes stocked into reservoirs in Ohio similarly approached zero after 14 d, although residual mortality due to predation was assumed to occur for an additional 6 weeks (Stahl et al. 1996). Predation on a number of other stocked fishes, including muskellunge...
There was no significant relationship between walleye predation mortality and walleye fall CPUE, although lower fall CPUE was correlated with largemouth bass densities above 24.9 fish/ha. A bioenergetics model of Whitefish Lake, Wisconsin, estimated that largemouth bass consumed all stocked walleyes and, in general, found high predation effects of largemouth bass on walleye (Fayram et al. 2005). Largemouth bass may also have affected walleye survival through nonconsumptive effects (Peckarsky et al. 2008), such as altering walleye behavior and growth or through competition for food resources (Parkos and Wahl 2010). Bluegills and gizzard shad were abundant in many of our impoundments, potentially competing for food with juvenile walleyes. Gizzard shad abundance is correlated with bluegill abundance, where they may act as alternative prey for largemouth bass (Aday et al. 2003). Similarly, availability of alternative prey may mediate largemouth bass predation on stocked walleyes.

Density-dependent relationships have been noted between largemouth bass populations and predation rates on stocked esocids (Carline et al. 1986; Szendrey and Wahl 1996) and walleye (Santucci and Wahl 1993). However, these studies were performed in a limited number of lakes and correlations may thus have been influenced by relatively small sample sizes. Our results across 77 impoundment-years suggest that there is not a density-dependent relationship between largemouth bass populations and survival of stocked walleyes. Fall CPUE of walleyes, however, did not exceed 10/fish in any impoundment-year when largemouth bass density was >25/ha. Long-term studies across a number of lakes are necessary to determine if similar patterns exist for other species and in other geographic areas.

**MANAGEMENT IMPLICATIONS**

Predator density can be an important consideration when stocking fish. For walleyes stocked into Illinois impoundments, however, it appears to play a relatively minor role in influencing walleye survival. Fall survival was >3%, while mortality due to largemouth bass predation was <1%; so, other factors are probably more important in determining stocking success and failure in our studied impoundments. Those 10 impoundments varied in size, but were all characterized as eutrophic to hypereutrophic and, thus, generally had high levels of food resources. Our results from Illinois may be applicable to other Midwestern and moderate-latitude lakes and impoundments, especially those with strong prey fish populations, but should be confirmed in systems in other geographic regions across productivity levels and predator and prey fish communities. Abundant prey may increase competition with walleye fingerlings and thus contribute to low survival of stocked fish, but abundant prey may also moderate predator effects. Modification of rearing habitat increases survival of stocked fish and should be implemented when possible to improve stocking success (Salvanes and Braithwaite 2006; Strand et al. 2010). Size at stocking of walleyes has been shown to be correlated with survival (Santucci and Wahl 1993; Brooks et al. 2002); however, this does not appear to be linked with predator density.
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Habitat Associations of Fish Species of Greatest Conservation Need at Multiple Spatial Scales in Wadeable Iowa Streams

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ARTICLE

Habitat Associations of Fish Species of Greatest Conservation Need at Multiple Spatial Scales in Wadeable Iowa Streams

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Abstract
Fish and habitat data were collected from 84 wadeable stream reaches in the Mississippi River drainage of Iowa to predict the occurrences of seven fish species of greatest conservation need and to identify the relative importance of habitat variables measured at small (e.g., depth, velocity, and substrate) and large (e.g., stream order, elevation, and gradient) scales in terms of their influence on species occurrences. Multiple logistic regression analysis was used to predict fish species occurrences, starting with all possible combinations of variables (5 large-scale variables, 13 small-scale variables, and all 18 variables) but limiting the final models to a maximum of five variables. Akaike’s information criterion was used to rank candidate models, weight model parameters, and calculate model-averaged predictions. On average, the correct classification rate (CCR = 80%) and Cohen’s kappa (κ = 0.59) were greatest for multiple-scale models (i.e., those including both large-scale and small-scale variables), intermediate for small-scale models (CCR = 75%; κ = 0.49), and lowest for large-scale models (CCR = 73%; κ = 0.44). The occurrence of each species was associated with a unique combination of large-scale and small-scale variables. Our results support the necessity of understanding factors that constrain the distribution of fishes across spatial scales to ensure that management decisions and actions occur at the appropriate scale.

Conservation of freshwater ecosystems is an important goal of resource managers and an understanding of species distributions and habitat requirements greatly increases the probability of successful ecosystem restoration and preservation. Furthermore, an understanding of species–habitat relationships can provide insight into the effects of land use practices, habitat alterations, and climate change on species distributions (Wang et al. 2003; Wall et al. 2004; Lyons et al. 2010). Modeling of species distributions is an important tool for addressing many issues in conservation (Guisan and Thuiller 2005), and the use of predictive occurrence models to further the understanding of fish species' relationships with habitat features in freshwater systems is common (e.g., Olden and Jackson 2001; Rich et al. 2003; Steen et al. 2008). As habitat loss and degradation...
continue to threaten fish biodiversity in North America (Miller et al. 1989; Richter et al. 1997; Jelks et al. 2008), species distribution models are playing an increasingly important role in conservation. However, predicting the distribution of fish species is challenging because fish species occurrences are influenced by a combination of abiotic and biotic processes acting across multiple spatial and temporal scales (Poff 1997; Marsh-Matthews and Matthews 2000; Jackson et al. 2001). A further challenge is that the most influential processes vary by species and system (Pont et al. 2005; Monti and Legendre 2009).

The link between landscapes and aquatic ecosystems has been appreciated for decades (Hynes 1975; Vannote et al. 1980; Allan 2004), and the relationships between processes acting at larger scales and habitats and biota at smaller scales are of great interest to aquatic ecologists (Richards et al. 1996; Wang et al. 2003; Hughes et al. 2006). Habitat variables measured at large scales are often able to explain substantial variation in fish assemblages, particularly in highly variable landscapes (e.g., Rocky Mountain streams; Rahel and Hubert 1991) or across large spatial scales (e.g., entire midwestern USA; Marsh-Matthews and Matthews 2000). Additionally, the modeling of species occurrences with large-scale habitat variables is economical because such variables are easily measured with a GIS, thereby reducing the need for costly field sampling (Oakes et al. 2005; Steen et al. 2008). However, in other regions, large-scale habitat variables such as land use may not effectively explain variation in fish assemblage structure (Rich et al. 2003; Heitke et al. 2006) or may only do so indirectly (Rowe et al. 2009a).

Relationships between fish assemblages and environmental features measured at small scales are also well documented (Gorman and Karr 1978; Schlosser 1982; Lobb and Orth 1991). The influence of instream physical habitat features (e.g., depth and substrate composition) on food, refuge, and spawning habitat availability is easy to conceptualize, and their influence on fish assemblages is well studied (Fischer and Paukert 2008; Rowe et al. 2009b). Thus, many studies have used instream habitat variables to explain the distribution or abundance of fish species (e.g., Hubert and Rahel 1989; Quist et al. 2005; Rashleigh et al. 2005). Furthermore, an understanding of the constraints on fish species occurrences measured at small scales (e.g., canopy cover) may be most useful for conservation efforts because small-scale characteristics can be more easily manipulated for restoration than landscape-scale features (e.g., elevation).

Identification of the factors and spatial scales influencing fish species occurrences remains a central focus of fisheries ecologists (e.g., Porter et al. 2000; Rich et al. 2003; Pont et al. 2005). Biotic communities are influenced by a hierarchical system of constraints in which large-scale processes constrain smaller-scale processes (Tonn 1990; Poff 1997; Quist et al. 2005). This is especially evident for stream habitats, which are hierarchically organized within catchments, segments, reaches, macrohabitats, and microhabitats (Frissel et al. 1986). Thus, species occurrence models that account for effects measured at multiple spatial scales may provide more predictive power and transferability than models that incorporate variables measured at a single spatial scale (Leftwich et al. 1997; Rich et al. 2003; Pont et al. 2005).

In Iowa, 68 of approximately 144 extant fish species are classified as species of greatest conservation need (SGCN), and the protection and enhancement of habitats to improve their status are of high priority (Zohrer 2005). Fifty percent of the fish SGCN examined by Sindt et al. (2012) were found to have declining distributions. Despite concern regarding their conservation status, the habitat associations of SGCN and most other Iowa stream fish species are poorly understood. Therefore, an understanding of factors influencing the occurrences of stream fish SGCN at multiple spatial scales is important for guiding the conservation of these species (Lewis et al. 1996; Rabeni and Sowa 1996; Durance et al. 2006; Dunham and Peterson 2010).

Our objectives were to (1) identify important large-scale and small-scale habitat features that influence the occurrence of each fish SGCN; (2) predict the occurrences of fish SGCN by using habitat variables measured at a large scale, a small scale, and both scales (i.e., multiple-scale variables); and (3) evaluate the relative influence of large-scale and small-scale habitat variables on fish species occurrences. Furthermore, because inaccurate species distribution models may be detrimental to conservation efforts, models were validated by using an independent data set to gauge confidence in model predictions and test model generality. We expected that (1) the habitat features with the greatest influence on species occurrence would vary among species due to species-specific habitat associations and (2) species occurrence models that included habitat variables measured at multiple spatial scales would explain the most variability in species occurrence and would exhibit the greatest model generality.

METHODS

Study area and field sampling.—Fish assemblages and small-scale physical habitat characteristics were sampled from 84 wadeable (i.e., second through fifth order) Iowa stream reaches during the spring and summer (May–August) of 2009 and 2010 (Figure 1). Rather than using a simple random sampling design, stream reaches were selected to maximize the number of reaches sampled for each SGCN in three stream segment categories for a concurrent study (Sindt et al. 2012). The three stream segment categories within each species’ respective distribution included (1) previously sampled stream segments where the species was documented to be present within the last 50 years (i.e., since 1958); (2) stream segments that had not been previously sampled but where the species was predicted to be present by an existing species distribution model (Iowa Aquatic Gap Analysis Project; Loan-Wilsey et al. 2005); and (3) stream segments that had not been previously sampled and where the species was not predicted to be present. Sixty-eight Iowa fish species are classified as SGCN, and knowledge about habitat associations for all SGCN is needed to guide conservation efforts (Zohrer 2005). However, only seven species were present in a sufficient number of the 84 sampled stream reaches to allow for modeling:

...

All sampled stream reaches were located in the Mississippi River drainage of Iowa, which contains 34 eight-digit hydrologic unit code (HUC) watersheds (HUCs designated by the U.S. Geological Survey) and portions of seven ecoregions (Des Moines Lobe, Loess Hills and Steeply Rolling Prairies, Southern Iowa Rolling Loess Prairies, Central Irregular Plains, Iowan Surface, Paleozoic Plateau, and Interior River Lowland; Griffith et al. 1994). The 84 stream reaches were sampled from 18 watersheds and included reaches from the Iowan Surface (*n* = 47 reaches), Des Moines Lobe (*n* = 15), Southern Iowa Rolling Loess Prairies (*n* = 14), and Paleozoic Plateau (*n* = 8) ecoregions. Stream reaches were also sampled from both of Iowa’s aquatic subregions (i.e., Eastern Broadleaf Forest and Central Plains), which have unique physiographic characteristics and riverine assemblages (Sowa et al. 2004). Aquatic subregions are similar to the ecoregion provinces defined by Bailey (1995), but the boundaries were delineated by the Missouri Resource Assessment Partnership (University of Missouri, Columbia) to align with drainage divides. Twenty-one of the sampled stream reaches were in the Central Plains aquatic subregion, which is characterized by thick loess deposits over flat to gently sloping terrain with wide stream valleys. Many Central Plains streams were historically dominated by fine silt and sand substrates, and sediment input has been exacerbated by the conversion of native prairie to cropland. The other 63 stream reaches were sampled in the Eastern Broadleaf Forest aquatic subregion of northeastern Iowa; this aquatic subregion is also highly altered from agricultural practices but is geologically more diverse than the Central Plains subregion. The Eastern Broadleaf Forest contains the Paleozoic Plateau ecoregion, which was less impacted by glaciation and is characterized by high topographic relief, rocky outcroppings, and dense forests (Griffith et al. 1994). Overall, Iowa’s landscape is relatively homogeneous, with
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elevation only varying from 146 to 509 m, and 72% of the land has been converted to row crop agriculture (U.S. Department of Agriculture 2007). Previous studies have found increasing aquatic ecological integrity (e.g., index of biotic integrity) from southwest Iowa to northeast Iowa (Wilton 2004; Heitke et al. 2006). Greater ecological integrity in northeast Iowa is likely a reflection of relatively high-quality habitat due to the greater topographic relief, less-disturbed riparian habitats, and coarser substrates than in other regions of Iowa.

Sample reaches were 300–400 m in length and were divided into macrohabitat units (riffles, pools, runs, or off-channel units). When feasible, sample reaches were selected to encompass as many different macrohabitat units as possible and to be more than 100 m from an artificial structure (e.g., a bridge or low-head dam). All sampling occurred during base flow conditions to minimize sampling inefficiencies associated with high flow, depth, and turbidity. Fish assemblages were sampled in each macrohabitat separately by using single-pass upstream electrofishing with a pulsed-DC electrofishing unit (Simonson and Lyons 1995). When feasible, a generator-powered, barge-mounted electrofishing unit with three anodes (Model VVP-15B; Smith-Root, Inc., Vancouver, Washington) was used. However, if streams were too shallow or were inaccessible, a battery-powered backpack electrofishing unit (Smith-Root LR-20) was used. For both backpack and barge-mounted electrofishing, three netters used 6.34-mm-mesh dip nets to collect fish. An effort was made to sample all accessible habitat types in each macrohabitat.

Voltage output was adjusted to maximize efficiency and reduce incidental mortality in each sample reach. Fish that were collected in each macrohabitat unit were examined for external abnormalities, identified, counted, and released. Up to five voucher specimens of each SGCN were preserved in a 10% solution of formalin. Fish that could not be identified in the field were preserved and transported to the laboratory for identification.

Habitat characteristics were quantified by measuring physical habitat features in each macrohabitat unit. The length of each macrohabitat unit was measured along the thalweg, and the width of each macrohabitat unit was measured along a transect perpendicular to the thalweg at 25, 50, and 75% of the macrohabitat length. Depth, current velocity, and substrate size were measured at 20, 40, 50, 60, and 80% of the length of each transect. Current velocity was measured with a portable velocity meter (Flo-Mate Model 2000; Marsh-McBirney, Inc., Frederick, Maryland) at 60% of the depth when depth was less than 0.75 m; at depths greater than 0.75 m, velocities were measured at 20% and 80% of the depth and the two values were averaged (Buchanan and Somers 1969). Substrate was classified as artificial (e.g., tire), soil, wood (e.g., submerged tree), detritus, hardpan, clay (<0.004 mm), silt (0.004–0.063 mm), sand (0.062–2.000 mm), gravel (2–16 mm), coarse gravel (16–64 mm), cobble (64–256 mm), boulder (>256 mm), or bedrock (i.e., modified Wentworth scale). Canopy cover was measured along each transect by using a spherical densiometer (1) at and facing each streambank and (2) facing upstream and downstream at the midpoint of the transect. Bank cover characteristics (percent coverage of woody vegetation, nonwoody vegetation, roots, boulders, eroding ground, and bare ground) and distance to anthropogenic disturbance (on the bank, ≤10 m from the bank, >10 m from the bank, or absent) were visually estimated for the left and right banks of each transect. One length measurement, three width measurements, and three depth measurements were recorded for each unit of instream cover (artificial structure, boulder, rip-rap, filamentous algae, aquatic macrophytes, terrestrial vegetation, overhanging vegetation, undercut bank, island, small brush, tree root, and large woody debris) at least 0.3 m in length within each macrohabitat.

The area of each macrohabitat unit was estimated by multiplying the thalweg length by the mean width. Mean depth, width, current velocity, canopy cover, and bank coverage percentages were calculated for each macrohabitat unit. Additionally, the CV in depth, width, current velocity, and canopy cover was calculated (CV = 100 × [SD/mean]). The proportions of each substrate type and distance to disturbance category were also quantified for each macrohabitat unit. All habitat characteristics (except instream cover, which was censused and not estimated) were averaged for each macrohabitat category (riffle, pool, run, and off-channel) within each stream reach. Furthermore, averaged values were weighted by the proportion of the total stream reach area that was represented by the respective macrohabitat category. Weighted values were summed to quantify habitat characteristics for the entire stream reach. Aerial coverage of each instream cover type was quantified as the proportion of reach area. Additional composite variables were created by summing two or more habitat variables (e.g., proportion of coarse substrates).

Independent variables.—Large-scale and small-scale habitat variables characterizing sampled stream reaches were selected as independent variables for SGCN occurrence models. Sixteen GIS-measured variables that were used to develop fish distribution models for the Iowa Aquatic Gap Analysis Project (Loan-Wilsey et al. 2005) were obtained using ArcMap version 9.3 (Environmental Systems Research Institute, Redlands, California) and were considered candidate large-scale variables. The 16 variables included one or more measures of flow (intermittent or permanent), stream order (Strahler 1957), channel gradient, elevation, soil type, aquatic subregion (Eastern Broadleaf Forest or Central Plains), temperature (coldwater or warmwater), and size discrepancy with downstream segment. The temperature variable was derived from the Iowa Department of Natural Resources’ coldwater streams designation, which is based on biotic communities and maximum summer temperatures. Candidate small-scale habitat variables characterizing channel morphology (e.g., width, depth, and macrohabitat composition), current velocity, canopy cover, bank cover, substrate composition, instream cover (e.g., woody debris and boulders), and distance to disturbance (e.g., row crop agriculture, pasture, and road) were obtained from field sampling.
TABLE 1. Large-scale and small-scale habitat variables for 84 wadeable Iowa stream reaches that were sampled during spring and summer 2009 and 2010; these variables were used as independent variables in fish species occurrence models (min = minimum; max = maximum).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Large-scale variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>Factor (1 = coldwater; 2 = warmwater)</td>
<td>1.93</td>
<td>0.26</td>
<td>1.00</td>
<td>2.00</td>
</tr>
<tr>
<td>Subregion</td>
<td>Factor (1 = Central Plains; 2 = Eastern Broadleaf Forest)</td>
<td>1.75</td>
<td>0.44</td>
<td>1.00</td>
<td>2.00</td>
</tr>
<tr>
<td>Order</td>
<td>Strahler stream order</td>
<td>3.11</td>
<td>0.76</td>
<td>2.00</td>
<td>5.00</td>
</tr>
<tr>
<td>Elevation</td>
<td>Elevation (m) of the upstream end of the stream segment</td>
<td>295.27</td>
<td>45.43</td>
<td>189.00</td>
<td>387.00</td>
</tr>
<tr>
<td>Gradient</td>
<td>Measure of reach gradient (1 = 0.0–0.4 m/km; 2 = 0.5–1.0 m/km; 3 = 1.1–2.0 m/km; 4 = 2.1–3.0 m/km; 5 = 3.1–5.0 m/km; 6 = 5.1–7.0 m/km; 7 = 7.1–10.0 m/km; 8 = 10.1–13.0 m/km; 9 = 13.1–17.0 m/km; 10 = ≥17.1 m/km)</td>
<td>3.18</td>
<td>1.46</td>
<td>1.00</td>
<td>8.00</td>
</tr>
<tr>
<td><strong>Small-scale variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width</td>
<td>Mean wetted channel width (m)</td>
<td>10.84</td>
<td>7.07</td>
<td>2.28</td>
<td>40.95</td>
</tr>
<tr>
<td>CVWidth</td>
<td>Mean CV of wetted channel width</td>
<td>14.93</td>
<td>5.91</td>
<td>4.69</td>
<td>32.29</td>
</tr>
<tr>
<td>Depth</td>
<td>Mean depth (m)</td>
<td>0.38</td>
<td>0.16</td>
<td>0.08</td>
<td>0.85</td>
</tr>
<tr>
<td>CVDepth</td>
<td>Mean CV of depth</td>
<td>39.87</td>
<td>12.50</td>
<td>10.97</td>
<td>68.37</td>
</tr>
<tr>
<td>Velocity</td>
<td>Mean current velocity (m/s)</td>
<td>0.30</td>
<td>0.13</td>
<td>0.09</td>
<td>0.65</td>
</tr>
<tr>
<td>Pool</td>
<td>Percentage of reach area as pool</td>
<td>5.43</td>
<td>10.41</td>
<td>0.00</td>
<td>53.31</td>
</tr>
<tr>
<td>Riffle</td>
<td>Percentage of reach area as riffle</td>
<td>17.24</td>
<td>17.98</td>
<td>0.00</td>
<td>74.21</td>
</tr>
<tr>
<td>Canopy</td>
<td>Mean canopy cover (%)</td>
<td>39.69</td>
<td>24.21</td>
<td>0.03</td>
<td>87.30</td>
</tr>
<tr>
<td>PetBankCover</td>
<td>Percentage of total bank covered (woody, nonwoody, boulder or rip-rap, and roots)</td>
<td>50.61</td>
<td>16.38</td>
<td>18.33</td>
<td>100.00</td>
</tr>
<tr>
<td>Coarse</td>
<td>Percentage of substrate that is coarse (coarse gravel, cobble, and boulder)</td>
<td>21.15</td>
<td>25.58</td>
<td>0.00</td>
<td>88.51</td>
</tr>
<tr>
<td>Dist10m</td>
<td>Percentage of banks with disturbance on the bank or within 10 m of the bank</td>
<td>25.69</td>
<td>38.89</td>
<td>0.00</td>
<td>100.00</td>
</tr>
<tr>
<td>WoodyCover</td>
<td>Percentage of reach area with woody debris, tree roots, or small brush as cover</td>
<td>5.75</td>
<td>5.86</td>
<td>0.00</td>
<td>23.04</td>
</tr>
<tr>
<td>VegCover</td>
<td>Percentage of reach area with filamentous algae, aquatic macrophytes, overhanging vegetation, or terrestrial vegetation as cover</td>
<td>5.96</td>
<td>10.33</td>
<td>0.00</td>
<td>50.06</td>
</tr>
</tbody>
</table>

Many of the large-scale variables were redundant (e.g., three variables described stream size). To avoid multicollinearity, the most ecologically relevant and interpretable variable from redundant groups was retained. The variable describing flow was excluded because streams with intermittent flow were not sampled. Pearson’s product-moment correlations were calculated for all pairs of large-scale variables to ensure that no highly correlated (Pearson’s $r \geq |0.70|$) variables were retained.

Small-scale habitat characteristics have been found to be associated with fish assemblage characteristics in Iowa (Rowe et al. 2009b). Thus, 62 small-scale variables were created to describe local physical habitat features. Reducing the number of variables was essential for removing multicollinearity between variables and improving model interpretability. Ecologically relevant small-scale variables were selected as potential explanatory variables. Pearson’s product-moment correlations were calculated for all pairs of small-scale variables. When two or more ecologically relevant variables were highly correlated, the most relevant and interpretable variable was retained.

Habitat variables that were used to develop species occurrence models included 5 large-scale variables and 13 small-scale variables (Table 1). The large-scale variables included temperature, subregion, stream order, elevation, and gradient. Temperature and subregion were categorical variables and therefore were treated as factors rather than as continuous variables in model development. The 13 small-scale variables included measures of channel morphology, current velocity, canopy cover, bank cover, substrate composition, instream cover, and distance to disturbance.

**Species occurrence models.**—We used an information theoretic approach (Burnham and Anderson 2002) to evaluate competing multiple logistic regression models and to identify habitat variables measured at multiple spatial scales that influence the occurrences of the seven fish SGCN. Multiple logistic
regression analysis is a common multivariate approach for predicting the binary response of fish species presence or absence (e.g., Porter et al. 2000; Rich et al. 2003; Rashleigh et al. 2005).

Using retained variables (i.e., the 5 large-scale variables and 13 small-scale variables), candidate multiple logistic regression models were created for all possible combinations of variables measured at a large scale, a small scale, and multiple scales (i.e., both large-scale and small-scale variables). Because large-scale models could include a maximum of five variables, up to five variables were allowed in all candidate models to eliminate the possibility of small-scale and multiple scales models explaining more variation than large-scale models simply due to the inclusion of more variables. Furthermore, to prevent model overfitting and spurious results, the maximum number of variables allowed in a candidate model was 10% of the number of stream reaches that were sampled within the species’ respective distribution (Table 2). For example, we sampled 34 stream reaches within the historical distribution of the central mudminnow, and thus we only allowed up to three variables to be included in models predicting the occurrence of central mudminnow.

Confidence model sets were selected from among all candidate models for each model type (large-scale, small-scale, and multiple-scale models) based on Akaike’s information criterion (AIC), and these confidence model sets were used to create model-averaged models. The AIC reflects model parsimony by measuring the goodness of fit while penalizing for the number of parameters (Burnham and Anderson 2002). Recently, the use of AIC corrected for small sample size (AICc) has been common; however, Richards (2005) found that AICc did not increase the likelihood of selecting the best-approximating model. Thus, we used AIC rather than AICc. Richards (2005) also suggested that an AIC difference (ΔAIC) between 4 and 7 should be used as a selection criterion for 95% confidence that the best-approximating model is included in the confidence model set. Thus, all candidate models with a ΔAIC of 6 or less were included in a given confidence model set. Furthermore, because more than one combination of variables was likely to have evidence of being the best-approximating model, all models that were included in confidence model sets were averaged to account for model selection uncertainty (Burnham and Anderson 2002). Model-averaged coefficients were calculated by weighting the coefficient values for each model in the confidence model set by the models’ respective Akaike weights. The relative importance of habitat variables in confidence model sets was assessed by summing the Akaike weights for all models within the confidence model set in which the variable of interest was included. Variables with summed Akaike weights of 0.60 or greater were interpreted as important. Summed relative weights must be interpreted carefully because they reflect the importance of the habitat variable but not the strength of the relationship (i.e., they do not account for coefficient values). All multiple logistic regression analyses were performed with R software (R Development Core Team 2009).

Logistic regression models predict the probability of species presence as a value ranging from 0 to 1. Thresholds of 0.5 are often used in species presence–absence models, with values greater than 0.5 being interpreted as presence and values less than 0.5 being interpreted as absence (e.g., Porter et al. 2000; Pont et al. 2005; Ruiz and Peterson 2007). However, 0.5 is not always the most appropriate threshold because species prevalence can bias logistic regression scores toward the larger group (i.e., present or absent; Fielding and Bell 1997). We used an approach similar to that described by Olden and Jackson (2001) to select optimum thresholds for maximizing the area under the curve of the receiver operating characteristic plot for the training data (i.e., the same data that were used to create the model). The receiver operating characteristic plot is a graph of model sensitivity versus 1 − specificity, where sensitivity is the proportion of observed presences that are correctly predicted and specificity is the proportion of observed absences that are correctly predicted. Optimal threshold values were chosen by assuming that the costs of misclassifying a species as absent or present were equal. The optimal threshold value and model-averaged predictions for each species occurrence model were used to calculate confusion matrix values and performance measures to self-evaluate model performance after re-substituting the same simulation.

### Table 2: Model performance measures for large-scale, small-scale, and multiple-scale models of occurrence for seven Iowa fish species of greatest conservation need (n = number of stream reaches sampled in each species’ historical distribution; CCR = correct classification rate expressed as a proportion; κ = Cohen’s kappa value; P is associated with the null hypothesis that κ = 0).

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Prevalence</th>
<th>CCR</th>
<th>κ</th>
<th>P</th>
<th>CCR</th>
<th>κ</th>
<th>P</th>
<th>CCR</th>
<th>κ</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banded darter</td>
<td>80</td>
<td>0.40</td>
<td>0.78</td>
<td>0.54</td>
<td>&lt;0.001</td>
<td>0.80</td>
<td>0.60</td>
<td>&lt;0.001</td>
<td>0.83</td>
<td>0.64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>American brook lamprey</td>
<td>53</td>
<td>0.32</td>
<td>0.51</td>
<td>0.14</td>
<td>0.118</td>
<td>0.55</td>
<td>0.21</td>
<td>0.041</td>
<td>0.58</td>
<td>0.27</td>
<td>0.011</td>
</tr>
<tr>
<td>Ozark minnow</td>
<td>63</td>
<td>0.25</td>
<td>0.59</td>
<td>0.27</td>
<td>0.007</td>
<td>0.70</td>
<td>0.39</td>
<td>0.001</td>
<td>0.79</td>
<td>0.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Blackside darter</td>
<td>83</td>
<td>0.27</td>
<td>0.72</td>
<td>0.37</td>
<td>0.001</td>
<td>0.64</td>
<td>0.33</td>
<td>&lt;0.001</td>
<td>0.80</td>
<td>0.54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Southern redbelly dace</td>
<td>77</td>
<td>0.55</td>
<td>0.77</td>
<td>0.51</td>
<td>&lt;0.001</td>
<td>0.71</td>
<td>0.40</td>
<td>&lt;0.001</td>
<td>0.79</td>
<td>0.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Longnose dace</td>
<td>50</td>
<td>0.20</td>
<td>0.92</td>
<td>0.75</td>
<td>&lt;0.001</td>
<td>0.92</td>
<td>0.77</td>
<td>&lt;0.001</td>
<td>0.96</td>
<td>0.88</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Central mudminnow</td>
<td>34</td>
<td>0.21</td>
<td>0.85</td>
<td>0.47</td>
<td>0.047</td>
<td>0.91</td>
<td>0.74</td>
<td>&lt;0.001</td>
<td>0.88</td>
<td>0.70</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
data that were used to parameterize the model (Fielding and Bell 1997). The correct classification rate (CCR) is a simple measure of the percentage of cases that are correctly predicted by a model, but its interpretation can be biased by species prevalence (Olden et al. 2002). Therefore, the primary statistic used to self-evaluate model performance was Cohen’s kappa (κ), an index used to assess the correct classification of events (presence or absence) relative to that expected by random chance (Cohen 1960). Kappa values less than or equal to zero indicate that model performance is no better than random chance, whereas a κ value of 1 indicates perfect model performance. Landis and Koch (1977) arbitrarily characterized κ values of less than 0.40 as indicating poor to fair model performance and κ values greater than 0.40 as indicating moderate to near-perfect model performance. Cohen’s κ is commonly used to evaluate fish species presence–absence models (e.g., Olden and Jackson 2001; Rashleigh et al. 2005; Hayer et al. 2008) and is also used in the medical and remote sensing fields (Congalton 1991; Manel et al. 2001). Kappa has limitations and may be overly sensitive to species prevalence (McPherson et al. 2004; Vaughan and Omerod 2005); however, Manel et al. (2001) found that κ was a robust indicator of model performance and was negligibly influenced by species prevalence. The SE, significance, and 95% confidence interval of κ can be calculated and used to test the null hypothesis that κ is equal to zero (Titus et al. 1984). The κ values were calculated and significance tests (κ = 0.05) were performed using the fmsb package in R (R Development Core Team 2009). The CCRs and κ values were used to assess the performance of models and to evaluate the relative influence of habitat variables measured at each spatial scale on species occurrences.

Model validation.—The most robust model validation techniques use data that are independent from those used to estimate the model parameters. Therefore, independent data were used to validate and test the generality of species occurrence models. Data were obtained from a previous study by Rowe et al. (2009b) in which fish assemblages were sampled via the Iowa Department of Natural Resources’ wadeable stream bioassessment protocol (Wilton 2004) and physical habitats were sampled by following the wadeable streams physical habitat protocol of the U.S. Environmental Protection Agency’s Environmental Monitoring and Assessment Program (EMAP; Peck et al. 2006). Rowe et al. (2009b) analyzed data from 93 randomly selected wadeable streams across Iowa. However, only 65 of the wadeable streams were sampled from the Mississippi River drainage to which our models were constrained. Similar methods were used to sample fish, but the methods used to quantify habitat characteristics were slightly different from those used to collect data for our study; however, in most applications it is unlikely that data will always be collected with the exact same protocol. Thus, our use of data collected with differing methodologies offers an opportunity to validate the models with an independent data set and to test the models’ generality for use with data collected by different methods, thereby presenting a “conservative” assessment of model accuracy.

Even though the habitat sampling methodologies of this study were not identical to those used to collect the independent data, many of the same small-scale habitat features were quantified, and the large-scale variables could be easily obtained with a GIS (ArcMap version 9.3). Rather than measuring depths across the width of the stream reach, the EMAP protocol only measures depths along the stream thalweg. To adjust the mean thalweg depth to better represent mean depth, linear regression analysis was used to estimate mean macrohabitat depth from the mean of the maximum macrohabitat transect depths by using data collected from all 84 stream reaches in our study. The linear regression explained a large amount of the variation in mean depth, with an r² of 0.91 (P < 0.0001). Therefore, mean depth was estimated using the equation

\[
\text{mean depth} = (0.773 \times \text{mean thalweg depth}) - 0.0224. 
\]

Similarly, the EMAP protocol does not include measurement of current velocity. Therefore, we estimated mean current velocity by using a linear regression equation developed with data collected during our study:

\[
\text{mean current velocity} = (0.0073 \times \text{mean channel width}) + 0.2209. 
\]

Mean channel width explained a small amount of the variation in mean current velocity (r² = 0.17; P < 0.0001), but this was the strongest relationship between it and any of the other habitat variables. We argue that using this equation to estimate mean current velocity was more appropriate than assuming a constant mean current velocity across sites. Among the small-scale variables that were used to develop our species occurrence models, the only one that could not be obtained from the EMAP protocol for the independent data set was the proportion of banks with disturbance on the bank or within 10 m of the bank. Because missing values resulting from different sampling protocols is a real-world scenario, all values for the distance to disturbance variable were set to zero to simulate missing data. We hypothesize that having disturbance within 10 m of the bank is likely to bias the models toward predicting the species as absent, and thus we will obtain a conservative estimate of model performance.

Model-averaged multiple logistic regression models developed with large-scale, small-scale, and multiple-scale data were used to predict the presence or absence of the seven SGCN by using the habitat variables from the independent data set. Optimal thresholds were used to determine whether each species was predicted to be present or absent in stream reaches that were sampled within the species’ respective distribution. Model-predicted presences and absences were compared with the actual presence or absence of each species and were used to calculate...
TABLE 3. Model-averaged parameters and optimal threshold values for large-scale (LS), small-scale (SS), and multiple-scale (MS) multiple logistic regression models of species occurrence. Multiple logistic regression equations are in the form of $P = \frac{e^{\beta_0 + \sum \beta_i x_i}}{1 + e^{\beta_0 + \sum \beta_i x_i}}$, where $P$ = probability of occurrence and $g(x) = b_0 + b_1x_1 + b_2x_2 + b_3x_3$ ($b_0$ is the intercept, $b_1$ to $b_3$ are coefficients, and $x_1$ to $x_3$ are the variables). If $P$ is greater than the optimal threshold value, the species is predicted to be present. See text for definition of optimal threshold; variables are defined in Table 1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Banded darter</th>
<th>American brook lamprey</th>
<th>Ozark minnow</th>
<th>Blackside darter</th>
<th>Southern redbelly dace</th>
<th>Longnose dace</th>
<th>Central mudminnow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LS or SS</td>
<td>MS</td>
<td>LS or SS</td>
<td>LS or SS</td>
<td>LS or SS</td>
<td>LS or SS</td>
<td>LS or SS</td>
</tr>
<tr>
<td>LS or MS optimal threshold</td>
<td>0.378</td>
<td>0.467</td>
<td>0.145</td>
<td>0.056</td>
<td>0.248</td>
<td>0.303</td>
<td>0.314</td>
</tr>
<tr>
<td>SS optimal threshold</td>
<td>0.316</td>
<td>0.206</td>
<td>0.206</td>
<td>0.206</td>
<td>0.212</td>
<td>0.417</td>
<td>0.442</td>
</tr>
</tbody>
</table>

**LS variables**

- Temperature 2 (warmwater): 0.205 ± 0.201
- Subregion 2 (Eastern Broadleaf Forest): 0.225 ± 0.117
- Order: 1.542 ± 0.280
- Elevation: 0.014 ± 0.008
- Gradient: 0.054 ± 0.014

**SS variables**

- Width: 0.205 ± 0.179
- CVWidth: 0.021 ± 0.012
- Depth: 0.655 ± 0.301
- CVDepth: 0.027 ± 0.020
- Velocity: 0.014 ± 0.110
- Pool: 0.001 ± 0.000
- Riffle: 0.000 ± 0.001
- Canopy: 0.000 ± 0.000
- PctBankCover: -0.055 ± 0.009
- Coarse: 0.030 ± 0.031
- Dist10m: 0.000 ± 0.000
- WoodyCover: -0.006 ± 0.005
- VegCover: -0.001 ± 0.002

The same model performance measures (CCR and $\kappa$ value) that were examined for the self-evaluation of model performance.

**RESULTS**

The number of stream reaches that were sampled within the historical distribution of the seven SGCN varied from 34 for the central mudminnow to 83 for the blackside darter, and frequency of occurrence varied from 0.20 for the longnose dace to 0.55 for the southern redbelly dace (Table 2). Large-scale, small-scale, and multiple-scale model-averaged models were created for all seven species; as expected, the optimal threshold values differed from the commonly used value of 0.5 (Table 3). Multiple-scale models had greater $\kappa$ values than most of the large- or small-scale models, and small-scale models tended to have greater $\kappa$ values than large-scale models.

Species occurrence models that were developed with large-scale habitat variables predicted the occurrences of six of the seven species significantly better than chance ($\kappa > 0.0$, $P \leq 0.05$), and $\kappa$ values varied from 0.14 for the American brook lamprey to 0.75 for the longnose dace (mean $\kappa = 0.44$, SE = 0.07; Table 2). Large-scale models correctly predicted 51–92% of species presences and absences, with a mean CCR of 73% (SE = 5). The sum of Akaike weights for all models in confidence model sets in which a variable occurred indicated that all five large-scale variables were important in at least one of the seven species models (Table 4). Stream order was an important variable in four species models, elevation and gradient were important in three models, subregion was important in two models, and temperature was important in one model. Four large-scale variables were important in the blackside darter model, and only one variable was important in Ozark minnow and central mudminnow models.
TABLE 4. Relative importance and the direction of influence for independent variables in large-scale (LS), small-scale (SS), and multiple-scale (MS) species occurrence models for seven Iowa fish species of greatest conservation need. Relative importance for a given variable is the sum of Akaike weights for all models in the confidence model set (i.e., with Akaike’s information criterion difference [AIC] ≤ 6) that included the variable of interest. Values greater than 0.60 (shown in bold italics) provide substantial evidence that the variable is important for predicting the occurrence of the species. Variables are defined in Table 1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Banded darter</th>
<th>American brook lamprey</th>
<th>Ozark minnow</th>
<th>Blackside darter</th>
<th>Southern redbelly dace</th>
<th>Longnose dace</th>
<th>Central mudminnow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
<td>LS or SS MS</td>
</tr>
<tr>
<td>Temperature 2</td>
<td>0.29</td>
<td>0.13</td>
<td>0.31</td>
<td>-0.08</td>
<td>-0.25 -0.14</td>
<td>0.65</td>
<td>0.32</td>
</tr>
<tr>
<td>(warmwater)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subregion 2 (Eastern Broadleaf Forest)</td>
<td>0.35</td>
<td>0.11</td>
<td>0.44</td>
<td>0.15</td>
<td>0.82</td>
<td>0.29</td>
<td>-0.30 -0.04</td>
</tr>
<tr>
<td>Order</td>
<td>1.00</td>
<td>0.25</td>
<td>0.84</td>
<td>0.11</td>
<td>-0.27 -0.10</td>
<td>-0.67</td>
<td>-0.48</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.89</td>
<td>0.49</td>
<td>1.00</td>
<td>1.00</td>
<td>0.59</td>
<td>0.56</td>
<td>-0.61 0.73</td>
</tr>
<tr>
<td>Gradient</td>
<td>0.33 -0.08</td>
<td>-0.32 -0.09</td>
<td>0.25</td>
<td>-0.04</td>
<td>-0.80 -0.28</td>
<td>0.37</td>
<td>0.15</td>
</tr>
<tr>
<td>Width</td>
<td>0.99</td>
<td>0.87</td>
<td>0.85</td>
<td>0.87</td>
<td>0.12</td>
<td>0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>CVWidth</td>
<td>0.27</td>
<td>0.16</td>
<td>0.27</td>
<td>0.15</td>
<td>0.18</td>
<td>0.08</td>
<td>-0.10 -0.04</td>
</tr>
<tr>
<td>Depth</td>
<td>0.22</td>
<td>0.10</td>
<td>0.15</td>
<td>0.12</td>
<td>0.11</td>
<td>0.05</td>
<td>0.37</td>
</tr>
<tr>
<td>CVDepth</td>
<td>0.44</td>
<td>0.33</td>
<td>0.60</td>
<td>0.18</td>
<td>0.99</td>
<td>1.00</td>
<td>-0.94 -0.62</td>
</tr>
<tr>
<td>Velocity</td>
<td>0.11</td>
<td>0.07</td>
<td>-0.16</td>
<td>-0.08</td>
<td>-0.48</td>
<td>-0.31</td>
<td>-0.62</td>
</tr>
<tr>
<td>Pool</td>
<td>0.11</td>
<td>0.05</td>
<td>0.33</td>
<td>0.16</td>
<td>0.61</td>
<td>-0.58</td>
<td>0.11</td>
</tr>
<tr>
<td>Riffle</td>
<td>-0.12</td>
<td>0.08</td>
<td>-0.50</td>
<td>-0.09</td>
<td>-0.11</td>
<td>-0.05</td>
<td>-0.14</td>
</tr>
<tr>
<td>Canopy</td>
<td>0.10</td>
<td>-0.05</td>
<td>0.10</td>
<td>-0.09</td>
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Species occurrence models that were developed with small-scale variables predicted the occurrences of all seven species significantly better than chance, with k values varying from 0.21 for the American brook lamprey to 0.77 for the longnose dace (mean k = 0.49, SE = 0.08). Small-scale models correctly classified 55–92% of species presences and absences, with a mean CCR of 75% (SE = 5). Of the 13 small-scale variables that were hypothesized to influence fish species distributions, 9 of the variables were identified as important in small-scale models (Table 4). Mean stream width and mean CV of depth were the variables that were most commonly designated as important; they were identified as important in the small-scale models for three species. The number of important small-scale variables varied from zero in the central mudminnow model to three in the banded darter, Ozark minnow, and blackside darter models. Although the small-scale model performed better than the large-scale model for central mudminnow, no small-scale variables were identified as important; this is likely attributable to the small number of stream segments (i.e., 34) that were sampled within the central mudminnow’s distribution, and spurious correlations probably accounted for the explained variation in occurrence.

For six of the seven species, multiple-scale models had a higher k value and CCR than either the large- or small-scale models (Table 2). The k values were significantly greater than zero for all multiple-scale models, varying from 0.27 for the American brook lamprey to 0.88 for the longnose dace (mean k = 0.59, SE = 0.07). Six of the multiple-scale models had k values greater than 0.40, suggesting moderate to substantial performance. The CCRs for most of the multiple-scale models were relatively high (79–96%), but the percentage of correctly predicted presences and absences was low (CCR = 58%) for the American brook lamprey (Table 2). As expected, the habitat variables identified as important in multiple-scale models were similar to those identified for the large-scale and small-scale models; however, only three of the large-scale variables were important in at least one multiple-scale model (Table 4). Although stream order was important in the large-scale models for four species, stream width (a small-scale variable) was selected as a more appropriate measure of stream size in the multiple-scale models. Six of the variables that were important in small-scale models were also important in multiple-scale models, and the variable representing the availability of instream vegetation cover (e.g., aquatic macrophytes and overhanging vegetation)
FIGURE 2. Qualitative associations of seven fish species of greatest conservation need with large-scale and small-scale habitat variables measured in wadeable Iowa streams. Quantitative relationships supporting these associations were primarily obtained from the multiple-scale model summary statistics shown in Tables 4 and 5.

was identified as important in the American brook lamprey’s multiple-scale model even though it was not important in the small-scale model.

Multiple-scale models predicted the occurrence of most fish SGCN with the greatest accuracy; thus, the habitat variables that were identified as important in each species’ multiple-scale model were weighted the most for interpretation. Stream size (stream order and stream width) or gradient variables were important in multiple-scale models for five of the seven species (Table 4). Thus, the importance of these variables in species occurrence models was used in combination with model-averaged coefficient values to conceptualize the relative associations with the occurrence of each species (Figure 2). For example, the occurrence of southern redbelly dace was associated with narrow streams, whereas the occurrence of banded darters and American brook lampreys was associated with larger streams. Similarly, the occurrence of longnose dace was associated with high-gradient streams, while central mudminnow occurrence was associated with low-gradient streams. Neither stream size nor gradient was important in the multiple-scale models for the blackside darter and Ozark minnow, but the large-scale model showed that blackside darter occurrence was associated with smaller, low-gradient streams. Furthermore, up to three other variables were identified as important in each species’ multiple-scale model.

Stream reaches in the independent data set were sampled from 28 of the 34 eight-digit HUC watersheds in the Mississippi River drainage of Iowa. From 15 to 54 stream reaches were sampled within the selected species’ historical distributions and each species was collected in 1 (Ozark minnow and central mudminnow) to 16 (southern redbelly dace) stream reaches (Table 5). When applied to the independent data set, large-scale models were able to predict the occurrences of banded darters, American brook lampreys, southern redbelly dace, and longnose dace significantly better than random chance, but they could not predict the occurrence of Ozark minnow, blackside darters, or central mudminnow better than random chance (Table 5). Although small-scale models performed better than large-scale models for the model development data set, when the small-scale models were applied to the independent data set, they only predicted the occurrences of banded darters and longnose dace better than would be expected by random chance. When variables measured at both the large and small scales were included in the multiple-scale models, the presence or absence of Ozark minnow, blackside darters, and central mudminnow was still not predicted more accurately than would be expected by chance. However, multiple-scale models predicted the occurrences of banded darters, southern redbelly dace, and longnose dace better than large- or small-scale models.
An understanding of factors that influence the distribution of fish species is vital for conservation success, and models that predict species occurrences may serve as a useful tool for fisheries managers. We developed models that accurately predicted the occurrences of all seven Iowa fish SGCN and identified important associations with both large-scale and small-scale habitat features. Most species occurrences were effectively predicted by using either large- or small-scale variables, and the most influential habitat features and spatial scale varied by species. As hypothesized, the inclusion of variables that were measured at both spatial scales predicted the occurrences of fish SGCN with the greatest accuracy.

Physical and biological changes along the longitudinal gradients of streams are well documented (Vannote et al. 1980), and large-scale environmental gradients have been shown to influence the longitudinal distribution of fish species (Rahel and Hubert 1991; Quist et al. 2004). Consistent with the results of others, we found that large-scale measures of stream order (Paller 1994), elevation (Quist et al. 2004), channel gradient (Pont et al. 2005), temperature (Buisson et al. 2008; Lyons et al. 2010), and aquatic subregion each had an important influence on the distribution of at least one of the seven fish species. Stream order, elevation, and gradient were among the most important variables in large-scale models, suggesting that Iowa stream fish assemblages may be strongly influenced by longitudinal gradients and stream size thresholds. Similarly, Quist et al. (2004) showed that fishes persisted within specific elevation and stream width boundaries in Wyoming streams. In the present study, we found that southern redbelly dace were common in small second- and third-order streams, but banded darters and American brook lampreys were never collected from a stream that was less than third order. Paller (1994) reported similar associations between fish assemblages and stream order in following patterns of species additions and replacements. Models for three Iowa fish SGCN identified important associations with stream gradient. Longnose dace were generally sampled from higher-gradient streams, including the two highest gradient streams sampled (i.e., 7.0–13.0 m/km). In contrast, blackside darters and central mudminnow were only sampled in low-gradient streams for which gradient did not exceed 3.0 m/km. The positive association between longnose dace occurrence and gradient likely reflects this species’ similar positive association with riffle habitat availability. This result is consistent with what others have reported as common longnose dace habitat in Iowa (Harlan and Speaker 1969). Central mudminnow are suggested to occupy habitats with little to no current, silty substrates, and usually the presence of vegetation (Harlan and Speaker 1969; Martin-Bergmann and Gee 1985); thus, high-gradient streams would not be expected to provide suitable habitat conditions for central mudminnow.

Iowa topography is relatively gentle, and the elevation of streams sampled for this study only varied from 189 to 387 m. Thus, the importance of elevation in the occurrence models for four of the species was unexpected. Quist et al. (2004) suggested that elevation acts as a proxy for temperature, which influences the survival, growth, reproduction, and distribution of fish (Buisson et al. 2008; Lyons et al. 2010; Robinson et al. 2010). Although elevation probably does not act as a surrogate measure for temperature in Iowa, differences in elevation likely correspond to differences in underlying geology and climate across the state. The subregion variable similarly differentiates between two Iowa regions that have different underlying physiographic features. Heitke et al. (2006) showed that fish assemblages and physical habitat conditions vary significantly across Iowa’s ecoregions. Subregions may also represent regions with unique aquatic biodiversity as a result of processes such as speciation, colonization, and extinction. For example, there is a unique group of fishes—including the Ozark minnow—that exhibits two disjunct distributions: one distribution extends into the Eastern Broadleaf Forest subregion of Iowa, and the other is found in the northern Ozarks of southern Missouri and surrounding states. Berendzen et al. (2010) showed that this unique, disjunct distribution is likely attributable to the expansion of fishes from the northern Ozarks into the Paleozoic Plateau of Iowa after glacial periods, followed by isolation of the two populations.
as suitable habitats between the two regions were lost due to glacial deposition of loess and till. Our results were consistent with this hypothesis and showed that the occurrences of Ozark minnow and southern redbelly dace were positively associated with the Eastern Broadleaf Forest subregion. Our results also suggest that southern redbelly dace are not constrained by specific small-scale habitat features within stream reaches where large-scale habitat conditions are suitable. These results are not surprising, as southern redbelly dace are recognized as being prevalent in headwater streams of the Eastern Broadleaf Forest subregion in Iowa (Harlan and Speaker 1969). Thus, the sole use of GIS-measured variables representing stream order and subregion can accurately predict southern redbelly dace occurrence in the Mississippi River drainage of Iowa. In contrast, even though the distribution of Ozark minnow is constrained to northeast Iowa (Harlan and Speaker 1969), small-scale variables predicted the occurrence of Ozark minnow better than the subregion variable or any combination of large-scale variables. Ultimately, the multiple-scale model was able to predict the occurrence of Ozark minnow with the greatest accuracy and indicated that Ozark minnow occurrence was positively associated with depth variability and negatively associated with proximity to anthropogenic disturbance. This is consistent with the work of Pfieger (1997) who reported that Ozark minnow inhabit areas of slow current in fast-flowing streams, which is indicative of high depth variability.

Similar to large-scale variables, we found that many small-scale variables were important for predicting the occurrence of fish SGCN. Understanding the small-scale physical habitat requirements of stream fish species has long been a central theme of fish ecologists (Schlosser 1982; Hubert and Rahel 1989). Early work by Gorman and Carr (1978) related fish species to specific instream physical habitat measures (e.g., depth, substrate, and velocity) and showed a positive relationship between species diversity and habitat diversity. Later, Leonard and Legendre (2009) showed that environmental factors were important in structuring biotic communities in high-flow lotic systems but that biotic interactions were more influential in low-flow lotic systems. Pont et al. (2005) showed that the influences of regional-scale and small-scale processes on species occurrence were species specific rather than system specific. Similarly, we found differences in the relative influence of large-scale and small-scale habitat features on each fish species. Thus, it is important to determine the appropriate scale for management efforts on a case-by-case basis because models that are developed in one region or for one species are unlikely to exhibit generality to another region or species. Many studies have focused on determining the spatial scale that is most influential on stream biotic communities, but the results are inconsistent. For example, Creque et al. (2005) developed models to predict the density of five sport fish species in Michigan rivers by using only GIS-measured landscape variables and only small-scale habitat variables; models that were developed with landscape variables explained more variation than models that were developed with small-scale variables. In contrast, Rich et al. (2003) found that variation in the occurrence of bull trout Salvelinus confluentus in a Montana watershed was explained to a greater extent by small-scale abiotic and biotic variables than by large-scale variables. Although either large- or small-scale variables may accurately predict the distribution of fish species, Leftwich et al. (1997) suggested that incorporating variables from multiple spatial scales is likely to improve the generality of models and to provide the greatest interpretive value. Our results support this conclusion in that models incorporating both large-scale and small-scale variables predicted fish species occurrences with the greatest accuracy. Specifically, our multiple-scale models correctly predicted the occurrences of the seven species 58–96% of the time, with κ values varying from 0.27 to 0.88. Pont et al. (2005) similarly used multiple logistic regression models with variables measured at multiple spatial scales to predict the occurrences of 13 common fish species in France; they reported CCRs of 71–92% and κ values from 0.10 to 0.61. When applied
to an independent data set, our multiple-scale models generally exhibited better performance than the large- or small-scale models. Specifically, the occurrences of banded darters, southern redbelly dace, and longnose dace were predicted considerably better by multiple-scale models than by single-scale models. These results emphasize the importance of understanding the influence of factors acting at multiple spatial scales before making important conservation decisions. The largest spatial scale at which factors are constraining species occurrences should be treated as a limiting factor; unless management efforts address issues at that scale, the success of such efforts will be limited. For example, increasing fish species diversity with small-scale habitat manipulations may be unsuccessful if water quality or connectivity issues are the limiting factor (Tonn 1990; Pretty et al. 2003). Results from this study suggest that habitat restoration efforts to create riffle habitats for longnose dace could be unsuccessful if implemented in low-gradient streams.

Despite the large number of habitat variables considered in our species occurrence models, none of the variables provided measures of temporal variability, which may have the ability to increase predictive power. For example, the timing of flooding events may greatly influence fish assemblages (Harvey 1987). In Oregon, Pearson et al. (1992) documented changes in fish assemblages before and after flood events and linked assemblage resilience to flood events with hydraulic complexity. As a result of agricultural practices (e.g., drainage tiling and channelization) in Iowa, the hydrologic regimes of stream systems are highly altered, and the intensity, timing, and frequency of flood events are likely to influence aquatic communities (Meyers et al. 2010). Similarly, the location and magnitude of fish barriers (e.g., dams, culverts, and grade-control structures) can fragment populations and prevent source populations from re-colonizing suitable habitats (Compton et al. 2008; Litvan et al. 2008). Variables that characterize water quality and biotic interactions may also explain further variation in species occurrences. For example, predation and competition have been shown to influence fish assemblage structure (Fausch and White 1981; Power et al. 1985), and variables characterizing the presence of predators or the abundance of predators have been used to improve predictive power in recent species distribution models (Rich et al. 2003; Quist et al. 2005). The number of factors that potentially influence fish assemblages and species distributions is immeasurable; therefore, understanding the factors that explain the most variation in species occurrences and the linkages between those factors across spatial scales will improve the efficiency of conservation efforts.

Our study is one of the few studies that have used an independent data set to validate fish species occurrence models and to quantify confidence in model predictions (e.g., Leftwich et al. 1997; Steen et al. 2008). Most often, species occurrence models fail to accurately predict species distributions outside of the region for which the models were developed. For instance, Porter et al. (2000) developed models that predicted the occurrence of 13 fish species in the Blackwater River drainage, British Columbia, with CCRs of 73–90%, but the accuracy of the models greatly decreased when they were applied to data collected in a distant drainage. Results of our model validation with an independent data set showed that large-scale and multiple-scale models were able to predict the occurrences of banded darters, American brook lampreys, southern redbelly dace, and longnose dace better than random chance. In a concurrent study (Sindt et al. 2012), we also found that models created with large-scale explanatory variables (Iowa Aquatic Gap Analysis Project models; Loan-Wilsey et al. 2005) predicted the occurrences of banded darters, southern redbelly dace, and longnose dace better than would be expected by random chance, but this was not the case for nine other species, including the American brook lamprey, Ozark minnow, and blackside darter. Thus, in Iowa, the most effective variables for predicting the occurrences of many fish SGCN, including the Ozark minnow and blackside darter, are still undetermined. The combined results of the present study and our previous study (Sindt et al. 2012) further emphasize the importance of understanding the most appropriate scale for management and conservation efforts on a species-by-species and system-by-system basis. Therefore, we caution that even though several of our models exhibited generality when validated with an independent data set, they might not be effective outside of the Mississippi River drainage in Iowa.

An understanding of factors that shape the distribution of fish species across spatial scales is important for resource managers and is vital to conservation success. For this study, we adopted an exploratory approach to identify abiotic variables measured at two spatial scales influencing the occurrences of fish SGCN in wadeable Iowa streams and to provide insight into species ecology. Our results suggest that managing for stream fish biodiversity requires the protection and restoration of habitat complexity across a broad spectrum of large-scale habitat conditions. The performance of our models complements other studies in which large-scale and small-scale habitat features were found to explain variability in species occurrences. However, we have also shown that the most influential spatial scale and habitat variables are species specific and that the incorporation of variables measured at multiple spatial scales provides the greatest model generality.

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The Potential for Vessel Interactions with Adult Atlantic Sturgeon in the James River, Virginia


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MANAGEMENT BRIEF

The Potential for Vessel Interactions with Adult Atlantic Sturgeon in the James River, Virginia

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Abstract

In 2012, all populations of Atlantic sturgeon Acipenser oxyrinchus oxyrinchus were listed as either threatened or endangered under the U.S. Endangered Species Act. During 2007–2010, researchers documented 31 carcasses of adult Atlantic sturgeon in the tidal freshwater portion of the James River, Virginia. Twenty-six of the carcasses had gashes from vessel propellers, and the remaining five carcasses were too decomposed to allow determination of the cause of death. The types of vessels responsible for these mortalities were not explicitly demonstrated. Most (84%) of the carcasses were found in a relatively narrow reach that was modified to increase shipping efficiency. To explore the number of Atlantic sturgeon being hit and their horizontal and depth distributions in relation to vessel draft, we conducted telemetry experiments on three living fish (all males) and six dead specimens. While staging (holding in an area from hours to days, with minimal upstream or downstream movements), the adult male Atlantic sturgeon spent most (62%) of the time within 1 m of the river bottom. Assuming that behavior is not modified by vessel noise, adult male Atlantic sturgeon in the James River would rarely encounter small recreational boats or tugboats with shallow drafts; instead, mortalities are likely caused by deep-draft ocean cargo ships, which have drafts that coincide with the distribution of the tracked adult males. Dead specimens (n = 6) drifted with the current for several hours to almost 4 d before beaching at distances ranging from 0.5 to over 50 river kilometers from the point of release. We estimated that current monitoring in the James River documents less than one-third of vessel strike mortalities. A better understanding of Atlantic sturgeon behavior in the presence of vessels will aid in restoring this federally endangered species.

The Atlantic sturgeon Acipenser oxyrinchus oxyrinchus is an anadromous fish that was abundant along the Atlantic slope of the USA until the early 20th century (Smith 1985; Bain 1997; Secor et al. 1997; Atlantic Sturgeon Status Review Team 2007). Due to unsustainable harvest, habitat loss, pollution, and
dam construction, Atlantic sturgeon populations are severely depleted in the USA (Boreman 1997; Smith and Clugston 1997). During peak harvest at the end of the 19th century, the Chesapeake Bay was the second-largest producer of Atlantic sturgeon products in the USA (Secor 2002); however, by the end of the 20th century, the Chesapeake Bay Atlantic sturgeon population was considered functionally extirpated (Secor 1996; Speir and O’Connell 1996). Because of high spawning fidelity, a genetically distinct population segment of Atlantic sturgeon has developed in the Chesapeake Bay (King et al. 2001). In 2012, the Chesapeake Bay distinct population segment was listed as endangered under the U.S. Endangered Species Act.

The James River, Virginia, is one of two Chesapeake Bay tributaries with verified spawning success of Atlantic sturgeon over the past decade (Atlantic Sturgeon Status Review Team 2007; H. Brooks, Virginia Institute of Marine Science, unpublished data). Between 2007 and 2011, over 130 adult Atlantic sturgeon were collected in the tidal freshwater portion of the James River above river kilometer (rkm) 108.

Vessel interactions with aquatic species may have serious consequences that hinder the recovery of endangered species, including the Florida manatee *Trichechus manatus latirostris* (Laist and Shaw 2006) and various sea turtle families (Cheloniidae and Dermochelyidae; Chaloupka et al. 2008). Vessel interactions with sturgeon species have been documented in the Mississippi River drainage (shovelnose sturgeon *Scaphirhynchus platorynchus*: Gutreuter 2003) and in the Delaware River (Atlantic sturgeon: Brown and Murphy 2010). Each year since 2007, adult Atlantic sturgeon carcasses have been found between rkm 102–126 during the fall (August 29–November 8), within the riparian zone of the tidal freshwater portion of the James River. Of the 31 recovered carcasses, 26 were dismembered or had gashes that resembled vessel propeller strikes (Figure 1) and the remaining five carcasses were too decomposed to permit determination of the cause of death. None of the recovered Atlantic sturgeon carcasses was without evidence of propeller strike, thus indicating that propeller injuries are the cause of the mortalities in the James River. During our observations, gash marks have only been found on the dorsal aspect except when the cut extends all the way through the fish. Fish must have had a normal, erect posture when struck and were likely alive at the time of the propeller strike because dead

![Image](https://example.com/image1)

**FIGURE 1.** Examples of Atlantic sturgeon that were hit by vessel propellers in the James River, Virginia, during fall (2007–2010). Most (84%) of the 31 carcasses were found above rkm 115, and all were estimated to be over 148 cm FL: (A) a postspawn female (183 cm FL) with large gashes on the dorsal side; (B) a male (162 cm FL), also with large gashes on the dorsum; and (C), (D) males (both ~150 cm FL) that were dismembered.
Atlantic sturgeon float ventral side up. Therefore, the gashes were unlikely to have occurred postmortem. Propeller marks have also been lacking on the ventral side of Atlantic sturgeon carcasses found in the Delaware River (Matthew Fisher, Delaware Department of Natural Resources and Environmental Control [DNREC], personal communication). On October 10, 2009, within 10 min after an ocean cargo ship passed by, a video was taken of an Atlantic sturgeon actively swimming at the surface with most of its head and tail dismembered. Although most of the carcasses have been found by researchers (Virginia Commonwealth University [VCU] and James River Association), there has been no designated project to monitor for Atlantic sturgeon carcasses in the James River. Several other Atlantic sturgeon carcasses were reported by recreational boaters during the study period, but most were not confirmed and therefore were not included in the present analysis.

The threat of vessel strike in riverine habitats could compromise Atlantic sturgeon recovery efforts by removing spawning adults from the population (Boreman 1997; Brown and Murphy 2010). Vessel interaction is listed as a contributing factor for the decline of Atlantic sturgeon (Atlantic Sturgeon Status Review Team 2007), but the actual number of vessel strike mortalities in the James River is unknown. The absence of information on population size makes it difficult to ascertain the proportion of spawning Atlantic sturgeon that are killed in the James River due to vessel strikes. The vessel types that are striking adult Atlantic sturgeon and the locations of such interactions in the James River are also unknown. The objectives of the present study were to (1) determine the amount of time spent by adult Atlantic sturgeon at depths corresponding to various vessel propeller drafts, (2) identify areas where interactions between vessels and adult Atlantic sturgeon are most likely to occur, and (3) estimate the proportion of undetected vessel strike mortalities of adult Atlantic sturgeon.

**STUDY AREA**

The James River is the southernmost major tributary of the Chesapeake Bay (Figure 2). The freshwater tidal portion of

![Figure 2](image-url)
the river extends upstream to Richmond, Virginia, at rkm 155. River width varies between 0.7 and 7.1 km up to rkm 120 and then narrows to a range of 0.1–0.4 km. The federal navigation channel that is maintained by the U.S. Army Corps of Engineers (USACE) extends from the river mouth to rkm 150. The channel is maintained to a minimum depth of 7.6 m and minimum width of 91.4 m. The Port of Richmond (at rkm 145) is the major destination for deep-draft vessel traffic occurring upstream of rkm 120 (i.e., where the river narrows). The area upstream of rkm 120 also accommodates tugboat and recreational boat traffic.

In 1934, the James River channel was modified by construction of a channel through an oxbow at rkm 120 to improve shipping efficiency. The smallest river width at this location is about 125 m. From 2007 to 2011, over 130 live adult Atlantic sturgeon have been caught and released within 2 rkm downstream of the modified river channel; thus, the area seems to be an aggregation spot for adult Atlantic sturgeon during the putative fall spawning period. Most (84%) of the 31 adult Atlantic sturgeon carcasses were found within 4 rkm of rkm 120 (Figure 2). Because of the large number of live adult Atlantic sturgeon that have been collected and the high percentage of carcasses that have been found in this area, we hypothesized that the narrow cut-through above rkm 120 represents a location where Atlantic sturgeon are being struck by vessel propellers. During the study period, an ocean cargo ship completed one round trip to the Port of Richmond each week, and tugboat and recreational boat traffic was common.

METHODS

Live fish tracking.—During fall 2008, three live adult male Atlantic sturgeon (spermiating males; fish A–C) were collected by gill nets within 3 rkm of rkm 120 (Figure 2) and received implanted (Kahn and Mohead 2010) Vemco V16 passive acoustic transmitters (estimated tag life = 1,630 d) and Vemco V13 ultrasonic transmitters (estimated tag life = 30 d) equipped with a depth sensor (range = 50 m; resolution = 0.22 m; accuracy = ±0.5%) set at 0.75-s bursts. Because female Atlantic sturgeon were rarely collected, no live females were tagged for the study. Range tests of the tracking tags were conducted by anchoring the boat in a fixed position and anchoring the tags at 10-m intervals between 10 and 200 m from the boat. Tags were tracked by using both omnidirectional and directional hydrophones. To minimize potential handling effects on fish behavior, data from the first 24 h of each track were excluded from the analysis. Individuals traveled a minimum of 2.7 km within the first 24 h and were therefore active after surgery. After the initial 24-h period, fish A was tracked for 33 h over the next 60 h, fish B was tracked for 55 h over the next 106 h, and fish C was tracked for 83 h over the next 172 h. Each fish was tracked by boat during daytime and nighttime. Tracks were edited for accuracy, and spatial analysis was conducted using ArcMap (ArcGIS version 10; ESRI).

Vemco ultrasonic tag transmissions may be received at a distance of up to 1.5 km (Vemco support, personal communication), which complicated our ability to determine a fish’s location. We used the Global Positioning System points of the tracking boat’s location for analysis. To best approximate the position of a tracked fish, the strongest signal from the first 30-s period and last 30-s period of each minute was used to infer the fish’s position. Because the channel width is a minimum of 91.4 m, we only used pings that were emitted within 100 m of the boat. River bathymetry was determined by using the approach harbor soundings point shapefile (National Oceanic and Atmospheric Administration, http://www.nauticalcharts.noaa.gov/csdl/ctp/encdirect_new.htm).

Three major vessel types frequent the tidal freshwater portion of the James River: ocean cargo ships, tugboats, and small recreational craft. The three vessel types have dissimilar drafts (≤1.0 m for small recreational craft; ≤2.3 m for tugboats; ≤7.3 m for ocean cargo ships when fully loaded); thus, their propellers are at different depths within the water column (Sarah Cameron, USACE Norfolk District, personal communication). Fish depths and locations were analyzed to determine the time spent by the fish within the draft depth of each vessel type. Bathymetry data were also used to determine water column preferences and time budgeting of tracked fish (100% = fish is at the surface; 0% = fish is at the bottom).

Carcass tracking.—Between September 2 and October 8, 2009, long-range (>1.6 km) radio tags (Advanced Telemetry Systems) were implanted into six carcasses of adult Atlantic sturgeon to assess mortality drift. Three of the carcasses were fresh mortalities with large gashes, and those carcasses were positively buoyant. Two previously frozen carcasses were placed into a holding pen in the river and were deployed after they became positively buoyant. A third frozen carcass was allowed to thaw and was released when its internal body temperature was equal to the water temperature; the carcass sank to the bottom during initial release. Carcasses were released at approximately rkm 120 during incoming or outgoing tides. Carcasses were re-deployed multiple times until they were too decomposed to handle; in total, 17 drifts were conducted. Carcasses were considered “deposited” if they remained in the same spot over a complete tide cycle. River discharge was monitored at rkm 110 to determine whether any abnormal discharge events occurred during the carcass tracking period, as such events might affect the locations of carcass deposition.

RESULTS

Live Fish Tracking

The three live Atlantic sturgeon were tracked over a 55-rkm stretch of the James River (rkm 76–131) over an 8-d period (Figure 3). The fish were present in the federal navigation channel 69% of the time while being tracked (Table 1), and there was no noticeable pattern to when or where they left the navigation channel. On average, fish spent 51% of the tracking time at depths that coincided with the deep-draft ocean cargo ship draft, whereas they were rarely located at
TABLE 1. Percentage of time (based on the total tracking time or the time within the federal navigation channel) for which three actively tracked adult male Atlantic sturgeon inhabited depths corresponding to the drafts of various vessel types. The average area of water column indicates the percentage of the water column that was inhabited by the tracked fish (100% = at the surface; 0% = at the bottom). The total tracking time was 33 h for fish A, 55 h for fish B, and 83 h for fish C.

<table>
<thead>
<tr>
<th>Vessel type (draft depth)</th>
<th>Small recreational craft (≤ 1.0 m)</th>
<th>Tugboat (≤ 2.3 m)</th>
<th>Ocean cargo ship (≤ 7.3 m)</th>
<th>Below all draft depths (%)</th>
<th>Average area water column (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>Time (%) in navigation channel</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>67</td>
<td>0</td>
<td>0</td>
<td>49</td>
<td>50</td>
</tr>
<tr>
<td>B</td>
<td>83</td>
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<tr>
<td>C</td>
<td>56</td>
<td>0</td>
<td>&lt;1</td>
<td>84</td>
<td>15</td>
</tr>
</tbody>
</table>

Total tracking time

| Fish | Time (%) in navigation channel | Small recreational craft (≤ 1.0 m) | Tugboat (≤ 2.3 m) | Ocean cargo ship (≤ 7.3 m) | Below all draft depths (%) | Average area water column (%) |
| A | 100 | 0 | 0 | 58 | 42 | 7 |
| B | 100 | 0 | 0 | 22 | 78 | 9 |
| C | 100 | 0 | <1 | 87 | 12 | 36 |

Time within the navigation channel

FIGURE 3. Map of the James River (river kilometer 72–134) channel and the active tracks of three tagged adult male Atlantic sturgeon. Fish were released at rkm 120, where the river’s width narrows by over 60%. Note that the fish tracks were mostly confined within the navigation channel. Fish A and B made no long, directional movements while being tracked; they mostly stayed stationary or slowly moved back and forth in a small area. In contrast, fish C made a 21-rkm downstream movement that took 7 h, and this fish maintained a depth of about 5 m below the surface.
the depths utilized by tugboats and small recreational craft (Table 1; Figure 4). Upstream of rkm 120, fish were within the draft of ocean cargo ships 93% of the time. Fish A and B moved slowly back and forth with and against tidal flow and remained within 2 m of the bottom about 80% of the time (Figure 4). When downstream of rkm 120, fish B spent 20 h (19% of the total hours of tracking) in deep holes and therefore was out of propeller range for all vessel types. While making a 7-h, 21-rkm downstream movement, fish C was within the navigation channel and ocean cargo ship draft 72% of the time. Fish C did not remain consistently on the bottom but maintained a depth of roughly 5 m below the surface, even in water that was deeper than 11 m (Figure 4). Cumulative histograms (Figure 4) indicated that fish A and B spent half of their time within 1 m of the bottom and fish C spent half of its time within 4 m of the bottom; fish C remained higher in the water column than fish A and B, which were relatively stationary while being tracked.

**Carcass Tracking**

During the carcass tracking period, there were no major discharge events that might have influenced carcass deposition locations. Carcasses ($n = 6$; deployed multiple times) were located after 16 of the 17 instances in which they were set adrift. The frozen carcass that initially sank stayed stationary on the bottom for almost 3 d until it became positively buoyant and started to move. Similarly, the two frozen carcasses that were placed into a pen became positively buoyant within 3 d. During tracking, positively buoyant carcasses remained at the surface in a ventral-side-up orientation until stranded. Distances of carcass drift from the release point ranged from 0.5 to 52.6 rkm, with an average of 10.8 rkm (SD = 13.8; Figure 2), and the average drift time was 40 h (SD = 24; range = 4–93 h). The drifting carcasses were observed moving back and forth with the tide several times before they were deposited. At least twice, a carcass was pushed onto the beach by the incoming tide but drifted off during the next outgoing tide. Carcass deposition was witnessed six times; in four of those cases, deposition occurred within 1 h of tide change. Only 5 (31%) of the 16 carcass deployments resulted in deposition of carcasses in areas where they would likely be found by using current monitoring techniques. For the remaining 11 deployments (69%), the carcasses were deposited in areas that are rarely frequented by researchers. Furthermore,
several carcasses were covered by vegetation or driftwood and were obscured from view when observed from the water; however, this factor was not used to determine whether the carcasses would be considered found or not.

**DISCUSSION**

The Atlantic Sturgeon Status Review Team (2007) stated that rivers with narrow channels and large-vessel traffic have high incidences of vessel strikes on adult Atlantic sturgeon. Brown and Murphy (2010) described the number of mortalities and the potential impact of vessel interactions on the Atlantic sturgeon population in the Delaware River. To our knowledge, the present study is the first published study involving the use of active telemetry to explore vessel interactions with adult Atlantic sturgeon. River morphology constrains adult Atlantic sturgeon to the navigation channel while they inhabit the tidal freshwater portion of the James River above rkm 120 during fall. Large ocean cargo ships are the main vessel type whose draft intersects with the distribution of adult male Atlantic sturgeon residing in the river during the fall.

Ryder (1890) noted that spawning Delaware River Atlantic sturgeon tended to stay on the bottom except when exhibiting rapid movements. Fish A and B moved minimally while being tracked, and they occupied a position within 1 m of the river bottom, similar to the behavior of white sturgeon *A. transmontanus* in the Kootenai River, British Columbia (Paragamian and Duehr 2005). Most areas of the James River above rkm 120 are maintained at the minimum navigable channel depth of 7.6 m; therefore, Atlantic sturgeon that utilize the tidal river above rkm 120 are consistently at ocean cargo ship propeller depth. The federal navigation channel occupies a 25-rkm stretch with a narrow width and channel depth, forming an area of increased injury and mortality risk from ocean cargo ships in comparison with downstream areas, which contain deepwater refuges for adult Atlantic sturgeon. While being tracked during a 7-h downstream movement of 21 rkm, fish C maintained a depth of about 5 m below the surface, even in water that was deeper than 11 m (Figure 4). Passive telemetry data from fish that returned twice in subsequent years indicated that the fish maintained depths similar to those indicated by the active tracking data. On one occasion, a fish was actively tracked during an encounter with an ocean cargo ship while in the cut-through above rkm 120. Because the tracking boat had evacuated the immediate vicinity, it was not possible to observe the fish’s behavior as the ocean cargo ship passed through the area. However, when we returned (moments after the cargo ship moved through that portion of the cut-through), we found that the fish had maintained approximately the same position before and after the passing of the ocean cargo ship. This observation was made within the first 24 h after tag implantation.

Atlantic sturgeon carcasses drifted much further than we hypothesized based on recovery distribution. Of the 16 deployments of carcasses that were later found, only 31% (*n* = 5) resulted in carcass deposition in areas that are frequented by researchers or the riverkeeper. The other 69% of deployments resulted in the carcasses being deposited in areas that are not monitored as part of other projects. If only 31% of the vessel strike mortalities that occurred from 2007 to 2010 were found, then extrapolation suggests that 80 adult Atlantic sturgeon were killed during that period. Only 21% of the constricted reach of the James River is monitored by other research projects in the area, leaving the remaining 79% of the reach mostly uninvestigated. Therefore, the estimate of 80 mortalities is extremely conservative. Gutreuter et al. (2003) estimated a propeller entrainment rate of 0.53 shovel-nose sturgeon per kilometer traveled by towboats in some areas of the Mississippi and Illinois rivers. The Gutreuter et al. (2003) study applies to commercial ships in narrow channels, similar to the situation with ocean cargo ships in the James River.

The drift movement of Atlantic sturgeon carcasses complicates the determination of vessel strike location. Carcasses can drift over 52 rkm in the James River, requiring a large area to be surveyed. We frequently found mortalities on bare beaches; however, many of the carcasses were deposited in areas covered by vegetation and driftwood, thus hindering researchers’ ability to locate dead Atlantic sturgeon when monitoring from boats.

Vessel traffic is expected to continue in the tidal freshwater portion of the James River. Due to the hard-bottom substrate, deeper channel dredging is unlikely to be implemented in this area. Therefore, vessel strikes will likely continue and may hinder the recovery of the Atlantic sturgeon population. Future work is needed to better understand Atlantic sturgeon behavior in the presence of vessels in order to reduce encounters. In addition, a dedicated monitoring program would allow a more accurate enumeration of adult Atlantic sturgeon mortalities during riverine residence.

**ACKNOWLEDGMENTS**

We thank Douglas Clarke and Charles Dickerson (USACE Engineer Research and Development Center); Peter Sturke, Brianna Langford, and David Hopler (VCU); and Christian Hager (Virginia Sea Grant) for their assistance with data development. We are also grateful to William Shuart and Jennifer Ciminelli (VCU) for GIS assistance; Eric Hilton (Virginia Institute of Marine Science), George Trice (commercial fisher), and Kelly Place (commercial fisher) for providing Atlantic sturgeon carcasses; and Tom Garin (Advanced Telemetry Systems) for donating radio tags. We appreciate Sarah Cameron (USACE Norfolk District) for supplying boat draft information and Jed Brown (U.S. Virgin Islands Division of Fish and Wildlife, St. Croix) and Matthew Fisher (Delaware DNREC, Division of Fish and Wildlife) for providing information on Delaware River Atlantic sturgeon vessel strikes. We thank the Professional Association of Diving Instructors Foundation for partial financial support. This is Contribution Number 25 of the VCU Rice Center.
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ARTICLE

Elevated Streamflows Increase Dam Passage by Juvenile Coho Salmon during Winter: Implications of Climate Change in the Pacific Northwest

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Abstract

A 4-year evaluation was conducted to determine the proportion of juvenile coho salmon *Oncorhynchus kisutch* passing Cowlitz Falls Dam, on the Cowlitz River, Washington, during winter. River and reservoir populations of coho salmon parr were monitored using radiotelemetry to determine if streamflow increases resulted in increased downstream movement and dam passage. This was of interest because fish that pass downstream of Cowlitz Falls Dam become landlocked in Riffe Lake and are lost to the anadromous population. Higher proportions of reservoir-released fish (0.391–0.480) passed Cowlitz Falls Dam than did river-released fish (0.037–0.119). Event-time analyses demonstrated that streamflow increases were important predictors of dam passage rates during the study. The estimated effect of increasing streamflows on the risk of dam passage varied annually and ranged from 9% to 75% for every 28.3 m³/s increase in streamflow. These results have current management implications because they demonstrate the significance of dam passage by juvenile coho salmon during winter months when juvenile fish collection facilities are typically not operating. The results also have future management implications because climate change predictions suggest that peak streamflow timing for many watersheds in the Pacific Northwest will shift from late spring and early summer to winter. Increased occurrence of intense winter flood events is also expected. Our results demonstrate that juvenile coho salmon respond readily to streamflow increases and initiate downstream movements during winter months, which could result in increased passage at dams during these periods if climate change predictions are realized in the coming decades.

Juvenile coho salmon *Oncorhynchus kisutch* typically reside in freshwater streams and rivers during their first winter of life. Because significant mortality can occur during this period, their ecology has been well studied (Bustard and Narver 1975; Tschapinski and Hartman 1983; Giannico and Hinch 2003). Coho salmon juveniles are commonly found in areas containing

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large woody debris during winter, and riverine ponds, alcoves, and side channels typically contain the highest densities of overwintering fish (Tschaplinski and Hartman 1983; McMahon and Hartman 1989; Shirvell 1990). These habitats provide cover and velocity refugia during high flow periods, which is important because juvenile coho salmon respond readily to streamflow increases by moving downstream in areas lacking woody debris and side-channel habitat (Bustard and Narver 1975; Hartman et al. 1982; Taylor 1988; Shirvell 1990). Downstream movements by juvenile coho salmon that occur prior to the spring migration period are associated with reduced survival, so minimizing this behavior during winter is important in areas where these populations can be managed (Thedinga and Koski 1984; Holtby 1988).

Although previous studies have been insightful for understanding the general behavior patterns of juvenile salmonids during winter months, additional research is required. Factors that affect the survival, behavior, and habitat use of juvenile salmonids in the winter are complex, and many of the previous studies have been limited due to the small size of fish and difficulties associated with sampling during this period (Huusko et al. 2007; Brown et al. 2011; Tiffan et al. 2012). Recent reviews by Huusko et al. (2007) and Brown et al. (2011) provide thorough summaries of the contemporary understanding of stream-rearing juvenile salmonids during winter months. Both papers call for additional research to better understand juvenile salmonid behavior during the winter and habitat use patterns and the effects of environmental (temperature, discharge) and physical (dams, reservoirs) factors on these relationships. Evolving technologies will undoubtedly aid in the development of studies to address these factors. For example, radio transmitters have recently been developed that are relatively small (<0.4 g) and operate for long periods of time (>100 d). Tiffan et al. (2012) used these transmitters to monitor downstream movements of juvenile fall-run Chinook salmon *O. tshawytscha* through reservoirs in the lower Snake River and were able to describe annual, seasonal, and spatial variations in downstream movement rates while also documenting dam passage during winter months. The availability of these radio transmitters and monitoring systems allowed the researchers to monitor individual fish throughout a relatively large study area (>150 river kilometers, hereafter rkm), whereas previous studies had to draw inferences about fish behavior using fine-scale observations and fish counts at various points during their study periods (Holtby 1988; Nickelson et al. 1992; Giannico and Hinch 2003).

Winter passage of juvenile coho salmon at Cowlitz Falls Dam, located on the Cowlitz River in southwestern Washington State (Figure 1), may result in significant losses to the coho salmon population, which is listed as threatened under the U.S. Endangered Species Act (NMFS 2005). Cowlitz Falls Dam provides flood control in the upper Cowlitz River during high-flow periods, which can result in large volumes of water passing...
through the dam when streamflow increases occur. Flood control operations are handled in various ways depending on the size of the flow increase. River flows $\leq 227$ m$^3$/s (measured at U.S. Geological Survey [USGS] Gauge #14231000) do not require flood control measures because the dam’s two turbines can accommodate flows at or below this level. Streamflows that range from 227 to 425 m$^3$/s are usually controlled by maximizing turbine output and passing additional water through spillbays or low-level sluiceways at the dam. However, once river flows exceed 425 m$^3$/s the dam is required to pass enough water (through turbines, spillbays, etc.) to lower the surface elevation of Lake Scanewa (the reservoir created by Cowlitz Falls Dam; Figure 1) by as much as 6 m (hereafter reservoir drawdown). On average, reservoir drawdowns have occurred 2.3 times (range = 0–6) during November–March each year between 1994 and 2010. Winter streamflow increases are believed to cause significant dam passage by juvenile coho salmon for the following reasons: (1) juvenile coho salmon are commonly observed rearing in Lake Scanewa during the fall and would be susceptible to dam passage during drawdown events; (2) the largest number of coho salmon smolts ever collected (334,718 fish compared with the 10-year average of 136,519 fish) at the Cowlitz Falls Fish Facility (CFFF) occurred during 2001, the only year in which a reservoir drawdown did not occur during the winter prior to a fish collection season; and (3) the CFFF is only operated during April–August each year, which means that fish moving downstream during high winter flow events are not collected and pass downstream of the dam. The fish that are collected at Cowlitz Falls Dam are transported downstream and released into the lower Cowlitz River, where they can migrate to the ocean, whereas fish that pass Cowlitz Falls Dam enter Riffe Lake, where they become landlocked and are lost to the anadromous fish population. Several anadromous fish species reside within the study area including coho salmon, steelhead $O$. mykiss, Chinook salmon, and cutthroat trout $O$. clarkii. The construction of Mossyrock Dam in 1968 threatened anadromous fish species upstream of rkm 105 because the dam blocked upstream volitional fish passage and created Riffe Lake (Figure 1). These species have persisted upstream of Mossyrock Dam because of a trap-and-haul program, which transports fish around the Cowlitz River hydropower system. Returning adults are captured downstream of Mayfield Dam (rkm 80), loaded onto trucks, and transported upstream of Cowlitz Falls Dam (rkm 143), where they are released (Figure 1). High quality spawning habitat is located throughout the basin upstream of Cowlitz Falls Dam, and progeny from the transported adults are distributed throughout river and reservoir habitats, where they rear before moving downstream toward the ocean. Juvenile out-migrants are collected at Cowlitz Falls Dam and transported downstream of Mayfield Dam, where they are released (Figure 1). Juvenile out-migrants that are not collected at Cowlitz Falls Dam pass downstream and enter Riffe Lake, where they become landlocked due to the large size of the reservoir and lack of fish collection facilities at Mossyrock Dam. Mark–recapture studies conducted by the Washington Department of Fish and Wildlife at Cowlitz Falls Dam from 1997 to 2009 show that about 32% of the coho salmon smolts are collected at Cowlitz Falls Dam each year, which means that approximately 2.3 million coho salmon smolts were passed into Riffe Lake during that period (Serl and Morrill 2011). This estimate demonstrated the losses of anadromous production that occur in the upper Cowlitz River basin when juvenile coho salmon smolts pass Cowlitz Falls Dam and become entrapped in Riffe Lake.

Climate change predictions for western Washington suggest that flow regimes will be significantly altered in the coming decades, which could increase the winter passage of juvenile coho salmon at Cowlitz Falls Dam. The Cowlitz River is classified as a transient watershed, which means that river flows are influenced by both rainfall and snowmelt events (Elsner et al. 2010; Mantua et al. 2010). Peak streamflow events typically occur twice annually in transient watersheds: once during the winter when seasonal precipitation peaks and once during the late spring or early summer when snowmelt occurs (Elsner et al. 2010). Climate change predictions suggest that annual air temperatures in the Pacific Northwest will increase by 3.0 °C (on average) by the 2080s, which is expected to have significant effects on hydrological regimes in western Washington (Elsner et al. 2010; Mote and Salathe 2010). Transient watersheds, like the Cowlitz River, are expected to experience a significant shift in streamflow timing that will include increased winter runoff and decreased summer runoff due to the shift towards more rain-dominated winter precipitation that does not contribute to the snowpack (Mote et al. 2003; Elsner et al. 2010; Mantua et al. 2010; Figure 2). Studies have shown that high streamflow events are significant factors in overwinter mortality of juvenile coho salmon, so predictions of increased peak flows during the winter may increase early life stage mortality of coho salmon (Reeves et al. 1989; Beechie et al. 1994; Mantua et al. 2010).

Frequent winter streamflow increases resulting in reservoir drawdowns prompted an evaluation of coho salmon passage at Cowlitz Falls Dam during winter. We conducted an evaluation of fish passage using radiotelemetry to monitor downstream movements and estimate dam passage during October–February from 2007 to 2011. Our objectives were to (1) quantify dam passage of juvenile coho salmon at Cowlitz Falls Dam during winter, (2) determine if river and reservoir populations of juvenile coho salmon experienced similar passage rates, and (3) identify potential long-term effects of climate change predictions to inform future management actions aimed at protecting anadromous fish populations in the upper Cowlitz River basin.

METHODS

Study site.—This study was conducted in the upper Cowlitz River, which is a tributary to the Columbia River, in southwestern Washington State. Tagged fish were monitored in two riverine reaches (Cowlitz and Cispus rivers) upstream of Lake
FIGURE 2. Relationship between historical streamflows (blue line) and predicted streamflows (red line; ensemble averaged estimates) for the Cowlitz River at Packwood, Washington during the 2020s, 2040s, and 2080s. The light red envelope represents the range of predicted streamflows, and A1B and B1 refer to two emission scenarios used for estimating future climate change scenarios. Values on the y-axis represent streamflows (ft$^3$/s) and values on the x-axis represent individual months beginning with October and ending with September. This figure was downloaded from the Columbia Basin Climate Change Scenarios Project website and was produced by the Climate Impacts Group at the University of Washington in collaboration with the Washington State Department of Ecology, Bonneville Power Administration, Northwest Power and Conservation Council, Oregon Water Resources Department, and the British Columbia Ministry of the Environment. [Figure available in color online.]

Scanewa, in Lake Scanewa, and downstream of Cowlitz Falls Dam (Figure 1). Lake Scanewa is a 284-ha reservoir that was created by the construction of Cowlitz Falls Dam in 1994. The confluence of the Cowlitz and Cispus rivers is located near the center of the reservoir (Figure 1).

The Cowlitz and Cispus rivers drain large areas on the western slope of the Cascade Mountains, and rainfall and snowmelt events control water temperatures and streamflows throughout the year. The Cowlitz River, upstream of Lake Scanewa, is larger and warmer than the Cispus River during most months of the year. Streamflows in the Cowlitz River averaged 82.0 m$^3$/s (range = 7.5–736.2 m$^3$/s; 264.9–25,991.6 ft$^3$/s) from January 2007 to March 2011 compared with 31.2 m$^3$/s (range = 7.4–257.4 m$^3$/s; 261.3–9,075.9 ft$^3$/s) in the Cispus River. River temperatures in the Cowlitz River averaged 4.8°C (range = 0–7.8°C) from December 2010 to March 2011 compared with 4.2°C (range = 0–7.2°C) in the Cispus River.

Fish collection and tagging.—Juvenile coho salmon were collected by angling or electrofishing, radio transmitters were surgically implanted, and tagged individuals were monitored to determine dam passage proportions and dam passage rates during our study. A total of 17 tag-and-release efforts were conducted during four field seasons, which included October to February of 2007–2011. Coho salmon juveniles were collected for tagging in Lake Scanewa during 2007, 2009, and 2010, and in the Cowlitz and Cispus rivers during 2008–2010 (Table 1). Reservoir collection efforts occurred primarily near rkm 1.0 on the Cispus River (Figure 1). River collection on the Cowlitz and Cispus rivers occurred near rkm 195.5 and 27.0, respectively. Following collection, juvenile coho salmon were transported to the CFFF, where they were held for 24–72 h in floating 208-L, perforated containers that received a continuous supply of flow-through river water. On each tagging date, fish were anesthetized using buffered tricaine methanesulfonate (70 mg/L) and radio transmitters (Model NTC-3-1; Lotek Wireless, Canada) were surgically implanted using techniques described by Adams et al. (1998). Radio transmitters were 13.5 mm long, 5.3 mm wide, and weighed 0.37 g in air. Transmitters included an antenna that was 16 cm long and emitted a signal every 20 s. A subsample of 25 transmitters was monitored in a laboratory setting during 2009 and we found that mean tag life was 104 d. Fish were not tagged if the radio transmitter weighed more than 5% of their body weight (in air) at the time of tagging. We were able to tag fish that were 7.4 g or larger. Following tagging, fish were held for 24 h and were then transported by truck to one of three release sites. Fish were segregated throughout the holding, tagging, and release process to ensure that tagged fish were released near the location where they were originally collected.

Monitoring system.—Fixed monitoring sites (hereafter fixed sites) were established and maintained to collect information about movement patterns of tagged fish during the study (Figure 1). Fixed sites were located on the Cowlitz River (rkm 173.2 and 193.9), Cispus River (rkm 3.2 and 9.6), in Lake Scanewa (rkm 136.7, 139.1 on the Cowlitz River; rkm 1.8 on the Cispus River), and on Cowlitz Falls Dam (rkm 135.5) to monitor fish movements prior to passage at the dam (Figure 1). Fixed sites in the tailrace of Cowlitz Falls Dam (rkm 135.2 and 135.3) monitored for tagged fish passing the dam. Two sites located downstream of the dam’s tailrace (rkm 130.3 and 131.6) provided a secondary array for confirming dam passage by tagged fish. Additionally, fixed sites were operated on Mossyrock Dam (rkm 105.8) during 2007–2009 to determine if tagged fish moved through Riffe Lake after passing Cowlitz Falls Dam.

Downloaded by [Department Of Fisheries] at 00:05 19 November 2012
TABLE 1. Release dates and the number of radio-tagged juvenile coho salmon that were released in the upper Cowlitz River basin during a 2007–2010 evaluation.

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Estimating passage proportions.—We used a Cormack–Jolly–Seber (CJS) mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) to estimate detection probabilities at fixed sites and the proportion of juvenile coho salmon that passed Cowlitz Falls Dam during our study. These models are commonly used to estimate recapture and survival probabilities from mark–recapture studies. We anticipated that some tagged fish that passed Cowlitz Falls Dam would not be detected by fixed sites in the tailrace of the dam because fish tended to move downstream quickly during high flow periods, the transmitters emitted a signal every 20 s, and the signal strength was relatively weak due to the small size of the transmitters. The use of the CJS model allowed us to obtain unbiased estimates of the proportion of tagged fish that passed Cowlitz Falls Dam during our study because these estimates were corrected for missed detections at fixed sites.

Release and detection records from river- and reservoir-released fish were summarized to create detection histories that were analyzed using Program MARK (White and Burnham 1999). A three-occasion detection history was created for each fish that was released during the study. Each detection history summarized the release and subsequent detection or nondetection of tagged fish at sites downstream of the dam. All fish received a “1” in the first occasion of the detection history, which represented tagged fish being released upstream of the dam. The last two occasions in the detection history represented detection or nondetection (0 = not detected; 1 = detected) in the tailrace of the dam and at fixed monitoring sites located approximately 5 rkm downstream of the dam. The CJS model produced three types of estimates: P_{dam}, which was the joint probability of tagged fish being released, surviving and moving downstream from the release sites, and passing Cowlitz Falls Dam; d, which was the detection probability of fixed sites located in the tailrace of the dam; and λ, which was the joint probability of tagged fish surviving, moving downstream from the tailrace, and being detected at fixed sites located 5 km downstream of the dam. Dam passage data for river-released fish during 2010 were sparse, so we pooled river-released groups of tagged fish from 2009 and 2010 for the CJS analysis. The fully parameterized model that we used contained 15 parameters, which included P_{dam}, d, and λ estimates for reservoir-released fish in 2007, 2009, and 2010 and river-released fish in 2008 and 2009–2010.

Estimating passage rates.—Cox proportional hazards regression was used to examine effects of covariates on rates of dam passage by tagged fish during the study period (Allison 1995; Castro-Santos and Haro 2003). Dam passage, as indicated by detection of individual tagged fish downstream of the dam, was the event of interest, and the hazard rate was the proportion of
tagged fish that passed the dam during each day of the study period. Four predictor variables were included in the analysis: release year (2007, 2008, 2009, 2010), fish size (<100 mm fork length; ≥100 mm fork length), release location (river, reservoir), and river flow. We used a 100-mm fork length criterion because this has been identified as a threshold for smoltification of coho salmon (Sandercok 1991) and is applicable to coho salmon in the Cowlitz River. River flow was included as a continuous predictor variable. Mean daily flow data were obtained from the USGS gauging station (#14231000) located near Randle, Washington. All fish not detected downstream of the dam were considered at risk of passing the dam until 105 d after release (the maximum observed time from release to passage), at which point they were censored.

The event-time analysis consisted of three general steps, which included identifying significant covariates and two-way interactions between covariates, assessing whether assumptions of the Cox proportional hazards model were satisfied for the data, and determining hazard ratios for significant predictor variables. Hazard ratios were used with river flow data to estimate the effects of river flow on risk of dam passage. Flow data were grouped by 28.3 m³/s bins, and a risk statistic, described by Allison (1995), was used to understand the relationship between river flow and dam passage. The risk statistic is informative because it described how risk of passing the dam changed relative to each 28.3 m³/s increase in river flow. The risk statistic was calculated as follows:

\[
\text{risk statistic} = 100 \times (\text{hazard ratio} - 1)
\]

The results from these analyses were used to understand the effects of covariates on the rates of dam passage during our study and to infer how coho salmon passage at Cowlitz Falls Dam could be affected in the future if climate change predictions are realized.

**River flows and climate change.**—As previously discussed, climate change predictions suggest that the timing of peak streamflow events will shift in future decades in the Pacific Northwest as a result of climate warming. Cowlitz River streamflow data were used to verify that historical and current streamflow responses support predicted shifts in streamflow timing. Cowlitz River monthly streamflow data were downloaded for the USGS flow gauging station #14226500 near Packwood, Washington (http://waterdata.usgs.gov/wa/nwis/) for the years 1930–2009. Area-averaged monthly temperature data were downloaded from the National Oceanic and Atmospheric Administration’s Climate Division dataset (http://www7.ncdc.noaa.gov/CDO/CDDivisionSelect.jsp) for Washington’s climate division 4 (East Olympic Cascade Foothills) for the same time period. Climate Division 4 includes the west slopes of the Cascade foothills, parts of southwestern Washington, and the east Olympic foothills and includes the upper Cowlitz River basin, where our study was conducted. Climate data from this region are represented as an area average using cooperative observer weather stations within the boundaries of the area.

We used Cowlitz River streamflow data to calculate a ratio that compared melting-season streamflows (May–July) to late-winter streamflows (January–March). The ratio was obtained by dividing the average melting-season streamflow by the average late-winter streamflow, representing the proportions of annual streamflow that occurred during the two periods. Higher flows during the melting season than during the late-winter period result in a relatively large ratio (>1). Conversely, the ratio would be near 1 or <1 when streamflow timing was composed of higher flows during the late-winter period than during the melting season. This ratio was then plotted against the average late-winter air temperature (January–March) to assess the relationship between streamflow timing and temperature.

**RESULTS**

A total of 856 juvenile coho salmon were collected during the study period and 428 of these fish were tagged and released. Of these, 262 fish were released in the reservoir and 166 fish were released in the Cowlitz and Cispus rivers (Table 1). Cispus River releases comprised 56% of the river realeses (93 total fish; 48 in 2008, 33 in 2009, 12 in 2010) compared with 44% for the Cowlitz River (73 total fish; 34 in 2008, 27 in 2009, 12 in 2010). During 2007 tagged fish were only released in the reservoir, and during 2008 tagged fish were only released in the rivers (Table 1). Mean weight and fork length of river-released fish was 10.4 g and 98.3 mm, respectively, compared with 10.5 g and 97.2 mm for reservoir-released fish. Mean fork length of fish that were not tagged during the study period was 82.1 mm and mean weight was 6.3 g.

More than one-third of the fish released in the reservoir passed Cowlitz Falls Dam during our study, whereas few of the river-released fish moved downstream of the dam. Tagged fish exhibited one of two behaviors during the study period, either remaining near the release location or moving downstream and passing Cowlitz Falls Dam. We did not observe downstream movements by tagged fish that did not pass the dam. A total of 102 (38.9%) juvenile coho salmon from the reservoir were detected downstream of Cowlitz Falls Dam during the study period compared with only 13 (7.8%) of the river-released fish. Of the river-released fish that passed downstream of Cowlitz Falls Dam, six fish were from the Cowlitz River release group and seven fish were from the Cispus River release group. The average elapsed time from release to dam passage by reservoir-released fish was 25.0 d (range = 1–85 d) compared with 54.8 d (range = 6–105 d) for river-released fish (Figure 3).

Some of the fish that passed Cowlitz Falls Dam were eventually detected at Mossyrock Dam. Eight of the fish known to have passed Cowlitz Falls Dam were detected at Mossyrock Dam during the study (3 in 2007, 2 in 2008, 3 in 2009). Mean elapsed time from passing Cowlitz Falls Dam to detection at Mossyrock Dam was 24.4 d (range = 3.4–69.7 d) and mean travel rate in Riffe Lake was 1.1 km/d (range = 0.1–2.4 km/d).
FIGURE 3. Kaplan–Meier survivorship function for tagged fish from river (dashed line) and reservoir (solid line) release locations. Open circles represent the time when data were censored due to expected failure of all radio transmitters in the study.

**Dam Passage Proportions**

We found that \( d \) varied throughout the study period and that \( P_{\text{dam}} \) was higher for reservoir-released fish than for river-released fish. Estimates of \( d \) ranged from 0.100 to 0.682 across release groups and study years (Table 2). Estimates of \( P_{\text{dam}} \) were relatively high for reservoir-released fish (0.391 in 2007, 0.480 in 2009, 0.445 in 2010) compared with river-released fish (0.037 in 2008, 0.119 in 2009 and 2010; Table 2). Estimates of \( \lambda \) ranged from 0.666 to 1.000 (Table 2).

**Dam Passage Rates**

Event-time analyses demonstrated that release location (\( P = 0.0051 \)), river flow (\( P < 0.0001 \)), and year (\( P < 0.0001 \)) were significant predictors of dam passage rates during the study period, whereas fish size was not (\( P = 0.2110 \)). We also observed that the two-way interaction between river flow and year was significant (\( P < 0.0001 \)) so the final model that was used for testing assumptions and determining hazard ratios included the following variables: release location, river flow, year, and the river flow \( \times \) year interaction. Multiple tests were conducted using techniques described by Patetta (2006) to confirm that assumptions of the Cox proportional hazards model were satisfied. Release location did not interact with other covariates during our study, so the hazard ratio of 6.493 demonstrates that reservoir-released fish had a dam passage rate that was nearly 6.5 times greater than that of river-released fish throughout the study period. Because we observed an interaction between river flow and year, hazard ratios were estimated for river flow during each year of the study. Hazard ratio estimates were 1.491 during 2007, 1.187 during 2008, 1.748 during 2009, and 1.086 during 2010, which means that the risk of dam passage increased by 49.1%, 18.7%, 74.8%, and 8.6% for every 28.3 m\(^3\)/s (1000 ft\(^3\)/s) increase in river flow during 2007, 2008, 2009, and 2010, respectively. Individual passage events were plotted with daily streamflow data to illustrate the relationship between dam passage and streamflow increases (Figure 4). This showed that most dam passage occurred during periods of increasing streamflow.

**River Flows and Climate Change**

The 80-year analysis of Cowlitz River streamflow patterns demonstrated that warm winters were characterized by increased river flows during late winter (January–March) and decreased flows during the melting season (May–July), and this relationship was reversed during cool winters (Figure 5). The melting-season flow to late-winter flow ratio is smaller during warm winters, which demonstrates that increased temperatures during winter months leads to higher winter flows and lower melting-season flows. The five warmest winters (1934, 1941, 1981, 1983, 1992) had an average late-winter flow of 48.2 m\(^3\)/s (1700 ft\(^3\)/s) and an average melting-season flow of 42.8 m\(^3\)/s (1510 ft\(^3\)/s), whereas the five coldest winters (1936, 1937, 1949, 1950, 1956) had an average late-winter flow of 29.2 m\(^3\)/s (1030 ft\(^3\)/s) and an average melting-season flow of 106.8 m\(^3\)/s (3770 ft\(^3\)/s). The 80-year historical record of streamflow on the Cowlitz River exhibits behaviors consistent with regional climate change predictions; the warming temperatures are expected to result in higher late-winter flow and lower melting-season flow as the basin becomes more rain dominant. These findings are consistent with predictions illustrated in Figure 2 from two climate change models. Expected warming patterns will increase December–February flows by about 30% by the 2020s, and flows are expected to double during this same period by the 2080s (Figure 2).

**DISCUSSION**

We used recent developments in radio transmitter technology to further advance the existing information about winter behavior of juvenile coho salmon. The ability to effectively evaluate parr-sized fish with telemetry technologies has traditionally been limited by the availability of small transmitters. However, recent efforts to reduce transmitter size and increase operating life resulted in the development of the transmitter that
we used, which weighed 0.37 g (in air) and operated for about 3 months. This transmitter allowed us to tag juvenile coho salmon as small as 7.4 g (approximately 85 mm fork length) and to monitor the movements of individual fish for 3 months throughout a study area that encompassed approximately 100 rkm. Previous studies did not have the advantage of using this technology, so most studies either relied on enumerating fish in certain habitats or monitoring fine-scale movements of individuals to draw inferences about juvenile coho salmon responses to streamflow increases (Shirvell 1990; Shirvell 1994; Giannico and Healey 1998). Our data support findings from these studies while also providing additional information (i.e., dam passage proportions, dam passage rates).

Our data showed that winter streamflow increases in the upper Cowlitz River resulted in increased dam passage by juvenile coho salmon at Cowlitz Falls Dam. Mean estimates of dam passage proportions during our study were 44% for reservoir-released fish and 8% for river-released fish. These findings are important because they identify a significant source of lost production to the anadromous coho salmon population of the upper Cowlitz River. Research has shown that large numbers of coho salmon smolts enter Riffe Lake during the fish passage season (April–August) each year (Serl and Morrill 2011), and fisheries managers have suspected that winter dam passage could be substantial at Cowlitz Falls Dam. Our study provided the first empirical estimates of dam passage by juvenile coho salmon during winter months in the system.

Reservoir populations of juvenile coho salmon appear to be more susceptible to dam passage than river populations in the
upper Cowlitz River. Our analyses estimated that nearly half of the reservoir-released fish (39–48%) passed Cowlitz Falls Dam during the study compared to 4–12% of the river-released fish. Both CJS modeling analyses and event-time analyses found these differences to be significant. The difference in dam passage between the two release groups can likely be attributed to habitat differences between the river and reservoir environments. Riverine habitat located between the river release sites and Lake Scanewa is complex and diverse, containing large accumulations of woody debris, numerous side channels, and deep pools, all of which have been shown to maintain high numbers of juvenile coho salmon during winter freshets (Tschaplinski and Hartman 1983; McMahon and Hartman 1989; Nickelson et al. 1992; Giannico and Hinch 2003). Conversely, habitat in Lake Scanewa is largely homogenous with steep-sided shorelines that contain little woody debris, and the areas that do contain woody debris are typically dewatered when the reservoir is drawn down. Drawdowns return much of the reservoir to riverine-like conditions, and the lack of suitable habitat for juvenile coho salmon to hold in may result in the increased dam passage that was observed during our study. McMahon and Hartman (1989) found that most coho salmon juveniles in their study emigrated from test channels during simulated freshets unless complex habitat conditions (i.e., low velocity, shade, woody debris) were present. Similarly, Tschaplinski and Hartman (1983) found that stream sections containing log jams, undercut banks, and debris retained high numbers of juvenile coho salmon during winter freshets compared with stream sections where these habitat characteristics were absent. Results from these studies suggest that dam passage by reservoir-released juvenile coho salmon in the upper Cowlitz River would exceed those of river-released fish, and our study confirmed this. It is possible that reservoir-released fish passed Cowlitz Falls Dam at a higher rate than river-released fish because of their proximity to the dam (river release sites >30 rkm from Cowlitz Falls Dam; reservoir release site = 3.1 rkm from Cowlitz Falls Dam). Although we cannot rule out the effects of this factor on our results, it seems apparent that coho salmon juveniles in Lake Scanewa are susceptible to winter dam passage. Based on these findings it is also clear that future evaluations will be required to understand how the juvenile coho salmon population is distributed between river and reservoir environments in the upper Cowlitz River basin. This information will be essential for understanding population loss during winter months.

We found that substantial numbers of tagged juvenile coho salmon responded to winter streamflow increases by moving downstream and passing Cowlitz Falls Dam, and this behavior suggests that winter dam passage will be exacerbated during coming decades if climate change predictions are realized. At the beginning of the study we assumed that large numbers of fish were passing Cowlitz Falls Dam during drawdowns, when river flows were >425 m³/s. We were surprised to find that the largest proportion of tagged fish passed during 2009, the only winter during our study when a drawdown did not occur. However, river flows peaked multiple times during 2009 and cumulative passage during that winter resulted in an estimated passage of 48% of the reservoir-released fish (Figure 4; Table 2). This observation supports our findings that flow increases lead to increased risk of dam passage, and large streamflow increases that occur occasionally may result in lower dam passage than moderate streamflow increases that occur frequently. The effects of flow-related winter passage by juvenile coho salmon are evident if we consider a simplistic example in which a population of 100 juvenile coho salmon are residing upstream of Cowlitz Falls Dam during winter months under the following two scenarios: (1) daily streamflows average 28.3 m³/s, representing current, cool winter conditions; and (2) daily streamflows average 84.9 m³/s, representing predicted future, warm winter conditions. We assumed that the risk of passing Cowlitz Falls Dam would increase by 38% for every 28.3 m³/s increase in streamflow, which is the 4-year average of risk estimates that we observed during our study. If 25 of the juvenile coho salmon pass Cowlitz Falls Dam under the first scenario, we would expect to see 44 juvenile coho salmon pass under the second climate change scenario. This finding indicates that substantial dam passage could occur during winter months in coming decades, which could result in additional losses to the anadromous coho salmon population of the upper Cowlitz River.

Although these data were collected in the Cowlitz River basin, the findings from this study have implications throughout the entire range of Pacific salmon _Oncorhynchus_ spp. Juvenile salmonid collection facilities are being developed, are under construction, or are in operation at hydroelectric facilities on midsized rivers (Baker River, Cowlitz River, Lewis River, Willamette River, etc.) located along the western slope of the Cascade Mountains, in Washington and Oregon, and are being considered in California. These facilities comprise a common strategy throughout the region for restoring anadromous salmon populations in watersheds where volitional access is no longer present due to dam construction, but important habitat is available upstream of dams. Our data suggest that out-migration timing at these locations will change in the coming decades. If this occurs, contemporary collection efforts that focus on smolt-sized fish that out-migrate during May–August will likely have to adapt to target parr-sized fish that move downstream during January–April. Given these concerns, future habitat restoration efforts upstream of Cowlitz Falls Dam, and at other locations, may be useful for increasing winter habitat for juvenile salmonids to reduce winter flow-related passage.

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Do Anglers Know What They Catch? Identification Accuracy and Its Effect on Angler Survey-Derived Catch Estimates

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Abstract

Angler surveys are reliant on the ability of anglers to accurately report various aspects of their fishing trips. Misidentification of sport fishes has been postulated as a source of error among angler surveys but has received little attention. We evaluated the overall ability of anglers to identify sport fishes common to Ohio and the potential impacts on catch estimates derived from angler surveys. During angler surveys conducted on lakes and reservoirs (2007, \( n = 34 \)) and Ohio River tailwaters (2010, \( n = 3 \)), anglers were presented with artist-rendered images of 18 different sport fishes common to these waters. Anglers (lake and reservoir, \( n = 2,442 \); Ohio River, \( n = 458 \)) were asked to identify sport fish by their common name. On average, anglers correctly identified sport fishes 42% of the time, but accuracy varied widely among species (lake and reservoir, range = 4.4–85.1%; Ohio River, range = 9.4–71.8%), with greater accuracy exhibited for the most common species (e.g., largemouth bass \( Micropterus salmoides \)). However, by grouping angler responses into species groups (e.g., black bass \( Micropterus \) spp., sunfish \( Lepomis \) spp.) angler identification of sport fishes was more reliable (lake and reservoir, mean = 83.4%; Ohio River, mean = 83.8%). Using these estimates of angler accuracy, we simulated the potential error in sport fish catch estimates using data from an angler survey conducted at one Ohio reservoir. These results suggested that misidentification error may result in a substantial error in catch estimates. A survey of North American fisheries management agencies regarding angler surveys and angler sport fish identification revealed that the majority of agencies group similar species for analysis and cited species misidentification by anglers as the primary reason for doing so.
Angler surveys are widely used to gather important information on recreational fisheries, such as effort, catch and harvest, fish lengths, and socioeconomic characteristics of anglers (Pollock et al. 1994; Malvestuto and Hudgins 1996; Wilde et al. 1996). While survey methods vary, they all depend on the accuracy of angler responses, and it is well recognized that angler surveys are prone to certain response errors (Pollock et al. 1994; National Academy of Sciences 2006). For example, surveys relying on angler recollection of fishing trips (e.g., mail and telephone surveys) commonly exhibit angler recall bias, resulting in the overestimation of angler participation (days fished; Thompson and Hubert 1990; Tarrent et al. 1993; Connelly and Brown 1995) and catch and harvest rates (Roach et al. 1999), as well as decreased precision in estimates as the recall period increases (Osborn and Matlock 2010). On-site surveys may minimize recall bias, but anglers have been shown to exaggerate catch numbers in an effort to appear more “successful” (prestige bias; Jacobson et al. 1983; Sullivan 2003), particularly when catch rates are low. Accuracy in angler-reported harvest during angler surveys may be influenced by multiple factors (Mallison and Cichra 2004), such as the presence of harvest limits (i.e., anglers are more conscious of harvest numbers when harvest limits are present) or the types and sizes of fish harvested (i.e., larger or unique fish are likely to be more memorable). Further, error in angler-reported sizes of fish caught and harvested can occur due to rounding (whole digit bias; level of attentiveness) or as a result of anglers using inconsistent measuring techniques (Ferguson et al. 1984; Page et al. 2004). In short, there are a variety of sources of error related to angler self-reporting of fisheries data that fisheries managers need to consider when conducting angler surveys. Understanding these errors may assist fisheries managers in adjusting for, or minimizing the effects of, these errors on estimates derived from these surveys (Connelly and Brown 1995; Mallison and Cichra 2004).

An additional source of error in angler-reported data that has been presumed, but has received little direct attention, is related to misidentification of sport fishes (Pollock et al. 1994; Roach et al. 1999; National Academy of Sciences 2006). Evidence from North American salmonid fisheries suggests that angler identification of sport fishes is largely unreliable. Stelfox et al. (2001) found that anglers in Alberta accurately identified nine salmonid species on average 69% of the time, with the lowest accuracy for brown trout Salmo trutta (60%) and the greatest for Arctic grayling Thymallus arcticus (86%). Similarly, Schmetterling and Long (1999) found that accuracy among Montana anglers in identifying six common salmonid species was, on average, only 63%, with the lowest accuracy for bull trout Salvelinus confluentus (44%) and the highest accuracy for cutthroat trout Oncorhynchus clarkii lewisi (89%). Accuracy among Idaho anglers (Lamansky et al. 2001) was found to be 54%, on average, for four salmonid species, with the lowest accuracy for brown trout (38%) and the greatest for rainbow trout Oncorhynchus mykiss (83%). In contrast, angler identification of salmonid species within Lake Ontario (Bowlby and Savoie 2011) was on average 82% accurate, with accuracy being lowest for coho salmon Oncorhynchus kisutch (60%) and greatest for lake trout Salvelinus namaycush (96%). For all studies, avid (experienced) anglers tended to be more proficient at identifying fishes (e.g., Schmetterling and Long 1999; Lamansky et al. 2001; Stelfox et al. 2001; Bowlby and Savoie 2011). Consequently, the ability of anglers to accurately identify particular sport fishes caught and harvested was expected to vary by angler experience and among fisheries. Comparative analyses of the proficiency of anglers in identifying sport fishes within freshwater fisheries would be useful for developing expectations as to the reliability of angler-reported data and developing strategies for minimizing error.

Given the uncertainty in the proficiency of anglers in identifying sport fishes, the Ohio Division of Wildlife (ODOW) has adopted a precautionary approach to this potential error when conducting angler surveys. Specifically, during annual on-site angler surveys, angler responses to queries on sport fishes caught and harvested are grouped into broad categories (e.g., black bass Micropterus spp., catfish Ictalurus and Pylodictis spp., crappie Pomoxis spp.) to reduce the potential error in estimates (e.g., catch rates) resulting from angler misidentification of sport fishes. This strategy assumes that anglers are more accurate at assigning fish to general groups (e.g., sunfish Lepomis spp.) than identifying specific species (e.g., bluegill Lepomis macrochirus). However, based on our knowledge, the efficacy of this grouping method has not been validated and it is unknown whether grouping angler-reported catch and harvest data into broad categories is necessary for all species, or if substantial error exists despite the grouping of responses. For this study, we sought to (1) evaluate the accuracy of Ohio anglers in identifying common sport fishes and assess the efficacy in grouping angler-reported catch data into species categories and (2) quantify the error in catch estimates associated with misidentification of sport fishes. Further, fisheries management agencies across the United States and Canada were surveyed to explore how misidentification of sport fishes by anglers is addressed for angler-reported catch data collected during on-site angler surveys.

METHODS

We tested the accuracy of Ohio anglers in identifying 18 different Ohio sport fishes using artist-rendered color images of sport fishes commissioned by the ODOW and used within fish identification publications (ODOW 2008). Anglers were able to identify sport fishes by color, markings, and meristic variation (e.g., number of dorsal spines). It should be noted that identification of Morone spp. using tongue patch configuration was not an option in this study; however, it is unknown how often this identification method is used by anglers. The fish species used were the most common sport fishes encountered by anglers on Ohio lakes and reservoirs (hereafter LR) and the Ohio River tailwaters (hereafter OR). The fishes shown to anglers represented six
sport fish groups: (1) black bass (largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, and spotted bass *M. punctulatus*), (2) catfish (blue catfish *Ictalurus furcatus*, channel catfish *I. punctatus*, and flathead catfish *Pylodictis olivaris*), (3) crappie (black crappie *Pomoxis nigromaculatus* and white crappie *P. annularis*), (4) *Sander* spp. (walleye *Sander vitreus*, sauger *S. canadensis*, and saugeye [walleye *S. vitreus* × sauger *S. canadensis*]), (5) sunfish (bluegill, green sunfish *Lepomis cyanellus*, pumpkinseed *L. gibbosus*, and redear sunfish *L. microlophus*), and (6) *Morone* spp. (striped bass *Morone saxatilis*, white bass *M. chrysops*, and hybrid striped bass [striped bass *M. saxatilis* × white bass *M. chrysops*]). Images were printed individually on 8.5 × 11 in white paper stock and laminated. Images were presented to anglers as a part of statewide LR and OR angler survey interviews. The suite of sport fishes presented to anglers surveyed on LR differed slightly from those presented to anglers surveyed on the OR due to differences in the species present (Table 1).

A roving angler survey design (Pollock et al. 1994) was used to survey anglers at 34 Ohio reservoirs during 2007. Each reservoir was sampled one weekend day each week from April 28th through July 29th. Images of three different sport fishes were randomly assigned, with replacement to each day and reservoir sampled. As part of the survey process, anglers were presented images one at a time and were asked to identify fish by species (i.e., common name; Table 1). Only responses from the angler party spokesperson were accepted. The spokesperson was the individual chosen by the party to speak on their behalf. Angler survey clerks presented fish images to an angler only once during the 2007 angler survey. Angler survey clerks also queried anglers on the type of fish they were seeking.

An access-point survey design was used to survey anglers at three tailwaters on the Ohio River during 2010. Each tailwater was sampled three weekdays and weekend days each week from March to August. Each angler interviewed was shown four images: a *Sander* species, a *Morone* species, a catfish species, and a species of black bass. The species used on a given survey day were assigned prior to the angler survey season by random selection without replacement.

**Species-specific and species group identification.**—To evaluate the accuracy of anglers at identifying each sport fish, anglers were divided into three groups based on their responses: (1) those that correctly identified a species by its common name (e.g., largemouth bass), (2) those that provided the common name of a related species (e.g., smallmouth bass instead of largemouth bass) or the species group name (e.g., black bass), and (3) those that provided inaccurate responses, which included colloquialisms (e.g., shovelhead or mudcat for flathead catfish) and “I don’t know” responses. We calculated the percentage of responses for each group. The percentage of anglers able to identify sport fishes to species group (i.e., cumulative percentage of angler groups 1 and 2) for each sport fish species was calculated. This allowed us to compare species-specific identification accuracy (group 1 anglers) to species group level accuracy. For each species, the most common incorrect species responses were also noted and the percentage of responses calculated. Analyses for the LR and OR angler surveys were conducted separately.

**Identification accuracy among angler groups.**—Accuracy among anglers seeking different sport fishes was evaluated. Based on angler responses to the question of what they were seeking, LR anglers were classified as those seeking “anything that bites” (hereafter, anything), black bass, catfish, crappie, *Sander* spp., sunfish, and other (<1% of all anglers interviewed). The OR anglers were classified as those seeking anything, black bass, catfish, *Morone* spp., and *Sander* spp. For each angler group, the percentage of accurate species-specific responses was calculated for each species group (e.g., combined percentage of accurate responses for largemouth bass and smallmouth bass calculated for LR anglers). A contingency chi-square analysis of proportions (Zar 1996) was used to test for differences in species-specific accuracy among angler groups for all species groups. The False Discovery Rate method (García 2004) was used to control the family-wise type I error rate by adjusting the significance value (*P* ≤ 0.05). Wherever chi-square analyses revealed significant differences among angler groups in identification accuracy after adjusting for the type I error, pairwise comparisons among angler groups were conducted using a multiple comparisons of proportions test (Zar 1996).

**Simulating the effects of identification error.**—Directly assessing error introduced into catch estimates derived from angler-reported survey data is difficult given that fish species caught cannot be verified (e.g., released fish). We developed a simulation to assess the error thatangler misidentification of sport fishes may introduce using angler survey data collected at Hoover Reservoir, Franklin County, Ohio, in 2010 to generate and compare an “actual” number of each species caught by anglers within the reservoir. We used actual angler survey data in the simulation as opposed to artificially derived data in order to incorporate realism into the simulation.

Angler survey data collected from Hoover Reservoir (ODOW, unpublished data) was used to derive a baseline of actual numbers of fish caught during a given month (30 d) for largemouth bass, smallmouth bass, channel catfish, black crappie, white crappie, white bass, saugeye, bluegill, pumpkinseed sunfish, and green sunfish. Estimates of mean daily angler-directed effort (h/d) and mean daily catch rates (fish/d) were used to derive the number of fish caught per species group (Pollock et al. 1994) by anglers seeking (angler type) the following: anything, crappie, black bass, *Sander* spp., catfish, *Morone* spp., and sunfish. These represented 29.4%, 26.4%, 19.2%, 12.9%, 4.8%, 4.1%, and 3.0% of the anglers interviewed on Hoover Reservoir, respectively. Daily directed effort was calculated as the percentage of anglers (weighted by hours fished) targeting a specific species group multiplied by the estimated total angler-hours fished that day (average of three angler counts × 14 h). Daily catch rate (fish/d) of each species group was calculated for each angler group by dividing the mean number of fish caught per species group per angler group by the mean number...
TABLE 1. Percent of anglers that were able to accurately identify sport fishes as the correct species (common name) or to the correct species group (e.g., black bass). The most common incorrect species responses and percent (all responses) are also provided.

<table>
<thead>
<tr>
<th>Species group and fishery</th>
<th>Responses</th>
<th>Correct species</th>
<th>Correct species group</th>
<th>Most common incorrect species response (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Black bass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>648</td>
<td>73.0</td>
<td>90.1</td>
<td>Smallmouth bass (7.7)</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>365</td>
<td>58.4</td>
<td>88.3</td>
<td>Largemouth bass (17.3)</td>
</tr>
<tr>
<td>Ohio River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>110</td>
<td>71.8</td>
<td>95.4</td>
<td>Smallmouth bass (13.6)</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>106</td>
<td>61.3</td>
<td>89.6</td>
<td>Largemouth bass (19.8)</td>
</tr>
<tr>
<td>Spotted bass</td>
<td>127</td>
<td>9.4</td>
<td>94.5</td>
<td>Largemouth bass (64.6)</td>
</tr>
<tr>
<td><strong>Catfish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Channel catfish</td>
<td>496</td>
<td>69.4</td>
<td>98.1</td>
<td>Blue catfish (7.9)</td>
</tr>
<tr>
<td>Flathead catfish</td>
<td>350</td>
<td>29.1</td>
<td>90.5</td>
<td>Channel catfish (43.1)</td>
</tr>
<tr>
<td>Ohio River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue catfish</td>
<td>106</td>
<td>55.7</td>
<td>100.0</td>
<td>Channel catfish (17.9)</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>128</td>
<td>57.8</td>
<td>98.5</td>
<td>Blue catfish (9.4)</td>
</tr>
<tr>
<td>Flathead catfish</td>
<td>110</td>
<td>30.0</td>
<td>85.4</td>
<td>Channel catfish (20.9)</td>
</tr>
<tr>
<td><strong>Crappie</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black crappie</td>
<td>459</td>
<td>47.3</td>
<td>81.7</td>
<td>White crappie (12.2)</td>
</tr>
<tr>
<td>White crappie</td>
<td>416</td>
<td>38.2</td>
<td>75.0</td>
<td>Black crappie (8.7)</td>
</tr>
<tr>
<td><strong>Morone spp.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hybrid striped bass</td>
<td>490</td>
<td>16.1</td>
<td>65.7</td>
<td>White bass (49.6)</td>
</tr>
<tr>
<td>White bass</td>
<td>324</td>
<td>50.3</td>
<td>61.7</td>
<td>Striped bass (11.4)</td>
</tr>
<tr>
<td>Ohio River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hybrid striped bass</td>
<td>110</td>
<td>16.4</td>
<td>60.0</td>
<td>White bass (43.6)</td>
</tr>
<tr>
<td>Striped bass</td>
<td>128</td>
<td>31.3</td>
<td>65.7</td>
<td>White bass (34.4)</td>
</tr>
<tr>
<td>White bass</td>
<td>106</td>
<td>30.2</td>
<td>59.4</td>
<td>Striped bass (29.2)</td>
</tr>
<tr>
<td><strong>Sunfish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bluegill</td>
<td>598</td>
<td>85.1</td>
<td>91.6</td>
<td>Pumpkinseed (1.3)</td>
</tr>
<tr>
<td>Green sunfish</td>
<td>450</td>
<td>4.4</td>
<td>79.5</td>
<td>Bluegill (58.2)</td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>397</td>
<td>8.3</td>
<td>88.9</td>
<td>Bluegill (59.7)</td>
</tr>
<tr>
<td>Redear sunfish</td>
<td>371</td>
<td>7.5</td>
<td>84.6</td>
<td>Bluegill (60.9)</td>
</tr>
<tr>
<td><strong>Sander spp.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saugeye</td>
<td>488</td>
<td>32.6</td>
<td>83.6</td>
<td>Walleye (51.0)</td>
</tr>
<tr>
<td>Walleye</td>
<td>442</td>
<td>70.8</td>
<td>87.7</td>
<td>Saugeye (16.7)</td>
</tr>
<tr>
<td>Ohio River</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sauger</td>
<td>106</td>
<td>67.0</td>
<td>93.4</td>
<td>Walleye (26.4)</td>
</tr>
<tr>
<td>Saugeye</td>
<td>127</td>
<td>19.7</td>
<td>95.3</td>
<td>Saugeye (75.6)</td>
</tr>
<tr>
<td>Walleye</td>
<td>110</td>
<td>60.9</td>
<td>97.9</td>
<td>Sauger (37.0)</td>
</tr>
<tr>
<td><strong>All species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lakes and reservoirs</td>
<td>2,442</td>
<td>42.2</td>
<td>83.4</td>
<td></td>
</tr>
<tr>
<td>Ohio River</td>
<td>458</td>
<td>42.6</td>
<td>83.8</td>
<td></td>
</tr>
</tbody>
</table>
of angler-hours fished per angler group (i.e., ratio of the means; Pollock et al. 1994). Since catch data were collected by species groups for this survey (e.g., black bass), we assumed the species-specific catch was proportional to the species composition estimated from fish population assessments (ODOW, unpublished data). The “reported” catch for each species was calculated by partitioning the actual catch for each angler group based on its response distribution for a given species (this study) and summing across angler groups. Finally, the percent difference between the actual and reported catch was calculated. We also evaluated the error in fish identification after grouping specific species into species groups (e.g., black bass, crappie).

**Fish management agency survey.**—We surveyed state and provincial fish management agencies across the United States and Canada to explore how other management agencies treat angler-reported data. During 2007 and 2008, we contacted 62 state and provincial management agencies by e-mail inviting them to respond to the survey online (Zoomerang online surveys, MarketTools). Respondents were asked nine questions (Appendix) regarding their opinions of and approaches for dealing with angler-reported data collected during angler surveys. Specifically, we wanted to know whether they grouped angler-reported data, and if so, the reasons for grouping and which species were grouped.

**RESULTS**

Species-Specific and Species Group Identification

We contacted and presented fish images to 2,442 anglers on LR and 458 anglers on the OR. On average, each fish image was presented to 456 anglers (range = 306–648) during LR surveys and 115 anglers (range = 106–128) during OR surveys. The accuracy of anglers at identifying fish species (Table 1) to common name averaged 42.2% for LR anglers and 42.6% for OR anglers and varied greatly among species (LR, range = 4.4–85.1%; OR, range = 9.4–71.8%). Accuracy was greatest for bluegill and lowest for green sunfish for LR anglers and greatest for largemouth bass and lowest for spotted bass among OR anglers. On average, “I don’t know” responses were 3.9% and 1.3% for LR and OR anglers, respectively.

When grouping responses by species groups, accuracy in identification was markedly improved among sport fishes (LR, mean = 83.4%, range = 61.8–98.0%; OR, mean = 83.8%, range = 79.1–100.0%). Identification to species group was greatest for catfish species among both LR anglers and OR anglers, whereas LR and OR anglers both identified *Morone* spp. to species group with the lowest accuracy.

**Identification Accuracy among Angler Type**

The ability to accurately identify specific sport fishes differed among LR anglers targeting different species groups (Table 2). Among OR anglers, accuracy differed among angler groups for only catfish, which is likely a function of small sample sizes. Among LR anglers, black bass and *Sander* spp. anglers were the most accurate, followed by crappie, catfish, and sunfish anglers. Anglers seeking anything were the least accurate.

**Simulating the Effects of Identification Error**

Error in catch estimates over a 30-d period differed by species (range = 0.2–386.0%; Table 3). The greatest error was observed for smallmouth bass and the least for channel catfish. However, differences between actual and angler response-based

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**Table 2.** Comparisons in identification accuracy among anglers seeking different species (angler groups) for lake and reservoir and Ohio River anglers. Angler responses for specific species were grouped into related species groups (e.g., black bass = largemouth bass, smallmouth bass, and spotted bass) for analysis. Values represent the percentage of accurate responses (common names) across all species within a group (e.g., total accurate responses/total responses). The chi-square analysis was used to test for significant differences among angler groups in identification accuracy. Within rows, significant (P < 0.05) pairwise differences (Zar 1996) were denoted with different lowercase letters.

<table>
<thead>
<tr>
<th>Species groups</th>
<th>Anything</th>
<th>Black bass</th>
<th>Crappie</th>
<th>Catfish</th>
<th><em>Sander</em></th>
<th><em>Morone</em></th>
<th>Sunfish</th>
<th>chi-square</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lakes and reservoirs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black bass</td>
<td>57 x</td>
<td>83 z</td>
<td>65 yx</td>
<td>69 zyx</td>
<td>80 zy</td>
<td>65 yx</td>
<td>45.41</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Catfish</td>
<td>59 y</td>
<td>80 z</td>
<td>72 zy</td>
<td>74 zy</td>
<td>82 z</td>
<td>52 y</td>
<td>35.78</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Crappie</td>
<td>28 y</td>
<td>39 y</td>
<td>59 z</td>
<td>21 y</td>
<td>64 z</td>
<td>42 zy</td>
<td>66.22</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td><em>Morone</em></td>
<td>22 y</td>
<td>39 z</td>
<td>30 zy</td>
<td>20 y</td>
<td>41 zy</td>
<td>29 zy</td>
<td>20.07</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td><em>Sander</em></td>
<td>41 y</td>
<td>59 z</td>
<td>50 zy</td>
<td>53 zy</td>
<td>63 z</td>
<td>57 zy</td>
<td>21.84</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Sunfish</td>
<td>28 z</td>
<td>33 z</td>
<td>35 z</td>
<td>30 z</td>
<td>39 z</td>
<td>45 z</td>
<td>8.54</td>
<td>0.129</td>
<td></td>
</tr>
<tr>
<td><strong>Ohio River</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black bass</td>
<td>35 z</td>
<td>43 z</td>
<td>43 z</td>
<td>53 z</td>
<td>49 z</td>
<td>6.96</td>
<td>0.138</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Catfish</td>
<td>46 z</td>
<td>43 z</td>
<td>45 z</td>
<td>48 z</td>
<td>49 z</td>
<td>0.33</td>
<td>0.988</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Morone</em></td>
<td>30 z</td>
<td>29 z</td>
<td>41 z</td>
<td>46 z</td>
<td>44 z</td>
<td>6.25</td>
<td>0.181</td>
<td></td>
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</tr>
<tr>
<td><em>Sander</em></td>
<td>40 zy</td>
<td>57 z</td>
<td>30 y</td>
<td>53 z</td>
<td>59 z</td>
<td>13.69</td>
<td>0.008</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3. Results of a simulation to evaluate the potential effects of angler misidentification of sport fishes on catch estimates. The estimated actual catch is compared with the catch reported by anglers. The actual numbers of fish caught were derived from an angler survey conducted at Hoover Reservoir in Ohio during 2010. The reported catch was derived by applying species-specific angler identification error to the actual catch. The comparisons of actual and reported catches are shown for both specific species and species groups.

<table>
<thead>
<tr>
<th>Species and species group</th>
<th>Actual catch</th>
<th>Reported catch</th>
<th>Percent difference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Specific species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>5,790</td>
<td>6,488</td>
<td>12.1</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>180</td>
<td>875</td>
<td>386.0</td>
</tr>
<tr>
<td>Channel catfish</td>
<td>1,740</td>
<td>1,736</td>
<td>–0.2</td>
</tr>
<tr>
<td>Black crappie</td>
<td>4,980</td>
<td>5,963</td>
<td>19.7</td>
</tr>
<tr>
<td>White crappie</td>
<td>14,910</td>
<td>12,122</td>
<td>–18.7</td>
</tr>
<tr>
<td>White bass</td>
<td>4,590</td>
<td>3,802</td>
<td>–17.2</td>
</tr>
<tr>
<td>Saugeye</td>
<td>1,410</td>
<td>1,384</td>
<td>–1.8</td>
</tr>
<tr>
<td>Bluegill</td>
<td>5,381</td>
<td>6,239</td>
<td>15.9</td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>633</td>
<td>33</td>
<td>–94.8</td>
</tr>
<tr>
<td>Green sunfish</td>
<td>317</td>
<td>20</td>
<td>–93.7</td>
</tr>
<tr>
<td><strong>Species groups</strong></td>
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<td></td>
</tr>
<tr>
<td>Black bass</td>
<td>5,970</td>
<td>7,363</td>
<td>23.3</td>
</tr>
<tr>
<td>Catfish</td>
<td>1,740</td>
<td>1,736</td>
<td>–0.2</td>
</tr>
<tr>
<td>Crappie</td>
<td>19,890</td>
<td>18,085</td>
<td>–9.1</td>
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<tr>
<td>Morone</td>
<td>4,590</td>
<td>3,802</td>
<td>–17.2</td>
</tr>
<tr>
<td>Sander</td>
<td>1,410</td>
<td>1,390</td>
<td>–1.4</td>
</tr>
<tr>
<td>Sunfish</td>
<td>6,330</td>
<td>6,292</td>
<td>–0.6</td>
</tr>
</tbody>
</table>

Angler accuracy in identifying sport fishes varied among species and depended appreciably on the specificity of identification, which may have implications for how angler surveys are conducted and how survey data are analyzed. Overall, angler accuracy in identifying sport fishes to species was low (LR, mean accuracy = 42.2%; OR, mean accuracy = 42.6%) and error was often a function of misidentifying sport fishes as either related species or identification as the species group name (e.g., crappie, catfish). Error among related species did not appear reciprocal as accuracy was greatest among the more common sport fishes by specific species only, but when analyzing angler-reported data, most agencies (56.6%) indicated that they analyzed angler-reported data on released fish by both specific species and species groups, depending on the species (Table 4). When asked to indicate the reasons for analyzing angler-reported data collected on released fish by species groups (60.4% of agencies; Table 5), “reliability of identification by anglers” (84.8%) was the most often cited and most important reason for grouping (mean rank = 1.8; 1 being most important and 5 being least important; Table 5), followed by “similar management objectives,” “low importance of certain species to the fishery,” “few numbers of certain species caught,” and “simplify analysis.” Crappie, sunfish, catfish, and black bass species were the most common species grouped by fisheries management agencies (Table 6).

**DISCUSSION**

Angler accuracy in identifying sport fishes varied among species and depended appreciably on the specificity of identification, which may have implications for how angler surveys are conducted and how survey data are analyzed. Overall, angler accuracy in identifying sport fishes to species was low (LR, mean accuracy = 42.2%; OR, mean accuracy = 42.6%) and error was often a function of misidentifying sport fishes as either related species or identification as the species group name (e.g., crappie, catfish). Error among related species did not appear reciprocal as accuracy was greatest among the more common sport fishes

**Fish Management Agency Survey**

Of the 62 state and provincial fisheries management agencies contacted, 54 (87.1%) responded to our survey and 53 indicated that they routinely conducted angler surveys and collected data from anglers on the fish they released. Most agencies (58.5%) indicated that they collected angler-reported data on released fish by specific species only, but when analyzing angler-reported data, most agencies (56.6%) indicated that they analyzed angler-reported data on released fish by both specific species and species groups, depending on the species (Table 4). When asked to indicate the reasons for analyzing angler-reported data collected on released fish by species groups (60.4% of agencies; Table 5), “reliability of identification by anglers” (84.8%) was the most often cited and most important reason for grouping (mean rank = 1.8; 1 being most important and 5 being least important; Table 5), followed by “similar management objectives,” “low importance of certain species to the fishery,” “few numbers of certain species caught,” and “simplify analysis.” Crappie, sunfish, catfish, and black bass species were the most common species grouped by fisheries management agencies (Table 6).

**TABLE 4.** Percentage of state and provincial fish management agencies that conduct angler surveys that indicated using the following method for collecting and analyzing angler-reported data on released fish (Questions 3 and 4; Appendix).

<table>
<thead>
<tr>
<th>Angler-reported data on released fish</th>
<th>Collected</th>
<th>Analyzed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species groups only (e.g., black bass, centrarchids)</td>
<td>3.8</td>
<td>3.8</td>
</tr>
<tr>
<td>Both specific species and species groups, depending on the species</td>
<td>37.7</td>
<td>56.6</td>
</tr>
<tr>
<td>Specific species only (e.g., largemouth bass)</td>
<td>58.5</td>
<td>39.6</td>
</tr>
</tbody>
</table>

**TABLE 5.** Reasons and levels of importance (1 = most important, 5 = least important) indicated by state and provincial fish management agencies as to why they grouped, by similar species, angler-reported data on released fish collected during angler surveys (Question 5; Appendix).

<table>
<thead>
<tr>
<th>Reasons for grouping by similar species</th>
<th>Percent</th>
<th>Mean importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reliability of identification by anglers</td>
<td>84.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Similar management objectives</td>
<td>72.7</td>
<td>2.2</td>
</tr>
<tr>
<td>Simplify analysis</td>
<td>48.5</td>
<td>3.7</td>
</tr>
<tr>
<td>Few numbers of certain species caught</td>
<td>45.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Low importance of certain species to the fishery</td>
<td>39.4</td>
<td>3.3</td>
</tr>
</tbody>
</table>
TABLE 6. Percentage of state and provincial fish management agencies surveyed that reported using the various fish species groupings for analyzing angler-reported catch data collected from angler surveys (Question 6; Appendix).

<table>
<thead>
<tr>
<th>Fish species grouping</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crappie</td>
<td>63.6</td>
</tr>
<tr>
<td>Sunfish (e.g., bluegill, pumpkinseed, redear sunfish . . .)</td>
<td>60.6</td>
</tr>
<tr>
<td>Catfish (e.g., channel catfish, flathead catfish, bullheads Ameiurus spp . . .)</td>
<td>57.6</td>
</tr>
<tr>
<td>Black bass (e.g., largemouth bass, smallmouth bass, spotted bass . . .)</td>
<td>51.5</td>
</tr>
<tr>
<td>Trout (e.g., brown trout, brook trout Salvelinus fontinalis, rainbow trout . . .)</td>
<td>45.5</td>
</tr>
<tr>
<td>Morone (e.g., striped bass, white bass, hybrids . . .)</td>
<td>24.2</td>
</tr>
<tr>
<td>Panfish (e.g., sunfish, crappie, yellow perch Perca flavescens . . .)</td>
<td>21.2</td>
</tr>
<tr>
<td>Percids (e.g., walleye, sauger, saugeye, yellow perch . . .)</td>
<td>18.2</td>
</tr>
<tr>
<td>Bullheads (bullhead spp.)</td>
<td>18.2</td>
</tr>
<tr>
<td>Salmon (e.g., Chinook salmon Oncorhynchus tshawytscha, coho salmon O. kisutch, kokanee O. nerka . . .)</td>
<td>9.1</td>
</tr>
<tr>
<td>Centrarchids (e.g., black bass, sunfish . . .)</td>
<td>6.1</td>
</tr>
<tr>
<td>Esocids (e.g., northern pike Esox lucius, pickerel Esox spp., muskellunge E. masquinongy . . .)</td>
<td>3.0</td>
</tr>
<tr>
<td>Char (e.g., lake trout Salvelinus namaycush, bull trout, Dolly Varden S. malma . . .)</td>
<td>3.0</td>
</tr>
<tr>
<td>Cichlids (e.g., tilapia Tilapia spp., red devil cichlid Cichlasoma citrinellum . . .)</td>
<td>3.0</td>
</tr>
</tbody>
</table>

(e.g., bluegill, channel catfish, largemouth bass, and walleye), and misidentification of congeners tended to be biased toward these common species. For example, accuracy of LR anglers at identifying bluegill was high (85.1%) with only 1.3% of the anglers identifying bluegill as a different sunfish species, whereas angler accuracy in identifying all other sunfish species was low (mean = 5.1%), with 60.0% of anglers identifying these sunfish species as bluegill. The OR anglers showed a similar bias in identifying both smallmouth bass and spotted bass as large-mouth bass, walleye and saugeye as sauger, and blue catfish and flathead catfish as channel catfish. These results were consistent with those of Schmetterling and Long (1999) who found that Montana anglers presented with replicas of various salmonid species typically confused related species. Conceivably, when species-specific responses are required during angler surveys, angler propensity to identify related sport fishes as the more common common congener may result in the overestimation of catch and harvest rates for common species and an underestimation of related species.

Angler accuracy in sport fish identification was greatly enhanced by including related species and corresponding species group responses as accurate responses. On average, anglers were able to identify a specific sport fish to at least the correct species group (e.g., black bass) more than 80% of the time (LR anglers = 83.4%; OR anglers = 83.8%). This suggests that analyzing catch information from angler surveys by species groups (e.g., crappie, black bass) may reduce identification-related error. However, it should be noted that misidentification of some sport fishes as nonrelated species was still prevalent. For example, Lepomis spp. were routinely misidentified as crappie, while white crappie were misidentified as bluegill in our study, suggesting that error in identification may remain an issue for these species even after consolidating angler responses by species group. This may explain, in part, why Mallison and Cichra (2004) found significant underreporting during angler surveys of sunfish (71%) and crappie (29%) harvested by crappie and sunfish anglers, respectively. In addition, the proficiency among anglers in identifying Morone species was low and reflected a propensity for anglers to confuse these fishes with other species (e.g., crappie) and to identify these fish with colloquialisms (e.g., striper, wiper, hybrid). The low angler demand (<1% of anglers seeking) and limited number of hybrid striped bass and striped bass fisheries outside of the OR may also have contributed to a lack of familiarity with these species. Further, there appeared to be no common unifying species group name for Morone species familiar to anglers, which may have contributed to low accuracies; however, accuracy among Sander species was high despite no common species group name. Grouping angler responses by species groups appears to be a valid method for reducing identification error among angler surveys in Ohio and possibly elsewhere, although notable error still exists among some species.

The level of confidence among anglers in identifying sport fish was not considered in this study. Given that anglers were encouraged to provide species-specific responses and few responded with “I don’t know,” it is conceivable that a substantial number of anglers may have provided their “best guess” when identifying sport fish. A tendency among anglers to guess the most common or familiar species may explain in part the bias toward misidentifying sport fish as the more common or familiar species but would also suggest that some portion of accurate responses for common and familiar sport fish were also guesses. It is unclear as to what extent responses reflected “best guesses” or how the confidence among anglers in identification of sport fish may influence angler-reported catch numbers collected during angler surveys, but it is plausible that uncertainty among anglers in their ability to provide accurate catch information during a survey could result in a nonresponse bias. For example,
lacking relevant knowledge about a subject has been identified as a source of item nonresponse behavior among survey respondents; that is, partially or completely refraining from responding to individual survey components (Fisher 1996; Leeuw et al. 2003). In short, accuracy levels presented in this paper may be overstating the true identification proficiency of anglers as there is an unknown proportion of anglers likely providing common and familiar sport fish names as guesses and not as reliable identifications. Further work evaluating angler confidence in identifying sport fishes would be helpful for interpreting the reliability of angler identification of sport fishes and its impacts on angler survey-derived catch estimates.

Accuracy among anglers in identifying sport fishes differed among the species groups being targeted, but differences were not consistent with expectations. We expected that anglers targeting particular species groups would more accurately identify the species within those groups as they likely possessed more experience and knowledge regarding the species they sought; however, results suggested that the accuracy of LR anglers at identifying specific sport fishes was more a function of overall angler fishing experience, than experience dedicated toward any specific species group. This may be attributed, in part, to differences in levels of fishing specialization among anglers. Highly specialized anglers tend to be more experienced and engaged in fishing-related activities (e.g., members of fishing clubs), more knowledgeable (Wilde and Ditton 1994; Ditton 1996; Wilde et al. 1998), and presumably more competent at identifying fish species. We found that black bass and *Sander* spp. anglers exhibited greater accuracy at identifying nearly all sport fishes, whereas anything anglers were often less accurate. Black bass, *Sander* spp., and anything anglers likely represented the extremes in specialization among anglers surveyed, with black bass and *Sander* spp. anglers being the most specialized and anything anglers being the least specialized. In fact, Ohio black bass and *Sander* spp. anglers have been shown to be nearly twice as avid as anything seeking anything, with the mean number of days fished being 61, 56, and 32 d/year, respectively (ODOW, unpublished data). Similarly, Schmetterling and Long (1999) found that more experienced anglers were more adept at identifying various salmonid species, with those anglers who had been fishing for more than 10 years exhibiting an accuracy of 74.1%, whereas those with less than 1 year of experience exhibited an accuracy of 35.8%. These results may be helpful for developing expectations as to the level of accuracy among anglers and may assist in identifying angler groups that could be targeted for education programs. Stelfox et al. (2001) found that education strategies improved the accuracy of angler identification for various trout species in Alberta by 23%, with the greatest improvement (46%) observed among less experienced anglers (i.e., fished <1 year). Bowly and Savoie (2011) surmised that the high accuracy among Lake Ontario anglers in identifying salmonid species may be related, in part, to the availability of educational resources (e.g., online publications and reports).

While it is apparent that angler accuracy in identifying sport fishes has the potential to influence fisheries estimates derived from angler surveys, the overall impact of misidentifications will ultimately depend on the composition of sport fishes, anglers, and catch within a fishery. For example, identification errors from black bass fisheries composed of a single species of black bass may be less prevalent or easier to identify and correct by fisheries managers, likely making grouping responses to reduce error unwarranted. Our simulation, that compared “actual” angler catches to angler “reported” catches (i.e., after applying error rates from this study) revealed potentially dramatic differences in misidentification error among sport fishes (range = 0.2–386.0%). The largest differences in actual and reported catch were found among species with the lowest angler catch rates such as smallmouth bass, pumpkinseed sunfish, and green sunfish. Grouping responses among related species substantially reduced identification error within our simulation but also revealed that the catch among non–black bass species groups appeared to be underestimated, while the catch of black bass was overestimated. Interestingly, 51.8% of fish that were not correctly assigned to non–black bass species groups were directed to the black bass species group, with 67.3% attributed to the misidentification of *Morone* spp. (i.e., white bass). These results may be helpful for understanding general trends in the impacts of identification error on fisheries estimates derived from angler surveys.

Based on our survey results, there appears to be an inferred appreciation among fisheries management agencies for the lack of proficiency among anglers in identifying sport fishes. Most agencies grouped angler responses collected from angler surveys into species groups to some extent, and reliability of fish identification was the most important reason for these groupings. Prevalence of various species likely dictated, in part, the frequency in the types of groupings used among agencies (e.g., cichlids), but the results were no less demonstrative of the fact that the practice of grouping appears to be an option used by agencies for a variety of species groups. Crappie, sunfish, catfish, and black bass were groupings used by over half of the agencies. Trout were also a common grouping and is consistent with previous studies showing a lack of proficiency among anglers in identifying these species (Schmetterling and Long 1999; Stelfox et al. 2001). Infrequent groupings of other species such as salmon and esocids may be indicative of greater confidence among agencies in angler identification of those species. For example, Bowly and Savoie (2011) found that Lake Ontario anglers identified some salmon species with a high degree of accuracy (e.g., 93% for Chinook salmon).

In general, results provided an inference for drawing expectations as to the accuracy of results from angler surveys, designing angler surveys, and understanding the factors contributing to angler accuracy in sport fish identification. It is evident that consolidating and analyzing angler responses by species groups may be an option for reducing error related to misidentification and appears to be a common practice among...
state and provincial fisheries management agencies. Managers may need to consider the bias among anglers in identifying sport fish as the common or more familiar species, even when species groups are used. Further, angler misidentification of sport fishes likely impedes effective communication of fisheries information and the success of management strategies such as daily bag and length limits. Education programs may improve identification and concomitantly communication, but the effectiveness of those programs will no doubt be dependent on the level of specialization or avidity among anglers.

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REFERENCES


## APPENDIX: ONLINE SURVEY

**Ohio DNR Survey:** Differences among natural resource agencies in the collection of creel data related to angler-released fishes.

1. Does your agency collect data on angler-released fish as a routine part of your creel surveys?
   - Yes
   - No

2. What data are typically collected on angler-released fish? Please check all that apply.
   - Numbers
   - Fish types (e.g., species, species groups, families)
   - Location caught
   - Condition upon release (e.g., good, fair, dead)
   - Other, please specify

3. If data on types of fish are collected, how are they collected?
   - By specific species (e.g., largemouth bass)
   - By species groups (e.g., black bass, centrarchidae)
   - By both specific species and species groups depending on the species.

4. If data on types of fish are collected, how are the data analyzed?
   - By specific species (e.g., largemouth bass)
   - By species groups (e.g., black bass, centrarchidae)
   - By both specific species and species groups depending on the species.
   - We do not use data on angler-released fish in our creel surveys.

5. If angler-released fish are grouped by similar species, what are the reasons for grouping species? Please rank in order of importance with 1 being most important, or check NA if the reason does not apply.
   - Reliability of identification by anglers.
   - Similar management goals.
   - Few numbers of certain species caught.
   - Low importance of certain species to the fishery.
   - Simplify analysis.

6. Please indicate below the general types of fish groupings used, if any. Please check all that apply.
   - Bullheads (bullhead spp.)
   - Morones (e.g., striped bass, white bass, hybrids...)
   - Sunfish (e.g., bluegill, pumpkinseed, redear...)
   - Percids (e.g., walleye, suger, saugeye, yellow perch...)
   - Esocids (e.g., northern pike, pickerel, muskie...)
   - Black bass (e.g., largemouth, smallmouth, spotted...)
   - Catfish (e.g., channel, flathead, bullheads...)
   - Trout (e.g., brown, brook, rainbow...)
   - Panfish (e.g., sunfish, crappie, yellow perch...)
   - Crappie
   - Salmon (e.g., Chinook, coho, kokonee...)
   - Centrarchids (e.g., black bass, sunfish...)
   - Other, please specify

7. For creel surveys in general, how would you rate your confidence in the accuracy of data provided by anglers on the fish they release? Please select one.
   - Very confident.
   - Confident.
   - Somewhat confident.
   - Not confident.
   - Depends on the type of data collected (e.g., species, numbers, lengths...).

8. For creel surveys in general, please rate your confidence in the accuracy of the specific data types provided by anglers on the fish they release. With 1 being very confident and 4 being not confident.

<table>
<thead>
<tr>
<th>Specific species (e.g., largemouth bass)</th>
<th>Very confident</th>
<th>Confident</th>
<th>Somewhat confident</th>
<th>Not confident</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species groups (e.g., black bass)</th>
<th>Very confident</th>
<th>Confident</th>
<th>Somewhat confident</th>
<th>Not confident</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Number released</th>
<th>Very confident</th>
<th>Confident</th>
<th>Somewhat confident</th>
<th>Not confident</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Location caught</th>
<th>Very confident</th>
<th>Confident</th>
<th>Somewhat confident</th>
<th>Not confident</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Condition upon release (e.g., good, fair, dead)</th>
<th>Very confident</th>
<th>Confident</th>
<th>Somewhat confident</th>
<th>Not confident</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

9. In what state or province is your agency located?

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FIGURE A.1. Online survey sent to state and provincial fisheries management agencies within the United States and Canadian during 2007–2008 regarding angler self-reported data collected during angler surveys.
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Effect of Survey Design and Catch Rate Estimation on Total Catch Estimates in Chinook Salmon Fisheries
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Effect of Survey Design and Catch Rate Estimation on Total Catch Estimates in Chinook Salmon Fisheries

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Abstract
Roving–roving and roving–access creel surveys are the primary techniques used to obtain information on harvest of Chinook salmon *Oncorhynchus tshawytscha* in Idaho sport fisheries. Once interviews are conducted using roving–roving or roving–access survey designs, mean catch rate can be estimated with the ratio-of-means (ROM) estimator, the mean-of-ratios (MOR) estimator, or the MOR estimator with exclusion of short-duration (≤0.5 h) trips. Our objective was to examine the relative bias and precision of total catch estimates obtained from use of the two survey designs and three catch rate estimators for Idaho Chinook salmon fisheries. Information on angling populations was obtained by direct visual observation of portions of Chinook salmon fisheries in three Idaho river systems over an 18-d period. Based on data from the angling populations, Monte Carlo simulations were performed to evaluate the properties of the catch rate estimators and survey designs. Among the three estimators, the ROM estimator provided the most accurate and precise estimates of mean catch rate and total catch for both roving–roving and roving–access surveys. On average, the root mean square error of simulated total catch estimates was 1.42 times greater and relative bias was 160.13 times greater for roving–roving surveys than for roving–access surveys. Length-of-stay bias and nonstationary catch rates in roving–roving surveys both appeared to affect catch rate and total catch estimates. Our results suggest that use of the ROM estimator in combination with an estimate of angler effort provided the least biased and most precise estimates of total catch for both survey designs. However, roving–access surveys were more accurate than roving–roving surveys for Chinook salmon fisheries in Idaho.

The abundance of wild adult spring- and summer-run Chinook salmon *Oncorhynchus tshawytscha* in the Columbia River basin has declined over the last several decades. In 1995, Snake River spring- and summer-run Chinook salmon were listed as threatened under the Endangered Species Act (ESA; Myers et al. 1998). As a result of these declines, hatchery production was adopted to mitigate for loss of wild stocks and to provide sport, commercial, and ceremonial tribal fisheries in the Snake River basin. Section 9 of the ESA prohibits direct take of listed species (i.e., wild salmon); therefore, the only harvestable salmon sport fisheries in Idaho are supported by hatchery salmon. Since the 1950s, sport fishery seasons, locations, and bag limits for spring- and summer-run Chinook salmon in Idaho have varied depending on adult returns (Sam Sharr, Idaho Department of Fish and Game [IDFG], personal communication).
Due to the status of Chinook salmon in Idaho, there are multiple constraints on sport fisheries. For instance, harvest of hatchery fish is managed based on a quota system that allows sufficient returns to hatcheries for maintaining broodstock. Preliminary estimates of adult returns are forecasted and updated as Chinook salmon enter the Columbia River and travel through fish passage facilities at Bonneville Dam on the Columbia River and at Lower Granite Dam on the Snake River. Sportfishing seasons are then established by IDFG based on estimated returns of hatchery salmon to their parent hatcheries throughout Idaho, and the number of harvestable fish is shared equally between sport and tribal fisheries (Janssen and Kiefer 1999). Mixed-stock fisheries (wild and hatchery fish and mixtures of hatchery stocks) are managed to allow the return of fish to upriver fisheries and hatcheries and to minimize potential effects on wild stocks. In sport fisheries that target hatchery fish (Snake River, Salmon River, and South Fork Salmon River [SFSR]), the ESA limits the allowable incidental mortality (e.g., hooking mortality) of listed wild salmon that are caught and released to 0–2% depending on the run size. Fisheries must be closed when this condition is met (Apperson and Wilson 1998). A constant mortality rate of 10% is assumed for all listed stocks of wild Chinook salmon that are caught and released.

In addition to the above incidental mortality quota, fisheries may be closed once the harvest share of hatchery fish has been met. Throughout most of the Snake River basin in Idaho, IDFG typically closes fisheries based on the harvest share before the incidental mortality quota is met (Dale Allen, IDFG, personal communication). Maximization of angling opportunity and harvest is the primary goal of the IDFG hatchery program. Thus, precise estimates of harvest and release of both wild and hatchery fish are required to maximize angling opportunity while minimizing the incidental mortality of wild fish.

Creel surveys are the primary technique used to obtain information on angler use and harvest in sport fisheries. The design and scale of creel surveys vary greatly depending on the sampling frame, desired precision, and available resources (Pollock et al. 1994). Roving creel surveys are typically conducted in fisheries that have diffuse access, whereas access surveys are conducted in fisheries that have few access points. Both survey designs may use an estimate of angling effort (i.e., based on angler counts) that is expanded over the hours in the fishing day to estimate total angler-hours (Robson 1960, 1961). Surveys may also include an angler interview component that is used to estimate mean catch rate, often based on incomplete trips for roving creel surveys and complete trips for access surveys. Estimates of angling effort are then multiplied by mean catch rate to estimate total catch (Robson 1961).

Pollock et al. (1997) provided a naming protocol to describe creel surveys that employ complemented designs; the name specifies the effort survey type followed by the interview survey type (e.g., “roving–access” design). The IDFG currently uses both roving–roving and roving–access survey designs in salmon fisheries depending on the characteristics of the fishery. To estimate catch rate in roving–roving surveys, angler interviews are conducted primarily while anglers are fishing (i.e., incomplete trips; Malvestuto 1983; Robson 1991; Pollock et al. 1994). In Idaho, creel clerks travel through the fishery in a vehicle or on foot and intercept shore anglers. Because anglers are intercepted during their fishing trips, the probability of being surveyed is not equal among all anglers. Instead, the probability of being surveyed is proportional to the angler’s trip length (Robson 1961; Hoening et al. 1997; Pollock et al. 1997). An unequal interview probability among anglers can introduce bias into estimates of mean catch rate if anglers who fish for different durations have different catch rates (e.g., anglers who fish longer have a higher catch rate than anglers who fish for a shorter duration; Malvestuto 1983; Pollock et al. 1994, 1997); this has been referred to as “length-of-stay bias.” In a roving–roving survey, because the anglers are interviewed before their trips are completed, it is also assumed that each angler’s catch rate is stationary and does not change after the angler is interviewed (MacKenzie 1991; Pollock et al. 1994, 1997). Thus, accuracy and precision of total catch estimates from roving–roving designs could be sensitive to both length-of-stay bias and nonstationary catch rates.

In roving–access surveys, anglers are intercepted as they exit the fishery at the completion of their fishing trips (Robson 1960; Hayne 1991; Pollock et al. 1994). Because interviews are based on completed trips, anglers have an equal probability of being interviewed and the catch rate estimates are not subject to length-of-stay bias. Contrary to roving–roving surveys, the assumption of stationary catch rates is not required for roving–access surveys because the actual final catch rate is observed. Although roving–access surveys are desirable because they require fewer assumptions than roving–roving creel surveys, they may be subject to bias if access points are numerous, not well defined, or overlooked by creel clerks (Pollock et al. 1994). As with most creel surveys, the choice of survey design (roving–access or roving–roving) for Chinook salmon fisheries in Idaho is typically determined by the number of access points. Access is diffuse throughout most salmon fisheries in Idaho, but a large proportion of angling effort takes place in a few localized areas. Such areas may be surveyed by using roving–access surveys, while the remaining areas of the fishery can be surveyed with a roving–roving design.

Regardless of the angler contact approach used, once the interviews are conducted the mean catch rate is estimated by using either the ratio-of-means (ROM) estimator or the mean-of-ratios (MOR) estimator depending on the survey design (Jones et al. 1995; Hoening et al. 1997; Pollock et al. 1997). The ROM estimator calculates mean catch rate as the total catch divided by the total time fished. For all anglers in the sample, thus producing an estimate of mean catch rate per day. The MOR estimator calculates mean catch rate as the mean of catch rates for all anglers who were interviewed and results in an estimate of mean catch rate per angler. The two estimators typically result in two different estimates of catch rate (Crone and Malvestuto 1991; Keeffe et al. 2009). Several authors have suggested that the ROM estimator should be used to estimate mean catch rate and...
total catch when anglers are surveyed with equal probability (roving–access surveys), whereas the MOR estimator should be used when anglers are surveyed with unequal probability (roving–roving surveys; Jones et al. 1995; Hoenig et al. 1997; Lockwood 1997; Pollock et al. 1997). Moreover, use of the MOR estimator in roving–roving surveys can result in estimates of mean catch rate with unstable variance if the interviewed anglers have large catches and short trip lengths (Jones et al. 1995; Hoenig et al. 1997; Pollock et al. 1997). However, if short trips (i.e., ≤0.5 h) are ignored, the variance of estimates of mean catch rate may stabilize with no appreciable bias (Hoenig et al. 1997; Pollock et al. 1997).

Previous research on survey designs and catch rate estimation has been based on simulation models of fisheries by using either completed trip data or simulated data (Jones et al. 1995; Hoenig et al. 1997). These simulation models do not account for actual temporal changes in catch rate, and they fail to capture the unique characteristics that define Chinook salmon fisheries in Idaho. Furthermore, such modeling is based on an assumed or simulated distribution instead of observed data (Hoenig et al. 1997; Dauk and Schwarz 2001; Lockwood 2004). Various authors (e.g., Hoenig et al. 1997; Pollock et al. 1997) have identified the need for additional research to determine the properties of catch rate estimates for fisheries with different specific characteristics (e.g., temporal changes in catch rate).

Due to the nature of Chinook salmon fisheries in Idaho and other fisheries across the Columbia River basin, poorly designed creel surveys or improper statistical analyses could result in premature closing of a fishery or insufficient adult returns to hatcheries. The results from angler surveys could affect future fisheries or could jeopardize the sustainability of a threatened species. Constraints on these fisheries (i.e., harvest share and catch-and-release quota) create the necessity for accurate and precise short-term (e.g., daily or weekly), in-season estimates of total catch. Therefore, the objective of this research was to compare angler interview strategies (roving–access and roving–roving) and catch rate estimators (ROM and MOR) for estimating total catch in Idaho Chinook salmon fisheries.

**METHODS**

**Study area.**—The Snake River originates in Jackson Lake (Grand Teton National Park), Wyoming. After draining much of the southern portion of Idaho, the Snake River flows north, forming the Oregon–Idaho border, and then enters the Columbia River at Burbank, Washington. Anadromous fishes currently have access to portions of the Snake River below Hells Canyon Dam. Major Idaho tributaries below Hells Canyon Dam include the Salmon River and the Clearwater River (CR). Angler observations were conducted on the CR, the SFSR, and the Little Salmon River (LSR) near its confluence with the Salmon River.

**Field methods.**—Censuses of angling activity were completed on 200–700-m reaches of three Chinook salmon fisheries in Idaho based on direct visual observations that served as a theoretical angling population. Resampling simulations were then conducted, and the resulting sampling distributions were evaluated to determine the effect of survey type and catch rate estimator on the bias and precision of total catch estimates. Based on instantaneous counts of anglers in the census reach compared with simultaneous counts of anglers in the entire fishery (i.e., conducted by IDFG creel clerks), the observed census reach accounted for approximately 28% of angling effort in the entire fishery of interest on the CR, 19% of angling effort on the LSR, and 6% of angling effort on the SFSR. We assumed that these nonrandomly selected observation reaches were representative of the target population. These distributions served as the theoretical angling population that was resampled using Monte Carlo simulations. Observations were conducted for 6 d at each fishery (CR, SFSR, and LSR), for a total of 18 observation days. On the SFSR, two different reaches were observed during the 6-d period due to spatial shifts in angling activity. On the CR and LSR, observations were conducted at the same site throughout the 6-d period. Observation reaches were selected nonrandomly based on known fishing locations that allowed for discreet observations of anglers and adequate sample sizes (i.e., angling effort and total catch). Observation days were also selected nonrandomly and were conducted near the peak of the fishing season in each fishery to maximize observation of angling activity. Fishing hours for all fisheries were during daylight; on a given observation day, observers were present before the start of the legal fishing period, and they remained until after the end of the legal fishing period.

Observers remained “hidden” so as not to influence angler decisions on fishing locations, fishing times, fish harvest, or reporting to IDFG creel clerks. On the CR and LSR, angling activity was observed from afar using spotting scopes. However, this was not possible on the SFSR. Consequently, two observers were used to monitor fishing activity on the SFSR: one observer fished and relayed information to the other observer, who discreetly recorded data. The recorded data included the time each angler entered and left the fishery, the total catch, the time of catch, the number of fish released, and the number of fish harvested. Each angler was assigned a unique arbitrary identification number, and a physical description was recorded.

The start of a fishing event was defined as the angler’s first cast, and the end of the fishing event was defined as the time the angler exited the fishing area and was no longer available for a roving interview. If an angler took a “break” and exited the fishery (i.e., was out of the field of visibility for the IDFG creel clerks who were conducting the roving counts) for a period of 5 min or greater, that angler was assumed to be unavailable for counting in a roving effort count. If an angler re-entered the fishery, that angler was re-assigned his initial identification number. All data were recorded on a per-angler basis to avoid bias or variance that may arise from estimates associated with angler groups or parties (e.g., pooled effort and catch; Lockwood 1997).

**Sampling strategies.**—Once the census data were collected, angling populations were created for simulation analysis. Angling populations were sampled using Monte Carlo simulations that employed various sampling and estimation strategies to
evaluate bias and precision. Simple random sampling without replacement was used to estimate total effort, mean catch rate, and their product (i.e., total catch) in each fishery from the census data set. Effort was estimated with a simple random sampling design, where minutes were defined as the sampling units (i.e., count times) and were selected with equal probability. The sampling frame for count times included all minutes during legal fishing hours. Four count times were selected for each fishery and day, and counts of anglers were conducted instantaneously. To evaluate mean catch rate estimation using the roving–roving method, simulated interviews of 60% of all anglers were conducted each day at random times during their fishing trips. Anglers were selected for interview with selection probabilities proportional to the time fished. To evaluate mean catch rate estimation using the roving–access survey method, simulated interviews of 60% of all anglers were conducted at the conclusion of their fishing trips. In the roving–access survey, anglers were selected for interview with equal selection probabilities. Total catch was estimated in both roving–roving and roving–access simulations and included fish that were harvested and fish that were released.

Effort, catch rate, and total catch estimation.—Total angling effort (\(E\)) in angler-hours in all simulated fisheries was estimated as

\[
E = T \bar{I},
\]

where \(T\) is the total number of hours in the fishing day and \(\bar{I}\) is the mean of the four angler counts. Mean daily catch rate in all simulated fisheries was estimated using the ROM estimator (\(\hat{R}_1\)),

\[
\hat{R}_1 = \frac{\sum_{i=1}^{n} c_i}{\sum_{i=1}^{n} L_i} / n,
\]

and the mean catch rate per angler was calculated using the MOR estimator (\(\hat{R}_2\)),

\[
\hat{R}_2 = \frac{\sum_{i=1}^{n} c_i / L_i}{n},
\]

where \(c_i\) is the number of fish caught by the \(i\)th angler, \(L_i\) is the number of hours fished by the \(i\)th angler, and \(n\) is the total number of anglers interviewed. Hoenig et al. (1997) and Pollock et al. (1997) suggested that the variance of mean catch rate estimates obtained by use of MOR could be stabilized by excluding the interviews of anglers whose trips were 0.5 h or less. Therefore, the MOR catch rate for each simulated fishery was estimated (1) with truncation of the data set to exclude short fishing trips of 0.5 h or less (\(\text{MOR}_t\)) and (2) without truncation. Total catch in each simulated fishery was estimated by using the ROM catch rate (total catch \(\hat{C}_1\)),

\[
\hat{C}_1 = E \times \hat{R}_1,
\]

and the MOR catch rate (total catch \(\hat{C}_2\); with and without exclusion of trips \(\leq 0.5\) h),

\[
\hat{C}_2 = E \times \hat{R}_2.
\]

For roving–roving surveys, mean catch rate was estimated using the three estimators (ROM, MOR, and MOR\(_t\)), whereas for roving–access surveys the mean catch rate was estimated using the MOR and ROM estimators only. Mean catch rate was estimated on the same sample of anglers selected for each survey design and estimator at each iteration of the simulation. Nonparametric bootstrap 95% CIs were calculated for each estimate using the percentile method (Efron and Tibshirani 1993).

Simulations and evaluation.—For each survey design (roving–roving or roving–access) and catch rate estimator, Monte Carlo simulations were conducted that included 1,000 iterations of effort, mean catch rate, and their product (i.e., total catch estimate). This provided an empirical sampling distribution. Bias was estimated as the difference between the mean of the sampling distribution and the true population parameter. Relative bias was estimated as bias divided by the true population parameter. To assess the accuracy and precision of each estimator, the root mean square error (RMSE) was estimated as the square root of the mean squared difference between the estimate (\(\hat{\theta}\)) and the true value (\(\theta\)):

\[
\text{RMSE}(\hat{\theta}) = \sqrt{\frac{\sum_{i=1}^{1,000} (\hat{\theta}_i - \theta)^2}{1,000}}.
\]

Coverage of the 95% CIs of total catch estimates was also evaluated. In theory, 95% of all bootstrap CIs should encompass the true population parameter, 2.5% should be below the true value, and 2.5% should be above the true value. The percentage of CIs that encompassed the true population parameter was determined along with the direction of CIs that did not encompass the known population value. Simulations and statistical analyses were conducted with R (R Development Core Team 2009).

When an angler is interviewed before their trip is complete (i.e., roving–roving surveys), the expectation is that the angler will be interviewed at the midpoint of the trip and that the angler’s catch rate is stationary during the trip (Pollock et al. 1994; Jones et al. 1995; Hoenig et al. 1997). Linear regression was used to examine the effect of this assumption on the relative bias of catch rate estimates. Relative bias in total catch estimates from simulations was regressed against the true mean change in catch rate from the midpoint of the trip to the completion of the trip for all anglers for each day in the fishery. The slope and coefficient of determination (\(r^2\)) from the linear regression models were used to evaluate the effect of nonstationary catch rates on relative bias for all three catch rate estimators in roving–roving surveys. Greater slopes and \(r^2\) values indicated greater effects of nonstationary catch rates on the relative bias of mean catch rate.
### TABLE 1. Summary of angling activity observed for 6 d on each of three Chinook salmon fisheries in Idaho (Clearwater, Little Salmon, and South Fork Salmon rivers) during the 2011 fishing season.

<table>
<thead>
<tr>
<th>Day</th>
<th>Total number of anglers</th>
<th>Total hours fished</th>
<th>Mean hours fished per angler</th>
<th>Number of fish caught</th>
<th>Daily catch rate (fish/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Clearwater River</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>49</td>
<td>254.6</td>
<td>5.2</td>
<td>8</td>
<td>0.031</td>
</tr>
<tr>
<td>2</td>
<td>47</td>
<td>264.2</td>
<td>5.6</td>
<td>8</td>
<td>0.030</td>
</tr>
<tr>
<td>3</td>
<td>31</td>
<td>251.1</td>
<td>8.1</td>
<td>9</td>
<td>0.036</td>
</tr>
<tr>
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<td>14</td>
<td>44.2</td>
<td>3.1</td>
<td>3</td>
<td>0.068</td>
</tr>
<tr>
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<td>37</td>
<td>122.9</td>
<td>3.3</td>
<td>6</td>
<td>0.049</td>
</tr>
<tr>
<td>6</td>
<td>42</td>
<td>123.5</td>
<td>2.9</td>
<td>4</td>
<td>0.032</td>
</tr>
<tr>
<td><strong>Little Salmon River</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>46</td>
<td>195.9</td>
<td>4.2</td>
<td>26</td>
<td>0.133</td>
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<td>0.229</td>
</tr>
<tr>
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<td>136.6</td>
<td>5.0</td>
<td>18</td>
<td>0.132</td>
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<tr>
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<td>40</td>
<td>183.8</td>
<td>4.6</td>
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<td>0.092</td>
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<td>37</td>
<td>116.7</td>
<td>3.1</td>
<td>19</td>
<td>0.163</td>
</tr>
<tr>
<td><strong>South Fork Salmon River</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>30.4</td>
<td>5.0</td>
<td>1</td>
<td>0.033</td>
</tr>
<tr>
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<td>5</td>
<td>43.0</td>
<td>8.6</td>
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<td>0.046</td>
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<td>59.8</td>
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<td>5</td>
<td>0.083</td>
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<tr>
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<td>8</td>
<td>71.1</td>
<td>8.8</td>
<td>6</td>
<td>0.084</td>
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<tr>
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<td>29</td>
<td>124.4</td>
<td>4.2</td>
<td>21</td>
<td>0.169</td>
</tr>
<tr>
<td>6</td>
<td>29</td>
<td>105.9</td>
<td>3.6</td>
<td>17</td>
<td>0.161</td>
</tr>
</tbody>
</table>

### RESULTS

Over the 18-d observation period, 2,296 h of angling effort and 501 angler trips were observed (Table 1). Observed anglers caught 207 Chinook salmon, with 10% of anglers catching 58% of the fish. Seventy-three percent of anglers were unsuccessful in catching a fish. Fishing time (mean ± SE) for all anglers was 4.6 ± 0.16 h (Figure 1). Fishing time for observed anglers who were successful in catching a fish averaged 6.9 ± 0.31 h, whereas anglers who were unsuccessful fished for an average of 3.7 ± 0.16 h. Total catch per day for all anglers varied from 1 to 26 fish (mean ± SE = 11.5 ± 1.84 fish). The true mean daily catch rate (ROM) for observed anglers varied from 0.030 to 0.229 fish/h and averaged 0.099 ± 0.0029 fish/h. Mean per-angler catch rate (MOR) varied from 0.000 to 0.677 fish/h and averaged 0.085 ± 0.0096 fish/h. For anglers who caught fish, the time of the first catch varied from 0.02 to 14.90 h (mean ± SE = 3.8 ± 0.27 h) after the beginning of the trip.

Simulations for all 18 observation days using simple random sampling to estimate angling effort resulted in relatively unbiased and precise estimates (Table 1; Figure 2). Relative bias in effort estimates varied from 0.25% to 1.22% (mean ± SE = 0.62 ± 0.064%). The RMSE of simulated estimates of angling effort varied from 7.72 to 64.65 h (mean ± SE = 25.00 ± 3.95 h). Bias and RMSE were highest for the CR fishery, where effort was the lowest. The direction of bias in total effort estimates was not consistent among days but tended toward negative bias. Effort was overestimated on 4 of the 18 survey days and was underestimated on 14 survey days. The largest bias in any one sampling distribution was less than 3 h (i.e., on day 2 for the CR fishery). Although estimates of effort added further variability to estimates of total catch when combined with mean catch rate, they added little to overall bias.

Overall, among the three estimators, the ROM estimator provided the most accurate and precise estimates of mean catch rate (Figure 3) and total catch (Figure 4) for both survey designs (Table 2). Although the MOR<sub>eff</sub> estimator generally performed better than the nontruncated MOR estimator, it did not perform as well as the ROM estimator. For roving–roving surveys, bias and RMSE of mean catch rate (Figure 3) and total catch (Figure 4) using the MOR estimator were highest on day 4 for the LSR fishery and day 6 for the SFSR fishery; bias was positive (i.e., mean catch rate and total catch were overestimated) on both days. The truncation of the data set to remove short-duration trips (MOR<sub>tr</sub> estimator) reduced bias and RMSE on these days. Direction of bias for roving–roving surveys was not consistent over the 18-d period for any of the estimators. Mean catch rate and total catch were overestimated on 7 d when the MOR and MOR<sub>tr</sub> estimators were used. The ROM estimator provided the most accurate and precise estimates of mean catch rate (Figure 3) and total catch (Figure 4) for both survey designs (Table 2). Although the MOR<sub>eff</sub> estimator generally performed better than the nontruncated MOR estimator, it did not perform as well as the ROM estimator.
catch rate and total catch on 6 d for the roving–roving survey design.

For the roving–roving design, the mean CI coverage of total catch estimates for all days was closest to 95% when the ROM estimator was used (mean ± SE = 87.8 ± 3.75%; Table 2). With use of the MOR_{tr} estimator, the CIs resulted in a mean coverage of 78.6 ± 4.00%, indicating slightly better performance than that of the nontruncated MOR estimator (mean ± SE = 75.0 ± 4.10%). For all estimators used with the roving–roving design, the CIs that did not contain the true total catch were typically biased low. For all estimators over the 18-d period, an underestimate of CI coverage was observed approximately 96% of the time (i.e., mean between days) when the CI did not encompass the true parameter.

Use of the ROM estimator in a roving–access survey consistently resulted in a smaller relative bias and higher precision than use of the MOR estimator (Figures 3, 4). The only exception was on day 6 for the CR fishery, when performance was similar between estimators. Bias from use of the ROM estimator was less than 0.6 fish for every day in the fishery. The direction of bias was not consistent between days for either estimator. Mean catch rate and total catch were overestimated on 11 d and
FIGURE 3. Bias and root mean square error (RMSE) of estimated mean catch rate (fish/h) from roving–roving (left panels) and roving–access (right panels) creel surveys conducted in three Chinook salmon fisheries (Clearwater River [CR], Little Salmon River [LSR], and South Fork Salmon River [SFSR], Idaho) during 2011. The mean-of-ratios (MOR) and ratio-of-means (ROM) estimators were calculated for simulated roving–roving and roving–access surveys. The MOR estimator with truncation of the data set to exclude 0.5-h or shorter fishing trips (MORtr) was also evaluated for the roving–roving surveys. Simulations for each fishery encompassed 6 d.

underestimated on 7 d when the ROM was used; with the MOR estimator, mean catch rate and total catch were overestimated on 13 d and underestimated on 5 d. For the roving–access design, mean CI coverage for all days was 95.3 ± 1.67% (mean ± SE) when using the ROM estimator and 83.7 ± 4.03% when using the MOR estimator (Table 2). Similar to the roving–roving survey design, CI coverage was biased low. Over the 18-d period, when the CIs did not encompass the true parameter, they were underestimated approximately 97% of the time for both estimators.

The RMSE of total catch estimates for roving–roving surveys was 1.42 times greater (range = 1.04–2.24 times greater) than that observed for roving–access surveys on average. This suggests that accuracy would be 1.42 times less in a roving–roving survey than in a roving–access survey. Roving–roving surveys resulted in total catch estimates that were 160.13 times more biased on average (range = 0.02–2,500.06 times more biased) than those from roving–access surveys.

Length-of-stay bias and nonstationary catch rates in roving–roving surveys appeared to affect estimates of mean catch rate and total catch. Figure 5 illustrates the potential effect of nonstationary catch rates on bias in roving–roving surveys; the three observation days depicted in the figure were selected because of the observed relative bias from the simulations. For instance, on day 6 for the SFSR fishery, anglers had a higher catch rate (on average) at the midpoint of their trips than at the completion of their trips (Figure 5), resulting in an overestimate of total catch by use of all three estimators (Figure 4). The opposite scenario was observed on day 2 for the LSR fishery, when anglers had a lower catch rate at the midpoint of their trips and the total catch was underestimated. On day 1 for the LSR fishery, anglers had a relatively small change in catch rate on average, and total catch
estimates were relatively unbiased. The three estimators were not equally sensitive to nonstationary catch rates. Nonstationary catch rates explained 64% of the variability in relative bias of total catch estimates from the MOR, 21% of the variability in relative bias from the MOR_t, and 14% of the variability in relative bias from the ROM (Figure 6). The slope of the regression line describing the change in catch rate versus relative bias of simulated total catch estimates from the MOR estimator was 2.4 times higher than the slope for the MOR_t estimator and 4.3 times higher than the slope for the ROM estimator.

**DISCUSSION**

Results from this study are consistent with recommendations from previous research with regard to roving–access surveys but differ from previous work on roving–roving surveys (Jones et al. 1995; Hoenig et al. 1997; Lockwood 1997; Pollock et al. 1997). Jones et al. (1995) suggested that the ROM and MOR estimators do not estimate the same theoretical catch rate. Instead, the ROM estimates the per-day catch rate and the MOR estimates the per-angler catch rate. When interviews are combined with an estimate of total effort, the ROM estimates total catch when interviews are from completed trips (i.e., roving–access surveys), whereas the MOR estimates total catch when interviews are from incomplete trips (i.e., roving–roving surveys). Hoenig et al. (1997) and Pollock et al. (1997) provided a theory to explain why the estimators are appropriate in different situations (i.e., complete versus incomplete trips), and showed that the MOR estimator could be improved by excluding interviews representing fishing trips that were 0.5 h or shorter in
TABLE 2. Percent CI coverage for simulated estimates of total catch (percentage of CIs that encompassed the true value of total catch) on 6 d for each of three Chinook salmon fisheries in Idaho (Clearwater, Little Salmon, and South Fork Salmon rivers) during the 2011 season. Two survey designs (roving–roving and roving–access surveys) were simulated. Three estimators of mean catch rate were used for roving–roving surveys (mean of ratios [MOR], ratio of means [ROM], and MOR with truncation of the data set to exclude fishing trips ≤ 0.5 h [MORtr]), and two estimators of catch rate were used for roving–access surveys (MOR and ROM).

<table>
<thead>
<tr>
<th>Day</th>
<th>Number of fish caught</th>
<th>Roving–roving survey</th>
<th>Roving–access survey</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MOR</td>
<td>ROM</td>
</tr>
<tr>
<td>Clearwater River</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>36.8</td>
<td>76.1</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>76.7</td>
<td>96.0</td>
</tr>
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</tr>
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<td>90.7</td>
</tr>
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<td>Little Salmon River</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>26</td>
<td>89.6</td>
<td>97.6</td>
</tr>
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<td>5</td>
<td>21</td>
<td>93.8</td>
<td>99.2</td>
</tr>
<tr>
<td>6</td>
<td>17</td>
<td>91.3</td>
<td>97.5</td>
</tr>
</tbody>
</table>

duration. Hoenig et al. (1997), Jones et al. (1995), Lockwood (1997), and Pollock et al. (1997) all presented simulation studies that were consistent with this theory. Our study results suggest that using the ROM estimator in combination with an estimate of angler effort provided the least biased and most precise estimates of total catch for both survey designs used in Idaho Chinook salmon fisheries.

The properties of the ROM estimator when used with roving–access surveys are well understood because anglers are interviewed with equal probability at the completion of their trips (Pollock et al. 1994, 1997; Jones et al. 1995). With few exceptions, mean catch rate estimates for roving–access surveys are not affected by bag limits, length-of-stay bias, or nonstationary catch rates (Pollock et al. 1994; Bernard et al. 1998; Rasmussen at al. 1998). Empirical studies have likely been consistent with regard to the correct estimator in roving–access surveys because of the properties of the ROM estimator and the lack of assumptions (e.g., stationary catch rates) in surveys based on access interviews. When multiplied by an estimate of effort, the ROM estimator provides an unbiased estimate of total catch. In contrast, when the MOR estimator is multiplied by an estimate of effort in a roving–access survey, it does not provide a true estimate of total catch (Jones et al. 1995; Pollock et al. 1997). Our results are consistent with previous research indicating that the ROM is the appropriate estimator in roving–access surveys when total catch is the parameter of interest (Jones et al. 1995; Lockwood 1997; Pollock et al. 1997).

Simulations based on effort and catch data from Chinook salmon fisheries in Idaho suggest that the ROM estimator was the least biased and most precise estimator for roving–roving creel surveys. This finding is inconsistent with simulation results presented by Jones et al. (1995) and Hoenig et al. (1997); however, their simulations were conducted for fisheries with characteristics that were vastly different from those of Chinook salmon fisheries in Idaho. Specifically, the disparity between successful and unsuccessful anglers in terms of catch rates (>70% of observed anglers did not catch any fish) and time fished was greater in the present study than in the previous studies. In addition, previous simulations did not account for actual changes in angler catch rates over time. Jones et al. (1995) suggested that the ROM estimator in roving–roving surveys typically overestimates catch, but this was generally not observed in our study. When simulated catch rates were overestimated in comparison with known values, we found that it was likely a result of
FIGURE 5. Probability that an angler would be interviewed versus the change in catch rate from the midpoint to the completion of the fishing trip for individual anglers in Chinook salmon fisheries, as illustrated by 2 d on the Little Salmon River (LSR) and 1 d on the South Fork Salmon River (SFSR), Idaho, in 2011. Theoretically, it is assumed that (1) anglers are interviewed at the midpoint of their fishing trips in a roving survey design and (2) the catch rate at the midpoint of an angler’s trip should represent the final catch rate for that trip (i.e., assumption of stationary catch rate).

FIGURE 6. Relationship between the mean change in catch rate (fish/h) from the midpoint of an angler’s fishing trip to the completion of the trip for all anglers on each day and the relative bias of total catch estimates from simulations using three catch rate estimators: (A) ratio of means, (B) mean of ratios, and (C) mean of ratios with truncation of the data set to exclude 0.5-h or shorter fishing trips. Chinook salmon fisheries on the Clearwater River (CR), Little Salmon River (LSR), and South Fork Salmon River (SFSR), Idaho, were each evaluated for 6 d (i.e., 18 total observation days).
interviewing a few anglers who fished for a relatively short time and caught a fish. Not surprisingly, these anglers had an extremely high catch rate, which biased estimates of mean catch rate. The ROM estimator was not affected by these anglers to the same extent as the MOR estimator. When the MOR estimator is used, each angler is equally weighted, whereas the ROM estimator involves weighting each angler by the length of time fished. The effect of high catch rates and low effort on mean catch rate has been recognized in the literature. For instance, Hoenig et al. (1997) reported that the MORtr and ROM estimators typically resulted in similar estimates on average, but the MORtr estimator resulted in a smaller mean square error. Our results are consistent in that the MORtr and ROM estimators resulted in similar estimates; however, the ROM estimator resulted in a lower RMSE, lower bias, and more accurate CI coverage than either of the MOR estimators. The removal of trips of different durations may have been more consistent with previous research (e.g., excluding trips ≤ 0.5 h instead of trips ≤ 1 h). Although bias was decreased by truncating short trips in this study, caution should be taken when subjectivity is used (i.e., deciding to ignore trips of a given length) in an attempt to improve estimates. Such actions may result in additional and unpredictable bias.

In addition to producing a smaller average bias and lower RMSE, the ROM estimator was associated with 95% CI coverage that was closest to targeted values for both the roving–roving and roving–access survey designs. However, the skewed distributions of catch rates (i.e., most anglers were unsuccessful in catching a fish) resulted in CIs that were biased low. Jones et al. (1997) found similar results (80–99% of the rejection area was concentrated in the left tail) when using closed-form variance estimators. Jones et al. (1997) suggested that a sample size of 100 interviews would result in CI coverage equal to targeted levels but that the coverage would still be asymmetrical due to the skewed distribution of catch rates. Chinook salmon fisheries in Idaho and elsewhere are characterized by high localized densities of angler effort relative to that observed for many other fisheries (Martinson and Shelby 1992). Interviewing 100 or more anglers on most survey days is a realistic and reasonable target when planning surveys and hiring creel survey personnel. However, catch rates in Idaho Chinook salmon fisheries are typically skewed to a greater extent than those in the fisheries described by Jones et al. (1997), and thus a higher sampling intensity may be necessary to reach targeted CIs.

In the roving–roving surveys, biased estimates of total catch may have resulted from both length-of-stay bias and nonstationary angler catch rates. Anglers who caught fish tended to have longer fishing durations and therefore a higher probability of being interviewed than anglers who were unsuccessful in catching fish (Pollock et al. 1994). Given the disparate distributions of trip duration between groups of anglers with differing catch rates, we would expect catch rate and total catch to be consistently overestimated because anglers with higher catch rates were more likely to be interviewed. However, with the exception of the SFSR fishery, use of all three estimators with the roving–roving surveys resulted in a negative bias on most days. This suggests that variable catch rates are more responsible for the bias observed in our study.

It is assumed that anglers are interviewed at the midpoint of their fishing trips in a roving survey, and their catch rate at that point is assumed to be constant (stationary catch rate; Pollock et al. 1994; Hoenig et al. 1997). In the Chinook salmon fisheries we studied, anglers failed to meet the stationary catch rate assumption on the days of observation. For instance, on day 6 for the SFSR fishery, successful anglers tended to have a higher catch rate at the midpoint of their trips relative to the end of their trips; this resulted in overestimation of catch rate and total catch for that day. The opposite scenario was observed on day 2 for the LSR fishery, where anglers had a lower catch rate at the midpoint than at the end of their trips and estimates were negatively biased. Individual anglers’ catch rates were not constant on LSR day 1, but the change in catch rate was inconsistent among anglers, thereby resulting in unbiased estimates of mean catch rate and ultimately total catch.

Multiple methods have been proposed to account for differences in catch rates between incomplete trips and completed trips. Pollock et al. (1997) suggested that complete and incomplete catch rates should be estimated on the same sample of anglers to validate the use of the MOR estimator with roving surveys. Keefe et al. (2009) provided methodology to use linear regression models that correct for apparent bias in catch rates based on incomplete trips. Dauk and Schwarz (2001) proposed a model that improved catch rate estimates for a gill-net fishery by assuming declining catch rates instead of stationary catch rates. However, in the three Chinook salmon fisheries we evaluated, the trajectory of catch rates through time was not consistent among the fisheries or among days, thus precluding use of the models similar to those proposed by Dauk and Schwarz (2001) and Keefe et al. (2009). Validation of catch rates from the same sample of anglers, as was suggested by Pollock et al. (1997), would be impractical because it would have to be performed daily due to inconsistency in catch rates. When properly designed, roving–access surveys are free from length-of-stay bias and the assumption of stationary catch rates. Consequently, access surveys are preferable whenever logistically possible.

Although use of the ROM estimator with roving–roving surveys provided the most precise and unbiased estimates in our study, use of the ROM with a roving–roving survey should be done with caution. Hoenig et al. (1997) showed that using the ROM catch rate estimator with a roving–roving survey did not provide the most unbiased and precise estimates of total catch. Instead, those authors recommended using the MORtr estimator.
Our simulations showed that the ROM is the preferred estimator for both roving–roving and roving–access surveys, probably due to the characteristics of Chinook salmon fisheries in Idaho. However, all of the mean catch rate and total catch estimates were biased when a roving–roving survey design was used. Given the inconsistent properties of estimators used with roving–roving creel surveys, roving–access surveys are preferable when circumstances allow.

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ARTICLE

Empirical Standard Weight Equation for the Aegean Chub Squalius fellowesii, an Endemic Freshwater Fish Species of Western Anatolia, Turkey

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Abstract

Data on length and weight of Aegean chub Squalius fellowesii, an endemic species distributed in the Aegean drainages of Anatolia, Turkey, were used to calculate a standard weight (Ws) equation by means of the empirical percentile (EmP) method. The resulting Ws equation was log10Ws = −3.801 + 1.783·log10TL + 0.329·(log10TL)². Over the range of application (70–220 mm TL), the EmP Ws equation was not biased by length, and the use of this equation is suggested as a way to calculate the relative weight (Wr) of Aegean chub throughout the species’ distribution area.

Analysis of length–weight relationships can provide important insights into the ecology of a species and can help in the assessment of populations of that species (Froese 2006). Body condition indexes are useful tools derived from length–weight relationships for a species (Blackwell et al. 2000) and provide a measure of the health of a fish population under the assumption that for fish of a given length, heavier individuals are in better condition than lighter individuals (Froese 2006). Because these indexes are based only on measurements of length and weight, there is no need to sacrifice any of the specimens, and large numbers of fish can be processed with minimal mortality (Fechhelm et al. 1995). Thus, body condition indexes have become important tools for fisheries management (Anderson and Neumann 1996; Blackwell et al. 2000). Among the condition indexes proposed in the literature (e.g., Fulton’s [1911] condition factor and Le Cren’s [1951] condition factor), relative weight (Wr; Wege and Anderson 1978) has the advantage of not being affected by length biases and changes in body shape. Therefore, the use of Wr allows comparative condition assessments of fish from different length-groups and from different populations (Murphy et al. 1991). Relative weight is calculated as the comparison between the actual weight of a specimen (W) and the standard weight (Ws), which is the weight of an ideal conspecific individual having the same length and exhibiting good physiological condition (Murphy et al. 1991). The Ws is predicted by a Wr equation, which is a length–weight regression that is typical of the species. Since its creation, the Wr index has been widely used to perform condition analyses of many species (Blackwell et al. 2000). However, its applicability is limited by the lack of species-specific Ws equations, as these equations must be developed by using samples of specimens collected throughout the area of distribution for the species of interest.

The Aegean chub Squalius fellowesii (Figure 1) is a cyprinid species that is endemic to the Aegean drainages of Anatolia, Turkey (Figure 2). The Squalius populations from the Esen, Dalaman, Büyük Menderes, Gediz, Bakır, and Madra drainages belong to this species (Ozuluğ and Freyhof 2011). The Aegean

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chub is one of the most common freshwater fish species in its area of distribution (Balık et al. 2004; Şaşı 2004; Dirican and Barlas 2007), and it is caught both as a game species and for consumption (Şaşı and Balık 2003; Koc et al. 2007). However, to date, only a few watercourses have been studied and such work has focused on limited basic biological features of this species, such as age, growth, and sex ratio (Şaşı and Balık 2003; Balık et al. 2004; Dirican and Barlas 2007; Koc et al. 2007).

Originally described as *Leuciscus fellowesii*, the Aegean chub was recently accepted as a valid species by Özuluğ and Freyhof (2011). Durand et al. (2000) and Sanjur et al. (2003) found molecular differences in chub populations from western Anatolia; those authors suggested that the group of “short-snouted chubs,” identified as a subspecies of the European chub *Squalius (Leuciscus) cephalus*, could be divided into different species within the genus *Squalius*. Özuluğ and Freyhof (2011) confirmed this hypothesis and reported the occurrence of 10 different *Squalius* species (four of them only recently described) in western and central Anatolia, and among these species was the Aegean chub.

The objective of this research was to develop a $W_s$ equation for Aegean chub. The empirical percentile (EmP) method proposed by Gerow et al. (2005) was used to develop the $W_s$ equation, as recent studies have encouraged the development of $W_s$ equations by use of this method (Richter 2007; Rennie and Verdon 2008; Rypel and Richter 2008; Angeli et al. 2009; Ogle and Winfield 2009; Gerow 2010; Giannetto et al. 2011, 2012a). Availability of a $W_s$ equation for the Aegean chub could be useful in the management of this endemic species, which has a restricted distribution and is threatened mainly by habitat loss (changes in land use), water pollution, nonnative species introductions, and seasonal droughts (Önsoy et al. 2011). At a broader scale, data on the condition of Aegean chub populations throughout the species’ distribution could be crucial in identifying important areas for species conservation. More specifically, those populations showing a high body condition could be considered as potential sources for future restocking practices, whereas populations with lower body condition should be selected for programs of conservation for the species or habitat rehabilitation.

METHODS

Data set selection.—Data on the TL (mm) and weight ($W$, g) of Aegean chub were collected throughout the distribution area of this species. The total data set was validated by using the procedure suggested by Giannetto et al. (2011, 2012c). First, the TL–$W$ regression of the total sample was examined, and all fish that were represented by large outliers were excluded, as these outliers were probably derived from incorrect measurements. All lengths that were measured only in terms of SL or FL (mm) were converted to TL (mm) by applying a general linear conversion model developed based on all fish from the data sets in which at least two types of length measurement were recorded (Ogle and Winfield 2009).

The log10 $W$ was plotted against log10TL for each population. Based on recommendations made by Froese (2006), all populations with an $r^2$ value less than 0.90 or a slope value outside the range of 2.5–3.5 were removed from the data set (Rypel and Richter 2008; Ogle and Winfield 2009).

The log10 $W$ was plotted against log10TL for each population. Based on recommendations made by Froese (2006), all populations with an $r^2$ value less than 0.90 or a slope value outside the range of 2.5–3.5 were removed from the data set because such values are often associated with samples that represent narrow size ranges (Froese and Pauly 2000).

The next step in computing the $W_s$ equation was the determination of an applicable length range. A minimum TL is required...
TABLE 1. Number of Aegean chub populations and individuals (per 10-mm length-class) that were used to develop the standard weight equation.

<table>
<thead>
<tr>
<th>Length-class (mm TL)</th>
<th>Number of populations</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>70</td>
<td>29</td>
<td>161</td>
</tr>
<tr>
<td>80</td>
<td>38</td>
<td>199</td>
</tr>
<tr>
<td>90</td>
<td>43</td>
<td>240</td>
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<td>100</td>
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<td>193</td>
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<td>110</td>
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<td>190</td>
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<td>120</td>
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<td>130</td>
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<td>11</td>
</tr>
<tr>
<td>210</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>220</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>

because of the high potential error that occurs in the measurement of small specimens in the field (Murphy et al. 1991); in addition, small fish display high variance in the weights values due to the differences in growth forms that arise in the juvenile stages. In accordance with Willis et al. (1991), the minimum TL was determined by examining the relationship between (1) the variance : mean ratio for log10 W and (2) TL at 10-mm intervals. The length at which the variance : mean ratio is stabilized and does not exceed 0.01 is identified and used as the minimum (Murphy et al. 1991). According to Gerow et al. (2005), the use of the Emp method for the development of a W equation also requires a maximum TL. The maximum was identified as the greatest length-class for which at least three fish populations were available in the data set (Table 1). All fish outside of this suitable length range were excluded from further analysis. Once the total data set was cleaned and validated, it was divided into two data sets: (1) a larger development data set, which was used to compute the W equation; and (2) a smaller validation data set, which was utilized to investigate potential length-related biases in the calculated W equation (Rypel and Richter 2008; Ogle and Winfield 2009; Giannetto et al. 2012c).

Development of the empirical percentile standard weight equation.—The mean empirical W (for each 10-mm TL-group) was calculated by using the log10 transformed TL and W of each population included in the development data set. The third quartile (i.e., 75th percentile) of these mean empirical W-values was then regressed against TL to develop the Emp W equation by using a weighted quadratic model (Gerow et al. 2005).

The resulting Emp W equation was used to calculate the W of each specimen from each population based on the equation provided by Wege and Anderson (1978):

\[ W_r = 100 \times (W/W_s), \]

where \( W \) is the weight (g) of an individual and \( W_s \) is the standard weight predicted by the \( W_r \) equation.

Validation of the empirical percentile standard weight equation.—An important characteristic of a good condition index is that it should be free from length-related biases, thus allowing comparison of condition assessments among fish of different sizes (Murphy et al. 1990; Anderson and Neumann 1996; Blackwell et al. 2000). Two different methods were used to validate the Emp W equation calculated for Aegean chub: (1) the analysis of residuals of the W equation to investigate whether the distribution of residuals exhibited evident patterns; and (2) the empirical quartiles (EmpQ) method (Gerow et al. 2004; as modified by Ogle and Winfield 2009) to determine whether the quadratic regression of the 75th-percentile mean W standardized by \( W_s \) against TL (at 10-mm intervals) had a slope of zero (Ogle and Winfield 2009; Giannetto et al. 2011). The EmpQ method was performed by using the FSA package (Ogle 2009) in R software.

RESULTS

The total sample comprised 2,188 individual Aegean chub with a mean TL of 103 mm (SD = 4; minimum = 24 mm; maximum = 225 mm) and a mean weight of 18 g (SD = 21; minimum = 1 g; maximum = 175 g). Among the 57 populations that made up the total sample, one population was excluded (in accordance with Froese 2006) because the slope of its log10 W–log10 TL relationship was less than 2.5. The log10 W–log10 TL equation calculated for the total sample was

\[ \log_{10} W = -5.244 + 3.154 \cdot \log_{10} TL \]

\( R^2 = 0.988, P < 0.001; n = 2,188 \). The development data set consisted of 1,900 fish, and the validation data set included 288 fish. In accordance with Rypel and Richter (2008), the small size of the validation data set was chosen so that the data set used to develop the Emp W equation would be as large as possible. The data were selected so that both data sets contained Aegean chub populations that were distributed throughout the geographical range of the species (Ogle and Winfield 2009).

The minimum TL for application of the \( W_r \) equation was identified as 70 mm (Figure 3); as a result, all specimens smaller than this size were excluded from subsequent analysis. The maximum TL was 220 mm, the length of the largest fish present in the development data set; this length was consistent with the maximum length reported for Aegean chub in the literature (Ozuluğ and Freyhof 2011). Thus, the length range that was judged to be suitable for the Emp W equation was 70–220 mm TL.
The Aegean chub $W_s$ equation calculated by means of the EmP method was

$$\log_{10} W_s = -3.801 + 1.783 \cdot \log_{10} \text{TL} + 0.329 \cdot (\log_{10} \text{TL})^2$$

($R^2 = 0.999$, $P < 0.001$). When we examined the residual values from this EmP $W_s$ equation to determine potential length-related biases, the residuals appeared to be distributed randomly and did not exhibit any evident patterns (Figure 4a). When the EmpQ method (Gerow et al. 2004) was applied to the validation data set, the EmP $W_s$ equation calculated for Aegean chub did not appear to be influenced by fish length since the slope of the quadratic regression of 75th-percentile mean $W$ standardized by $W_s$ against TL was not significantly different from zero for either the linear term or the quadratic term of the equation ($P_{\text{quadratic}} = 0.706$, $P_{\text{linear}} = 0.713$; Figure 4b).

**DISCUSSION**

According to Bister et al. (2000), because of the positive correlation between fish growth and environmental quality, $W_r$ could be an easy and powerful tool for recognizing environmental changes (Gabelhouse 1991; Hubert et al. 1994; Liao et al. 1995) or ecological changes, such as interspecies or intraspecies competition (Johnson 1992; Giannetto et al. 2012b). Previous studies have clearly indicated habitat-dependent variations in age and growth features of Aegean chub (Balık et al. 2004; Dirican and Barlas 2007). This was more obvious in differences between Aegean chub in lentic and lotic areas, suggesting that growth conditions were better for the lentic populations than for lotic populations, and such differences have been observed in other *Squalius* species distributed in different regions of Anatolia (Şaş and Balık 2003; Torcu et al. 2007). However, at present, there are no $W_r$ equations available in the literature for other *Squalius* species distributed in Anatolia or for the European chub. For this reason, the application of $W_r$ to compare conditions among these species is currently limited.

Based on our results, the use of the EmP equation to determine $W_r$ for the Aegean chub throughout its area of distribution is recommended. Further research is encouraged to extend this methodology to other species distributed in the Aegean chub's range; particular attention should be given to species that are endemic, rarely studied, and, at this time, threatened by the presence of an increasing number of nonnative species that are commonly introduced into Turkish waters by stocking practices with the aim of increasing fish production and sportfishing.
FIGURE 4. Plots showing (a) the distribution of standardized residuals from the standard weight ($W_s$) equation (fitted values = values obtained by the model fit) and (b) the results of applying the empirical quartiles (EmpQ) method to investigate potential length-related bias in the $W_s$ equation for Aegean chub (standardized 75th-percentile mean weight $[W]$ was calculated with the $W_s$ equation).

(İnal and Erk’akan 2006; Aydn et al. 2011; Önsoy et al. 2011; Tarkan et al. 2012). Nonnative species introductions, together with habitat degradation, are probably responsible for the recent notable decline in Aegean chub density throughout this species’ distribution area (Önsoy et al. 2011). For this reason and as was previously demonstrated by Giannetto et al. (2012b), the methodology proposed here can be very useful in assessing the impact of nonnative species on natural and endemic species. For example, Giannetto et al. (2012b) used covariance analysis to compare the mean $W_s$ of native fish species of the Tiber River basin (central Italy) in the absence and presence of nonnative species (assuming a status of same ecological conditions by using the environmental variables as a covariate); the condition of some of the endemic species was found to be significantly worse when nonnative species were present than when nonnative species were absent.

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**Article**

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**Abstract**

Hoop nets are rapidly becoming the preferred gear type used to sample channel catfish *Ictalurus punctatus*, and many managers have reported that hoop nets effectively sample channel catfish in small impoundments (<200 ha). However, the utility and precision of this approach in larger impoundments have not been tested. We sought to determine how the number of tandem hoop net series affected the catch of channel catfish and the time involved in using 16 tandem hoop net series in larger impoundments (>200 ha). Hoop net series were fished once, set for 3 d; then we used Monte Carlo bootstrapping techniques that allowed us to estimate the number of net series required to achieve two levels of precision (relative standard errors [RSEs] of 15 and 25) at two levels of confidence (80% and 95%). Sixteen hoop net series were effective at obtaining an RSE of 25 with 80% and 95% confidence in all but one reservoir. Achieving an RSE of 15 was often less effective and required 18–96 hoop net series given the desired level of confidence. We estimated that an hour was needed, on average, to deploy and retrieve three hoop net series, which meant that 16 hoop net series per reservoir could be “set” and “retrieved” within a day, respectively. The estimated number of net series to achieve an RSE of 25 or 15 was positively associated with the coefficient of variation (CV) of the sample but not with reservoir surface area or relative abundance. Our results suggest that hoop nets are capable of providing reasonably precise estimates of channel catfish relative abundance and that the relationship with the CV of the sample reported herein can be used to determine the sampling effort for a desired level of precision.

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Channel catfish *Ictalurus punctatus* are highly sought by anglers in the USA and pursued in environments ranging from small earthen ponds to large rivers (USCB 2006). In many reservoir environments, channel catfish are managed by maintenance stocking and populations are assessed by sampling events considered either routine or experimental. Many fishery managers have used gill nets, trap nets, and boat electrofishing to sample channel catfish (Hanson 1986; Stevenson and Day 1986; Wilde 1995; Howell and Betsill 1999; Mitzner 1999; Santucci et al. 1999; Michaletz and Sullivan 2002), but these methods have large biases with respect to abundance and size structure. Baited hoop nets are increasing in popularity as a sampling gear and have been shown to sample channel catfish in proportion to their abundance without size bias (Buckmeier and Schlechte 2009). Various studies have attempted to increase their efficiency: single net sets have been replaced with sets of three tied in tandem (Walker et al. 1996), and the escapement of fish was greatly reduced by constricting the rear throat (Michaletz and Sullivan 2002; Porath et al. 2011).
Methods devised by Michaletz and Sullivan (2002) have become a fundamental part of many studies using hoop nets to sample channel catfish (e.g., Michaletz 2005, 2006, 2009; Richters and Pope 2011), but these methods are based on samples from small impoundments (<200 ha) with catch rates of 90.5 fish per tandem hoop net series on average. Recent studies have suggested that hoop nets are less efficient in larger impoundments (>200 ha) and that more than nine hoop net series would be needed to effectively sample those channel catfish populations (Richters and Pope 2011). Neely and Dumont (2011) found that hoop nets precisely sampled three large impoundments (contingent on soak duration), but these estimates were based on a resampling technique that used six to eight hoop net series with unrestricted rear throat configurations.

To properly sample any fish species, one needs to develop a strategy that yields robust results. Previous studies (e.g., Wilde 1995; Michaletz and Sullivan 2002) have estimated sample size to achieve a desired level of precision (i.e., coefficient of variation [CV]) or used simple formulae such as $N = (CV/RSE)^2$, where RSE is the relative standard error (e.g., DeVries et al. 1995). Recently, Dumont and Schlechte (2004) proposed an alternative technique that uses bootstrapping to predict the number of samples needed to meet a level of precision (RSE). Bootstrapping, though, is atypical for most fisheries managers and requires a large number of samples ($N > 10$) to produce results with high power (Lunneborg 2000; Dumont and Schlechte 2004), so few studies have used it. We sought to estimate the number of tandem hoop net sets needed to obtain two levels of precision (RSE = 25 and 15) using bootstrapping with 80% and 95% confidence by sampling larger impoundments (>200 ha) with 16 hoop net series. We examined whether the sample sizes necessary to obtain the two levels of precision were related to measures of catfish catch and impoundment size and sought to determine the time commitment required to set and retrieve additional hoop net series.

Channel catfish were counted, measured (total length; mm), and released at the site of capture. Relative abundance (CPUE) was expressed as the average number of channel catfish captured per hoop net series per 72 h set. We recorded the amount of time needed to deploy and retrieve 8- and 16-net series in a day. A workday was defined as the period between the time when the boat left the boat ramp and the time when it returned. Travel time to and from reservoirs was not included because of inherent variability in the distance from field station to reservoir.

The number of samples required to achieve the desired levels of precision was calculated by resampling the empirical data from each reservoir 1,000 times (with replacement) using Monte Carlo bootstrapping techniques in Microsoft Excel with a macro developed by Dumont and Schlechte (2004). Relative standard error was calculated to provide an estimate of the precision around the population mean (Dumont and Schlechte 2004); the resampling routine estimated the number of series necessary to achieve two levels of precision, RSE$_{25}$ and RSE$_{15}$, at the 80th and 95th percentiles (i.e., confidence levels) of 1,000 random samples.

Linear regression models were developed to determine the relationships between the projected number of net series needed to achieve RSE$_{25}$ and RSE$_{15}$ and associated measures of channel catfish relative abundance (mean CPUE, CV) and reservoir surface area. A power analysis was used to determine the probability of rejecting a false relationship because only six reservoirs were sampled (Kuehl 2000). A model was considered significant at $P < 0.05$, and all analyses were conducted using program R (version 2.14.1; R Development Core Team 2011).

RESULTS

Catch rates of channel catfish and measures of variation ranged widely among our study impoundments (Table 1). A total of 4,807 channel catfish were collected during the sampling period, with catch rates ranging from 1 to 220 per series. The estimated number of net series to achieve RSE$_{25}$ and RSE$_{15}$ with 80% and 95% confidence was variable among reservoirs but often less than 16. Sixteen hoop net series were more than adequate to achieve RSE$_{25}$ with 80% and 95% confidence in all but one impoundment (i.e., Lake Ponca), which required 34–40 net series. A sample size of sixteen hoop net series achieved RSE$_{15}$ for only two impoundments (i.e., Lake McMurtry); most sample requirements ranged from 18 to 96.

Linear regression models relating the required sample size to reservoir surface area and channel catfish catch statistics were nonsignificant except for those involving the CV of channel catfish CPUE (Table 2; Figure 1). All relationships between the required sample sizes and CV of channel catfish CPUE were significant ($r^2 > 0.90; P = 0.01$) with high statistical power ($\geq 0.98$). Statistical power was $<0.23$ for nonsignificant models and often required sample size estimates that ranged from 20 to 390 in order to attain power of at least 0.80.
TABLE 1. Summary of relative abundance (mean CPUE) and coefficient of variation (CV) estimates for channel catfish from sixteen hoop net series in six Oklahoma impoundments >200 ha. The numbers of hoop net series (effort) needed to achieve two estimates of sampling precision (relative standard error) at two levels of confidence are given.

<table>
<thead>
<tr>
<th>Impoundment</th>
<th>Area (ha)</th>
<th>N</th>
<th>CPUE</th>
<th>Range</th>
<th>CV</th>
<th>RSE25, 80%</th>
<th>RSE25, 95%</th>
<th>RSE15, 80%</th>
<th>RSE15, 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake McMurtry</td>
<td>465</td>
<td>1,487</td>
<td>92.9</td>
<td>47–146</td>
<td>0.42</td>
<td>3</td>
<td>4</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>Lake Greenleaf</td>
<td>372</td>
<td>136</td>
<td>8.5</td>
<td>2–17</td>
<td>0.82</td>
<td>9</td>
<td>11</td>
<td>22</td>
<td>26</td>
</tr>
<tr>
<td>Lake Ponca</td>
<td>326</td>
<td>167</td>
<td>10.4</td>
<td>1–63</td>
<td>1.49</td>
<td>34</td>
<td>40</td>
<td>90</td>
<td>96</td>
</tr>
<tr>
<td>Lake Okmulgee</td>
<td>270</td>
<td>440</td>
<td>27.5</td>
<td>2–57</td>
<td>0.67</td>
<td>9</td>
<td>12</td>
<td>21</td>
<td>25</td>
</tr>
<tr>
<td>Lake Okemah</td>
<td>270</td>
<td>1,289</td>
<td>80.6</td>
<td>5–136</td>
<td>0.46</td>
<td>6</td>
<td>9</td>
<td>13</td>
<td>18</td>
</tr>
<tr>
<td>Lake Lone Chimney</td>
<td>223</td>
<td>1,288</td>
<td>80.5</td>
<td>1–220</td>
<td>0.76</td>
<td>12</td>
<td>15</td>
<td>29</td>
<td>33</td>
</tr>
</tbody>
</table>

Deploying all 16 hoop net series in a single event resulted in concomitant increases in time, but retrieving 16 hoop net series rather than 8 did not increase the time required in a similar fashion. For example, deploying 16 net series required approximately twice the amount of effort (3.8 h) as deploying 8; however, retrieving 16 net series required 8.9 h on average, approximately $1.5 \times$ the effort of retrieving 8.

DISCUSSION

We found hoop nets to be effective in estimating channel catfish relative abundance in larger impoundments, generally requiring less than 16 net series. Estimating the number of hoop net series based on a given level of precision was dependent on the CV of the sample. That is in contrast with studies that have based the number of net series on reservoir size (e.g., Michaletz 2005, 2006, 2009; Richters and Pope 2011). The relationship between the number of net series and impoundment size was not significant and had low power to detect a relationship. It would require considerable effort to acquire sufficient statistical power to detect a valid relationship between required sample size and impoundment surface area, and it is likely that a relationship does not exist.

Fish sampling efforts have often been based on the assumption that fish abundance is directly correlated with impoundment size (Wilde 1995), which, on its surface, seems like a logical—although untested—assumption. We failed to find evidence of a relationship between reservoir size and the required sample size, suggesting that more nets per reservoir area will not necessarily result in a concomitant increase in sampled fish in larger reservoirs. Still, larger bodies of water necessarily provide more aquatic habitat and should therefore contain more fish, and our relationship between the CV of the sample and required sample size suggests using a factor related to fish distribution in these larger reservoirs as a mitigating factor. While we did not expressly test hypotheses for these functions, we find some explanatory reasoning in the established ecological theory of island biogeography (MacArthur and Wilson 1967). Part of island biogeography theory is the long-known understanding (e.g., Cain 1938) that increased habitat area (i.e., reservoir size) and species diversity are positively related. This phenomenon is more pronounced for smaller habitats than larger habitats, as has been demonstrated for fish species in lakes (Griffiths 1997) and

TABLE 2. Summary of linear regression models relating the required number of hoop net series to reservoir surface area and channel catfish catch statistics at two levels of confidence (80% and 95%). Effort is the estimated number of tandem hoop net series needed to achieve a statistical power (1 – $\beta$) of 0.80.

<table>
<thead>
<tr>
<th>RSE</th>
<th>Independent variable</th>
<th>Model</th>
<th>$r^2$</th>
<th>$P$</th>
<th>Power</th>
<th>Effort</th>
<th>Model</th>
<th>$r^2$</th>
<th>$P$</th>
<th>Power</th>
<th>Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>Area (ha)</td>
<td>$y = 46.08 - 0.05_{\text{Area}}$</td>
<td>0.02</td>
<td>0.79</td>
<td>0.06</td>
<td>390</td>
<td>$y = 54.05 - 0.06_{\text{Area}}$</td>
<td>0.03</td>
<td>0.75</td>
<td>0.06</td>
<td>259</td>
</tr>
<tr>
<td></td>
<td>$N$</td>
<td>$y = 52.76 - 0.03_N$</td>
<td>0.33</td>
<td>0.23</td>
<td>0.23</td>
<td>21</td>
<td>$y = 57.94 - 0.03_N$</td>
<td>0.34</td>
<td>0.23</td>
<td>0.23</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>CPUE</td>
<td>$y = 52.76 - 0.44_{\text{CPUE}}$</td>
<td>0.33</td>
<td>0.23</td>
<td>0.23</td>
<td>21</td>
<td>$y = 57.94 - 0.47_{\text{CPUE}}$</td>
<td>0.34</td>
<td>0.23</td>
<td>0.23</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>$y = -27.72 + 75.61_{\text{CV}}$</td>
<td>0.95</td>
<td>0.01</td>
<td>0.99</td>
<td>4</td>
<td>$y = -25.96 + 78.52_{\text{CV}}$</td>
<td>0.95</td>
<td>0.01</td>
<td>0.99</td>
<td>4</td>
</tr>
<tr>
<td>25</td>
<td>Area (ha)</td>
<td>$y = 19.57 - 0.02_{\text{Area}}$</td>
<td>0.03</td>
<td>0.73</td>
<td>0.06</td>
<td>259</td>
<td>$y = 25.29 - 0.03_{\text{Area}}$</td>
<td>0.05</td>
<td>0.68</td>
<td>0.07</td>
<td>154</td>
</tr>
<tr>
<td></td>
<td>$N$</td>
<td>$y = 20.50 - 0.01_N$</td>
<td>0.34</td>
<td>0.23</td>
<td>0.23</td>
<td>20</td>
<td>$y = 24.59 - 0.01_N$</td>
<td>0.33</td>
<td>0.23</td>
<td>0.23</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>CPUE</td>
<td>$y = 20.50 - 0.17_{\text{CPUE}}$</td>
<td>0.34</td>
<td>0.23</td>
<td>0.23</td>
<td>20</td>
<td>$y = 24.59 - 0.19_{\text{CPUE}}$</td>
<td>0.33</td>
<td>0.23</td>
<td>0.23</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>$y = -9.41 + 28.02_{\text{CV}}$</td>
<td>0.95</td>
<td>0.01</td>
<td>0.99</td>
<td>4</td>
<td>$y = -9.29 + 31.76_{\text{CV}}$</td>
<td>0.94</td>
<td>0.01</td>
<td>0.98</td>
<td>5</td>
</tr>
</tbody>
</table>
river basins (Watters 1992). Thus, channel catfish populations in larger impoundments are not necessarily more abundant but are in contact with more species, leading to increased interspecific competition for resources. The niche compression hypothesis (MacArthur and Wilson 1967; Pianka 1994) predicts that as interspecific competition increases, habitat use becomes more specialized. Channel catfish that would use the entirety of habitats in small lakes might be more habitat specific in larger impoundments. As reservoir size increases, a manager might need to set more nets to meet a predefined threshold of precision, but this level would depend on the habitats of the reservoir and how channel catfish are using those habitats, not on the size of the reservoir. This would explain why in our study the estimated sample size needed was related to the CV of channel catfish CPUE and not reservoir size (i.e., habitat is reservoir specific).

Well-designed experiments in the future that test these relationships between the number of samples needed in relation to the CV of CPUE and impoundment size would aid the development of robust sampling strategies for channel catfish in reservoirs. Moreover, this line of reasoning suggests that research on how channel catfish use and perceive habitat in reservoirs of varying sizes in relation to other species is needed. Further understanding of these relationships could result in more efficient sampling strategies.

Other studies have reported that a high number of net series (ranging from >12 to >40) would be needed to attain moderate (CV = 0.20) and fine (CV = 0.10) precision levels for most channel catfish populations (Michaletz and Sullivan 2002; Neely and Dumont 2011). For five of our six reservoirs, we estimated that from 4 to 15 hoop net series would typically be needed to attain moderate precision (RSE\textsubscript{25}) with 95% confidence, but in only one reservoir was less than 8 series adequate. Because a variety of channel catfish sampling studies are using a maximum of 8 net series (e.g., Michaletz 2005, 2006, 2009; Neely and Dumont 2011) and studies are showing that more are necessary (e.g., this study: Michaletz and Sullivan 2002), we believe that it was imperative to estimate the time associated with this extra effort.

Most of our impoundments required 9–15 hoop net series to achieve RSE\textsubscript{25} at 95% confidence, which suggests that the additional effort needed is minimal. This, of course, depends on the amount of fish captured, the travel time to sampling sites, delays in sampling, and crew efficiency. The additional amount of effort (from 1 to 6 net series) required to increase the level of confidence seems negligible for a given level of precision. However, increasing precision from RSE\textsubscript{25} to RSE\textsubscript{15} became unrealistic, often doubling the number of net series needed up to 96. Sixteen hoop net series took us about one-half day to set and a whole day to retrieve, which seems reasonable given that most crews would typically only set nets in one reservoir per day given the travel time involved and the number of net series a typical office may have available. Should time or the availability of nets become a constraint, the evidence suggests that using a 2-d soak duration instead of a 3-d duration will provide adequate precision for channel catfish relative abundance (Neely and Dumont 2011); however, we did not directly test these methods.

Our results suggest that hoop nets provided precise relative abundance estimates for channel catfish in larger impoundments. A fishery manager could use the CV of the sample from a priori sampling events to predict the total number of samples needed to achieve a desired level of precision. The relationship between CV and effort modeled in this paper could be used to provide this estimate quickly without having to perform the resampling routine we employed.

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Improving Size Selectivity of Shrimp Trawls in the Gulf of Maine with a Modified Dual-Grid Size-Sorting System
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ARTICLE

Improving Size Selectivity of Shrimp Trawls in the Gulf of Maine with a Modified Dual-Grid Size-Sorting System

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Abstract

Finfish bycatch has been drastically reduced since the Nordmøre grid became mandatory in 1992 in the Gulf of Maine shrimp fishery. However, the Nordmøre grid does not improve northern shrimp size selection, catching large numbers of small shrimp when they are mixed with large mature shrimp. To reduce the catch of small northern shrimp, a new dual-grid shrimp size-sorting system was developed and tested in a flume tank and at sea to evaluate its potential for reducing catch of juvenile and male shrimp in the Gulf of Maine shrimp fishery and to optimize rigging. These tests used a trouser trawl system consisting of one trawl leading to two separate cod ends, which compared a cod end with a dual-grid size-sorting system with another identical cod end without a size-sorting grid. The size-sorting grid had 11-mm bar spacing. The dual-grid size-sorting system significantly reduced the number of small northern shrimp with a carapace length of 22 mm or less and slightly increased catch of large shrimp with a carapace length of 23 mm or larger, when compared with the Nordmøre grid without a size-sorting grid. There was a slight reduction of northern shrimp catch rates due to the release of smaller shrimp but with no significant differences in the number or quantity of major bycatch species between the regular grid and the size-sorting grid. The new dual-grid system was practical to operate and a significant improvement over an earlier version of the size-sorting grid in design, rigging, and handling. The application may reduce small shrimp in other northern shrimp fisheries and other shrimp and prawn fisheries with suitable modification to the design.

Northern shrimp (in some earlier publications referred to as “pink shrimp”) *Pandalus borealis* are distributed in the northern Atlantic Ocean and the Arctic Sea (Shumway et al. 1985). A similar species in the northern Pacific Ocean is now considered to be a separate species, *Pandalus eoeus* (Squires 1992; Bergström 2000; McLaughlin et al. 2005). Due to their small size, northern shrimp are harvested using small-mesh cod ends (typically 50 mm or less) in shrimp fisheries, but the small-mesh cod end can result in a large amount of finfish bycatch (Howell and Langan 1992). The Nordmøre grid that was developed in northern Norway in the late 1980s (Isaksen et al. 1992) greatly reduced finfish bycatch and was well received by the Gulf of Maine shrimp fishing industry on the northeastern coast of the USA in 1990. It became mandatory in the spring of 1992 in the fishery (Kenney et al. 1992; Clark et al. 2000).

While the Nordmøre grid is very effective at excluding large fish, it cannot reduce the amount of small fish and small shrimp that can pass through the space between the bars (maximum 25 mm in the Gulf of Maine) (Clark et al. 2000). Northern shrimp are hermaphrodites; born as male and transitioning to female at about age 3.5 years (ASMFC 2011). Small shrimp are usually juveniles, mature males, or transitional shrimp aged 3.5 years or younger. These shrimp typically measure about 22 mm carapace length (CL) or less; in Canada they use 20 mm or 21 mm CL as the cut-off length (Brothers 1998). In the Gulf of Maine, these small shrimp stay in deeper waters until they are ready to

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release of shrimp and finfish bycatch (He and Balzano 2011, 2012). This paper is one of a series of papers describing modifications to the system. This paper reports subsequent improvement to the system. Several attempts have been made to reduce the catch of small northern shrimp in the USA, Canada, and Europe. Increasing mesh sizes did not increase size selectivity as shown by Valdemarsen (1989) in Norway and by Tait and Tait (1993) in Canada. Square-mesh cod ends have shown some reduction in catch of immature small shrimp in some tests, but not in others (Hickey et al. 1993; Lehmann et al. 1993). In addition, mesh breakage and loss of market-size shrimp were reported when using square-mesh cod ends (Hickey et al. 1993).

During the capture process northern shrimp are passively carried by the flow inside the net, which may be significantly reduced when the cod end is full of catch (Valdemarsen 1989). With strong flow outside of the cod end, there would not be much active cross flow to take small shrimp out of the cod end. A funnel-shaped design, called a Radial Escape Section, installed in the rear section of the belly was tested to force small shrimp out of the trawl (Valdemarsen 1989). The device showed reductions in small shrimp, but blocking of the funnel by debris and complicated rigging requirements prevented its wide use.

A dual-grid system was tested in Newfoundland and the Gulf of Maine in the mid-1990s (DFO 1995, 1998; Brothers 1998; Schick et al. 1999). In these systems, the size-sorting grid was installed behind the regular Nordmøre Grid, which had limited success due to reduced flow rates at the second grid (FTU 1996). He and Balzano (2007) tested a size-sorting grid installed in front of the Nordmøre grid that produced promising results. However, this design was difficult to rig and maintain, especially when slightly different mesh size netting was used in the grid section. As a result, greater shrimp loss was observed in this system. This paper reports subsequent improvement to the previous work, with the new design and the new experimental method. This paper is one of a series of papers describing modifications to the Nordmøre grid to reduce small northern shrimp and finfish bycatch (He and Balzano 2011, 2012).

METHODS

Grid design.—The size-sorting grid was installed in front of the regular Nordmøre grid and thus became a dual-grid system. The regular Nordmøre grid was the same as that used in He and Balzano (2007), with external dimensions (width × length) of 965 mm × 1,470 mm and 25-mm bar spacing, made of high density polyethylene. The size-sorting grid had 11-mm bar spacing and 10-mm bar width (Figure 1). The external grid size (width × length) was 965 mm × 1,140 mm and was also made of high density polyethylene. Instead of using ropes to form the desired structure and grid angles as done in He and Balzano (2007), the new design used conventional industry-preferred weights (4.5-kg chain on the leading edge) and floats (4 × 204 mm diameter trawl floats) (Figure 2). The rear edge of the size-sorting grid ends at the gore (selvage). The size-sorting grid was installed at a 30° angle and the Nordmøre grid was around 50°. The final rigging and design detail are shown in Figure 2 (He and Balzano 2012).

Flume tank tests.—The full-scale dual-grid size-sorting system was tested at the flume tank of the Fisheries and Marine Institute at Memorial University of Newfoundland in St. John’s, Newfoundland, Canada. The test of the grid system was combined with a full-scale trouser trawl section to ensure both cod ends (with or without a size-sorting grid, or with different size-sorting grids) could be towed behind the trawl. A trouser trawl has the front end of the trawl similar to a regular trawl and an added trouser trawl section that leads to two cod ends, as described in He and Balzano (2011). The details of the rigging were perfected during the flume tank testing. The tested full-scale trouser trawl section and grid systems were shipped to Portland, Maine, where sea trials were carried out.

Sea trials.—A commercial shrimp trawl was modified into a trouser trawl for comparative fishing trials by attaching the trouser trawl section tested in the flume tank. The front part of the trawl was not changed and remained the same as a regular commercial shrimp trawl and was equipped with 305-mm-diameter rockhopper groundgear.

Sea trials were carried out during the traditional fishing season (between 10 April and 18 April 2009) on the traditional commercial shrimping grounds off Portland, Maine, at a depth between 115 m and 159 m. The FV North Star, a 14-m inshore shrimp trawler was used for comparative fishing trials with the second author (V. Balzano) as the captain. Both cod ends were identical and were made of 43-mm mesh size (inside knot measurement) braided nylon material. The test cod end with an 11-mm dual-grid size-sorting system (11RNG) and the control cod end with a regular Nordmøre grid (RNG) were switched in ABBA and BAAB sequence to eliminate the effect of side (port and starboard) and time of day (four tows per day). The trouser trawl was towed for 1 h at the towing speed of 2.4 knots (1.22 m/s).

Catch sampling and analysis.—The catch of target and bycatch species were sorted and measured after each tow. The northern shrimp catch was weighed to the nearest kilogram. One 1-kg sample of northern shrimp from each tow and each cod end was kept for size count and CL measurement in the laboratory. Carapace lengths were measured to the nearest millimeter. Bycatch was sorted to species and weighed to the nearest 0.05 kg. Individuals were measured to the nearest centimeter. Subsamples of about 50–70 individuals per cod end were taken when a large number of bycatch for a given species was caught.

The bycatch species were analyzed for “major bycatch species” with mean catch amounts greater than 0.1 kg/h and
SIZE SELECTIVITY OF SHRIMP TRAWLS

FIGURE 1. The specifications of the high density polyethylene size-sorting grid: external dimension 965 mm × 1,143 mm, grid spacing 11 mm, bar width 10 mm, grid thickness 25 mm, colored black. [Figure available in color online.]

The proportion of catch retained at CL by 11RNG cod end, Φ(CL), can be expressed for each CL and each tow as follows:

\[ \Phi(CL) = \frac{N_{CL,11RNG}}{N_{CL,11RNG} + N_{CL,RNG}} \]

where \( N_{CL,11RNG} \) and \( N_{CL,RNG} \) are the number of northern shrimp at CL measured for the experiment cod end (11RNG) and the control cod end (RNG), respectively. A value of \( \Phi = 0.5 \) indicates that there are no differences in the catch between the two cod ends at length CL. The catch proportion, \( \Phi(CL) \), for northern shrimp from the two cod ends was analyzed using the generalized linear mixed model (GLMM) with CL as the explanatory variable, \( \Phi \) as the response variable, the individual tow as the random effect, and subsample ratio as an offset, following the technique described in Holst and Revill (2009). In this analysis the GLMM was implemented using the occurring in every tow and for the “controlled groundfish species,” which includes American plaice Hippoglossoides platessaoides, witch flounder Glyptocephalus cynoglossus, yellowtail flounder Limanda ferruginea, goosefish Lophius americanus, cusk Brosme brosme, Atlantic cod Gadus morhua, fourspot flounder Paralichthys oblongus, and Atlantic halibut Hippoglossus hippoglossus.

The amount of catch (northern shrimp) and bycatch (finfish) per tow (i.e., per hour) was analyzed using a paired t-test to determine differences in catch rates of northern shrimp and bycatch species (kg/h). Comparisons were also made between the size-sorting grid and the regular Nordmøre grid for small shrimp 22 mm CL or less and for large shrimp 23 mm CL or larger. The number of northern shrimp in 1-mm-CL categories for each tow and each cod end was extrapolated from the subsamples, and the length-frequency distribution was generated for both experimental (11RNG) and control (RNG) cod ends.
The polynomial regression GLMM was used to fit curves for the expected proportions of the catch retained by the experimental cod end (11RNG), after logit transformation, as follows:

$$\text{logit}\Phi(CL) = \beta_0 + \beta_1 CL + \beta_2 CL^2 + \beta_3 CL^3,$$

where $\beta$ represents regression coefficients.

The analysis was proceeded by fitting the third order polynomials followed by subsequent reductions until all terms showed significance ($P < 0.05$). Reductions were based on Wald’s test, with removal of one term at a time to determine the best-fit model as recommended by Holst and Revill (2009).

**RESULTS**

**Northern Shrimp**

The average catch rate of northern shrimp from two cod ends combined was 132.2 kg/h during the 24 trouser trawl tows, which can be considered as commercial catch rates. Tow-by-tow catch rates of northern shrimp and four major bycatch species during 24 trouser trawl tows are shown in Table 1. The cod end with the dual-grid system (11RNG) caught less shrimp in 16 out of 24 tows (Figure 3). There was an average 9.7% reduction in shrimp catch rates in the cod end with a dual-grid size-sorting system (11RNG) compared with a cod end with a regular Nordmøre grid (RNG). The RNG cod end caught an average of 69.4 kg/h (SE, 3.80), while the 11RNG cod end caught an average of 62.7 kg/h (SE, 3.90). The difference was
TABLE 1. Tow-by-tow catch of northern shrimp and five major bycatch species (in kg/h): silver hake, American plaice, red hake, witch flounder, and yellowtail flounder. Abbreviations are as follows: 11RNG = 11-mm dual-grid size-sorting system, RNG = regular Nordmøre Grid, \( t \) = \( t \)-value from paired \( t \)-test (df = 23), \( P \) = probability as tested by paired \( t \)-test (one-tail), double asterisks indicate significance at the 0.01 level, and NS = not significant.

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When dividing northern shrimp into small (\( \leq 22 \text{ mm CL} \)) and large (\( \geq 23 \text{ mm CL} \)), the 11-mm size-sorting grid (11RNG) caught significantly fewer small shrimp than RNG both in weight (13.74 and 19.26 kg/h, respectively; paired \( t \)-test: \( t = -5.8537, \text{df} = 23, P < 0.001 \)) and in number (3,173 and 4,923 shrimp/h, respectively; \( t = -7.5118, \text{df} = 23, P < 0.001 \)) (Figure 5).

Carapace length-frequency distribution indicates that the 11RNG cod end caught more northern shrimp 23 mm CL or larger, while the RNG cod end caught more shrimp 22 mm CL.
FIGURE 3. Tow-by-tow catch comparison of northern shrimp between a cod end with a regular Nordmøre grid (RNG) and one with an 11-mm size-sorting grid (11RNG). Average catch rates were 67.8 kg/h for RNG and 62.8 kg/h for 11RNG. They are statistically different ($P = 0.012$).

CL or smaller (Figure 6a). The GLMM modeling of catch proportion ($\Phi$) at different CL indicates that the data fit best with the linear model based on the model fitting results shown in Table 2. The results showed significantly fewer shrimp caught by 11RNG for shrimp less than 23 mm CL (Figure 6b). The modeling also reveals that the 11RNG actually caught statistically significantly more shrimp larger than 27 mm CL.

**Finfish Bycatch**

Major bycatch species (average of 0.1 kg/h or greater and occurring in most tows), in the decreasing amount order, were silver hake *Merluccius bilinearis*, American plaice, red hake *Urophycis chuss*, witch flounder, and yellowtail flounder. There was a small amount of other bycatch species (<0.06 kg/h): Acadian redfish *Sebastes fasciatus*, Atlantic cod, Atlantic

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halibut, Atlantic herring *Clupea harengus*, cusk, fourspot flounder, goosefish, scup *Stenotomus chrysops*, and wrymouth *Cryptacanthodes maculatus*. They occurred in less than 60% of tows. The total bycatch of all species was about 7% of the total catch, and controlled groundfish species were about 2% of the total catch. Silver hake was the most abundant bycatch species (and the only bycatch species for which subsamples were taken), with an average catch rate of 2.80 kg/h (for 11RNG) and 3.22 kg/h (for RNG), followed by American plaice that averaged about 1.35 kg/h (Figure 7a). There were no statistical differences for each and every major bycatch species, or all species combined, either in weight or in numbers (Figure 7a, b), between the regular Nordmøre grid (RNG) and the dual-grid size-sorting system (11RNG) (Table 1).

**DISCUSSION**

The catch of small shrimp represents the waste of a resource. In quota-controlled fisheries, it can represent an economic loss to the vessel because small northern shrimp usually have very little value but are counted as a part of the landing quota (Brothers and Boulos 1996). Efforts to reduce small shrimp in trawls have concentrated on increasing mesh sizes and changing mesh shapes (e.g., square mesh) (Hickey et al. 1993; Lehman et al. 1993; Tait and Tait 1993; Broadhurst 2000) and on the size-sorting grid (DFO 1995, 1998; Brothers and Boulos 1996; FTU 1996; Brothers 1998; Schick et al. 1999; He and Balzano 2007, 2012). Merely changing mesh size and shape did not reduce catch of small northern shrimp due to the behavior and escape capability of the species (Valdemarsen 1989). The rear-installed size-sorting grid with small-mesh guiding panels was not very successful due to reduced flow rate at the size-sorting grid, which was believed to be as little as 40% of the towing velocity of the net (FTU 1996). Reduced flow rate reduces sorting effectiveness as less force is applied to push small shrimp through the size-sorting grid. As a result, northern shrimp were observed to “sit” on the size-sorting grid instead of passing through it. The size-sorting grid installed in front of the Nordmøre grid did not have this problem as seen on video (P. He, unpublished, video available on request).

With combined northern shrimp catch rates of 132 kg/h, the new dual-grid size-sorting system functioned as expected, reducing shrimp counts from 142 to 124 shrimp/kg. While He and Balzano (2007) designed and tested an earlier version of the size-sorting grid and found it effective in improving the size selectivity of shrimp, the current design is easier to rig and maintain. The previous design relied on measured length of ropes to form desired grid angles and integrity of the system (both grids).
Any slight change in mesh size (or stretch) in the grid section (which often occurs among netting manufacturers) and elongation of ropes would alter the grid angle and the performance of the sorting system. The current design used conventional floats and weight to form a desired grid angle and was much easier to rig, handle, and maintain. The grid configuration retained its shape after repeated use.

The current study revealed three modes in the length-frequency distribution in the northern shrimp catch of both RNG and 11RNG (Figure 6a). The first mode (8–16 mm CL) represents primarily age 2 juveniles and males. The second mode (16–22 mm CL) represents age 3 males, transitional and some primiparous females, while the third mode (≥23 mm CL) is mostly multiparous females age 4 and older (Parsons et al. 1986). Reductions of catch by 11RNG are primarily from the first and second mode, with a slight increase in the third mode.

In a subsequent experiment by the same authors, they found that the escape of northern shrimp between the bars is related to the carapace width of the shrimp (He and Balzano 2012). Northern shrimp whose carapace widths are 0.5 mm smaller than the bar spacing would be able to escape through the size-sorting grid. In this case, 11-mm bar spacing would allow shrimp of 10.5-mm carapace width to escape. A northern shrimp with a 10.5-mm carapace width is equivalent to a CL of 22 mm (He and Balzano 2012) or 7 g in weight.

In the previous study conducted in the 2006 northern shrimp season (He and Balzano 2007), the shrimp count was reduced from 193 to 147 shrimp/kg. During this experiment, which was conducted in the 2009 shrimp season, the count was reduced from 142 to 124 shrimp/kg. Many more small transitional and male northern shrimp of the strong 2003 and 2004 year-classes (2–3 years old) were present in the 2006 shrimp season than in the 2009 shrimp season (ASMFC 2011). For the same grid spacing (11 mm) of a size-sorting grid, a larger number of small shrimp would be able to escape if the size of the shrimp in the stock is relatively small (e.g., the 2006 season). On the other hand, if the stock consists of relatively large shrimp (e.g., the 2009 season), fewer shrimp would be able to escape through the space between the bars.

As in the previous study (He and Balzano 2007), the release of small northern shrimp was accompanied by some loss of shrimp catch both in weight and in numbers. During this study, the catch rate of 11RNG was 9.7% less on average than the control RNG cod end, while 15–43% of catch reduction was experienced in the previous study. As expected, a larger reduction in shrimp count (fewer small shrimps) was likely accompanied by a greater...
loss in catch both in number per hour and in kilogram per hour. This study demonstrated that the 11RNG performed equally well or better for large shrimp equal to or larger than 23 mm CL (mostly age 4 and older females) when compared with RNG.

In fact, a slight increase in the number or amount of larger shrimp 23 mm CL or larger was observed (Figure 5) and was statistically significant for all shrimp larger than 27 mm CL (age 5 multiparasous females) as seen in Figure 6b. The release of small shrimp in front of the regular Nordmøre grid may have provided a better condition for larger shrimp to pass through the Nordmøre grid as the total number of shrimp in front of the grid was reduced.

As expected, the installation of a size-sorting grid did not significantly change the amount of finfish bycatch or composition of the bycatch when compared with the Nordmøre grid alone. We do not expect that a substantial number of finfish would escape from the 11-mm spaces between the size-sorting grid bars.

In summary, the new modified dual-grid size-sorting system with the size-sorting grid placed before the Nordmøre grid reduced the number of small shrimp 22 mm CL or less in the Gulf of Maine northern shrimp fishery without loss of larger shrimp 23 mm CL or larger. The system was easier to rig, handle, and maintain than the previous designs. The design can readily be commercialized in the Gulf of Maine northern shrimp fishery with minimal investment and without changes in regulations. The design may also be used in other pandalid shrimp fisheries in the northern Atlantic and Pacific oceans with suitable adjustments to the grid spacing to match available shrimp size in the stock and desirable shrimp sizes to be retained. Application of the design principle in other shrimp and prawn fisheries around the world may also be possible with additional experimentation, adjusting for shrimp behavior and morphology, gear size, towing speed, and bycatch species.
ACKNOWLEDGMENTS

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Incorporating Movement Patterns to Improve Survival Estimates for Juvenile Bull Trout

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ARTICLE

Incorporating Movement Patterns to Improve Survival Estimates for Juvenile Bull Trout

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Abstract

Populations of many fish species are sensitive to changes in vital rates during early life stages, but our understanding of the factors affecting growth, survival, and movement patterns is often extremely limited for juvenile fish. These critical information gaps are particularly evident for bull trout Salvelinus confluentus, a threatened Pacific Northwest char. We combined several active and passive mark–recapture and resight techniques to assess migration rates and estimate survival for juvenile bull trout (70–170 mm total length). We evaluated the relative performance of multiple survival estimation techniques by comparing results from a common Cormack–Jolly–Seber (CJS) model, the less widely used Barker model, and a simple return rate (an index of survival). Juvenile bull trout of all sizes emigrated from their natal habitat throughout the year, and thereafter migrated up to 50 km downstream. With the CJS model, high emigration rates led to an extreme underestimate of apparent survival, a combined estimate of site fidelity and survival. In contrast, the Barker model, which allows survival and emigration to be modeled as separate parameters, produced estimates of survival that were much less biased than the return rate. Estimates of age-class-specific annual survival from the Barker model based on all available data were $0.218 \pm 0.028$ (estimate $\pm$ SE) for age-1 bull trout and $0.231 \pm 0.065$ for age-2 bull trout. This research demonstrates the importance of incorporating movement patterns into survival analyses, and we provide one of the first field-based estimates of juvenile bull trout annual survival in relatively pristine rearing conditions. These estimates can provide a baseline for comparison with future studies in more impacted systems and will help managers develop reliable stage-structured population models to evaluate future recovery strategies.

Knowledge of a species’ life history and associated vital rates is crucial for development of effective conservation and recovery strategies (Williams et al. 2002). For many fish species, population dynamics are extremely sensitive to changes in survival at early life stages (Houde 1994; Hilborn et al. 2003). However, demographic rates are often difficult to assess between egg deposition and subadult stages, in part because survival rates during early stages are typically relatively low and can be highly variable (Bradford 1995). Although they are sometimes costly to obtain, life-stage-specific estimates of survival can be used to evaluate the relative contribution of various subadult stages to overall population change and identify targets for management (Caswell 2001; Morris and Doak 2003; Gross et al. 2006). Further, precise estimates of survival can help managers comprehend the magnitude of variability that may occur naturally as a result of environmental factors, such as density-dependent interactions, relative to anthropogenic influences (e.g., Johnston et al. 2007).

Mark–recapture studies provide a way to estimate survival and other key demographic information specific to individual
cohorts or life stages (e.g., Lebreton et al. 1992; White and Burnham 1999). However, estimation of demographic rates may be complicated for highly migratory species, both because of the effort needed to recapture mobile individuals and because animal movement patterns can affect interpretation of survival estimates (Cilimburg et al. 2002; Horton and Letcher 2008). For example, estimates of apparent survival ($\hat{\phi}$) generated using the common Cormack–Jolly–Seber (CJS) model are a combined estimate of true survival and site fidelity, the probability that an animal remains available for recapture within the study area (White and Burnham 1999; Sandercock 2006). With CJS estimates, it is not possible to distinguish permanent emigration from mortality or temporary emigration from capture probability (Barker et al. 2004; Horton and Letcher 2008). As a result, frequent emigration of marked organisms from the study area can confound estimates of apparent survival, and this issue has previously limited studies that sought to estimate the survival of migratory stream-dwelling fishes (e.g., Paul et al. 2000; Letcher et al. 2002). However, recent advances in technology have allowed researchers to improve recapture and resighting probabilities, while new analytical techniques have improved the ability to incorporate movement patterns into mark–recapture survival analyses.

The use of passive integrated transponder (PIT) tags has become increasingly common in fisheries research. Novel technology, including mobile PIT tag readers and passive (stationary) in-stream antennas, now often accompany the use of PIT tags. These technical advances offer a promising means of increasing the spatial and temporal extent of resight information (Zydlewski et al. 2006). Fish marked with PIT tags can be located by a researcher actively moving a mobile PIT tag reader through a study site (e.g., Roussel et al. 2000). In comparison, a passive in-stream antenna (PIA) can be operated continually to detect PIT-tagged fish as they swim past a stationary location in the stream. Both of these methods allow detection (i.e., resight) of marked individuals without handling or harassment.

Although PIT tag data acquired at PIAs can help describe fish movement patterns within a stream system, resight data collected on a continual basis cannot be incorporated into many standard mark–recapture survival models. In the common CJS model, for example, captures and recaptures must take place over a short time period relative to the time between sampling events to ensure that survival probability is constant among individuals (Lebreton et al. 1992). A more recent model developed by Barker (1997) similarly requires captures during discrete events, but can also incorporate resights of marked animals during the intervals between discrete sampling periods. Whereas captures usually occur within a specific study area, resights of marked animals are assumed to take place throughout the range of the population of interest. Inclusion of this information allows for direct estimation of true survival and site fidelity as distinct parameters (Barker and White 2001; Barker et al. 2004). This model is uncommon in the fisheries literature (but see Buzby and Deegan 2004; Al-Chokhachy and Budy 2008), although it appears promising for studies that include numerous data types (Barker et al. 2004) or for fishes that exhibit coexisting life history strategies and diverse migration patterns (Buzby and Deegan 2004; Horton and Letcher 2008).

One such fish species that demonstrates a range of movement patterns is the bull trout Salvelinus confluentus. The bull trout is a threatened species of stream-dwelling char that exhibits variability in life history types, migration patterns, and maturation schedules (Bahr and Shrimpton 2004; Johnston and Post 2009). Bull trout populations often include both migratory and nonmigratory (resident) life history types (McPhail and Baxter 1996; Homel et al. 2008). Adults typically spawn in cold headwater streams which also serve as rearing habitat for juveniles. Bull trout usually disperse between ages 1 and 4, migrating downstream into larger river systems and lakes where they may reside for several years before returning to natal waters to spawn, although resident adult bull trout may inhabit the upper portions of a watershed throughout their lives (Fraley and Shepard 1989; Ratliff 1992; Rieman and McIntyre 1993). For bull trout, high within-population variability and behavioral plasticity encumber the quantification of movement patterns and survival estimates. Bull trout migration distances can range from just a few kilometers to more than 200 km (McPhail and Baxter 1996; Hogen and Scarnecchia 2006), further complicating the estimation of demographic parameters.

Considerable research has been conducted to describe migratory behavior and habitat use for individual bull trout populations (Swanberg 1997; Bahr and Shrimpton 2004; Watry and Scarnecchia 2008), but the majority of these studies have focused on adults. Information about bull trout life history requirements and vital rates is still relatively sparse, particularly for early life stages. Very few studies have assessed juvenile bull trout migration patterns, rates of survival, or the environmental factors affecting survival. Life-stage-based population projection models developed for bull trout suggest that population growth may be most sensitive to changes in the survival of large adults and early life stages (Rieman and McIntyre 1993; Al-Chokhachy 2006). However, the predictive ability of such models is currently limited by a lack of empirical survival estimates specific to subadult stages.

To our knowledge, reliable estimates of survival for juvenile age-classes (\(< 120 \text{ mm total length [TL]}\)) are unavailable for bull trout. Previous studies assessed relative survival for early age-classes of bull trout by comparing abundances between years but did not produce precise juvenile survival estimates (Paul et al. 2000; Johnston et al. 2007). Al-Chokhachy and Budy (2008) used mark–recapture methods to develop stage-specific survival estimates for bull trout larger than 120 mm TL, but their study did not include smaller individuals. Obtaining survival estimates specific to juvenile stage classes will help fill an important gap in our understanding of factors that determine bull trout survival at different life stages. Estimates of stage-specific survival rates will also aid in identifying the life stages to target for recovery and improve the ability of population
models to predict population-level responses to environmental changes.

To evaluate migration patterns and estimate survival rates for juvenile bull trout, we conducted an intensive mark–recapture study within one of several important spawning areas used by a relatively large population of bull trout in the South Fork Walla Walla River (SFWW), Oregon. The population of bull trout in the SFWW exhibits both migratory and resident life history forms (Homel et al. 2008), and migration distance and timing can be highly variable (Homel and Budy 2008). Prior to this study, little was known about juvenile bull trout dispersal and survival rates in this system.

The overall goal of this research was to provide insight into a stage of bull trout life history which has previously not been well quantified and which has important implications for understanding how juvenile life stages affect population growth and persistence. To meet this goal, the specific objectives of this study were to (1) quantify and better understand the movement patterns exhibited by juvenile bull trout (70–170 mm TL) and (2) incorporate knowledge of juvenile migration rates into mark–recapture analyses to obtain the most precise estimates of survival for bull trout during these influential early life stages.

**METHODS**

**Study Area**

We conducted this study over approximately 600 m of Skiphorton Creek directly upstream of the confluence with the SFWW (Figure 1). Skiphorton Creek originates in the foothills of the Blue Mountains in northeastern Oregon and enters the SFWW approximately 113 km upstream from the Columbia River. The Skiphorton Creek study area has an average slope of 3–5%, a mean width of 5 m, and a mean water depth of 0.24 m. The study area is characterized by complex habitat, including numerous small side channels, pools, undercut banks, and large woody debris. Bull trout primarily use Skiphorton Creek for spawning and juvenile rearing, and the fish assemblage is composed of juvenile or small resident bull trout (primarily <170 mm TL) and rainbow trout *Oncorhynchus mykiss* and/or juvenile steelhead (anadromous rainbow trout). Skiphorton Creek is located on roadless forest lands, and owing to the remote location, sampling was limited to the snow-free months of June through October.

We also gathered additional data throughout the SFWW and main-stem Walla Walla River (WW), both considerably larger
streams than Skiphorton Creek. Bull trout spawn throughout approximately 20 km of the upper SFWW and its tributaries, and adult and subadult bull trout use the entire SFWW and WW (43 and 81 km in length, respectively) for migration and overwintering habitat (Anglin et al. 2009).

Mark, Recapture, and Resight Techniques

Mark and recapture.—We conducted two discrete mark–recapture sampling events during the summers of 2007 and 2009 and three in 2008 (Table 1). We captured bull trout in Skiphorton Creek by chasing fish with a low-voltage electrical current downstream into a seine (hereafter referred to as “electroseining”). We constrained the number of electroseining events to minimize the stress to juvenile fish, and we gathered initial data on all captured fish between 70 and 170 mm TL. We anaesthetized, weighed, measured, and marked bull trout with both an external fin clip and an internal PIT tag (12.5 mm Full Duplex 134.2 kHz) surgically inserted into the peritoneal cavity. We double-marked all individuals to identify recaptures and quantify tag retention rates. We checked all recaptured fish for tag loss and recorded the unique PIT tag code. We released all fish near the point of capture after full equilibrium had been restored.

Mobile resights.—In 2008 and 2009, we also used a mobile PIT tag reader to detect marked fish throughout the Skiphorton Creek study area. We refer to this type of sampling as “mobile resight” surveys to remain consistent with the literature on Barker models, in which the term “resight” has been used to refer to any method for obtaining observations of marked animals other than physical live recaptures. The mobile reader consisted of a backpack-mounted tuner and receiver connected to a 0.35-m × 0.35-m triangular antenna at the end of an extendable pole (Biomark BP portable antenna; see Roussel et al. 2000; Cucherousset et al. 2005; Keeler et al. 2007). The reader’s maximum vertical PIT tag detection distance ranged between 0.15 and 0.35 m, depending on the orientation of the tag and the reader’s tuning. Lateral read range was extremely limited, such that a PIT tag had to be directly below the triangular antenna to be identified.

During each mobile resight survey, the operator waded upstream through the entire study area, passing the reader over all areas of the streambed at a height that would allow for PIT tag detection. The operator recorded the date, time, and exact location of each PIT tag. Each mobile resight sampling period took approximately 8 h, and all surveys were conducted by the same person to minimize sampling variability. We performed mobile resight surveys both during the day and at night and compared the recapture probabilities between these two time periods. We generally conducted mobile resight sampling approximately 1 week after electroseining mark–recapture events (Table 1) to assess mortalities following tagging.

Tag recoveries.—During the mobile resight surveys, we did not actually see marked fish, so we could not be certain whether (1) the PIT tag had been shed from a fish that was still alive, (2) the PIT tag was in a live fish, or (3) the marked fish had died but the tag remained in the river. We addressed the first possibility by double-marking all fish with both a PIT tag and external fin clip. Because the observed rate of PIT tag retention was high (see Results), we assumed that immobile tags represented dead fish. We distinguished between a live resight and a “tag recovery” in the following manner: after detecting a PIT tag with the mobile

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Resight interval (d)</th>
<th>Number marked</th>
<th>Live recaptures/resights</th>
<th>Live resight</th>
<th>Dead recoveries</th>
<th>Sampling method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jul 10–13, 2007</td>
<td>34</td>
<td>86</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>ES</td>
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<td>14</td>
<td>6</td>
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<td>May 2–3, 2008</td>
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<td>52</td>
<td>5</td>
<td>2</td>
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<td>ES</td>
</tr>
<tr>
<td>Jul 7–8, 2008</td>
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<td>94</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>ES</td>
</tr>
<tr>
<td>Aug 13–19, 2008</td>
<td>293</td>
<td>123</td>
<td>23</td>
<td>62</td>
<td>5</td>
<td>ES + MPR</td>
</tr>
<tr>
<td>Jun 8–15, 2009</td>
<td>36</td>
<td>107</td>
<td>12</td>
<td>34</td>
<td>0</td>
<td>ES + MPR</td>
</tr>
<tr>
<td>Jul 21–31, 2009</td>
<td>363</td>
<td>142</td>
<td>79</td>
<td>101</td>
<td>4</td>
<td>ES + MPR</td>
</tr>
<tr>
<td>Total</td>
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<td>669</td>
<td>136</td>
<td>209</td>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 1. Sampling schedule and methods used to capture, recapture, or resight juvenile bull trout. Fish were captured by electroseining (ES) and resighted with a mobile PIT tag reader (MPR) in Skiphorton Creek. Marked fish were resighted during intervals between discrete sampling events at a passive in-stream antenna at the downstream end of the study area (PIA<sub>SH</sub>) and at five passive in-stream antennas (PIA<sub>WW</sub>) as well as via ancillary capture (ANC) throughout the South Fork Walla Walla and Walla Walla rivers.
reader, the operator tapped on the substrate adjacent to the tag location, and if the tag was in a different place following the disturbance, the observation was considered a live resight. To be considered a tag recovery, a PIT tag had to be found immobile in the same location during two consecutive mobile surveys. Although we did not actually observe dead fish, we used the term “recovery” to describe detections of immobile PIT tags, to remain consistent with previous mark-recapture literature in which the term “dead recovery” has been used (Barker et al. 2004).

Passive in-stream antenna arrays and ancillary resight data.— In addition to sampling within the Skiphorton Creek study area, we collected continuous resight data from marked fish as they swam past stationary PIAs. As part of a large-scale, multiyear research project (see Al-Chokhachy and Budy 2008), five PIAs operated in the SFWW and WW river system located approximately 7, 16, 38, 52, and 103 km downstream from the Skiphorton Creek study area (Figure 1). The devices operated year-round, except for short periods when maintenance was required, and enabled us to gather resight data at multiple locations outside of the immediate study area. In 2008 and 2009, we installed one additional PIA at the downstream end of Skiphorton Creek (Skiphorton PIA) to identify when fish emigrated from the study area. We used a solar panel to generate power for the remote site; the PIA only operated between 24 July and 28 September 2008 and from 8 June to 30 September 2009, when sufficient sunlight was available.

Bull trout marked in Skiphorton Creek were also recaptured throughout the entire SFWW and WW system via several different methods. Each summer, as part of the larger study mentioned previously, approximately 20 km of the SFWW were sampled for bull trout via electroseining, and all recaptures of fish marked in Skiphorton Creek were recorded. Marked bull trout were also recaptured throughout the year at screw traps and via research-related angling at multiple locations on the WW. Fish recaptured in the SFWW or WW were considered “ancillary resights” collected during the intervals between discrete mark-recapture sampling periods. Although ancillary resights made up a small proportion of the total data, this additional sampling allowed us to consider marked fish to be at risk of recapture anywhere in the geographic range of interest (Barker 1997; Barker et al. 2004).

Juvenile Movement Patterns

We evaluated the timing, direction, distance, and frequency of juvenile bull trout movement within the study area and throughout the SFWW and WW based on data combined from all of the sampling methods described above. We assumed that any marked fish that was detected in the SFWW or WW or resighted at the Skiphorton PIA had emigrated from the study area. We considered the assumption of emigration valid for the duration of our study because we observed no marked fish to have reentered Skiphorton Creek after having left. For fish detected at the Skiphorton PIA, we used data from physical recaptures to estimate the length at emigration based on a linear equation for the absolute growth rate applicable to short time scales (Isely and Grabowski 2007), namely,

\[ \text{Length}_{\text{emigration}} = \text{Length}_{\text{tagging}} + 5.23 + 0.099 \times (\text{time}_{\text{emigration}} - \text{time}_{\text{tagging}}). \] (1)

We used movement observations to describe emigration rates and timing and examined the impact of emigration on survival estimates.

Survival Analyses

We estimated annual survival probability for two separate age-classes of juvenile bull trout: age 1 (70–120 mm TL) and age 2 (121–170 mm TL), where length at age at initial capture was estimated based on combined length-frequency analyses and otolith aging (Al-Chokhachy and Budy 2008; Budy et al. 2011). All survival analyses were conducted in Program MARK (White and Burnham 1999). First, we estimated apparent survival from a CJS model (Cormack 1964; Jolly 1965; Seber 1965), a model commonly used to assess survival probabilities for a wide range of taxa (e.g., Lebreton et al. 1992; Muir et al. 2001; Letcher et al. 2002). The CJS model only incorporates data obtained from discrete mark-recapture sampling periods, so we only used data collected during electroseining mark-recapture and mobile resight sampling in Skiphorton Creek. We combined mobile resights with active captures in the same discrete sampling period, as mobile resight surveys were conducted shortly after mark-recapture periods. The two parameters estimated by the CJS model are apparent survival (\( q_i \); the probability that an animal survives and remains in the sample from time \( i \) to \( i + 1 \)) and \( p_i \) (the probability of encountering an individual given that it is alive and in the sample). Because emigration can confound these two parameters, we also used an ad hoc method in the CJS model to account for known emigration: when we observed an individual emigrate from the study area, we removed its contribution to survival parameter estimation at that time (see Horton and Letcher 2008). We included only known emigrants in this approach, which did not allow us to account for incomplete detection of emigrants.

We compared estimates of apparent survival from the standard and ad hoc CJS models with estimates of survival from the Barker model (Barker 1997; Barker and White 2001). As in the CJS model, mobile antenna resights from within the study area were incorporated into the data from the previous mark-recapture period. In addition to this data, the Barker model also allowed inclusion of data obtained during the interval from \( i \) to \( i + 1 \) between discrete sampling events, which included tag recoveries, resights at PIAs, and ancillary resights throughout the SFWW and WW. If an individual was either recaptured or resighted on more than one occasion during the interval from \( i \) to \( i + 1 \), only a single detection was recorded in the encounter history (Barker et al. 2004). The model complexity necessary to accommodate this additional data results in a total of seven
parameters in the Barker model (Barker 1997). In addition to survival \((S_i)\) and recapture \((p_i)\) probabilities, the model parameters include \(F_i\) (the probability that an animal at risk of capture at time \(i\) is at risk of capture at time \(i + 1\) [i.e., has not emigrated from the study area]), \(F'\) (the probability that an animal not at risk of capture at time \(i\) is at risk of capture at time \(i + 1\) [e.g., temporary emigration]), \(R_i\) (the probability that an animal alive at time \(i\) is resighted alive in the interval from \(i\) to \(i + 1\)), and \(R'_i\) (the probability that an animal is resighted before it dies in the interval from \(i\) to \(i + 1\)). A final parameter, \(r\) (the probability that an animal dies and is found dead in the interval from \(i\) to \(i + 1\)) allowed us to incorporate data from tag recoveries. Because we recovered only a relatively small number of tags, we also compared survival estimates between a data set that included tag recoveries and another which did not, where we set \(r = 0\).

We assessed model fit using the median \(\hat{c}\) approach in program MARK to estimate a variance inflation factor \((\hat{c})\) for the most saturated model given available data (e.g., Horton et al. 2011). Because the variance inflation factor was reasonable (1.98) and we expected that model fit improved with the inclusion of individual covariates, we based model selection on Akaike’s information criterion corrected for effective sample size \((\text{AIC}_c)\). We considered models with a difference of 0–2 in \(\text{AIC}_c\) to have substantial support, models with >4 to have considerably less support, and models with >10 to have virtually no support (Burnham and Anderson 2002). Data limitations and model parsimony led us to model some parameters as constant across time and between size-classes.

Our primary parameter of interest was survival, so we used a two-step approach to the model selection process. Initially, we retained high dimensionality in our survival parameters \((\varphi\text{ in the CJS model and } S \text{ in the Barker model})\) and iteratively modeled the remaining parameters based on a priori knowledge of sampling efficiency and bull trout ecology. With the CJS model, model selection of the less pertinent parameter (recapture probability \([p]\)) resulted in a set of candidate models for which \(p\) varied as a function of an increasing trend across sampling periods and with length as an individual covariate. For all candidate Barker models, we modeled \(p\) as a function of individual length and \(r\) as constant over time and among size-classes. Owing to the variability in resights among sampling intervals (Table 1), we modeled both \(R\) and \(R'\) as functions of time. Finally, we found strong support for models in which we explicitly modeled permanent emigration by setting \(F'\) to 0 and we allowed \(F\) to vary as a function of individual length.

After selecting the model structure for the less pertinent parameters, we then focused on modeling survival, the parameter of greatest interest (e.g., Slattery and Alisauskas 2002; Collins and Doherty 2006). In both the CJS and Barker candidate model sets, we estimated survival for the two different age-classes as separate groups and modeled survival in relation to factors determined a priori, including annual variation, time interval, season, and individual covariates measured at the time of tagging, such as length. In addition, we included models with a marking effect to test the hypothesis that survival rates would be lower during the time interval immediately following initial capture. To facilitate comparison of survival estimates and variance between the CJS and Barker model types, we present estimates from the single best model from the set of candidate models.

We compared survival estimates from the top CJS and Barker models with an estimate of the return rate, an index of survival. Return rates can be considered a minimum estimate of true survival, because they do not account for detection probability or site fidelity (Sandercock 2006). We estimated a simple return rate by calculating the proportion of marked fish in each size-class that were recaptured or resighted nine or more months after initial tagging (fish that survived until the subsequent field season and afterward). We estimated a return rate \((\hat{RR})\) for marked fish from a simple proportion with binomial variance using

\[
\hat{RR} = \frac{Y}{N},
\]

\[
\text{var}(\hat{RR}) = \frac{\hat{RR}(1 - \hat{RR})}{N},
\]

where \(Y\) represents the number of marked fish that were resighted and \(N\) is the total number of marked fish.

**RESULTS**

**Recaptures and Resights of Marked Fish**

Between 2007 and 2009, we marked 669 bull trout in Skiphorton Creek. Nearly 50% were recaptured or resighted at least once \((n = 327)\), and approximately 11% multiple times \((n = 71)\). The total number of unmarked fish caught in a single mark-recapture sampling period ranged between 52 in May 2008 and 142 in July 2009 (Table 1). The majority of bull trout captured and PIT-tagged were in the age-1 size-class, whereas only 25% of the marked individuals were > 120 mm TL (Figure 2).

Multiple techniques were necessary to obtain sufficient data to track the movement patterns of marked individuals and evaluate survival rates, although the efficiency of resighting techniques varied. Data from the mobile PIT tag reader, all PIAs combined, and ancillary resights accounted for 62, 36, and 2% of total resight observations, respectively. The number of fish resighted during each interval between discrete sampling periods increased over the duration of the study (Table 1), as both the number of marked fish and sampling effort increased. In 2007, we resighted no fish between the two summer capture periods and only six between the 2007 and 2008 field seasons. After we added the PIA at the lower end of the Skiphorton Creek study area during 2008 and 2009, PIA resights increased dramatically.

The mobile PIT tag reader enabled us to resight marked bull trout while minimizing disturbance to the stream and fish and was particularly effective when used at night (Table 2). The recapture probability with the mobile PIT tag reader at night
FIGURE 2. (A) Length at capture of juvenile bull trout caught in Skiphorton Creek and marked with PIT tags and (B) proportion of marked fish in each size-group for which the exact date of emigration from the Skiphorton Creek study area was known. Emigration was determined when PIT-tagged fish were detected at a passive in-stream antenna located at the lower boundary of the study area. Length at emigration was estimated based on a linear growth relationship developed for the study population. 

\[ p = 0.51 \pm 0.04; \text{estimate} \pm \text{SE} \] was 4.5 times that of the mobile reader during the day \( (p = 0.11 \pm 0.02) \) and 2.5 times that of electroseine sampling \( (p = 0.22 \pm 0.03) \). We recaptured only one fish that had shed its PIT tag, resulting in an estimate of 98.8% tag retention. Given this high rate of tag retention, we did not explicitly account for tag loss and considered the 12 tag recoveries found during 2008 and 2009 to represent mortalities in our analyses.

### Juvenile Bull Trout Movement Patterns

Recapture data collected via multiple methods allowed us to determine when juvenile bull trout emigrated from the natal spawning/rearing tributary and enabled us to observe bull trout movements throughout the study area and the larger SFWW and WW system. Within the Skiphorton Creek study area, juvenile bull trout moved both upstream and downstream, but the predominant direction of movement was downstream (Figure 3). Movement in the upstream direction occurred at low frequencies within the study area, and the largest recorded upstream movement was only 0.2 km. We observed numerous juvenile bull trout that remained for more than 1 month within 50 m of their original capture location, and in many instances those fish were located in the same habitat unit (e.g., a small pool or eddy) during numerous consecutive sampling periods. The majority of marked fish remained within 0.5 km of their initial capture location until they began a downstream migration, after which many moved rapidly downstream, some traveling up to 6 km in 3 d. We resighted marked fish at various locations throughout the larger SFWW and WW, and the greatest observed travel distance was 53 km downstream from the study area. We did not detect a relationship between stream discharge and movement patterns (Figure 3).

Juvenile bull trout emigrated from the study area at a range of sizes and during all seasons. Based on a linear relationship between juvenile bull trout growth and time, we estimated the length of marked fish for which the exact date of emigration was known (i.e., fish detected passing the Skiphorton PIA). Juvenile bull trout of all sizes exceeding 80 mm TL emigrated from the study area, although the majority of emigrants were longer than 100 mm (Figure 2). The proportion of emigrants increased with fish length, but we did not observe a distinct size threshold at which movement was initiated. Emigration occurred throughout the year, with a slight increase in the emigration rate from late August through October. In the age-1 age-class, 52% of the fish recaptured between 4 and 12 months after initial capture had moved more than 4 km downstream of the study area, and 92%

### Table 2. Comparison of capture probabilities for the capture and recapture/resight methods used to estimate juvenile bull trout movement and survival.

<table>
<thead>
<tr>
<th>Sampling method</th>
<th>Data type</th>
<th>Capture probability ( (p \text{ or } R) )</th>
<th>SE</th>
<th>Average recapture/ sampling hour</th>
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</thead>
<tbody>
<tr>
<td>Electroseining</td>
<td>Live recapture</td>
<td>( p = 0.22 )</td>
<td>0.03</td>
<td>0.76</td>
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<td>Live resight in study area/dead recovery</td>
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<td>Live resight in study area/dead recovery</td>
<td>( p = 0.51 )</td>
<td>0.04</td>
<td>7.55</td>
</tr>
<tr>
<td>PIAs + ancillary</td>
<td>Live resight outside study area</td>
<td>( R = 0.19^a )</td>
<td>0.06</td>
<td>n.a.</td>
</tr>
<tr>
<td>PIAs + ancillary</td>
<td>Live resight outside study area</td>
<td>( R' = 0.16^a )</td>
<td>0.01</td>
<td>n.a.</td>
</tr>
</tbody>
</table>

\( ^a \)For the time period when the Skiphorton PIA was operating continuously (maximum observed \( R \)).
of the age-2 fish appeared to have emigrated (Figure 4). As a result of high emigration rates and variable emigration timing, a substantial proportion of the marked fish were unavailable for recapture during subsequent sampling periods. Furthermore, no marked fish were detected within the study area more than 18 months after tagging, suggesting that nearly all juveniles emigrated from their natal habitat between age 1 and age 3.

**Juvenile Bull Trout Survival Rates**

Estimates of survival based on the simple return rate were $0.171 \pm 0.017$ (estimate ± SE) for the age-1 class and $0.190 \pm 0.030$ for the age-2 class (Figure 5). Compared with the return rate, the estimates of apparent survival from the naïve CJS model were extremely biased downward but improved when emigration was included in the models via the ad hoc approach. Point estimates of annual survival using the Barker model were higher than the return rate, and the 95% confidence intervals encompassed the return rate. Across models, the variance associated with survival estimates was greater for age-2 fish, as there were fewer fish marked in this size-class.

The CJS model that minimized AICc was constant across time and included separate estimates of apparent survival for the two age-classes and fish length as an individual covariate (Table 3). From this model, the estimate of apparent annual survival for the age-1 class was $0.090 \pm 0.018$ for a fish with a mean length of 100 mm TL and $0.009 \pm 0.009$ for the age-2 class based on a mean length of 133 mm. Compared with the return rate, the CJS estimates accounted for only 52% and 5% of the return rate for the two size-classes, respectively (Figure 5). The ad hoc CJS approach resulted in the same best model as the naïve CJS model, and with emigration explicitly incorporated, survival estimates were $0.142 \pm 0.023$ for the age-1 class (similar to the return rate), but $0.069 \pm 0.030$ for the age-2 class (only 36% of the return rate). Model selection showed much less support for the model that included a tagging effect, and a likelihood ratio test provided no evidence of a difference in survival during the time period immediately following tagging ($\chi^2 = 1.112, df = 2, P = 0.57$).

In contrast to the CJS model results, the annual survival estimates from the Barker model were somewhat higher than those from the return rate (Figure 5). Model selection produced identical model ranking for data with and without tag recoveries but led to slightly different estimates of survival with similar precision. For both data sets, the model with the greatest support was one in which survival was constant across time and varied between size-classes (Table 3). Estimated annual survival for the Barker model including dead recoveries was $0.218 \pm 0.028$ for fish in the age-1 class and $0.232 \pm 0.065$ for age-2 fish. When tag recoveries were omitted from the data ($r = 0$), the same best-ranking model provided similar estimates of $\hat{S}$ ($0.195 \pm 0.026$ and $0.191 \pm 0.062$, respectively). Based on the AICc values, there was little support for the model that included annual variability in survival, although this was unsurprising...
FIGURE 5. Estimates of survival probability for age-1 and age-2 bull trout marked in Skiphorton Creek calculated using different methods (RR = return rate, CJS = naïve Cormack–Jolly–Seber, CJSem = ad hoc CJS with emigration included, BD = Barker model with dead recoveries, BN = Barker model without dead recoveries). Error bars represent 95% confidence intervals.

given that there were only 3 years of data. There was also considerably less support for a model that included a tagging effect, and a likelihood ratio test provided no evidence of lower survival during the time period directly following tagging ($\chi^2 = 1.768$, df = 2, $P = 0.41$).

In addition to providing robust estimates of survival, the Barker model included specific parameters to estimate site fidelity, providing additional insight into juvenile bull trout migration patterns. Model selection demonstrated stronger support for a model in which we explicitly modeled permanent emigration ($F^\prime = 0$) than for a model that included random emigration (Barker and White 2001), which was consistent with our movement observations. In this model, $F$ varied as a function of individual length and parameter estimates indicated that $F$ was negatively related to fish length at marking and decreased sharply for fish larger than 100 mm. Estimates of $F$ were $0.735 \pm 0.151$ for a fish measuring 90 mm TL, compared with $0.125 \pm 0.063$ for a 110-mm TL bull trout. This sharp decline in the probability of an individual’s remaining at risk of capture was consistent with our observations of emigration rates for bull trout across this range of sizes.

DISCUSSION

Our results provide some of the first estimates of annual survival rates for age-1 and age-2 bull trout based on individual mark–recapture information. Use of multiple recapture and resighting techniques allowed us to assess rates of emigration from natal habitat and to describe the movement patterns of juvenile bull trout. In addition, incorporating emigration into our survival analyses improved the accuracy of annual survival estimates for juvenile bull trout. The results from the Barker model appeared to be the least-biased estimates of survival based on the model types we considered and are the most precise field-based survival rates available for juvenile bull trout of which we are aware. Our study demonstrates the importance of incorporating movement patterns into survival analyses for migratory species and provides an important comparison of contemporary capture–recapture techniques in stream systems.

Mark, Recapture, and Resight Techniques

The use of PIT tags was highly effective in this study, as it enabled us to detect marked fish across a large geographic range with minimal handling. We found 2 of the 12 recovered tags during the sampling period directly after tagging, but we found no evidence that PIT-tagging individuals affected survival estimates. These results correspond with those of previous studies of juvenile salmonids, which have likewise detected no discernible difference in survival between PIT-tagged and nontagged fish held in a controlled setting (Prentice et al. 1990; Gries and Letcher 2002) or in the wild (Ombredane et al. 1998).

The use of the mobile PIT tag reader allowed us to increase the probability of resighting a marked individual while causing little disturbance to the stream and fish. The mobile reader also enabled us to make an efficient use of our sampling time, as it required only one person to operate (compared with three for the electroseining method) and the entire study area could be scanned in 8 h. The mobile reader was most effective when operated at night, when juvenile bull trout often moved very little from their location as the reader passed over them, even after the operator tapped on the substrate (in contrast with daytime sampling, when fish usually moved immediately). As a result, five resights were initially misidentified as tag recoveries, but the marked fish subsequently changed locations or were detected at downstream PIAs. Thus, we only classified tags as recoveries when they were found in the same place during at least two consecutive sampling periods.

We recovered only 12 tags, and this relatively small number may not have been sufficient to improve the precision of survival estimates from the Barker model. Nonetheless, it is reasonable to expect that larger numbers of tag recoveries would yield greater precision in estimating the parameters of interest (Barker and Kavalieris 2001). Tag recoveries could also have represented
TABLE 3. Survival models for juvenile bull trout captured and marked in Skiphorton Creek, 2007–2009. Two age-classes were modeled as separate groups: age 1 (70–120 mm TL) and age 2 (121–170 mm). Periods indicate no difference across time or among groups, plus signs denote additive parameters, and = 0 indicate parameters set to 0; length at capture was included as an individual covariate. See text for variable descriptions.

<table>
<thead>
<tr>
<th>Survival varies by</th>
<th>Candidate model</th>
<th>AICc</th>
<th>Model likelihood</th>
<th>Number of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age group + length</td>
<td>$\phi_{\text{group + length}} P_{\text{timetrend + length}}$</td>
<td>664.95</td>
<td>1.00</td>
<td>7</td>
</tr>
<tr>
<td>Age group</td>
<td>$\phi_{\text{group}} P_{\text{timetrend + length}}$</td>
<td>668.87</td>
<td>0.14</td>
<td>5</td>
</tr>
<tr>
<td>Year</td>
<td>$\phi_{\text{year}} P_{\text{timetrend + length}}$</td>
<td>681.87</td>
<td>0.04</td>
<td>6</td>
</tr>
<tr>
<td>Group + tag effect</td>
<td>$\phi_{\text{group + tag effect}} P_{\text{timetrend + length}}$</td>
<td>673.25</td>
<td>0.00</td>
<td>9</td>
</tr>
</tbody>
</table>

**CJS models**

**Barker models**

| Age group + length | $S_{\text{group + length}} P_{\text{length}} R_{\text{time}}$ | 1,839.63 | 1.00 | 18 |
| Age group + tag effect | $S_{\text{group + tag effect}} P_{\text{length}} R_{\text{time}}$ | 1,841.49 | 0.39 | 19 |
| Age group + tag effect | $S_{\text{group + tag effect}} P_{\text{length}} R_{\text{time}}$ | 1,844.35 | 0.09 | 20 |
| Year | $S_{\text{year}} P_{\text{length}} R_{\text{time}}$ | 1,860.91 | 0.00 | 19 |

PIT tags that were shed from fish that were still alive rather than true mortalities. However, based on the high rate of PIT tag retention that we observed, we considered the probability of a shed tag unlikely and therefore did not incorporate tag loss rates in our survival estimates. Other studies of similar-sized juvenile fish have also shown high rates of PIT tag retention (Ombredane et al. 1998; Gries and Letcher 2002). If PIT tag retention were lower than we observed, we would have underestimated true survival (Knudsen et al. 2009) and our annual survival estimates would be conservative.

Passive in-stream antenna arrays stationed at six locations throughout the geographic range of the population allowed us to collect data continually throughout the year, including in winter when our remote field site was inaccessible. Use of multiple PIAs also helped us develop a detailed spatial and temporal understanding of juvenile bull trout movement patterns and emigration rates. Detection efficiency varied among PIAs and at different discharges, but we did not have sufficient data or the analytical ability to incorporate this variability into our analyses. Operation of the PIA at the downstream end of the study area over the entire year would certainly have increased our knowledge of emigration timing and improved the survival estimates from the ad hoc CJS method. However, the Barker model can incorporate data collected opportunistically (Barker 1997) and thus allowed for the inclusion of PIA data even when sites operated at less than 100% detection efficiency.

We observed an increasing trend in the number of recaptures/resights over the course of the study, which likely occurred as a result of increased effort and efficiency over time. This increase in efficiency resulted from the installation of the Skiphorton PIA, the use of the mobile PIT tag reader at night, and the potential improvement in the skill of the person operating the mobile reader. Due to the high emigration rates, variation in emigration timing, and low capture probabilities of juvenile bull trout, multiple resight techniques were necessary to obtain sufficient resight data to estimate survival and characterize movement patterns. Each of these techniques provided data that informed estimates of survival and emigration in a different way. While the use of the mobile PIT tag reader at night resulted in a relatively high capture probability compared with other methods, it only allowed detection of fish that remained in the study area. Data collected at PIAs were integral in monitoring movements throughout the broader range of the population, but the spatial and temporal scope of this research was possible only because there was a preexisting infrastructure of PIAs within the river system. The high cost of obtaining this type of information, both in terms of money and effort, may be prohibitive in many studies. In our research, it would not have been possible to reliably estimate survival without the use of additional resight methods both within and outside of the Skiphorton Creek study area. Thus, the cost of using various sampling techniques relative to the information gained should be weighed carefully within the context of overall study objectives (e.g., Al-Chokhachy et al. 2009).

**Juvenile Bull Trout Movement Patterns**

Migratory behavior is known to vary among different age-classes of bull trout and among populations (McPhail and Baxter 1996; Monnot et al. 2008). For the population of juvenile bull trout in Skiphorton Creek, emigration from the natal stream occurred across a range of sizes > 80 mm TL, and rates of emigration increased with fish length. These results are consistent with those of research in other locations where juvenile bull trout typically migrate from rearing areas into larger rivers between age 1 and 3, with the majority migrating at age 2 (Oliver 1979; McPhail and Baxter 1996). However, our research demonstrated that a surprisingly large proportion of age-1 juveniles emigrated from rearing habitat into the larger SFWW. These data suggest that as juveniles grow larger, selective forces favor migration downstream into larger, warmer, and more productive habitat, despite potentially greater risk of mortality from predators (e.g.,...
adult bull trout) and environmental catastrophes, such as flooding. Our data also showed that after leaving their natal stream juvenile bull trout migrated throughout more than 50 km of downstream habitat in the SFWW and WW, indicating that immature fluvial bull trout used a wide range of rearing habitat throughout the entire river network.

Over the course of this study, juvenile bull trout emigrated from spawning and rearing habitat continuously throughout the year. We observed a pulse of emigration into the SFWW and WW from July through October, when stream discharge is at its lowest and instream barriers may be more difficult to pass. Increased observations during this time period may have been influenced by higher sampling intensity during these months, although other research has similarly demonstrated higher rates of downstream subadult migration during late summer and fall (Oliver 1979; Homel and Budy 2008). Immature bull trout also migrated downstream throughout the remainder of the year, including during winter months, a time period during which adult bull trout are often considered sedentary (Bahr and Shrimpton 2004; Watry and Scarnecchia 2008). These data illustrate the variability of juvenile bull trout migratory behavior, a component of the fluvial life history which is not always considered in management objectives.

Mark–Recapture Models and Annual Survival Estimates

Migration rates and distances are often difficult to quantify for species that exhibit diverse life history characteristics or variation in both migratory behavior and home range size, such as bull trout, coastal cutthroat trout _O. clarkii clarkii_, rainbow trout, and brook trout _Salvelinus fontinalis_ (e.g., Trotter 1989; Rodríguez 2002; Meka et al. 2003). Nonetheless, understanding and incorporating movement patterns into capture–recapture studies can dramatically improve estimates of survival and other important vital rates (Cliumbug et al. 2002; Horton and Letcher 2008). In our study, continuous emigration from the study area resulted in a constant loss of marked fish from the study population. The return rate (the minimum estimate of true survival) was higher than the estimates of apparent survival using the CJS model because it included data from individuals resighted anywhere in the geographic range of the population, including fish that had emigrated from Skiphorton Creek. In contrast, the naïve CJS model only used data collected within the study area, from which marked fish emigrated continually, resulting in estimates of apparent survival that were considerably lower than the return rate. This bias was more pronounced for the age-2 class because fish in this size range demonstrated higher emigration rates. When we incorporated emigration directly into encounter histories we observed an improvement over the naïve CJS model, but the ad hoc approach still produced estimates of apparent survival that were biased downward, particularly for the age-2 size-class.

In contrast to the CJS model, the Barker model produced estimates of annual survival which were higher than the observed return rate and similar between the two size-classes (or slightly greater for the age-2 size-class). This latter observation indicates that bull trout survival rates may increase with size and age, which is consistent with many other fish species (Lorenzen 2006). Although we have no way of knowing the true survival rates in the wild, it is reasonable to expect that the true survival rates would be higher than the return rate, which does not account for recapture probability (Martin et al. 1995; Sandercock 2006). In simulation analyses, Horton and Letcher (2008) found that the Barker model yielded robust estimates of survival with very little bias, regardless of whether emigration was temporary or permanent. Given the robust nature of the Barker model and the relative agreement between annual survival estimates derived from this model and observed return rates, we believe that the best estimates for juvenile bull trout annual survival from our study are those obtained from the Barker model.

Our study provides an important baseline of field-based annual survival estimates for age-1 bull trout (70–120 mm TL). Prior to our study, the survival of this age-class represented a significant gap in our understanding of bull trout demography. Our estimates of annual survival rates are within the range of other annual survival estimates for juvenile brook trout, a closely related species (mean ± SE apparent survival = 0.218 ± 0.149; Petty et al. 2005). For age-2 bull trout, survival estimates for the fish marked in Skiphorton Creek were higher than those for fish from the larger SFWW River (Al-Chokhachy and Budy 2008), where estimates of annual survival for subadult bull trout (120–170 mm TL) varied between 0.025 ± 0.009 and 0.154 ± 0.052, depending on the year. Our results were also comparable to the highest annual return rates for subadult bull trout (<270 mm fork length) observed in Mill Creek, another tributary to the Walla Walla River (P. Howell, U.S. Forest Service, unpublished data).

While the higher estimates of annual age-2 bull trout survival in this study may in part reflect the greater sampling intensity in our study design, they may also represent true biological differences in survival between stream types. Our results indicate that survival rates for juvenile bull trout are higher in small tributaries than in larger rivers but also that fish emigrate from these tributaries as they mature. Together, these observations suggest that there may be a trade-off in fitness between the increased risks faced in large rivers (e.g., predation, displacement by flooding) and the faster growth rates associated with warmer, more productive waters (Selong et al. 2001). While emigration from small, hydrologically stable headwater streams may decrease the probability of survival, fish that do survive likely grow faster than their later-emigrating counterparts. The variability in size at which juvenile bull trout emigrate from natal streams may represent an important adaptation that allows populations to hedge their bets in an unpredictable environment (Olofsson et al. 2009).

Conservation and Management Implications

This research describes movement patterns and survival rates for juvenile bull trout (<170 mm TL) and provides insight into
a life stage that is not well understood. Our data demonstrate that juvenile (ages 1 and 2) fluvial bull trout exhibit a range of migratory behaviors. In the SFWW, juveniles moved from natal rearing habitat to larger rivers throughout the year and across a range of sizes. Based on these data, maintaining diversity in life history adaptations, including the variability in juvenile migratory behavior, may be important for long-term population persistence. Further, juvenile bull trout from 80 to 100 mm TL and larger used habitat throughout the SFWW and mainstem WW in all seasons, suggesting that these size-classes should be considered in management decisions regarding flow regulation and fish passage. In addition to documenting juvenile migratory behavior, our research demonstrates the importance of incorporating emigration rates into survival analyses for species that exhibit variable migration patterns and improves our understanding of the influence of migration on survival rates.

We provide some of the first field-based, empirical estimates of juvenile bull trout annual survival based on marked individuals. These estimates can provide a baseline against which to compare the results of future studies of juvenile bull trout survival in more impacted systems as well as improve our understanding of how various management actions may affect bull trout at specific life stages. Given the sensitivity of bull trout population growth to survival rates at early life stages, stage-specific estimates of vital rates are important for the development and use of reliable stage-structured population models. The survival estimates from this research will help improve the predictive ability of bull trout population viability analyses, which can be used to evaluate population-level responses to different management scenarios and to develop sound recovery plans for this imperiled species.

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experiment examining covariate effects on first-year survival in Ross’s geese


Performance of Surplus Production Models with Time-Varying Parameters for Assessing Multispecies Assemblages

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Performance of Surplus Production Models with Time-Varying Parameters for Assessing Multispecies Assemblages

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Abstract

Single-species surplus production models are often used to assess multispecies assemblages in data-poor situations where catch and effort data are insufficient to perform individual species assessments. We examined the performance of single-species surplus production models applied to aggregated multispecies assemblages and explored the incorporation of time-varying parameters to improve model estimates. We simulated the dynamics of three species with different intrinsic growth rates and survey catchabilities over 50 years in the presence of fishing and a single fishery-independent survey. Schaefer surplus production models with and without time-varying growth rate and catchability were fitted to simulated data. We then compared the ability of each model to accurately estimate multispecies maximum sustainable yield and terminal year biomass and to accurately reflect overall trends in individual component stocks. All models produced biased estimates, but the accuracy of multispecies assemblage maximum sustainable yield was improved with the incorporation of time-varying parameters. The terminal biomass of the assemblage was best estimated by a basic production model in two of three scenarios. Multispecies assemblage trends were not reflective of all individual component species, resulting in situations in which some species were overexploited and others underexploited. Although the incorporation of time-varying parameters improved the accuracy of some estimates in this application, the direction and magnitude of bias may not be predictable unless the relative differences in growth rate and catchability among species in the assemblage are known. If single-species surplus production models are the only viable option for modeling assemblages, precautionary reference points should be adopted. Scaling the level of precaution to the range of growth rates among species in the assemblage is recommended.

Determining the status of data-poor fish species is an important challenge facing many fisheries management agencies. Interest in assessing data-poor fish stocks has increased in recent years in the USA following the reauthorization of the Magnuson–Stevens Act of 2006, which required catch limits for all marine and anadromous species with federal fishery management plans. However, many data-poor species lack the catch, effort, and life history information necessary to conduct single-species assessments for specifying catch limits either because several species in the same region are difficult to distinguish or collecting species-specific data is cost prohibitive. In such circumstances, one approach is to aggregate and assess multiple species using a single-species surplus production model (SSPM; Pauly 1984; Sparre and Venema 1998). Single-species surplus production models have been applied to many multispecies assemblages, including tropical fishes (Ralston and Polovina 1982), sharks (McAllister et al. 2001; SEDAR 2006, 2007; Jiao et al. 2009), demersal fishes (Brander 1977; Mueter and Megrey...
The ability to assess data-poor stocks with SSPMs is appealing in its simplicity. However, such assessments are likely to violate the underlying assumption that the data used in an SSPM come from a homogeneous stock (Prager 1994; Quinn and Deriso 1999). This assumption will almost always be violated because catchability, life history, and fishing pressure likely differ among the individual species in an assemblage (Fox 1974; Brandon 1977; Pauly 1984; Sparre and Venema 1998). In the extreme case, managing according to the results of an assessment in which the assumption of stock homogeneity is violated has the potential to functionally extirpate one or more species within the assemblage because the parabolic yield curve underlying an SSPM may not be reversible (Kirkwood 1982; Pauly 1984; Sparre and Venema 1998). Consider a hypothetical example in which growth rates differ among the species in an assemblage and management is aimed at achieving multispecies maximum sustainable yield (MSMSY; Figure 1). Species 1 would be extirpated if exploitation was sustained above level E3, and species 2 would be extirpated above level E2. In this example, exploitation levels above MSMSY cannot necessarily be reduced with the expectation that yields will return to MSMSY.

Although the theoretical implications of applying SSPMs to multispecies assemblages have been explored (Brown et al. 1976; Pope 1976a, 1979; Kirkwood 1982; Pauly 1984), the performance of statistically fitted, nonequilibrium SSPMs in assessing heterogeneous multispecies assemblages has not been rigorously evaluated. Kleiber and Maunder (2008) demonstrated the consequences of pooling catch-per-unit-effort (CPUE) data across multiple species to form a single index of abundance. The resulting index was found to be reflective of the changes in true abundance only in the unlikely event that all species have the same catchability. Aggregate CPUE did not track aggregate abundance even in situations where the component single-species indices were accurate. Although aggregating CPUE may be a convenient way to treat data, aggregate CPUE is likely to provide misleading trends in relative abundance and should not be relied upon for management (Maunder et al. 2006; Kleiber and Maunder 2008).

One potential method of implicitly accounting for changes in the aggregate catchability or life history parameters of a multispecies assemblage is to allow parameters to vary over time. If individual biomass trends differ among species in an assemblage as a result of variation in life history characteristics (e.g., growth or availability to survey gear), the aggregate parameters describing multispecies assemblage dynamics (e.g., assemblage growth rate or catchability) will change over time. For example, if an assemblage such as the hypothetical example in Figure 1 is managed to achieve MSMSY, species 3 will decline over time and become a smaller proportion of the assemblage; as a result, the average aggregate growth rate will increase. If an SSPM is used to assess a heterogeneous multispecies assemblage, the incorporation of time-varying growth or catchability parameters may help account for the resulting changes in aggregate dynamics and improve model performance. Wilberg et al. (2010) reviewed the estimation of time-varying catchability in SSPMs and suggested the use of such parameters to account for multiple known or unknown causes of changing catchability when assessing a single stock; however, to our knowledge, time-varying parameters have not been applied to SSPMs in multispecies assemblage assessments.

In this study we examined the implications of using SSPMs to assess multispecies assemblages when growth rate and catchability differ among species. The goals of our study were to (1) evaluate the ability of traditional SSPMs to assess multispecies dynamics, (2) determine whether SSPMs with time-varying parameters improve model performance, and (3) assess the potential ramifications of using SSPM-based assemblage reference points when conservation of individual species within the assemblage is desired. We were specifically interested in the ability of SSPMs to provide accurate stock status information for management of a multispecies assemblage and to monitor its component stocks. Therefore, we compared the relative errors in MSMSY and terminal biomass estimates generated by SSPMs with and without time-varying parameters. We also explored the use of SSPMs to monitor individual stocks by comparing the overall estimated trend in total multispecies assemblage biomass with that of its individual component stocks.

**METHODS**

We conducted a simulation study to evaluate the ability of SSPMs to estimate the dynamics of multispecies assemblages. We simulated the dynamics of an assemblage of three...
noninteracting species with different intrinsic growth rates and catchabilities over 50 years in the presence of fishing and a single fishery-independent survey. Three SSPMs were fitted to the simulated data: a traditional SSPM, an SSPM with a time-varying intrinsic growth rate, and an SSPM with time-varying catchability. We then compared the ability of each model to accurately estimate MSMSY and terminal assemblage biomass and to reflect the changes over time in the relative biomass of individual component stocks. The simulations were performed in AD Model Builder (Fournier et al. 2012).

**Simulation model.**—We simulated the population dynamics of three species individually using an independent, discrete-time, deterministic, logistic population model, namely,

$$B_{s,t+1} = B_{s,t} + r_s B_{s,t} \left(1 - \frac{B_{s,t}}{K_s}\right) \left(1 - U_t\right), \quad (1)$$

where $B_{s,t}$ was the biomass in year $t$ for species $s$, $r_s$ was the intrinsic rate of increase for species $s$, $K_s$ was carrying capacity for species $s$, and $U_t$ was the fishery exploitation rate in year $t$. We assumed that $B_{s,0}$ was equal to $K_s$ in the first year and that the fishery occurred at the end of each year. To avoid complications that arise when SSPMs are confronted with uninformative time series, we simulated fisheries dynamics in which $U_t$ varied over time. The exploitation rate of the simulated fishery increased from 2.5% in year 1 to a peak of 20% in year 15. The exploitation rate then decreased to 10% for years 16–24 and to 5% for years 25–50. This exploitation rate time series avoided the generation of unidirectional trends in biomass that would prevent independent estimation of the $r$ and $K$ parameters (i.e., one-way trips; Hilborn and Walters 1992). The same time series of $U_t$ was applied to each species in a given year. We summed catch across all three species in each year to generate total fishery catch ($C$) for input into the estimation model, that is,

$$C_t = \sum_{s=1}^{3} \left[ B_{s,t} + r_s B_{s,t} \left(1 - \frac{B_{s,t}}{K_s}\right) \right] U_t. \quad (2)$$

We generated an index of biomass ($I$) for the multispecies assemblage from a simulated survey that encountered all three species, namely,

$$I_t = \left( \sum_{s=1}^{3} q_s B_{s,t} \right) e^{\varepsilon_t}, \quad (3)$$

where $q_s$ was the catchability of species $s$ and $\varepsilon_t$ were observation errors from a normal distribution with a mean of zero and a standard deviation (SD) of 0.2. We also considered observation errors with an SD of 0.5. All assessment models exhibited wider variability in their estimates, but the overall performance was similar to the results with an SD of 0.2; therefore, we only present results with the lower observation error.

**Estimation model.**—We fit a Schaefer surplus production model (Quinn and Deriso 1999) to aggregate catch and an index of biomass. Assemblage biomass followed the logistic growth model

$$\hat{B}_{t+1} = \hat{B}_t + \hat{r}_t \hat{B}_t \left(1 - \frac{\hat{B}_t}{\hat{K}}\right) - C_t. \quad (4)$$

where $\hat{B}_t$, $\hat{r}_t$, and $\hat{K}$ were the estimated assemblage biomass at time $t$, the intrinsic growth rate at time $t$, and carrying capacity, respectively. The estimated index of biomass, $\hat{I}_t$, was the product of catchability and assemblage biomass, that is,

$$\hat{I}_t = q_t \hat{B}_t, \quad (5)$$

where $q_t$ was survey catchability at time $t$. The estimation model assumed that total catch was known without error. For models with time-varying parameters, either $\hat{r}$ or $\hat{q}$ was allowed to vary according to a random walk on the log scale, that is,

$$\log_e \hat{q}_{t+1} = \log_e \hat{q}_t + \omega_t, \quad \text{or} \quad (6)$$

$$\log_e \hat{r}_{t+1} = \log_e \hat{r}_t + \omega_t, \quad (7)$$

with annual deviations ($\omega_t$) from a normal distribution with a mean of zero and a standard deviation of 0.1. Although larger standard deviation values are typically used when modeling time-varying parameters as random walks (e.g., Wilberg and Bence 2006; Fenske et al. 2011), we found that SSPMs would not converge to unique solutions if the random walk was allowed too much flexibility. Assuming a small standard deviation implies that $r$ and $q$ should exhibit large interannual fluctuations, which is to be expected given that these parameters reflect changes due to gradual shifts in species composition. Assemblage growth rate or survey catchability in the first year was an estimated parameter.

We obtained parameter estimates by minimizing the concentrated negative log-likelihood function

$$-LL_1 = \frac{n}{2} \log_e \left( \sum (\log_e (I_t) - \log_e (\hat{I}_t))^2 \right). \quad (8)$$

We assumed multiplicative lognormal observation errors for the index of biomass. For models with time-varying growth or catchability, an additional likelihood term, $-LL_2$, defined as

$$-LL_2 = \frac{1}{2\sigma^2} \sum \omega_t^2, \quad (9)$$

was included for the random walk deviations.

We generated starting parameter values for the multispecies assemblage $r$ and $q$ by calculating the biomass-weighted $r$ and $q$ averaged across all species and years. The starting value for the multispecies assemblage $K$ was simply the sum of individual species’ $K_s$. We assumed that $\hat{B}_0$ was equal to $K$. 

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TABLE 1. Intrinsic growth rates (r) and catchabilities (q) used in the three simulation model scenarios.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Species 1</th>
<th>Species 2</th>
<th>Species 3</th>
<th>Species 1</th>
<th>Species 2</th>
<th>Species 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.2</td>
<td>0.13</td>
<td>0.06</td>
<td>0.13</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>B</td>
<td>0.2</td>
<td>0.13</td>
<td>0.06</td>
<td>0.2</td>
<td>0.13</td>
<td>0.06</td>
</tr>
<tr>
<td>C</td>
<td>0.2</td>
<td>0.13</td>
<td>0.06</td>
<td>0.06</td>
<td>0.13</td>
<td>0.2</td>
</tr>
</tbody>
</table>

Scenarios.—We developed three scenarios that differed in relative survey catchability for each species (Table 1). For all scenarios, we simulated population growth assuming intrinsic growth rates of 0.2, 0.13, and 0.06 for the three species, reflecting a realistic range of estimated rates found among members of the small coastal shark complex (blacknose shark *Carcharhinus acronotus*, finetooth shark *Carcharhinus isodon*, Atlantic sharpnose shark *Rhizoprionodon terraenovae*, and bonnethead *Sphyra tiburo*; SEDAR 2007). Survey catchability was either (A) the same for all species, (B) higher for species with faster growth rates, or (C) lower for species with faster growth rates (Table 1). We chose these scenarios to reflect simplified cases in which the assumption of constant catchability would be met for the index of abundance, the index would overweight the most productive species, or the index would overweight the least productive species. We set carrying capacity at the same value (1,000,000) for all three species. For each scenario, 1,000 data sets were generated assuming the log-scale standard deviation (SD) of observation error in the survey was 0.2.

Model performance evaluation.—Our evaluation of the SSPMs applied to multispecies assemblage data concentrated on three characteristics important to fisheries management, namely, the models’ ability to (1) estimate the true MSMSY, (2) estimate the terminal biomass of the multispecies assemblage, and (3) reflect overall trends in single-species dynamics.

The estimate of MSMSY for the assemblage was calculated as the peak yield from the logistic model (Quinn and Deriso 1999), that is,

\[
\text{MSMSY} = \frac{(\hat{K}\hat{r})}{4}.
\]

Because current conditions are often of greatest interest in fisheries management, we used the terminal year estimates of \(\hat{r}\) to calculate MSMSY for models with time-varying parameters.

We calculated the relative error (RE) in MSMSY and terminal biomass as

\[
\text{RE} = \frac{\text{estimated} - \text{true}}{\text{true}} \times 100.
\]

Positive values of RE indicated overestimation, whereas negative values indicated underestimation. We used the median of the absolute values of the relative errors as a measure of accuracy.

The change in assemblage biomass relative to the change in the biomass of each species across the time series was used as an indicator of the overall direction and magnitude of biomass trends. The change in assemblage biomass (i.e., relative biomass \(\hat{RB}\)) was calculated as the proportion of biomass in the last year relative to that in the first year, namely,

\[
\hat{RB} = \frac{\hat{B}_{t=50}}{\hat{B}_{t=1}}.
\]

and single-species relative biomass was estimated as

\[
RB_s = \frac{B_{s,t=50}}{B_{s,t=1}}.
\]

The relative difference (RD) between multispecies change in biomass and single-species change in biomass was represented as

\[
\text{RD}_s = \frac{D_s - \hat{D}}{D_s} \times 100.
\]

Positive values of RD indicated overestimation, whereas negative values indicated underestimation.

RESULTS

Simulated Population Dynamics

Total biomass and species composition changed throughout the simulation (Figure 2). As the exploitation rate increased from 2.5% to 20% over the first 15 years, the biomass of each species declined steadily. With the decrease in the exploitation rate to 10% in years 16–24, the rate of decline in assemblage biomass decreased. In the last 25 years of the simulation, the assemblage biomass began to increase again at an exploitation rate of 5%. The species with the highest growth rate (species 1) gradually became the most abundant species in the assemblage. The species with the lowest growth rate (species 3) followed the same biomass trend as the other two species, but eventually comprised only 12% of the biomass. The relative biomass was 0.72, 0.51, and 0.16 for species 1, 2, and 3, respectively.
FIGURE 2. Trends in the relative biomass of three species with different intrinsic growth rates being managed as a multispecies assemblage.

Estimation Model Performance

Both the basic SSPMs and models with time-varying parameters produced positively biased estimates of MSMSY in all scenarios; however, the most accurate model in each scenario was either the time-varying $r$ or $q$ model (Figure 3). The median relative errors for MSMSY were positively biased by 7–29% across scenarios. Although the time-varying models produced more variable estimates than the basic SSPM, their estimates of MSMSY were more accurate (Table 2). The time-varying $r$ model produced the most accurate estimates of MSMSY when catchability was constant across species. The time-varying $q$ model produced the most accurate estimates of MSMSY when both $r$ and $q$ varied among species.

The median relative errors of terminal assemblage biomass were positively biased by 12–41% (Figure 4). However, some scenarios resulted in median estimates of terminal biomass that were negatively biased by 4–29%, particularly scenario C. As with MSMSY, the estimates from the basic SSPM produced the lowest variation in relative error across scenarios. The basic SSPM produced the most accurate estimates of terminal assemblage biomass for scenarios A and C (Table 2). Time-varying models exhibited more variability within a scenario, but the amount of bias depended on the scenario. The time-varying $q$ model was most accurate when the species with the lowest $q$ also had the lowest $r$.

Multispecies assemblage trends were not reflective of all individual component species such that relative biomass was overestimated for some species and underestimated for others. All of the assessment models produced biased estimates of relative biomass for individual species in almost all scenarios (Figure 5). The relative difference between multispecies and single-species change in biomass was generally overestimated for species 1 (ranging from 12% to 49%), was scenario and model dependent for species 2 (ranging from −23% to +28%), and was grossly underestimated for species 3 (ranging from −291% to

<table>
<thead>
<tr>
<th>Variable</th>
<th>Scenario</th>
<th>Base</th>
<th>TVr</th>
<th>TVq</th>
</tr>
</thead>
<tbody>
<tr>
<td>MSMSY</td>
<td>A</td>
<td>18</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>25</td>
<td>29</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>17</td>
<td>17</td>
<td>13</td>
</tr>
<tr>
<td>Terminal biomass</td>
<td>A</td>
<td>12</td>
<td>16</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>38</td>
<td>41</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>18</td>
<td>20</td>
<td>29</td>
</tr>
</tbody>
</table>
The relative biomass of species 2, the species with average values of $r$ and $q$, was most similar to that of the entire assemblage; such an averaging effect would be expected in circumstances where a single model used to represent multiple species returns estimates of the average species conditions. The relative biomass of species 2 was slightly lower than that of the assemblage when the species with the lowest $q$ also had the lowest $r$ (Figure 5B) and slightly higher than that of the assemblage when the species with the highest $q$ had the lowest $r$ (Figure 5C). In contrast, assemblage relative biomass was almost always higher than that of species 1 (highest $r$), resulting in positive RDs for most simulations. The relative biomass of species 3 (lowest $r$) was always much higher than that of the assemblage, resulting in extremely large negative RD values for all simulations. The incorporation of time-varying parameters did not substantially improve RD.

DISCUSSION

Our simulation study showed how the estimates of important management quantities such as MSMSY and terminal biomass generated by SSPMs are biased if the assemblage being assessed is heterogeneous with regard to intrinsic growth rate and catchability. Kleiber and Maunder (2008) demonstrated how multistock-aggregated CPUE is not an acceptable index of abundance unless catchability is the same among all stocks. Our study expands upon their work by fitting SSPMs with and without time-varying parameters to aggregated multispecies data and showing that, even when catchabilities are the same, model estimates will still be biased if growth rates differ among stocks. In all of our scenarios, MSMSY was overestimated, while the direction and magnitude of the bias in assemblage biomass depended on the growth rates and catchabilities of the individual species within the assemblage and the parameter chosen to vary over time. In many data-poor situations, too little information is available on individual species’ life histories and relative catchability to confidently select which parameter (if any) to vary over time. Although intrinsic growth rate can be estimated using known life history characteristics, catchability is likely to be unknown in most data-poor situations.

Our results underestimate the potential bias in SSPM estimates because model-fitting conditions were simplified...
in several ways: (1) the correct assessment model was used given the logistic growth pattern used to simulate population dynamics for each species, (2) fishery catch was provided to the model without error, (3) the parameters for each species were constant over time (i.e., there was no process error), and (4) all species were subject to the same highly informative pattern of fishing mortality. These simplifications were chosen so that the evaluation of SSPM performance in regard to multispecies assemblages could be evaluated separately from more general production model performance issues that have been thoroughly examined already (Prager 1994). The incorporation of more realistic modeling situations (e.g., errors in catch, one-way trip time series) would decrease model performance.

Several simplifying assumptions were also made when simulating multispecies dynamics: (1) fishing mortality was assumed to be the same across all species, (2) all species had the same carrying capacity, (3) species did not interact, and (4) the fishery did not switch target species, as is often observed in developing fisheries (e.g., Regier and Loftus 1972). Real-world assemblages experience some or all of these complicating factors and may have more complicated and potentially unpredictable dynamics (Pope 1976b; Ralston and Polovina 1982; Sparre and Venema 1998). However, it is unlikely that these more complicated situations would result in better model performance than that of the simplified situations presented in this study. Therefore, biased estimates of MSMSY and terminal biomass should be anticipated when SSPMs are used to assess multispecies assemblages.

We encourage stock assessment scientists to carefully consider the assumptions that will be violated and how those violations will affect the management advice provided by an SSPM (Schnute and Richards 2001). The application of single-species surplus production models to multispecies assemblages has been shown to produce more precise results than single-species assessments (Pope 1979; Ralston and Polovina 1982), but we have shown in this study that SSPMs also tend to produce biased results. Increased precision should not be achieved at the expense of decreased accuracy. Both precision and accuracy should be considered when weighing the relative benefits of adopting a single versus a multispecies approach.

We found that the incorporation of time-varying growth and catchability parameters using random walks could improve the accuracy of MSMSY and terminal biomass estimates. We caution that time-varying parameters may not be estimable in many real-world situations because times series data tend to be less informative than those we simulated. In four out of six scenarios, models with time-varying parameters produced the most accurate results (Table 2; Figures 4B, 5B); however, the basic SSPM produced more accurate estimates of terminal biomass, whereas models with time-varying parameters tended to produce the most accurate estimates of MSMSY. When faced with a data-poor situation in which an SSPM is the only viable modeling option, the incorporation of time-varying parameters may be the most reasonable approach if MSMSY is the management goal.

However, the best choice of parameters to vary over time and the direction and magnitude of the resulting bias may not be predictable unless the relative difference in r and q among species in the assemblage is known. Another advantage of incorporating time-varying parameters may be that estimates of uncertainty are more realistically represented; in our study, models with time-varying parameters produced a wider range of estimates (i.e., wider confidence intervals) than traditional SSPMs.

Bayesian estimation of SSPM parameters has been suggested as a better method for assessing multispecies assemblages (McAllister et al. 2001; Jiao et al. 2009). Bayesian estimation methods that assume constant r and q will also produce biased estimates if the composition of the multispecies complexity changes over time due to overexploitation of some species and underexploitation of others. Bayesian estimation techniques may, however, provide a workable solution in one-way trip situations if credible informative priors can be developed for some or all of the parameters. Likewise, strongly informative priors that are accurately specified may reduce the bias in estimates.

Even if less biased estimates could be generated with the use of time-varying parameters in SSPMs, severe overexploitation of species within the assemblage and the potential loss of yield may still occur. Fishing at a rate to achieve a target biomass of a multispecies assemblage may be a risky management strategy if all components of the assemblage are valued enough to be conserved (May et al. 1979; Larkin 1982). As shown in Figure 1, if MSMSY target estimates are biased, one or more component species could be functionally extirpated while total yield for the assemblage remains high (Paulik et al. 1967; Pauly 1984; Jensen 1991). We found the species with the lowest r was severely depleted by the end of the time series even though the biomass of the multispecies assemblage was increasing (Figure 2). In contrast, the species with the highest r was underexploited, resulting in lost yield and a missed opportunity for the fishery. Several authors have argued that a fishery cannot be optimized for more than one species at a time and that, ultimately, some species in a multispecies fishery will be overexploited while others are underexploited (Jensen 1991, 1999; Dichmont et al. 2006). Pope (1974) showed theoretically how a multispecies fishery MSMSY could be attained only though a set of complicated catch quotas. Jensen (1999) simulated the population and fishery dynamics of eight Great Lakes cisco species Coregonus spp. caught in the same multispecies fishery and with the same gear and assessed them using a two-species surplus production model with no interspecific interactions; extinction of up to half of the species was a common result in his simulations. Using a similar model for two species, Jensen (1991) showed that fishing at the multispecies fishing mortality rate that produces the maximum sustainable yield (Fmsy) would lead to the extirpation of lake trout Salvelinus namaycush if managed and assessed jointly with lake whitefish Coregonus clupeaformis. Dichmont et al. (2006) performed a management strategy evaluation on a two-species tiger prawn Penaeus esculentus and P. semisulcatus fishery and
detected that none of the proposed management strategies allowed the stock size of both species to remain above the spawning stock size at maximum sustainable yield. Preventing overfishing of some members of a multispecies assemblage may be impossible if life histories or catchabilities differ or the multispecies fishery uses unselactive gear (Pope 1976b, 1979; Pauly 1984).

For U.S. marine fisheries, the 2006 reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act requires the management of individual fish stocks as a unit throughout their range; if that is not practical, a group of interrelated fish stocks may be managed as a unit. Due to the lack of species-specific data collection and the logistical challenges of assessing numerous species, many regional fisheries management councils have moved toward assessing some groups of species as stock complexes (Carmichael and Fenske 2011). For this approach to be successful, the life history and fishery characteristics of the species in the complex must be homogeneous (Cope et al. 2011). Defining appropriate stock complexes that, when assessed as a group, will not result in overexploitation of component stocks will be a serious challenge in regions with limited life history research and data collection programs (Carmichael and Fenske 2011). For management of stock complexes to be effective, stocks must be grouped into assemblages based on their productivity and catchability, with the groupings being as similar as possible. In many cases, though, species have been grouped together based on the similarity of appearance or taxonomy, which may not correspond to the similarity in productivity or catchability (e.g., sharks).

When adequate data are available, species should be assessed individually, jointly (Punt et al. 2011), or as a multi-species assemblage using stock assessment models that specifically account for interspecific or fishery gear interactions among component stocks (Hollowed et al. 2000), such as multispecies configurations of the surplus production model (Pope 1976b; Arreguin-Sanchez et al. 1992; Spencer and Collie 1997; Gamble and Link 2009), yield-per-recruit model (Pikitch 1987), or multispecies age-structured stock assessment methods (Helgason and Gislason 1979; Gislason and Helgason 1985; Jurado-Molina et al. 2005). We acknowledge that data limitations prohibit the use of multispecies models in many cases. If a few years of recent species-specific catch or survey data are available, the performance of production models may be improved if they can be modified to incorporate species-specific data at the end of the time series. However, if species-specific data are not available and SSPMs are the only viable modeling option, precautionary reference points should be adopted. More precaution than is typically considered reasonable for single-species fisheries may be needed to account for the expected bias in SSPM estimates of MSMSY. A reasonable ad hoc approach may be to scale the level of precaution to the range of growth rates among species in the assemblage, such that more precautionary management is adopted as the range in $r$ increases among species in the assemblage.

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Influence of Environmental Variables and Species Interactions on Sport Fish Communities in Small Missouri Impoundments

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Influence of Environmental Variables and Species Interactions on Sport Fish Communities in Small Missouri Impoundments

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Abstract

Small impoundments (<400 ha) are numerous and provide close-to-home fishing opportunities for millions of anglers throughout the United States (Willis et al. 2010). Many agencies in the Midwestern and southern states have constructed and managed small impoundments for the primary purpose of sportfishing. Other impoundments owned by municipalities are similarly managed through cooperative agreements. Some small public impoundments are intensively managed through stocking, fertilization, supplemental feeding, selective or complete prescribed fish kills, water level regulation, and restrictive harvest regulations (Shaner et al. 1996; Olive et al. 2005), but most are managed primarily by harvest regulations and the stocking of channel catfish Ictalurus punctatus.

Although these small public impoundments are numerous, many of them do not support optimal sport fisheries, demonstrating poor growth, poor size structure, or both for one or more sport fish species. In this study, we examined the relative importance of watershed characteristics, impoundment morphology, water quality, and species interactions in explaining differences in abundance, growth, and size structure of five sport fish species (largemouth bass Micropterus salmoides, bluegill Lepomis macrochirus, redear sunfish L. microlophus, white crappie Pomoxis annularis, and black crappie P. nigromaculatus) among 89 small Missouri impoundments spanning a large fertility gradient. Using regression analysis, we found that variables associated with predation, competition, and lake fertility were most important in explaining variation in sport fish demographics, whereas watershed and impoundment morphology variables were typically less important. Lakes with dense largemouth bass populations commonly contained sunfish and crappie populations with desirable size structure and growth, implying that predation was a strong structuring force. Density-dependent growth was common among all sport fish species. White crappies and black crappies had better growth or size structure in lakes with fewer bluegills, suggesting competition among these species. Lakes containing common carp Cyprinus carpio had fewer largemouth bass and slower-growing black crappies than lakes without common carp. The presence of gizzard shad Dorosoma cepedianum benefited largemouth bass populations but negatively affected bluegill and black crappie populations. Growth and size structure of sport fishes usually improved with increasing lake fertility. Predation and competition seemed to be most important in structuring sport fish communities in these impoundments provided that lake fertility was adequate to sustain acceptable abundances and growth rates of these fishes.
more sport fish species. There are probably many causes for these less-than-ideal populations, including overharvest, poor water quality and habitat, and deleterious species interactions. Early studies of these systems documented the overharvest of largemouth bass *Micropterus salmoides*, which led to the restriction of angler harvest by imposing minimum length limits (Funk 1974) and various other length restrictions, including slot limits (Anderson 1976; Eder 1984; Novinger 1990). Currently, overharvest of largemouth bass may be relatively uncommon because of these length limits and the common practice of catch and release (Quinn 1996; Siepker et al. 2007; Myers et al. 2008).

High angler exploitation of other common species, such as the bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*, and white crappie *Pomoxis annularis* (Coble 1988; Eder 1990; Bister 2002), can result in poor fish size structure by directly removing large fish and creating shifts in life history strategies (Beard et al. 1997; Drake et al. 1997). Although length limits have been imposed for some small impoundments, these regulations frequently have not improved fish size structure and have not been well received by anglers (e.g., Bister 2002; Hurley and Jackson 2002; Ott et al. 2003). Poor growth or high natural mortality probably limits the effectiveness of length limits for panfish in many small impoundments (Allen and Miranda 1995; Beard et al. 1997; Crawford and Allen 2006).

Within small impoundments, water quality and habitat as determined by watershed characteristics (e.g., land use, geology, and basin morphometry; Knoll et al. 2003; Jones et al. 2004, 2008a; Breminagan et al. 2008) may also influence fish population dynamics. For example, impoundments in agricultural landscapes typically contain higher nutrient levels than impoundments in forests (Jones et al. 2004). Within either landscape type, impoundments with high flushing rates, which are a function of watershed and impoundment morphometry, tend to have higher nutrient concentrations than those with long water retention (Breminagan et al. 2008; Jones et al. 2008a). Sport fish biomass and harvest tend to increase with lake fertility (Hanson and Leggett 1982; Jones and Hoyer 1982). Growth and size structure of sport fishes are often positively correlated with water fertility (e.g., Tomcko and Pierce 2005; Wagner et al. 2007; Schultz et al. 2008; Hoxmeier et al. 2009), probably because of the greater prey abundance in more fertile waters. However, undesirable fish species are common in highly fertile systems (Bachmann et al. 1996; Egertson and Downing 2004). McInerny and Cross (1999) found that the first-year growth of black crappies increased with chlorophyll concentrations up to a threshold of approximately 100 µg/L, after which growth was reduced. This finding suggests that excessive nutrient concentrations can lead to undesirable growth and size structure of sport fishes, similar to the relationship observed for biomass. Many of these highly fertile systems also suffer from low dissolved oxygen levels and periodic fish kills (Moyle 1949; Mericas and Malone 1984).

Abundance, growth, and size structure of sport fishes have been also linked to lake morphometry and aquatic vegetation. Lake morphometric variables, such as water depth (Tomcko and Pierce 2001; Paukert and Willis 2004; Schultz et al. 2008), surface area (Cross and McInerny 2005; Tomcko and Pierce 2005), volume (Shoup et al. 2007), basin slope (Hill 1984), shoreline complexity (Guy and Willis 1995; Schultz et al. 2008), and percent littoral area (Tomcko and Pierce 2001; Shoup et al. 2007), are often correlated with various sport fish demographic variables, sometimes with conflicting results. For example, desirable growth or size structure of bluegills was positively related to water depth in Iowa lakes (Schultz et al. 2008) but negatively related to water depth in Minnesota lakes (Tomcko and Pierce 2001). Similarly, the reported relationships between aquatic macrophyte coverage and sport fish demographics have been inconsistent (Savino et al. 1992; Hoyer and Canfield 1996; Pothonen et al. 1999; Paukert and Willis 2004; Cheruvil et al. 2005). Dibble et al. (1996) suggested that the growth of sport fishes should be optimized at some intermediate plant density because excessive macrophyte coverage could lead to excessive fish densities and corresponding slow growth, whereas sparse vegetation could result in slow growth because of the depletion of food resources. Others have not detected this unimodal relationship between sport fish growth and plant density (Savino et al. 1992; Cheruvil et al. 2005).

Fish population dynamics are commonly structured by competitive and predator–prey interactions both among and within species. Intraspecific competition is common in small lakes and impoundments because of density-dependent growth within sport fish species (Guy and Willis 1995; Paukert and Willis 2004; Tomcko and Pierce 2005). Interspecific competition among sport fish species is also common in small impoundments. For example, bluegills may compete with juvenile largemouth bass for food resources (Brenden and Murphy 2004; Aday et al. 2005). Competition from and habitat alterations caused by invasive or introduced species, such as the common carp *Cyprinus carpio* and gizzard shad *Dorosoma cepedianum*, can result in suboptimal sport fish populations (Aday et al. 2003; Michaletz and Bonneau 2005; Weber and Brown 2009; Jackson et al. 2010). Lastly, predation by apex predators, such as largemouth bass, can strongly influence growth and size structure of bluegill and crappie populations (Gabelhouse 1984; Guy and Willis 1990; Olive et al. 2005; Schultz et al. 2008).

Clearly, numerous factors influence sport fish populations in small impoundments, and there is uncertainty about which variables are most important. However, few studies of small Midwestern impoundments have simultaneously examined the relative influences of watershed, lake morphology, water quality, and species interactions on several sport fish species across a relatively large spatial scale and a large range of impoundment fertility levels. Most sport fish populations are managed by harvest restrictions, but these restrictions may be ineffective if watershed or impoundment characteristics are directly shaping population dynamics. Thus, to effectively manage these small impoundments, a better understanding of the relative importance of watershed, impoundment, water quality, and species interaction variables is necessary. Using regression analysis,
we examined the relative importance of these variables for 89 small Missouri impoundments. Specifically, our objective was to determine the relative importance of watershed, impoundment, water quality, and species interactions for explaining differences in relative abundance, growth, and size structure of largemouth bass, bluegills, redear sunfish L. microlophus, white crappies, and black crappies among small impoundments at a statewide scale.

**METHODS**

*Study sites.*—Variables influencing sport fish demographics were examined in 89 small impoundments (hereafter, “lakes”) scattered across the state of Missouri. Most of the lakes were located in the Glacial Plains physiographic section of the state ($N = 48$), whereas fewer lakes were situated in the Ozark Border ($N = 6$), Osage Plains ($N = 16$), Ozark Highlands ($N = 18$), and Mississippi Lowlands ($N = 1$) physiographic sections (see locations of physiographic sections in Figure 1 of Jones et al. 2008b). Small lakes were included in our study if (1) at least 3 years of sport fish and water quality data were available, (2) the presence or absence of gizzard shad and common carp was known, and (3) macrophyte coverage was indexed (see below). The study lakes spanned a broad range of conditions that were representative of Missouri’s small lakes; lake size ranged from 2 to 408 ha, and trophic state ranged from oligotrophic to hypereutrophic (Table 1). Fish communities consisted primarily of largemouth bass, bluegills, channel catfish, crappies, and other sunfishes Lepomis spp., sometimes including redear sunfish. Harvest restrictions varied among lakes, but most included either a 384-mm minimum total length (TL) limit or a 305–384-mm TL slot limit and a daily creel limit of six fish for largemouth bass. Length limits were rare for other species, and harvest of these species was mostly regulated by daily creel limits of 20–30 fish for sunfishes and crappies and 4 fish for catfishes Ictalurus spp. and flathead catfish Pylodictis olivaris combined.

**Fish demographic data.**—Sport fish demographic data were obtained from standardized spring electrofishing surveys that were conducted from 1969 to 2009 by Missouri Department of Conservation (MDC) fisheries management biologists. However, over 98% of the data were collected in 1978 and later years. Surveys were conducted nearly annually in some lakes but only occasionally in others (mean $= 13.5$ sample years; range $= 3–34$ sample years). For a sample year, one or more electrofishing surveys were conducted during late April to early June. Electrofishing effort averaged 1.9 h (range $= 0.6–11.3$ h) per sample year in each lake. Fish that were collected during these surveys were measured for TL (nearst 2.5 mm). Fish ages were estimated from scales collected during some surveys from a subsample of fish (usually 5 fish per 12.7-mm TL group). Although otoliths are preferred structures for determining fish age, scales are likely to be reasonably accurate for fish younger than 5–6 years of age (Maceina et al. 2007). Fish with assigned ages were used to construct an age–length key that was then applied to the entire sample to estimate mean length at age. Sampling was conducted mostly during the daytime in turbid lakes and at night in clear lakes; however, some lakes were sampled during the day in some years and at night in other years.

**TABLE 1.** Summary statistics describing the environmental variables measured from 89 small Missouri impoundments. For water quality data, four lakes were represented two times each due to changes in the presence or absence of common carp or gizzard shad (see text for details).

<table>
<thead>
<tr>
<th>Variable</th>
<th>$N$</th>
<th>Mean</th>
<th>SE</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
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<tr>
<td><strong>Watershed</strong></td>
<td></td>
<td></td>
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<tr>
<td>Watershed area (ha)</td>
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<td>2,194</td>
<td>767</td>
<td>689</td>
<td>20</td>
<td>66,622</td>
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<td><strong>Lake morphometry</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake surface area (ha)</td>
<td>89</td>
<td>61</td>
<td>8</td>
<td>31</td>
<td>2</td>
<td>408</td>
</tr>
<tr>
<td>Dam height (m)</td>
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<td>13.0</td>
<td>0.6</td>
<td>12.5</td>
<td>4.6</td>
<td>33.6</td>
</tr>
<tr>
<td>Volume ($m^3 \times 1,000$)</td>
<td>89</td>
<td>3,307</td>
<td>666</td>
<td>1,271</td>
<td>59</td>
<td>34,146</td>
</tr>
<tr>
<td>Watershed area : lake surface area ratio</td>
<td>89</td>
<td>36</td>
<td>8</td>
<td>18</td>
<td>4</td>
<td>592</td>
</tr>
<tr>
<td>Flushing index (times/year)</td>
<td>87</td>
<td>3.4</td>
<td>1.2</td>
<td>1.0</td>
<td>0.1</td>
<td>87.0</td>
</tr>
<tr>
<td>Shoreline development index$^a$</td>
<td>89</td>
<td>2.6</td>
<td>0.1</td>
<td>2.4</td>
<td>1.1</td>
<td>6.3</td>
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<tr>
<td>Chlorophyll ($\mu g/L$)</td>
<td>93</td>
<td>21</td>
<td>2</td>
<td>17</td>
<td>2</td>
<td>114</td>
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<tr>
<td>Total phosphorus ($\mu g/L$)</td>
<td>93</td>
<td>51</td>
<td>4</td>
<td>45</td>
<td>8</td>
<td>188</td>
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<tr>
<td>Total nitrogen ($\mu g/L$)</td>
<td>92</td>
<td>783</td>
<td>34</td>
<td>775</td>
<td>185</td>
<td>1,920</td>
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<tr>
<td>Volatile suspended solids (mg/L)</td>
<td>92</td>
<td>3.8</td>
<td>0.2</td>
<td>3.2</td>
<td>0.8</td>
<td>13.8</td>
</tr>
<tr>
<td>Nonvolatile suspended solids (mg/L)</td>
<td>93</td>
<td>4.5</td>
<td>0.5</td>
<td>3.1</td>
<td>0.5</td>
<td>35.9</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>93</td>
<td>1.1</td>
<td>0.1</td>
<td>0.9</td>
<td>0.2</td>
<td>3.2</td>
</tr>
<tr>
<td>Conductivity ($\mu S$)</td>
<td>93</td>
<td>197</td>
<td>8</td>
<td>197</td>
<td>40</td>
<td>417</td>
</tr>
</tbody>
</table>

$^a$ Ratio of shoreline length to the circumference of a circle having the same area as the lake.
The electrofishing data were obtained from management biologists in various forms, including raw field data sheets, output from various software programs, and lake management reports. From these sources, catch per effort (CPE) for stock-size and larger fish (number of fish/h of electrofishing), proportional size distribution (Guy et al. 2007) for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) were determined for largemouth bass, bluegills, redear sunfish, white crappies, and black crappies. The stock, quality, and preferred sizes (TL) for these species are from Anderson and Gutreuter (1983). Mean TL at age 3 was chosen for our growth variable because it was the standard parameter presented in lake management reports. Not all of the fish variables were available for every lake; data sets for largemouth bass and bluegills were the most complete because these fishes were the primary targets of standardized sampling. Because the number of annual surveys varied greatly among lakes, we averaged sport fish demographic estimates across all years for each lake (see below for some exceptions). For lakes with multiple surveys within a year, we first averaged estimates from these surveys before averaging across all years. Although fish populations can change over time, we consider these averages to be the best representation of sport fish demographics for these lakes.

From MDC management biologists, we also obtained data on the presence (index = 1) or absence (index = 0) of common carp and gizzard shad in the study lakes. We were unable to acquire relative abundance, size structure, or growth information for these species because this information is not routinely collected. For four of the lakes, the presence–absence of common carp or gizzard shad varied over time due to fish invasions or removals. For these lakes, we considered such periods separately in our analysis (see below). Thus, the four lakes were represented twice in the analysis.

Environmental data.—Watershed, lake morphometry, and water quality data (Table 1) were largely from Jones et al. (2004, 2008a, 2008b). Dam height was used as a surrogate for water depth because it was strongly and positively correlated with mean depth (Jones et al. 2004), which was unmeasured for some lakes. Limnological data were sampled seasonally on three or four occasions during May–August from surface waters near the dam of each lake. Data from these collections were averaged to obtain annual means for each variable. Detailed sampling and analytical procedures are described by Jones et al. (2008a, 2008b). Some additional unpublished water quality data were obtained by using these same methods. Limnological data were collected between 1978 and 2009. Shoreline development index was calculated as the ratio of the lake perimeter (determined with GIS software) to the circumference of a circle having the same area as the lake. Aquatic macrophyte coverage (VEG) was indexed as absent, moderate (<50% of the littoral zone), or abundant (≥50% of the littoral zone) by MDC fisheries management biologists. However, for analysis (see below), we combined the absent and moderate categories of VEG into a single category. Therefore, VEG was indexed as either sparse (index = 0) or abundant (index = 1).

As with fish data, the frequency of annual collections of limnological data varied among lakes, with some lakes being sampled nearly every year and others being sampled less frequently (mean = 7.5 sample years; range = 3–21 sample years). We attempted to match limnological data with fish data that were collected during the same time period. However, when that was not possible (<20% of cases), we used the long-term average limnological data presented by Jones et al. (2008b). Similar to how we handled the fish data, we averaged the limnological data over all sample years for each lake. For the four lakes where the presence–absence of common carp or gizzard shad varied among years, limnological data were averaged for separate time periods.

Analysis.—Prior to conducting regression analysis, we reduced the number of environmental variables using principal components analysis (PCA; PRINCOMP procedure in the Statistical Analysis System [SAS] version 9.2). All of the variables (Table 1) were log10(X) transformed to normalize the data prior to analysis. The correlation matrix was used as input for the analysis. Following the procedures of Cross and McInerny (2005), environmental variables that were highly correlated to individual principal components (PCs) were used as proxy variables in the regression analysis instead of the PC scores. The use of actual environmental variables allowed for easier interpretation of relationships between environmental and fish variables.

Regression analysis (REG procedure in SAS version 9.2) was used to assess relationships between environmental variables and fish variables. Preliminary analysis indicated that linear regression provided better model fits than regression tree analysis (De’ath and Fabricus 2000; De’ath 2002). Exploratory variables chosen for inclusion in the regression models were (1) the environmental variables identified with the PCA, (2) various sport fish demographic variables (Tables 2, 3), and (3) dummy variables for VEG, common carp, and gizzard shad. We used the log10(X)-transformed environmental variables as in the PCA.

To normalize the fish data, we transformed most of the fish variables by using either log10(X) or arcsine (X0.5) for proportional data. The ML3 data were normally distributed and were not transformed, and the three dummy variables were also not transformed. Sport fish demographics that could be associated with competition or predation were included as potential explanatory variables. For example, largemouth bass metrics (relative abundance and size structure) were included as explanatory variables for bluegill demographics because largemouth bass predation can structure bluegill populations (Guy and Willis 1990; Olive et al. 2005; Schultz et al. 2008). The intensity of largemouth bass predation is partially determined by their abundance and size. Bluegill CPE was likewise included in largemouth bass demographic models because bluegills can be prey and competitors for largemouth bass (Guy and Willis 1990; Brenden and Murphy 2004; Aday et al. 2005; Olive et al. 2005).

We compared the fit of various combinations of explanatory variables by using the information-theoretic approach (Burnham and Anderson 2002) and Akaike’s information criterion corrected for small sample size (AICc). All models with an AICc
TABLE 2. Summary statistics describing catch per effort (CPE; fish/h of electrofishing) of stock-size and larger fish, proportional size distributions for quality-size (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for largemouth bass, bluegills, redear sunfish, white crappies, and black crappies in 89 small Missouri impoundments. Four lakes are represented two times due to changes in the presence or absence of common carp or gizzard shad (see text for details).

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>SE</th>
<th>Median</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Largemouth bass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CPE</td>
<td>93</td>
<td>85</td>
<td>3</td>
<td>85</td>
<td>3</td>
<td>159</td>
</tr>
<tr>
<td>PSD</td>
<td>93</td>
<td>45</td>
<td>2</td>
<td>44</td>
<td>8</td>
<td>84</td>
</tr>
<tr>
<td>PSD-P</td>
<td>93</td>
<td>17</td>
<td>1</td>
<td>15</td>
<td>0</td>
<td>51</td>
</tr>
<tr>
<td>ML3</td>
<td>52</td>
<td>278</td>
<td>4</td>
<td>274</td>
<td>210</td>
<td>364</td>
</tr>
<tr>
<td>Bluegill</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>CPE</td>
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<td>135</td>
<td>7</td>
<td>123</td>
<td>41</td>
<td>369</td>
</tr>
<tr>
<td>PSD</td>
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<td>33</td>
<td>1</td>
<td>32</td>
<td>5</td>
<td>70</td>
</tr>
<tr>
<td>PSD-P</td>
<td>93</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>ML3</td>
<td>56</td>
<td>136</td>
<td>2</td>
<td>134</td>
<td>101</td>
<td>183</td>
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<tr>
<td>Redear sunfish</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CPE</td>
<td>49</td>
<td>35</td>
<td>4</td>
<td>24</td>
<td>1</td>
<td>143</td>
</tr>
<tr>
<td>PSD</td>
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<td>3</td>
<td>70</td>
<td>16</td>
<td>100</td>
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<td>PSD-P</td>
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<tr>
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<td>168</td>
<td>5</td>
<td>173</td>
<td>121</td>
<td>198</td>
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<tr>
<td>White crappie</td>
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<td></td>
</tr>
<tr>
<td>CPE</td>
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<td>37</td>
<td>5</td>
<td>24</td>
<td>1</td>
<td>143</td>
</tr>
<tr>
<td>PSD</td>
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<td>49</td>
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<td>48</td>
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<tr>
<td>PSD-P</td>
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<td>17</td>
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<tr>
<td>Black crappie</td>
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<tr>
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<tr>
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<td>228</td>
<td>14</td>
<td>239</td>
<td>145</td>
<td>280</td>
</tr>
</tbody>
</table>

difference (ΔAICc) of 2 or less in comparison with the most parsimonious model (i.e., the model with the lowest AICc value) were considered statistically similar. Preliminary analyses indicated that models with more than four explanatory variables did not significantly improve model fit relative to models with four or fewer variables. Thus, to avoid overfitting the models, we restricted the maximum number of explanatory variables to four for all dependent variables except ML3 for redbear sunfish (maximum of three explanatory variables), white crappies (maximum of three explanatory variables), and black crappies (maximum of two explanatory variables) due to small sample sizes. Models were only included for consideration if they did not exhibit multicollinearity among the regressors. Models were checked for multicollinearity by using diagnostic tools (options VIF, TOL, and COLLINOINT) within the REG procedure in SAS. For each dependent variable, we sought the simplest models with an ΔAICc of 2 or less. Models that included the same explanatory variables as a simpler model (i.e., one having fewer variables) with a smaller AIC value are not presented.

RESULTS

The study lakes exhibited a diverse array of environmental and sport fish characteristics. Lakes varied from shallow to deep, from oligotrophic to hypereutrophic, from having simple shorelines to having complex shorelines, and from being void of aquatic macrophytes to being extensively vegetated (Table 1). Likewise, sport fish demographics varied from low to high relative abundance, from small to large fish sizes, and from slow to fast growth (Table 2). Common carp were present in 45 lakes and absent from 42 lakes; in two other lakes, their presence varied over time. Gizzard shad were present in 54 lakes and absent from 31 lakes; in four other lakes, the presence of gizzard shad varied over time.

The number of potential explanatory environmental variables was reduced to six: five proxy variables identified by using PCA and one dummy variable (VEG). The first five PCs (PC1–PC5) explained 94% of the variance in the data set. The sixth PC and subsequent PCs each explained less than 3% of additional variance and were excluded from further consideration. Total phosphorus (TP), total nitrogen, Secchi depth, and
TABLE 3. Sport fish variables that were used as potential explanatory variables in regression models of largemouth bass (LMB), bluegill (BLG), redear sunfish (RED), white crappie (WHC), and black crappie (BLC) demographic response variables for 89 small impoundments. Variables are defined in Table 2.

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>LMB_CPE</th>
<th>LMB_PSD</th>
<th>LMB_PSD-P</th>
<th>BLG_CPE</th>
<th>BLG_PSD</th>
<th>BLG_PSD-P</th>
<th>RED_CPE</th>
<th>RED_PSD</th>
<th>RED_PSD-P</th>
<th>RED_ML3</th>
<th>WHC_CPE</th>
<th>WHC_PSD</th>
<th>WHC_PSD-P</th>
<th>BLC_CPE</th>
<th>BLC_PSD</th>
<th>BLC_PSD-P</th>
<th>BLC_ML3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
| chlorophyll were most strongly correlated with PC1 (Table 4). We chose TP as the proxy variable for PC1 because TP is strongly correlated with all trophic state metrics in Missouri reservoirs (Jones et al. 2008b). Lake surface area (SA), lake volume, and shoreline development index were most strongly correlated with PC2, and SA was chosen as the proxy variable. Lake volume had a slightly stronger correlation with PC2, but SA was selected because it is more commonly used as a lake size variable. The watershed area : lake surface area ratio (WSA) and the flushing index were most strongly correlated with PC3; the WSA was used as the proxy variable. Conductivity (COND) and nonvolatile suspended solids concentration (NVSS) were used as proxy variables for PC4 and PC5, respectively. Thus, TP, SA, WSA, COND, and NVSS were included as potential environmental variables (along with VEG) in the regression models.

Largemouth Bass Demographics

Variations in largemouth bass demographics were primarily explained by lake fertility (i.e., TP) and fish variables (Table 5). Relative abundance of largemouth bass was greatest in lakes with large numbers of bluegills, low TP, low WSA, low NVSS, and an absence of common carp. Bluegill CPE accounted for about one-half of the variance explained by the models. The negative relationship between largemouth bass CPE and TP was apparently driven by data from one hypereutrophic lake in which TP exceeded 150 µg/L, as there was little relationship between TP and largemouth bass CPE for the other lakes (Figure 1). Largemouth bass populations typically exhibited faster growth and contained a higher proportion of large individuals...
TABLE 4. Principal component (PC) loadings (correlation coefficients) and the percentage of variation explained by the first five PCs (PC1–PC5) on environmental variables for 89 small impoundments. Loadings in bold italics indicate the variables that were selected for inclusion in regression analyses. Units for the variables are provided in Table 1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Watershed area</td>
<td>0.055</td>
<td>0.392</td>
<td>0.352</td>
<td>−0.207</td>
<td>0.064</td>
</tr>
<tr>
<td>Lake surface area</td>
<td>0.081</td>
<td></td>
<td></td>
<td>−0.253</td>
<td>−0.053</td>
</tr>
<tr>
<td>Dam height</td>
<td>−0.064</td>
<td>0.401</td>
<td>−0.139</td>
<td>0.126</td>
<td>0.203</td>
</tr>
<tr>
<td>Volume</td>
<td>0.027</td>
<td>0.465</td>
<td>−0.095</td>
<td>−0.178</td>
<td>0.011</td>
</tr>
<tr>
<td>Watershed area : lake surface area ratio</td>
<td>−0.016</td>
<td>0.041</td>
<td></td>
<td>0.014</td>
<td>0.177</td>
</tr>
<tr>
<td>Flushing index</td>
<td>−0.051</td>
<td>−0.129</td>
<td>0.602</td>
<td>−0.220</td>
<td>0.054</td>
</tr>
<tr>
<td>Shoreline development index</td>
<td>0.047</td>
<td>0.425</td>
<td>−0.059</td>
<td>−0.021</td>
<td>−0.062</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>0.390</td>
<td>−0.064</td>
<td>−0.084</td>
<td>−0.124</td>
<td>0.474</td>
</tr>
<tr>
<td>Total phosphorus</td>
<td></td>
<td>0.429</td>
<td>−0.047</td>
<td>0.056</td>
<td>−0.043</td>
</tr>
<tr>
<td>Total nitrogen</td>
<td>0.412</td>
<td>−0.051</td>
<td>−0.103</td>
<td>−0.029</td>
<td>0.145</td>
</tr>
<tr>
<td>Volatile suspended solids</td>
<td>0.408</td>
<td>−0.086</td>
<td>−0.057</td>
<td>−0.033</td>
<td>0.325</td>
</tr>
<tr>
<td>Nonvolatile suspended solids</td>
<td>0.354</td>
<td>0.066</td>
<td>0.103</td>
<td>0.140</td>
<td>0.641</td>
</tr>
<tr>
<td>Secchi depth</td>
<td>−0.408</td>
<td>0.047</td>
<td>−0.086</td>
<td>0.077</td>
<td>0.363</td>
</tr>
<tr>
<td>Conductivity</td>
<td>0.125</td>
<td>0.208</td>
<td>0.191</td>
<td>0.139</td>
<td></td>
</tr>
<tr>
<td>Explained variation (%)</td>
<td>36.7</td>
<td>30.2</td>
<td>16.5</td>
<td>5.8</td>
<td>4.7</td>
</tr>
</tbody>
</table>

in larger, fertile lakes with a high abundance of small bluegills, the presence of gizzard shad, and a low abundance of largemouth bass. Largemouth bass populations in turbid lakes (high NVSS) usually had slower growth but higher PSD-P values than populations in clearer lakes.

Bluegill Demographics

The demographics of bluegill populations were most strongly associated with largemouth bass variables and the presence–absence of gizzard shad (Table 6). Bluegills were most abundant in lakes with an abundance of large-size largemouth bass, high

TABLE 5. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for largemouth bass (LMB) in small Missouri impoundments (N = number of lakes). Explanatory variables are macrophyte coverage (VEG), gizzard shad presence or absence (GIZ), common carp presence or absence (CARP), total phosphorus (TP), lake surface area (SA), watershed area : lake surface area ratio (WSA), conductivity (COND), nonvolatile suspended solids concentration (NVSS), and various fish variables (LMB; BLG = bluegill; RED = redear sunfish; WHC = white crappie; BLC = black crappie). Explanatory variables are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses. Models were compared by use of Akaike’s information criterion corrected for small sample size (AICc); ΔAICc is the difference in AICc values between the candidate model and the model with the lowest AICc value.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>R²</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>LMB_CPE (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BLG_CPE (+), TP (−), WSA (−)</td>
<td>0.285</td>
<td>0</td>
</tr>
<tr>
<td>BLG_CPE (+), NVSS (−), WSA (−)</td>
<td>0.272</td>
<td>1.63</td>
</tr>
<tr>
<td>BLG_CPE (+), TP (−), CARP (−)</td>
<td>0.270</td>
<td>1.88</td>
</tr>
<tr>
<td><strong>LMB_PSD (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TP (+), SA (+), COND (+), BLG_PSD (−)</td>
<td>0.498</td>
<td>0</td>
</tr>
<tr>
<td>TP (+), GIZ (+), COND (+), BLG_PSD (−)</td>
<td>0.497</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>LMB_PSD-P (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BLG_CPE (+), GIZ (+), LMB_CPE (−), NVSS (+)</td>
<td>0.519</td>
<td>0</td>
</tr>
<tr>
<td>TP (+), SA (+), BLG_PSD (−), COND (+)</td>
<td>0.512</td>
<td>1.33</td>
</tr>
<tr>
<td>BLG_CPE (+), GIZ (+), LMB_CPE (−), COND (+)</td>
<td>0.510</td>
<td>1.57</td>
</tr>
<tr>
<td>BLG_CPE (+), NVSS (+), SA (+), LMB_CPE (−)</td>
<td>0.510</td>
<td>1.57</td>
</tr>
<tr>
<td><strong>LMB_ML3 (N = 52)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA (+), NVSS (−), TP (+)</td>
<td>0.290</td>
<td>0</td>
</tr>
</tbody>
</table>
TABLE 6. Regression models explaining variation in catch per effort (CPE; fish/h of electrofishing), proportional size distribution for quality-size fish (PSD) and preferred-size fish (PSD-P), and mean TL (mm) at age 3 (ML3) for bluegills (BLG) in small Missouri impoundments (N = number of lakes; ΔAICc is defined in Table 5). Explanatory variables are defined in Table 5 and are listed in order of importance based on partial correlation coefficients. The signs of the regression coefficients for the explanatory variables are shown in parentheses.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>R²</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>BLG_CPE (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LMB_PSD-P (+), LMB_CPE (+), NVSS (−), TP (+)</td>
<td>0.433</td>
<td>0</td>
</tr>
<tr>
<td>LMB_PSD-P (+), LMB_CPE (+), TP (+), GIZ (−)</td>
<td>0.430</td>
<td>0.64</td>
</tr>
<tr>
<td><strong>BLG_PSD (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LMB_CPE (+), COND (+), LMB_PSD-P (−), TP (+)</td>
<td>0.345</td>
<td>0</td>
</tr>
<tr>
<td>LMB_CPE (+), COND (+), LMB_PSD-P (−)</td>
<td>0.318</td>
<td>1.55</td>
</tr>
<tr>
<td><strong>BLG_PSD-P (N = 93)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LMB_CPE (+), GIZ (−), BLG_CPE (−)</td>
<td>0.204</td>
<td>0</td>
</tr>
<tr>
<td>LMB_CPE (+), GIZ (−), NVSS (−)</td>
<td>0.203</td>
<td>0.10</td>
</tr>
<tr>
<td>LMB_CPE (+), NVSS (−), COND (+)</td>
<td>0.203</td>
<td>0.13</td>
</tr>
<tr>
<td>LMB_CPE (+), NVSS (−)</td>
<td>0.177</td>
<td>0.90</td>
</tr>
<tr>
<td><strong>BLG ML3 (N = 56)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LMB_PSD-P (−), NVSS (−), COND (+), TP (+)</td>
<td>0.321</td>
<td>0</td>
</tr>
<tr>
<td>LMB_PSD-P (−), GIZ (−), NVSS (−), TP (+)</td>
<td>0.315</td>
<td>0.52</td>
</tr>
<tr>
<td>LMB_PSD-P (−), GIZ (−), CARP (+)</td>
<td>0.270</td>
<td>1.61</td>
</tr>
<tr>
<td>LMB_PSD-P (−), GIZ (−)</td>
<td>0.238</td>
<td>1.69</td>
</tr>
<tr>
<td>GIZ (−), NVSS (−), TP (+)</td>
<td>0.266</td>
<td>1.97</td>
</tr>
</tbody>
</table>

TP, and low NVSS. Bluegill populations exhibited the fastest growth and contained the highest proportion of large individuals in lakes with a high abundance of small largemouth bass, an absence of gizzard shad, high fertility, low NVSS, and a low abundance of bluegills.

Redear Sunfish Demographics

Redear sunfish demographics were mostly associated with fish, lake fertility, and lake size variables (Table 7). Smaller lakes containing small largemouth bass and large numbers of bluegills exhibited the highest abundances of redear sunfish.

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>R²</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RED_CPE (N = 49)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LMB_PSD (−), SA (−), BLG_CPE (+)</td>
<td>0.328</td>
<td>0</td>
</tr>
<tr>
<td>LMB_PSD-P (−), BLG_CPE (+), SA (−), LMB_CPE (−)</td>
<td>0.347</td>
<td>1.08</td>
</tr>
<tr>
<td>LMB_PSD-P (−), BLG_CPE (+), SA (−)</td>
<td>0.302</td>
<td>1.84</td>
</tr>
<tr>
<td><strong>RED_PSD (N = 49)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RED_CPE (−), TP (+), LMB_PSD-P (−)</td>
<td>0.381</td>
<td>0</td>
</tr>
<tr>
<td>RED_CPE (−), TP (+), LMB_PSD (−)</td>
<td>0.380</td>
<td>0.13</td>
</tr>
<tr>
<td>RED_CPE (−), LMB_PSD (−)</td>
<td>0.344</td>
<td>0.52</td>
</tr>
<tr>
<td>RED_CPE (−), LMB_PSD-P (−)</td>
<td>0.343</td>
<td>0.55</td>
</tr>
<tr>
<td>RED_CPE (−), WSA (−)</td>
<td>0.336</td>
<td>1.13</td>
</tr>
<tr>
<td><strong>RED_PSD-P (N = 49)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RED_CPE (−), LMB_PSD-P (−)</td>
<td>0.286</td>
<td>0</td>
</tr>
<tr>
<td><strong>RED ML3 (N = 21)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TP (+), SA (+), LMB_PSD-P (−)</td>
<td>0.507</td>
<td>0</td>
</tr>
<tr>
<td>TP (+), SA (+), LMB_PSD (−)</td>
<td>0.502</td>
<td>0.22</td>
</tr>
</tbody>
</table>
Populations of redear sunfish with the fastest growth and the highest proportion of large individuals were found in larger, fertile lakes characterized by (1) low abundances of redear sunfish and (2) largemouth bass populations consisting of small individuals.

White Crappie Demographics

White crappie demographics were primarily associated with fish variables, NVSS, and SA (Table 8). White crappies were typically most abundant in turbid lakes containing largemouth bass populations with high PSD-P and the presence of gizzard shad. Larger lakes with greater abundances of largemouth bass and lesser abundances of white crappies and bluegills usually contained white crappie populations with the fastest growth and highest proportions of large individuals. The presence of common carp and gizzard shad also seemed to have a negative influence on the growth and size structure of white crappies.

Black Crappie Demographics

The demographics of black crappies were mostly associated with fish variables (Table 9). Models explaining black crappie CPE were weak but suggested that black crappies were most abundant in lakes with low COND and with largemouth bass populations composed of a high proportion of large individuals. A variety of variables was included in models explaining variation in growth and size structure of black crappies. However, the most important variables for promoting black crappie populations with fast growth and a high proportion of large individuals were low abundances of black crappies and bluegills, a high abundance of largemouth bass, abundant vegetation (i.e., high VEG), low NVSS, and an absence of common carp and gizzard shad.

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DISCUSSION

Our broad-scale analysis of factors affecting sport fish communities in small Missouri lakes revealed that variables associated with predation, competition, and lake fertility were the most important in explaining variation in sport fish demographics. Our results are congruent with those of previous studies that have recognized the importance of predation and competition in structuring fish communities. There was evidence for competition both within and among species, and density-dependent growth was observed for each of the sport fish species we examined. As was previously observed (Novinger and Dillard 1978; Gabelhouse 1984; Guy and Willis 1990; Olive et al. 2005), largemouth bass predation was a strong force in structuring sunfish and crappie populations. Lakes with dense largemouth bass populations typically contained sunfish and crappie populations with desirable size structure and growth, but the largemouth bass were mostly small individuals owing to density-dependent growth (Reynolds and Babb 1978; Paukert and Willis 2004).

As has been reported by others (Guy and Willis 1995; Pope et al. 2004; Tomcko and Pierce 2005), size structure and growth within a given species were poorer as density increased. Interspecific competition may also structure sport fish populations in these small lakes. The size structure of white crappies and the growth of black crappies declined with increasing bluegill abundance, suggesting competition for prey resources. Similar to our findings, Cicha et al. (1983) found that lakes dominated by intermediate-size bluegills (100–159 mm TL) contained stunted white crappie populations. Gabelhouse (1984) found a positive relationship between crappie PSD and bluegill PSD, possibly because bluegill abundance was lower in lakes with a higher bluegill PSD. Interestingly, bluegill CPE was positively correlated with largemouth bass CPE and redear sunfish CPE. Although juvenile largemouth bass and bluegills may compete for food resources (Brenden and Murphy 2004; Aday et al. 2005), the correlated abundances of stock-size and larger fish may simply indicate that the conditions suitable for recruitment are similar between these species.

Common carp and gizzard shad exhibited variable effects on sport fish populations. Lakes containing common carp had lower abundances of largemouth bass, poorer size structure of white crappies, and slower growth of black crappies; however, few other negative effects on sport fish species were found. Negative effects on sport fish seem to occur when common carp reach an abundance threshold, beyond which the abundances of sport fishes are reduced (Jackson et al. 2010; Weber and Brown 2011). Unfortunately, we lacked the necessary data for examining these relationships in our study lakes. Common carp are known to destroy aquatic macrophytes (Parkos et al. 2003; Weber and Brown 2009); such destruction would reduce nursery areas for juvenile fishes, thereby potentially reducing sport fish recruitment. Furthermore, aquatic macrophyte elimination and benthic foraging by common carp may also reduce macroinvertebrate densities, which in turn could reduce the growth of fishes that feed on macroinvertebrate prey (Parkos et al. 2003; Wahl et al. 2011). The growth of black crappies, which are known to feed on macroinvertebrates (Ball and Kilambi 1973; Ellison 1984; Tuten et al. 2008), may have suffered in lakes containing common carp because of lower prey resources. Lakes that contained gizzard shad usually had poorer growth and size structure of bluegills and black crappies but a better size structure of largemouth bass than lakes that lacked gizzard shad. Although the actual mechanisms are unknown, negative effects of gizzard shad on bluegills have been commonly reported (Aday et al. 2003; Michaletz and Bonneau 2005; Porath and Hurley 2005).

Conversely, gizzard shad constitute an important prey resource for largemouth bass and may improve growth of this predator species (Storck 1986; Michaletz 1997). Increases in lake fertility (as measured by TP) generally enhanced the growth and size structure of sport fishes in the study lakes. The TP variable was positively associated with growth and size structure of largemouth bass, bluegills, and redear sunfish. The slight negative relationship between TP and largemouth bass CPE appeared to be driven by data from one lake, and TP did not explain more than 10% of the variation in largemouth bass CPE. Relationships between sport fish demographics and lake fertility variables are probably nonlinear (Kautz 1982; McInerney and Cross 1999; Egerton and Downing 2004), but apparently few of our study lakes contained nutrient levels that were high enough to allow the detection of negative effects on sport fish populations.

Other variables were occasionally important in explaining variation in sport fish demographics. The NVSS variable was usually negatively associated with sport fish demographic variables except for a positive association with white crappie CPE. Turbidity caused by inorganic suspended solids can reduce foraging and reproductive success of fishes (Miner and Stein 1996; Trebitz et al. 2007; Shoup and Wahl 2009). However, white crappies seem to be more tolerant of turbidity than other centrarchids and can exist in turbid lakes at high densities (Ellison 1984; Muoneke et al. 1992). White crappies in these dense populations are typically slow growing, and most do not reach large sizes (Ellison 1984; Muoneke et al. 1992; present study). The COND variable had a positive influence on the growth and size structure of largemouth bass and bluegills but a negative influence on the growth and abundance of black crappies. Conductivity is closely associated with total dissolved solids, which in turn have been positively related to fish yield (Ryder 1982). Black crappie PSD was positively associated with the VEG index. Black crappies may have benefited from the macroinvertebrates associated with macrophytes (McDonough and Buchanan 1991; Martin et al. 1992). Large lakes tended to contain largemouth bass, redear sunfish, and white crappies that exhibited faster growth or better size structure. Consistent with our findings, largemouth bass grew faster in larger Nebraska lakes (Paukert and Willis 2004). Cross and McInerney (2005) found that bluegills fared better in smaller Minnesota lakes, but we found no significant relationships between bluegill demographics and SA. Finally, WSA was sometimes included in models and was...
negatively associated with fish variables except for black crappie growth. Black crappies seemed to grow faster in lakes with a larger WSA, perhaps because these lakes tended to be more fertile owing to higher flushing rates (Bremigan et al. 2008; Jones et al. 2008a). However, sample size was small and other models that did not include WSA explained as much or more of the variation in black crappie growth, indicating uncertainty in the relationship between WSA and growth of this species.

Although most of the models explained less than half of the variation in sport fish demographics, they provide information that will be useful to fisheries managers. Many small lakes are managed primarily by restricting angler harvest, especially the harvest of largemouth bass. Our study confirms the importance of manipulating largemouth bass densities to improve largemouth bass or panfish populations. Provided that lake fertility is adequate, the manipulation of largemouth bass densities may be the most important management strategy for many of these small lakes. Acceptable sport fisheries for both largemouth bass and panfish can be achieved by maintaining moderate densities and size structure of largemouth bass (Swingle 1950; Novinger and Legler 1978). Creation of a panfish population with many large individuals may require elevated densities of largemouth bass, thus sacrificing the growth and size structure of these predators (Gabelhouse 1984; Willis et al. 2010). High-quality bluegill populations will probably only be achieved in productive lakes that have high densities of largemouth bass and no gizzard shad. Conversely, high-quality largemouth bass populations will most likely occur in lakes that are characterized by low densities of largemouth bass, moderate to high densities of small bluegills, and the presence of gizzard shad (Willis et al. 2010). Consequently, lakes containing gizzard shad may be best managed for large-size largemouth bass instead of large bluegills because the selective removal of gizzard shad is costly and unlikely to achieve long-term positive results (DeVries and Stein 1990; Kim and DeVries 2000). Intense largemouth bass predation and lower abundances of bluegills seem necessary for desirable reedear sunfish and crappie populations. Additionally, eradication of common carp may benefit sport fish populations, but the abundance at which common carp harm sport fish populations in these small lakes is unknown.

Management efforts within watersheds have become more common with the increased recognition of the importance of watershed characteristics for lake sport fisheries (Miranda 2008; Schultz et al. 2008; Willis et al. 2010). Many of these efforts have been directed toward reducing nutrient and sediment input into lakes. Such efforts have benefited sport fisheries in lakes that formerly received large amounts of nutrients and sediments from their watersheds (Schultz et al. 2008). Our results indicate that reducing sediment loads into lakes could benefit sport fisheries and would increase the life span of the lakes. Inorganic suspended solid concentrations generally had a negative effect on sport fish populations. However, caution should be used in attempting to reduce nutrient input into lakes, as moderate levels of nutrients are necessary to support sport fish communities.

Substantial reductions in nutrient inputs have led to declines in sport fisheries in some lakes (Yurk and Ney 1989; Ney 1996). Our data suggest that the potential for harmful effects of high nutrient concentrations on warmwater sport fish populations occurs only in hypereutrophic lakes.

Diurnal timing of sampling could have affected our estimates of sport fish demographics. Electrofishing catch rates of bluegills or largemouth bass can sometimes be greater at night than during the day, especially in clear lakes (Dumont and Dennis 1997; McNerny and Cross 2000; Pierce et al. 2001). In some waters, no differences in daytime and nighttime catch rates were found for largemouth bass (Malvestuto and Sonski 1990; Dumont and Dennis 1997). Size structure estimates for largemouth bass and bluegills do not seem to vary between daytime and nighttime electrofishing samples (Dumont and Dennis 1997; Pierce et al. 2001). We acknowledge that diurnal differences in sampling could have affected our catch rate estimates, but this potential bias is relatively minor given the large range in catch rates among the study lakes (Table 2).

ACKNOWLEDGMENTS

We thank the many current and past biologists and technicians who collected and provided the data used in this study. We also thank Steffanie Abel for her efforts in acquiring and developing the fish data set. Tim Bixler and Philip Marley provided the lake perimeter and surface area data that were necessary to compute the shoreline development index. Comments provided by two anonymous reviewers were helpful in improving the manuscript.

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Sampling Glacial Lake Littoral Fish Assemblages with Four Gears

Daniel J. Dembkowski a, Melissa R. Wuellner a & David W. Willis a

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Sampling Glacial Lake Littoral Fish Assemblages with Four Gears

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Abstract
Littoral zone fish assemblages are important components of freshwater lakes. Monitoring of littoral fish assemblage structure is important because littoral fishes often comprise the majority of the entire fish assemblage, and fluctuations in the structure and abundance of the littoral fish assemblage can influence trophic interactions and fishery yields at the ecosystem level. Single-gear sampling designs, however, may only capture a subset of the fish assemblage, resulting in a skewed representation of fish assemblage structure. Use of multiple gears can be justified if they provide complementary fish assemblage information. Our objective was to compare glacial lake fish assemblage structure as represented by four gears and to assess whether the gears provide redundant or complementary fish assemblage information. Two northeastern South Dakota glacial lakes were sampled with a beach seine, benthic sled, drop net, and push trawl in August 2011. Results indicated that fish assemblage structure did not differ significantly among gears. However, fish assemblage descriptors (metrics of species richness, diversity, dominance, and evenness) and rates of species accumulation did differ among gears; in comparison with the drop net, the beach seine, benthic sled, and push trawl collected more individuals with qualitatively greater species richness and diversity at a faster rate. The beach seine collected the most individuals representing the greatest number of species with the least amount of sampling effort (i.e., fastest rate of species accumulation); thus, we recommend the use of beach seines for monitoring and assessment of littoral fish assemblages in glacial lakes.

The littoral zone fish assemblage is an important ecological component of freshwater lakes (Northcote 1988), and in some lakes littoral fishes account for a majority of the entire fish assemblage (Keast and Harker 1977). Fish use littoral habitats for spawning, foraging, and obtaining cover from predators (Hall and Werner 1977; Keast and Harker 1977; Mittelbach 1981; Trautman 1981; Ross 2001). Because of the importance of the littoral zone and littoral fishes in lake ecosystems, fluctuations in the abundance and structure of the littoral fish assemblage can potentially influence trophic interactions and fishery yields at the ecosystem level (Pierce et al. 2001). Thus, the monitoring of littoral fish assemblage structure is crucial.

Although the sampling of littoral fish assemblages is essential for monitoring and ecological assessment, littoral fish assemblages are difficult to sample and assess (Weaver et al. 1993). Littoral sampling difficulties often arise from factors such as heterogeneous distribution of fishes (Pierce et al. 1990; Bryan and Scarnecchia 1992; Weaver et al. 1993), structurally complex habitats (Lewin et al. 2004), and inherent limitations of the sampling gear (Weaver et al. 1993; Hayes et al. 1996; Hubert 1996). Many gear options are available for sampling littoral habitats, but a single sampling gear rarely captures all species and sizes, resulting in a skewed representation of the fish assemblage (Hayes et al. 1996; Hubert 1996; Eggleton et al. 2010). Accordingly, fish assemblage structure may be better represented using multiple gears rather than a single gear (Weaver et al. 1993; Tischler et al. 2000; Lapointe et al. 2006). However, logistical complications may arise during the use of multiple gears because such protocols may require more specialized equipment, additional personnel, or more time invested into sampling effort. Furthermore, gear standardization and comparison may prove difficult (Kjelson et al. 1975). Use of multiple gears can be justified if the gears do not provide redundant representations of fish assemblage structure (Ruetz et al. 2007).

Comparisons of catch per effort and basic catch characteristics among gears are common in the fisheries literature (e.g., Pope and Willis 1996; Peterson and Paukert 2009), but relatively less research has focused on examining the differences in overall fish assemblage structure depicted by different gears (Eggleton et al. 2010). Extant studies evaluating differences in fish assemblage structure among gears generally indicate that multiple gears provide complementary rather than redundant...
assemblage information (Lapointe et al. 2006; Ruetz et al. 2007; Eggleton et al. 2010). However, we are not aware of any studies that have focused on fish assemblages—much less littoral fish assemblages—in glacial lakes of the northern Great Plains ecoregion. Thus, the objective of this study was to (1) compare fish assemblage structure in two glacial lakes as represented by samples collected with four gears (beach seine, benthic sled, drop net, and push trawl) and (2) determine whether the gears provided complementary or redundant information on littoral fish assemblage structure. The present study is the first to assess differences in fish assemblage structure among this particular set of sampling gears.

**METHODS**

*Study lakes.—* Pickerel Lake (Day County, South Dakota) and Clear Lake (Marshall County, South Dakota) were sampled during August 2011. The two lakes are located in northeastern South Dakota, are of glacial origin, and are relatively similar in their local abiotic attributes. In terms of trophic status (Carlson 1977), Pickerel Lake is considered mesotrophic and Clear Lake is considered eutrophic. Pickerel Lake has a surface area of 397 ha, a mean depth of 4.8 m, and a shoreline development index of 2.2; Clear Lake has a surface area of 474 ha, a mean depth of 3.8 m, and a shoreline development index of 1.5 (Stueven and Stewart 1996). In comparison with Clear Lake, Pickerel Lake has a relatively steep basin morphometry. Natural riparian vegetation surrounding both lakes is limited owing to anthropogenic development, and littoral habitat consists largely of bare rock and sand substrate interspersed with stands of submerged macrophytes (sago pondweed *Stuckenia pectinata* and coontail *Ceratophyllum demersum*) and emergent macrophytes (bulrushes *Scirpus* spp. and cattails *Typha* spp.).

Fish assemblages in both lakes are relatively simple and consist primarily of species belonging to the centrarchid, percid, ictalurid, cyprinid, esocid, moronid, and catostomid families. Most of the species that are present in Pickerel and Clear lakes are ubiquitous in glacial lakes throughout northeastern South Dakota (B. Blackwell, South Dakota Department of Game, Fish and Parks, personal communication). Pickerel Lake is managed for panfish (i.e., black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, and yellow perch *Perca flavescens*), smallmouth bass *Micropterus dolomieu*, and wall-eye *Sander vitreus* fisheries. Management efforts in Clear Lake likewise focus on walleye and smallmouth bass but also include largemouth bass *Micropterus salmoides*.

*Fish collection.—* Fish assemblages were sampled using four different gears (beach seine, benthic sled, push trawl, and drop net). Each lake was sampled during daytime hours on 1, 8, and 15 August 2011. At each lake on each date, two sites were sampled with the beach seine, benthic sled, and push trawl, and four sites were sampled with the drop net. For each gear, half of the sites were located in submerged vegetated habitats and half were located in nonvegetated habitats. Sample sites were stratified by habitat (i.e., vegetated or nonvegetated), randomly selected, and fixed throughout the study duration. More samples were collected with the drop net to equalize the volume of water sampled with each gear. Due to logistical constraints, no samples were collected with the drop net on 15 August 2011. In total, six beach seine samples, six benthic sled samples, six push-trawl samples, and eight drop-net samples were collected from each lake.

A 27.4- × 1.8-m bag seine (3-mm bar mesh) was deployed in a circle by wading, and an onshore point was used as the starting and ending point. To enclose the sample, the lead line was pulled toward shore from both ends until the collected fish were confined in the bag of the seine.

The benthic sled (*sensu* Niles and Hartman 2007) was 3 m long and was constructed of 3-mm bar-mesh netting attached to a rigid, galvanized-steel frame (1.2 × 0.9 m). The frame and net assembly were fastened to two 1.2-m, galvanized-steel skis separated by a 102-mm-diameter polyvinyl chloride (PVC) roll bar that enabled the sled to roll over obstructions in the water. The skis of the benthic sled were filled with sand and capped to provide ballast. The benthic sled was outfitted with towing bridle, which were attached to lines running down booms that extended outward from the bow of a 5.5-m boat equipped with a 115-hp outboard motor. The sled was pushed along each transect for a target distance of 100 m at a speed of 1–2 m/s.

The push trawl consisted of a 3-m-long bottom trawl with 3-mm bar mesh, a zipper-style cod end, and a 3.75-m headrope. Because the push trawl did not have a rigid frame, a rope was threaded around the mouth of the net in a rectangular fashion, allowing the mouth to open and maintain a surface area of 1.1 m², after which a stop knot engaged and prevented the mouth from opening any further. For volumetric measures, we assumed that the mouth of the push trawl opened to its fullest extent during each transect throughout the study. On 1 and 15 August, submerged vegetation at the vegetated site in Pickerel Lake was too thick, causing the mouth of the push trawl to collapse. In those instances, the sample was not collected and a different, less-vegetated location nearby was selected for sampling.

The drop net (Kahl 1963) consisted of a cast net (6.2-m diameter; 5-mm bar mesh) suspended from a 4.8-m² floating frame constructed of 20-mm-diameter PVC. Each corner of the PVC frame consisted of a 1.2-m piece of aluminum pipe with a buoy attached to the surface end. The edges of the cast net were pinched in four areas to form corners, and each corner was attached to a 100-mm-long piece of steel pipe (hereafter, “collar”), which was slightly larger in diameter than the corner posts. The collars were fitted over the corner posts, and each collar rested on top of a Lynchpin that was attached to a trip-cord, enabling remote deployment of the drop net (Dewey 1992). Lynchpins were removed by pulling on the trip-cord, causing the collars to slide down the corner posts until the net fell to the lake bottom. The drop net was set and was left undisturbed for 120 min prior to removal of the lynchpins. The sample was
enclosed within the cast net by tightening the cast net’s hand line from above.

Fish were identified to species and counted before their release near the site of capture. Fish that were too difficult to identify in the field (i.e., small cyprinids and percids) were preserved in a 70% solution of ethanol and were transported to the laboratory for positive identification with taxonomic keys (Trautman 1981). For all fishes collected, catch per effort was expressed as the number of fish per cubic meter of water. The volume of water sampled with each gear was calculated via the methods of Dembkowski et al. (in press).

Statistical analyses.—Nonmetric multidimensional scaling (NMS; Clarke and Warwick 2001) was used to explore differences in fish assemblage structure among the benthic sled, beach seine, drop-net, and push-trawl samples. The NMS procedure identifies patterns in multivariate data sets by plotting similar samples close together and dissimilar samples farther apart (Clarke 1993; Clarke and Warwick 2001). Furthermore, the NMS procedure is appropriate for assemblage-level data because (1) it is free of assumptions that inhibit the use of other ordination techniques, (2) it is well suited for use with nonnormal data, and (3) it can be performed using any ecological distance measure (Clarke and Warwick 2001; McCune and Grace 2002).

The NMS procedure was conducted using a relativized Manhattan distance measure (Faith et al. 1987) that was applied to fourth-root-transformed catch-per-effort data, with each value in the data matrix representing the abundance of a given species at a given site. The fourth-root transformation was selected because it reduced the skewness of the data better than more-conventional transformations (Miranda 2011). A two-dimensional solution was used for the NMS because the reduction in stress (i.e., improvement in fit of the data) was negligible with higher dimensionality (McCune and Grace 2002). Additionally, the two-dimensional solution frequently provides the most easily interpreted graphical depiction and summary of the data (Clarke and Warwick 2001). Potential differences in fish assemblage structure among gears at each lake were tested using a permutation-based multivariate analysis of variance (PERMANOVA; Anderson 2001). The PERMANOVA procedure was applied to detect an overall difference among gears and to perform pairwise comparisons between gears. To remove the undue influence of rare species on potential differences in assemblage structure among gears, species that were represented by only one or two individuals were removed from fish assemblage analyses.

Raw species richness, rarefied species richness, Shannon’s diversity, Pielou’s evenness, and Simpson’s dominance indices were calculated for the samples collected with each gear at each lake. Rarefied species richness estimates are essentially species richness values that are standardized to the minimum sample size (i.e., the smallest number of individuals collected). Differences in richness, diversity, dominance, and evenness indices were not tested for statistical significance; instead, they were used to provide a qualitative indication of fish assemblage characteristics provided by each gear. Species accumulation curves were generated for each gear based on rarefied species richness estimates. Curves were linearized and differences in the regression coefficients (i.e., rate of species accumulation) among gears were tested using an analysis of covariance (ANCOVA). Statistical significance (α) was set at 0.05 for all statistical procedures. The α value was not adjusted for pairwise comparisons because this would have resulted in significance levels that were too conservative for our interests. The NMS analysis, PERMANOVA, and fish assemblage descriptor calculations were performed with the PERMANOVA+ add-on for PRIMER-E software (PRIMER-E Ltd., Plymouth, UK; Clarke and Gorley 2006). Species accumulation curves were generated by using Paleontological Statistics software (Hammer et al. 2001), and ANCOVAs were performed with the Statistical Analysis System (SAS Institute 2010).

RESULTS

Throughout the sampling period, we collected 7,590 fish representing 17 species (12 species in Clear Lake; 17 species in Pickerel Lake) and eight families. Of the total catch at Clear Lake, bluegills were collected most frequently (48% by number), followed by yellow perch (37%), black crappies (11%), and Johnny darters Etheostoma nigrum (2%; Table 1). In Clear Lake, the beach seine captured 1,563 fish representing 11 species; the benthic sled collected 952 fish representing eight species; the drop net captured 10 fish representing two species; and the push trawl sampled 1,383 fish representing 12 species (Table 1). Of the total catch at Pickerel Lake, black crappies were collected most frequently (38% by number), followed by bluegills (32%), yellow perch (20%), and black bullheads (7%; Table 1). In Pickerel Lake, the beach seine collected 1,379 fish representing 11 species; the benthic sled caught 1,014 fish representing nine species; the drop net sampled 308 fish representing six species; and the push trawl captured 981 fish representing 10 species. Although fish ages were not estimated, most of the centrarchid, percid, esocid, ictalurid, and moronid fishes collected were juveniles (<100 mm TL).

Several species were considered rare and were collected in only one of the four sampling gears. Green sunfish (n = 1) were only collected with the benthic sled; emerald shiners (n = 1) and white bass (n = 1) were only collected with the drop net; white suckers (n = 1) were only collected with the beach seine; and brook sticklebacks (n = 2) were only collected with the push trawl (Table 1). These rare species were not included in any of the subsequent analyses.

Fish assemblage structure did not differ among gears (Figure 1). Stress values for the two-dimensional NMS solution stabilized at 0.12 after 25 iterations, indicating that the two-dimensional solution provided a useful summarization of fish assemblage structure for each gear (Clarke and Warwick 2001). Although significant differences in overall fish assemblage structure were detected for each lake (P = 0.05 for both lakes),
TABLE 1. Total fish counts of species collected by four different sampling gears in two northeastern South Dakota glacial lakes during August 2011. Species denoted with asterisks were considered rare and were not included in fish assemblage analyses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Clear Lake</th>
<th>Pickerel Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Beach seine</td>
<td>Benthic sled</td>
</tr>
<tr>
<td>Black bullhead <em>Ameiurus melas</em></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Black crappie</td>
<td>226</td>
<td>112</td>
</tr>
<tr>
<td>Bluegill</td>
<td>613</td>
<td>574</td>
</tr>
<tr>
<td>Brook stickleback <em>Culaea inconstans</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Emerald shiner <em>Notropis atherinoides</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fathead minnow <em>Pimephales promelas</em></td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Green sunfish <em>Lepomis cyanellus</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Greenside darter <em>Etheostoma blennioides</em></td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Iowa darter <em>Etheostoma exile</em></td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Johnny darter</td>
<td>38</td>
<td>13</td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>Northern pike <em>Esox lucius</em></td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>24</td>
<td>0</td>
</tr>
<tr>
<td>Spottail shiner <em>Notropis hudsonius</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>White bass <em>Morone chrysops</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>White sucker <em>Catostomus commersonii</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Yellow perch</td>
<td>652</td>
<td>214</td>
</tr>
<tr>
<td>All species</td>
<td>1,563</td>
<td>952</td>
</tr>
</tbody>
</table>

comparisons of all pairwise gear combinations indicated no significant differences between gears. Stratification of analyses by habitat did not change our overall conclusions. Metrics of species richness, diversity, dominance, and evenness were variable between lakes and across gears (Table 2). In general, fish assemblage descriptors that were calculated for the beach seine, benthic sled, and push trawl were more similar to one another than to the descriptors calculated for the drop net.

Rates of species accumulation differed significantly among sampling gears for both lakes (Pickerel Lake: $F_{7, 18} = 84.39$, $P < 0.001$; Clear Lake: $F_{7, 18} = 183.64$, $P < 0.001$; Figure 2). At Pickerel Lake, the drop net had a significantly slower rate of species accumulation than the beach seine ($F_{1, 10} = 69.76$, $P < 0.001$), benthic sled ($F_{1, 10} = 29.92$, $P = 0.001$), and push trawl ($F_{1, 10} = 39.78$, $P < 0.001$). A similar trend was observed for Clear Lake, where the drop net also had a significantly slower rate of species accumulation than the beach seine ($F_{1, 10} = 138$, $P < 0.001$), benthic sled ($F_{1, 10} = 33.91$, $P < 0.001$), and push trawl ($F_{1, 10} = 89.52$, $P < 0.001$). No significant differences in species accumulation rates were detected among the beach seine, benthic sled, and push trawl at either lake. These trends are consistent with the qualitative differences in fish assemblage descriptors observed for the drop net in comparison with the other three gears (Table 2).

**DISCUSSION**

Although representation of fish assemblage structure did not differ among gears, we observed substantial differences in fish assemblage attributes (species richness, diversity, dominance, and evenness indices) and rates of species accumulation among...
TABLE 2. Fish assemblage descriptors for four gears that were used to sample the littoral fish assemblages of two glacial lakes in northeastern South Dakota during August 2011.

<table>
<thead>
<tr>
<th>Gear</th>
<th>Species richness</th>
<th>Rarefied species richness</th>
<th>Shannon’s diversity</th>
<th>Simpson’s dominance</th>
<th>Pielou’s evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pickerel Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beach seine</td>
<td>10</td>
<td>6.77</td>
<td>1.11</td>
<td>0.62</td>
<td>0.48</td>
</tr>
<tr>
<td>Benthic sled</td>
<td>8</td>
<td>6.81</td>
<td>1.25</td>
<td>0.66</td>
<td>0.60</td>
</tr>
<tr>
<td>Drop net</td>
<td>4</td>
<td>4</td>
<td>0.86</td>
<td>0.53</td>
<td>0.62</td>
</tr>
<tr>
<td>Push trawl</td>
<td>9</td>
<td>6.56</td>
<td>1.03</td>
<td>0.54</td>
<td>0.47</td>
</tr>
<tr>
<td><strong>Clear Lake</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beach seine</td>
<td>11</td>
<td>3.21</td>
<td>1.21</td>
<td>0.65</td>
<td>0.50</td>
</tr>
<tr>
<td>Benthic sled</td>
<td>8</td>
<td>3.15</td>
<td>1.12</td>
<td>0.57</td>
<td>0.54</td>
</tr>
<tr>
<td>Drop net</td>
<td>2</td>
<td>2</td>
<td>0.50</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>Push trawl</td>
<td>11</td>
<td>2.88</td>
<td>1.10</td>
<td>0.59</td>
<td>0.50</td>
</tr>
</tbody>
</table>

FIGURE 2. Species accumulation curves derived from beach seine, benthic sled, drop-net, and push-trawl samples collected in two northeastern South Dakota glacial lakes during August 2011. For a given lake, gears denoted by the same lowercase letter did not have significantly different (α = 0.05) regression coefficients (i.e., rates of species accumulation).

beach seine, benthic sled, drop-net, and push-trawl samples. More individuals of greater species richness and diversity were collected at a faster rate with the beach seine, benthic sled, and push trawl than with the drop net. Despite the similarity in fish assemblage representation among the tested gears, our results suggest that certain gears (beach seine, push trawl, and, to a lesser extent, benthic sled) are better than others (drop net) at sampling littoral fish assemblages in glacial lakes, as indicated by fish assemblage attributes and species accumulation rates.

Our findings are inconsistent with the results of previous studies examining differences in fish assemblage structure among gears; however, our study is the first to assess differences among this particular combination of gears. Ruetz et al. (2007) found that the combined use of small-mesh fyke nets and boat electrofishers was better than the use of either gear alone for representing fish assemblage structure in Muskegon Lake, Michigan. Similarly, Lapointe et al. (2006) reported that the combined use of seines, boat electrofishers, hoop nets, and Windermere traps (i.e., large minnow traps) increased the number of species captured and provided a more holistic view of the fish assemblage. Eggleton et al. (2010) also concluded that a multiple-gear sampling approach (boat electrofishers, gill nets, and mini fyke nets) was needed to characterize littoral zone fish assemblages in floodplain lakes. Combined use of different gears or gear types (i.e., active and passive gears) is presumably advantageous because the different gear types target both mobile and sedentary portions of the fish assemblage (Hayes et al. 1996; Hubert 1996). However, if the use of multiple gears or gear types is not justifiable (i.e., if the gears provide redundant fish assemblage information, as was observed in our study), a single gear should be used to avoid the logistical and standardization complications (e.g., Kjelson et al. 1975) that are associated with multiple-gear sampling protocols.

Because fish assemblage representation did not differ among gears, our recommendation of the most suitable gear for sampling littoral fish assemblages in glacial lakes is based on indices of fish assemblage attributes (species richness and diversity) and
rates of species accumulation. The beach seine, benthic sled, and push trawl consistently sampled more individuals, had qualitatively greater species richness and diversity, and accumulated new species at a faster rate than the drop net. Furthermore, in comparison with the drop net, the three other gears we examined require substantially less operational effort in the field (Dembkowski et al., in press). Because drop-net samples were relatively depauperate in terms of the number of individuals sampled, species richness, and species diversity, we do not recommend use of the drop net for sampling littoral fish assemblages. The beach seine, benthic sled, and push trawl were all effective at capturing the most common species as identified by this study; therefore, any of these gears are likely sufficient for monitoring the structure and abundance of the most numerous members of the assemblage, including most of the primary management species. However, an ideal standardized sampling protocol (see Bonar et al. 2009) for comprehensive assemblage-level monitoring should collect the most individuals representing the most species with the least amount of sampling effort. Based on these criteria, either the beach seine or the push trawl was the most suitable for sampling littoral fish assemblages in our study lakes. Because of the complications we experienced with the push trawl in thick stands of aquatic macrophytes, the beach seine is likely to be of greater utility than the push trawl. Sampling characteristics of the beach seine (i.e., collecting the greatest number of individuals; representing the greatest number of species; and exhibiting a relatively fast rate of species accumulation) meet the need for development of synoptic fish assemblage sampling protocols as a response to the paradigm shift from a single-species approach to an ecosystem-level approach (Hughes and Noss 1992; Eggleton et al. 2010) in fisheries management and research.

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Impacts of Highway Construction on Redd Counts of Stream-Dwelling Brook Trout

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Impacts of Highway Construction on Redd Counts of Stream-Dwelling Brook Trout

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Abstract
Sedimentation during road construction is a human impact that threatens aquatic ecosystems. Despite a large body of literature on the effect of fine sediments on the initial developmental stages of fish, we do not know of any studies that have investigated the return of spawners to spawning grounds in streams impacted by sediment from road construction. The objective of this study was to quantify the return to spawning grounds of brook trout Salvelinus fontinalis at different stages of highway construction (before, during, and after construction). Redd counts were made at a fine spatial resolution (<0.5 m) over two consecutive years in 12 reaches distributed along a 115-km stretch of highway in the Laurentides Wildlife Reserve, Quebec. We found a significant decrease in redd counts in reaches affected by construction during the second year but no evidence of impacts in reaches affected by construction during the first year. A possible explanation is that sediment releases were well controlled during construction except after an extreme weather event occurring during the spawning season of the second year. However, we observed that a reach heavily impacted by sediments still supported high densities of spawners. Overall, we found a significant decrease in the absolute number of redd counts in the second year but strong consistency in the spatial distribution of the spawning sites, both within and among reaches and for all stages of highway construction and sediment loadings, which suggests that the return of spawners is more constrained by habitat variables than by sediment from highway construction.

Human-induced sedimentation is an impact that threatens aquatic ecosystems (Waters 1995; Sutherland et al. 2002; Kemp et al. 2011) and is a growing concern due to expanding land use and climate change (Scheurer et al. 2009). Sediment transport and deposition are especially problematic in streams during road construction because of erosion and alteration of the hydrologic network at intersections with roads, resulting in higher peak flows and sedimentation (Forman and Alexander 1998; Jones et al. 2000; Benda et al. 2004; Wheeler et al. 2005). Currently, measures to mitigate impacts from road construction are not entirely effective and sedimentation still remains a concern (Shields 2009; Collins et al. 2010).

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Salmonid species that require clean gravel substratum for spawning are thought to be the most affected by sedimentation (Sutherland et al. 2002; Scheurer et al. 2009) and are very sensitive to fine sediments (Chapman 1988; Lisle 1989; Jensen et al. 2009). Most studies on the impacts of sediments on salmonids have focused on the initial developmental stages, from egg deposition to emergence (Bernier-Bourgault and Magnan 2002; Julien and Bergeron 2006; Guillemette et al. 2011). The mechanisms proposed to explain the decrease in survival-to-emergence in the presence of fine sediments are reduction of oxygenated water supply to embryos (Greig et al. 2005; Heywood and Walling 2007) and restriction of free movement at emergence (MacCrimmon and Gots 1986; Fudge et al. 2008; Sternecker and Geist 2010; Franssen et al. 2012). Despite the large body of literature on the effect of fine sediments, we do not know of any studies that have investigated the return of spawners to spawning grounds impacted by sedimentation. More specifically, road construction can (1) reduce the amount of suitable habitat for spawning due to sedimentation (Alexander and Hansen 1986; Magee et al. 1996) and (2) cause gill damage due to increased water turbidity (Berg and Northcote 1985; Lazar et al. 2010). In both cases, a reduction in spawner abundance is expected (spawners can move outside the zone of influence of highway construction or decide to spawn in other reaches). Cumulative effects of emergence success and spawner avoidance could result in a decline of stream-dwelling populations near roads. For example, Baxter et al. (1999) reported a negative correlation between the number of redds and the density of forest roads.

The objective of this study was to quantify the spawning return of brook trout Salvelinus fontinalis in relation to the stage of highway construction (before, during, and after construction). More specifically, we predicted a reduction in the number of spawners occurring in reaches affected by highway construction. We used redd count as an index of spawner abundance and reported changes in spawner distribution at fine spatial resolution (<0.5 m) within reaches spread along a 115-km stretch of highway.

**METHODS**

*Study area.*—The study was carried out in 12 streams of the Laurentides Wildlife Reserve (47°45’N, 71°15’W), Quebec, which is located on the Laurentian Plateau at altitudes between 360 and 820 m (Figure 1). The area has a humid continental climate with harsh winters (mean annual temperature = 0.3°C, annual snowfall = 639 cm). Vegetation cover is continuous boreal forest dominated by balsam fir Abies balsamea and white birch Betula papyrifera. Watershed geology is largely homogeneous and consists of a metamorphic basement (gneiss) with intrusive rocks (mainly mangerites); stream formation is primarily by glacial deposits and outwash. The annual discharge regime has a dominant peak in the spring at snowmelt and seasonal lows in late summer.

FIGURE 1. Locations of the 12 stream reaches (open circles) distributed along Highway 73–175 (black line) in the Laurentides Wildlife Reserve, Quebec. The intensity of shading is proportional to altitude. Dashed lines show the boundaries of four watersheds.
TABLE 1. Stream characteristics and number of sediment traps for the 12 reaches along Highway 73–175 in the Laurentides Wildlife Reserve, Quebec. Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08).

<table>
<thead>
<tr>
<th>Reach</th>
<th>Strahler order</th>
<th>Width (m)</th>
<th>Slope (%)</th>
<th>Number of traps</th>
</tr>
</thead>
<tbody>
<tr>
<td>94.59</td>
<td>2</td>
<td>5.7</td>
<td>4.0</td>
<td>3</td>
</tr>
<tr>
<td>96.37</td>
<td>1</td>
<td>1.3</td>
<td>12.8</td>
<td>2</td>
</tr>
<tr>
<td>101.63</td>
<td>1</td>
<td>1.1</td>
<td>3.3</td>
<td>0</td>
</tr>
<tr>
<td>104.10</td>
<td>1</td>
<td>2.9</td>
<td>2.7</td>
<td>0</td>
</tr>
<tr>
<td>104.67</td>
<td>1</td>
<td>3.5</td>
<td>1.4</td>
<td>0</td>
</tr>
<tr>
<td>113.32</td>
<td>1</td>
<td>1.9</td>
<td>2.3</td>
<td>0</td>
</tr>
<tr>
<td>133.11</td>
<td>2</td>
<td>3.1</td>
<td>1.0</td>
<td>3</td>
</tr>
<tr>
<td>143.75</td>
<td>3</td>
<td>5.2</td>
<td>0.3</td>
<td>4</td>
</tr>
<tr>
<td>161.70</td>
<td>2</td>
<td>1.9</td>
<td>1.1</td>
<td>2</td>
</tr>
<tr>
<td>165.93</td>
<td>1</td>
<td>1.8</td>
<td>2.0</td>
<td>2</td>
</tr>
<tr>
<td>174.33</td>
<td>1</td>
<td>1.4</td>
<td>3.1</td>
<td>0</td>
</tr>
<tr>
<td>209.08</td>
<td>2</td>
<td>2.5</td>
<td>2.6</td>
<td>0</td>
</tr>
</tbody>
</table>

Highway 73–175, which runs between Quebec and Sagueneay cities, Quebec, was built in 1948. A major construction project, undertaken during the period 2006–2012, widened the highway from two to four traffic lanes. The mean width of the highway’s zone of influence (including the traffic lanes and all areas required for road security and maintenance, such as ditches and additional strips of land) increased from 30 m to 120 m. Measures implemented to reduce sedimentation during construction included use of erosion control mattresses to stabilize stream banks, gravel filters placed along construction ditches to promote sediment retention, and geotextile curtains to limit dispersal of suspended particulate matter. The highway is the only apparent source of human disturbance on the aquatic environment in the Laurentides Wildlife Reserve.

We selected 12 reaches along a 115-km stretch of the highway to estimate the spawning abundance of brook trout in 2007 and 2008. The reaches are in small tributaries (Strahler order 1–3; Table 1) that are all crossed by the highway. The distance sampled in the reaches was on average 400 m and ranged from 110 m to 1,100 m (Figure 2). The distance sampled was not affected by the widening of the highway, except for the reach 113.32 that was shortened by 200 m in 2008 (see details on Figure 2). These reaches have a median slope of 2.5% (range 0.3–12.8%; Table 1) and a gravel bed substrate; these features provide suitable habitat for the reproduction of brook trout (Witzel and MacCrimmon 1983; Kondolf and Wolman 1993; Curry et al. 2002). Underwater visibility was high (i.e., bed substrate clearly visible with polarized sunglasses) and allowed for observation of spawning.

**Redd counts.**—Each reach was visited weekly to count the number of redds in 2007 (5 September to 17 October) and 2008 (15 August to 19 October). The visits began prior to the spawning season and continued until the end of the spawning season. During a visit, redds were counted by walking slowly in an upstream direction along the stream bank. When a potential redd was detected, the observer would crouch down and wait for at least 3 min to check for the presence of spawners. The observer was equipped with polarized sunglasses, and visits were always conducted in high visibility conditions (e.g., no sediment event, substrate always visible) to ensure consistency in the detection of redds. Redds were confirmed by the observation of a clearly defined nest (disturbed streambed sediments with a characteristic pit tailspill formation), an actively digging female, or a male fighting for a stationary female (Crisp and Carling 1989; Blanchfield and Ridgway 1999). The longitudinal position of each redd was recorded (nearest 0.5 m) using a measuring tape and flags spaced at 20-m intervals. The center of the highway was defined as the origin of the longitudinal position. Upstream and downstream locations were assigned negative and positive distances from the origin, respectively. The same observer identified redds following this protocol in 2007 and 2008, which reduced bias in redd detectability.

**Sediment and water level data.**—Sediment traps were used to determine the magnitude and duration of fine sediment increase resulting from highway construction. Two to four traps (depending on stream width) were installed in six reaches at downstream locations (Table 1). The sediment trap consisted of a bucket set into the streambed, incorporating a void space and nested in a slightly larger bucket (for ease of replacement; Lisle 1989). Buckets were installed with their rims 2.5 cm above
the streambed to avoid excess collection of bed load. In reach 94.59, the streambed could not be excavated to install the usual bucket-type trap because of obstruction by large boulders and bedrock. Thus, we built a sediment trap consisting of a hollow collection tube that was closed at one end and secured within a concrete block anchored to the streambed. Both types of sediment traps were removed and replaced (hereafter reset) with an empty trap at regular time intervals (2–4 weeks) from May 2006 to October 2009. Trap contents were dried and sieved for particle size analysis using standard methods (ASTM 2006). We considered fine sediments as the total mass of sediments <0.5 mm in diameter.

The upstream section of reach 143.75 was instrumented with a permanent recording station that monitored water level using a Submersible Pressure Transducer (range: 0–2 m; accuracy: 0.25% static; Keller America). Sediment and water level data originated from a complementary project and were not designed to fit with the spawning records presented here. No statistical analyses were done with fine sediments or water level data because of the lack of replication, but graphical analyses were used to interpret the impacts of highway construction on redd counts.

**Statistical analyses.**—Depending on the reach, highway construction occurred during the first year (thus yielding a “during–after” study period; \( n = 4 \)), the second year (a “before–during” study period; \( n = 5 \)), or not at all (a “before–before” study period; \( n = 3 \)). This classification was used to define a three-level treatment variable. The response variable was the difference in redd counts obtained by subtracting redd counts recorded in 2008 from those recorded in 2007. The impact of highway construction on the total number of redds was analyzed by one-way analysis of variance (ANOVA) with the difference in redd counts as the response variable and the treatment as the fixed factor (Green 1993). Since we had 2 years of observations, the one-way ANOVA was a simpler alternative to repeated-measures ANOVA on redd counts with treatment, time, and time × treatment interaction as fixed factors and reach as a random variable (see Green 1993 for more details). Group-wise differences were assessed with a post hoc Tukey test.

The spatial distribution of redds within each reach was estimated by kernel density functions, a form of smoothing curves that provide a continuous approximation to the underlying data distribution (Silverman 1986). The bandwidth of the kernel density was set to 12.5 for all distributions for consistency in the comparison of spatial distributions of redds between years and among reaches. This bandwidth provided a suitable compromise that avoided over- and undersmoothing of the spatial distributions of redds. The kernel density estimates were used to assess if highway construction modified the spatial distribution of redds within each reach. All analyses were done in the R environment (R Development Core Team 2010).

**RESULTS**

Redd counts were recorded from 5 September until 17 October 2007 and from 23 August to 19 October 2008 (Figure 3). The timing of arrival of spawners on their spawning ground was consistent between the 2 years, with the peak of redd counts occurring the last week of September (Figure 3). Redds were always observed in the 12 reaches for both years (Figure 4). Overall, redd counts were higher in 2008 \((n = 551)\) than in 2007 \((n = 450)\). The water level was on average higher in 2008 than in 2007 (Figure 3).

The one-way ANOVA of differences in redd counts revealed a significant effect of the treatment \((F_{2,9} = 4.263, P < 0.05)\). A post hoc Tukey test indicated that the only significant difference was between before–before and before–during treatments \((P < 0.05)\). On average, redd counts increased from 2007 to 2008 by 44% in all reaches of the before–before and during–after treatments, whereas redd counts decreased from 2007 to 2008 by 3% in reaches of the before–during treatment (Figure 4). The spatial distribution of redds within reaches was stable and consistent between years regardless of the stage of highway construction (Figure 5). The strong overlap in the distributions of redds between years indicated no change in location of spawning. More specifically, the reaches that had many spawners during the first year continued to have many spawners during the second year (e.g., reaches 94.59, 96.37, 104.67, 161.70; Figure 5). The spawning aggregations occurred within 200-m reach lengths.

Among the six reaches where fine sediments were collected, a major increase of fine sediments occurred in reach 96.37...
FIGURE 4. Highway construction impacts on redd counts according to treatment (BB: “before–before”; BD: “before–during”; DA: “during–after”). Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08).

FIGURE 5. Spatial distribution of redds shown by kernel density functions. The horizontal grey lines show the stream sections where redds were recorded. Reaches are identified by milepost distance from south (km 94.59) to north (km 209.08). Distances from the highway are positive downstream and negative upstream.

FIGURE 6. Fine sediments (total mass of sediments < 0.5 mm) sampled by sediment traps from May 2006 to October 2009 in six reaches. Grey vertical bars represent the 2007 and 2008 spawning seasons. Reaches are identified by milepost distance from south (km 94.59) to north (km 165.93). No other reach collecting fine sediment data was in construction during this event, which limits inference to other reaches in construction during this event. However, reaches that were not in construction in the 2008 spawning season nor other reaches outside the 2008 spawning season were affected by fine sediments (Figure 6).

DISCUSSION
To our knowledge, this is the first study quantifying the impact of different stages of highway construction on return
of spawners. Overall, the increase in redd count observed in undisturbed reaches in 2008 (44% on average) could have been the result of (1) higher discharge during the spawning periods and subsequent increase in the ability of spawners to migrate (Taylor et al. 2010) or (2) natural variability. Controlling for this variability (Green 1993), our results showed that highway construction induced a significant decrease in redd count in reaches under construction in 2008 (i.e., 3% on average), but there was no evidence of impacts in reaches under construction in 2007. A possible explanation could be that sediment releases were well controlled during construction except after an extreme weather event, tropical cyclone Ike, which occurred during the spawning season of the second year. The decrease in redd count might have been caused by increase in water turbidity, which influences spawners during migration (Whitman et al. 1982; Servizi and Martens 1992), or to the availability of clean gravel substratum for spawning (Kondolf and Wolman 1993; Magee et al. 1996).

Highway construction impacts were reported on short temporal scales and on local spatial scales (i.e., within the first kilometres of the highway). In addition, sediment data showed a rapid return (< 1 year) to their initial levels after impacts, perhaps because of rapid evacuation of surface accumulations of finer sediments in headwater streams (Verstraeten et al. 2007; Lachance et al. 2008), suggesting that highway construction can affect spawning sites on short temporal scales near the highway. However, at the landscape scale, the accumulation of sediments in the watershed has been shown to induce dramatic changes in aquatic ecosystems (Waters 1995; Sutherland et al. 2002; Donohue and Molinos 2009). For example, the accumulation of sediments in lakes can modify the ecological processes and re-structure energy flow pathways; these modifications frequently result in reduced biological diversity and productivity (Donohue and Molinos 2009). Thus, future investigations should evaluate sediment effects on population dynamics at the watershed scale to ensure that the observed effects were not underestimated at larger spatial scales (Fausch et al. 2002; Harvey and Railsback 2009; Scheurer et al. 2009).

Contrary to our prediction, the reach heavily impacted by fine sediments (reach 96.37; fine sediment accumulation from 7 g/d in the 2007 spawning season to 86 g/d in the 2008 spawning season; Figures 6, 7) still supported a high return of spawners (Figures 4, 5). Although we had no evidence of the completion of spawning, active reproductive behaviors (e.g., female digging and male combat) were observed in this reach during the 2008 spawning season (Figure 8). No attempt was made to assess the presence of eggs, egg viability, and the overall success of

FIGURE 7. Sediment traps on reach 96.37 (A) before (15 October 2006) and (B) after (19 September 2008) the tropical cyclone Ike.

FIGURE 8. Sequential photos showing a brook trout female digging into substrate filled by fine sediments. The excavation is clearly identifiable under the female on the photo 1. The female excavated the lower part of the redd after male courtship (quivering).
reproduction in order to preserve the spawning sites and to not disturb spawning activity. Sampling the young of the year the next year could be a safe alternative to estimate individual fitness through recruitment. Nevertheless, we suggest that the return of spawners in these degraded habitats will result in a reduction of individual fitness due to energetic expenditure or fine sediment accumulation in the substrate; this latter effect was already well documented in previous studies (Bernier-Bourgault and Magnan 2002; Jensen et al. 2009; Guillemette et al. 2011). This in turn could lead to population decline (Alexander and Hansen 1986; Nakamura et al. 1994; Baxter et al. 1999). Targeting multiple life history stages would improve our understanding of the mechanisms involved in the evolution of brook trout population in disturbed habitats (Curry and MacNeill 2004; Pépino et al. 2012).

Highway construction led to a significant decrease in the return of spawners in the second year, presumably because of sedimentation occurring after an extreme weather event in reaches affected by highway construction. However, the observed stability of the spatial distribution of spawning sites between the 2 years, both within and among reaches and at all stages of highway construction and levels of sediment loading, suggests that spawning areas are determined by habitat features. Therefore, the development of tools that predict the spawning areas from habitat variables should help managers identify and protect critical fish habitats from human disturbances, as has been proposed for some salmonid species in other contexts (Steel et al. 2004; Poplar-Jeffers et al. 2009).

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Latitudinal Influence on Age Estimates Derived from Scales and Otoliths for Bluegills

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Latitudinal Influence on Age Estimates Derived from Scales and Otoliths for Bluegills

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Abstract
Scales are perceived to give reliable estimates of age of fish in northern latitudes and unreliable estimates of age in southern latitudes, whereas otoliths are perceived to give reliable estimates of age regardless of latitude. The objective of our study was to assess the influence of latitude on the estimates of ages derived from scales and otoliths for bluegill *Lepomis macrochirus*. Our hypothesis was that a south-to-north gradient exists for precision between scales and otoliths with partial agreement between age estimates derived from scales and otoliths for fish in southern latitudes and nearly complete agreement between age estimates derived from scales and otoliths for fish in northern latitudes. Fish were sampled from Louisiana (latitude \(30^\circ 43' 48''\) N) to North Dakota (latitude \(47^\circ 05' 49''\) N). Contrary to a priori expectations, we did not find greater agreement in age estimates between structures in northern bluegill stocks than in those in the southern USA. The low agreement between structures increases uncertainty in the source of aging error, given that both scales and otoliths are valid structures (i.e., age estimates validated as accurate) for estimating ages of bluegills. Biologists should not compare age-dependent parameters for bluegill populations derived from different aging structures.

Scales and otoliths, two calcified structures in which annual marks (i.e., annuli) are formed, are widely used for estimating the age of fish (DeVries and Frie 1996; Campana and Thorrold 2001). Annuli are formed in calcified structures during periods of slow growth, generally associated with cold weather in temperate climates (DeVries and Frie 1996). Age estimates derived from scales have been validated for bluegill *Lepomis macrochirus* using known-age fish in New York (Regier 1962), and age estimates derived from otoliths have been validated for bluegills using marginal-increment analysis in South Carolina (Hales and Belk 1992). Lucchesi and Johnson (2006) compared the amount of time for removal and processing of scales and otoliths to estimate ages for walleye *Sander vitreus* and yellow perch *Perca flavescens*; they reported a similar amount of time to read and process each structure. Collection of scales is frequently preferred to collection of otoliths because fish from which only scales have been taken can be released alive.

Accurate age estimates are vital for quantifying population dynamics (e.g., recruitment, growth, and mortality) and assessing age structure of a population. Furthermore, a recent emphasis has been placed on standardization of methods to compare data gathered across large geographic areas (Bonar and Hubert 2002; Bonar et al. 2009). Inaccuracy in age estimation of fishes is caused by error associated with interpretation of annuli (Campana 2001), which is compounded by variability in the quality of annuli. Quality of annuli can differ among populations and years due to environmental factors that influence physiological mechanisms controlling formation of annuli; quality can also differ between the calcified structures being examined. Not all calcified structures in fish form a complete growth sequence throughout the lifetime of the animal (Casselman 1990). Therefore, aging techniques that produce accurate estimates are essential for analysis of population dynamics (Summerfelt and Hall 1987; Campana 2001).

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Quantification of the accuracy of age estimates is typically determined when estimating age of known-age fish or through marginal-increment analysis—information that typically is not available when sampling wild populations. In contrast, quantification of the precision of age estimates derived from two different calcified structures from the same fish (e.g., scales and otoliths) can be easily obtained. Although an estimate of precision and associated error does not provide an estimate of the true value of the quantity being measured, it does provide a distribution from which the probability of the existence of an independent random variable can be determined. Given that both age estimation methods we evaluated have been validated, we considered precision of estimates between structures as a measure of uncertainty that is introduced in age estimation.

Latitude of origin has a potential impact on the precision of age estimates of fish. The lack of a definitive cold season in southern latitudes affects physiological mechanisms that control annuli formation. In contrast, fish populations from northern latitudes typically experience definitive periods of fast growth associated with warm temperatures and slow growth associated with cool temperatures. Decreased precision between age estimates derived from scales and otoliths has been documented in fish from southern latitudes (Schramm and Doerzbacher 1985; Boxrucker 1986; Hammers and Miranda 1991). The loss of precision in age estimates between structures has been attributed to a reader’s inability to distinguish annuli formation on scales because of the effects of climate on the seasonal growth and metabolic activity of fish (Schramm and Doerzbacher 1985; Boxrucker 1986; Hoxmeier et al. 2001). Thus, fish from southern latitudes, with shorter or intermittent cold seasons, may have indistinguishable annuli on scales. In contrast, otoliths have been used to accurately age fish from both southern and northern latitudes (Schramm and Doerzbacher 1985; Boxrucker 1986; Kruse et al. 1993; Hoxmeier et al. 2001). A reader’s ability to accurately estimate age with scales and otoliths has been studied at relatively small spatial ranges (Boxrucker 1986; Hammers and Miranda 1991; Kruse et al. 1993; Hoxmeier et al. 2001). Thus, we considered precision of estimates between structures as a measure of uncertainty that is introduced in age estimation.

RESULTS AND DISCUSSION

We expected to find significant differences between regression lines and the 1:1 line in southern populations and no differences in northern populations. Contrary to a priori expectations, however, we found no evidence of a latitudinal gradient in any agreement of age estimates derived from scales and otoliths of bluegill. Age estimates derived from scales and otoliths were significantly different in 14 of 15 populations assessed (Figure 1). We found five populations in which the slope of the regression line did not differ from 1, but only one population in which slope did not differ from 1 and the y-intercept different from 0. We estimated growth parameters (asymptotic average length \(L_\infty\) and growth rate coefficient \(K\)) and instantaneous mortality \(Z\) using our study fish to illustrate potential influences of discrepancies in age estimates; we caution readers that the bluegill samples provided for this study were not representative of actual populations because we requested samples weighted toward older (i.e., larger) fish.

METHODS

Collection of bluegills.—We analyzed scales and otoliths of bluegills from populations centered along a line (longitude = 93°42’48”W to 97°07’09”W) from the Texas–Louisiana border north to the North Dakota–Minnesota border (latitudes = 30°43’48”N through 47°05’49”N). Bluegill samples were provided by biologists representing state agencies along the latitudinal gradient. Each biologist was asked to collect bluegills from all age groups present during sampling and to weight the sampling toward older age groups because we assumed discrepancies in age estimates would be more prevalent in older fish. Fish were frozen and shipped to University of Nebraska–Lincoln Fishery Science Laboratory for processing. In the laboratory, each fish was thawed and individually numbered. Scales (collected from under the tip of the pectoral fin when pressed against the body) and otoliths were removed for age analyses following procedures described by DeVries and Frie (1996).

Structure aging.—Scales were pressed onto acetate slides and viewed through a microfiche reader. Scale annuli were identified by close spacing of the circuli and cross-over points (Jerald 1983; Kruse et al. 1993). Whole otoliths were submerged in a black petri dish filled with water and viewed through a dissecting microscope with reflected light. Otolith annuli were identified as lighter colored, opaque bands (representing reduced growth increments) separated by darker colored, translucent bands (representing increased growth increments). All scales and otoliths were read separately by two independent readers to estimate fish age. To reduce reader bias, we resolved all discrepancies in age estimates between readers with a concert read (Campa 2001; Buckmeier et al. 2002). Age bias plots with linear regression were constructed for each population to examine the precision of age estimates derived from scales and otoliths (Phelps et al. 2007). Analysis of variance (ANOVA) was used to determine whether the slope of the regression line differed from 1, and in cases in which it did not differ from 1, to determine whether the y-intercept differed from 0. We estimated growth parameters (asymptotic average length \(L_\infty\) and growth rate coefficient \(K\)) and instantaneous mortality \(Z\) using our study fish to illustrate potential influences of discrepancies in age estimates; we caution readers that the bluegill samples provided for this study were not representative of actual populations because we requested samples weighted toward older (i.e., larger) fish.
FIGURE 1. Age bias plots for 15 bluegill populations. Linear regression indicated by solid black line. All regressions were significant ($P < 0.001$). The 1:1 dotted line (age estimates derived from scales = age estimates derived from otoliths) is provided for reference. The number of bluegills represented by each data point is indicated by size of data point: 1–4 bluegills for small points, 5–9 bluegills for medium points, and 10 or more bluegills for large points. Asterisk denotes regression slope = 1, and $y$-intercept = 0. Sample size ($n$) and structure agreement (agree; %) are provided for each population.

1. Brewer Lake, ND  
   $n = 55$, agree = 76%
2. Heinrich-Martin Dam, ND  
   $n = 52$, agree = 71%
3. Pheasant Lake, ND  
   $n = 55$, agree = 20%
4. Czechland Reservoir, NE  
   $n = 37$, agree = 49%
5. Walnut Creek Reservoir, NE  
   $n = 64$, agree = 47%
6. Higginsville City Lake, MO  
   $n = 53$, agree = 55%
7. Crawford State Lake, KS  
   $n = 122$, agree = 64%
8. Haskell City Lake, OK  
   $n = 51$, agree = 41%
9. Vian City Lake, OK  
   $n = 51$, agree = 43%
10. Muldrow City Lake, OK  
    $n = 80$, agree = 39%
11. Grandview Lake #1, AR  
    $n = 61$, agree = 60%
12. Gilmer Reservoir, TX  
    $n = 51$, agree = 53%
13. Pinkston Reservoir, TX  
    $n = 46$, agree = 37%
14. Kurth Reservoir, TX *  
    $n = 51$, agree = 45%
15. Bundick Lake, LA  
    $n = 62$, agree = 76%
FIGURE 2. Logistic regression of agreement of age estimates derived from scales and from otoliths plotted as a function of total length (mm) for bluegills (n = 891). A 50% likelihood of agreement occurred at a total length of 150 mm.

TABLE 1. Comparison of asymptotic average length ($L_\infty$) and growth rate coefficient (K) from the Von Bertalanffy growth equation and instantaneous mortality rate (Z) between models by using ages derived from scales and from otoliths for each bluegill population. Percent difference was calculated for parameter estimates according to the formula ($\left(\frac{X_{\text{scale}} - X_{\text{otolith}}}{0.5(X_{\text{scale}} + X_{\text{otolith}})}\right) \times 100$).

<table>
<thead>
<tr>
<th>Reservoir</th>
<th>Age derived from</th>
<th>Age derived from</th>
<th>Age derived from</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Scales</td>
<td>Otoliths</td>
<td>% Diff.</td>
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<tr>
<td>Brewer Lake, ND</td>
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<td>*</td>
<td>*</td>
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<tr>
<td>Heinrich Martin Dam, ND</td>
<td>238</td>
<td>*</td>
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<tr>
<td>Phesant Lake, ND</td>
<td>270</td>
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<tr>
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<td>211</td>
<td>228</td>
<td>0.540</td>
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<td>200</td>
<td>194</td>
<td>0.471</td>
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<tr>
<td>Higginsville City Lake, MO</td>
<td>168</td>
<td>156</td>
<td>0.437</td>
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<td>0.725</td>
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<td>241</td>
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<tr>
<td>Vian City Lake, OK</td>
<td>225</td>
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<tr>
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<td>Bundick Lake, LA</td>
<td>574</td>
<td>344</td>
<td>0.077</td>
</tr>
</tbody>
</table>

* We recognize Z cannot be negative; values are reported only for comparison purposes, to illustrate differences in estimates.
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ARTICLE

Privately Owned Small Impoundments in Central Alabama: A Survey and Evaluation of Management Techniques for Largemouth Bass and Bluegill

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Abstract
Small impoundments or ponds represent important fisheries resources, both recreationally and economically. These systems are small relative to most large public reservoirs and natural lakes and thus they are more easily manipulated to improve fishing quality. The utility of some pond management techniques in improving fisheries is not well understood. We combined a telephone survey and field sampling to quantify the characteristics and use(s) of private ponds in central Alabama and determine the efficacy of the most often used pond fishery enhancement techniques. The three most common techniques were fertilization (used by 48% of surveyed pond owners), supplemental feeding with pellets (45%), and the stocking of supplemental prey for largemouth bass Micropterus salmoides (12%; the species most often stocked was threadfin shad Dorosoma petenense). We sampled 66 ponds using boat electrofishing to assess largemouth bass and Lepomis spp. population responses to these management techniques. Fish populations varied greatly within management categories. However, ponds with threadfin shad exhibited overall greater largemouth bass length, length frequency indices (PSD and PSD-P, -M), growth, body condition, and density than ponds without threadfin shad. Bluegill Lepomis macrochirus population characteristics were similar among all ponds using fertilizer and threadfin shad. Of these techniques, we found that fertilization improved bluegill populations and that threadfin shad can improve largemouth bass populations without compromising bluegill size structure and abundance.

Small impoundments or ponds are abundant throughout the USA, with more than 2.6 million located on privately owned land. These ponds support a large portion of recreational fishing effort (Smith et al. 2002). While there are some accepted standard approaches to pond management (Willis et al. 2010), pond owners often manage these systems in a variety of ways to attempt to meet their goals of either “balanced” conditions, i.e., the abundance and size structure of predator and prey fish populations that support satisfactory sustainable harvest (Swingle 1950) or enhanced fishing. Unfortunately, many of these approaches have not been critically evaluated. Successful management requires that these tools be assessed such that outcomes can be reasonably predicted.

The most common stocking combination for warmwater ponds throughout the USA is largemouth bass Micropterus salmoides and bluegill Lepomis macrochirus, given their compatible predator–prey relationship and value as sport fishes (Swingle and Smith 1940; Modde 1980). The interactions between these species and their management have been relatively well studied (Olson et al. 1995; Brenden and Murphy 2004; Olive et al. 2005; Willis et al. 2010). Bluegills exhibit several qualities that make them a suitable prey fish for largemouth
bass (e.g., they are tolerant of a wide range of temperatures, they are omnivorous, they mature early, and they can have multiple reproduction events within a year; Swingle and Smith 1940). However, given that bluegills also outgrow the gape of largemouth bass (Hambright 1991), have effective defensive spines, have lower caloric density than some other prey fish species (Miranda and Muncy 1991; Eggleton and Schramm 2002), and have strong predator avoidance behaviors (e.g., Werner and Hall 1988), other prey have been considered for stocking in combination with them to enhance largemouth bass growth.

Threadfin shad *Dorosoma petenense* is often stocked to enhance piscivorous sport fish populations in ponds, large reservoirs, and lakes (reviewed in DeVries and Stein 1990). While the effects of threadfin shad on largemouth bass and bluegill populations have been examined in large reservoirs and natural lakes (Fast et al. 1982; DeVries and Stein 1990; DeVries et al. 1991; Garvey et al. 1998), these same interactions have been less carefully evaluated in ponds. In larger systems, threadfin shad can positively affect largemouth bass growth (Tharratt 1966; Miller 1971; von Geldern and Mitchell 1975) because they can be consumed by age-0, juvenile, and adult largemouth bass (Kimsey et al. 1957; Goodson 1965; von Geldern and Mitchell 1975; Wanjala et al. 1986). However, even in systems containing *Dorosoma* spp., centrarchids often remain the primary prey for largemouth bass (Timmons et al. 1980; Jackson et al. 1992; Bettolli et al. 1992; Irwin et al. 2003). Threadfin shad can severely reduce zooplankton density (Ziebell et al. 1986; Prophet 1988; DeVries et al. 1991; Garvey and Stein 1998), with negative effects on age-0 bluegill and largemouth bass recruitment and condition having been documented in these larger systems (DeVries et al. 1991; Stein et al. 1995; Garvey and Stein 1998).

Other common management techniques used in ponds include fertilization and providing pelleted food as a supplement to bluegills (Nail and Powell 1975; Fisher 1979; Berger 1982; Porath et al. 2003). Fertilization can increase fish biomass three- to four-fold depending on the natural fertility of the pond soils (Swingle 1950) and thus is commonly used to increase fish productivity. For bluegills, pellet feeding can increase growth (Porath and Hurley 2005), condition (Schmittou 1969; Berger 1982), density (Schmittou 1969), and size structure (Nail and Powell 1975) while providing the added benefit of increasing angler success and harvest by serving as a fish attractor (Berger 1982).

Despite the importance and abundance of ponds, relatively little is known about the degree to which pond owners follow both standard and enhanced management approaches or about the influence of some of the more often used management techniques on sport fishes in ponds. This information would be of importance to managers charged with maintaining pond fishing quality as well as to scientists studying the ecology of these systems. Here we used a combination of approaches to address two objectives: first, we used a telephone survey to identify the management techniques used by private pond owners in central Alabama; second, we compared the growth, condition, and structure of the bluegill and largemouth bass populations in private ponds where one or more of the most common management techniques (fertilizing, applying pellet feed, or stocking threadfin shad) were used.

**METHODS**

**Pond owner survey.**—Our study area included 23 counties across the central region of Alabama generally known as the “Black Belt Region” (Figure 1), which is characterized by gray–black clay-based soils derived from ancient marine sediments (Scarseth 1932). We conducted a survey of private pond owners throughout the study area to determine pond characteristics and uses, management objectives, the management techniques that were used, and owners’ awareness of available pond management services (see the appendix in Haley 2009 for a copy of the survey instrument). Twelve ponds were randomly selected from...
each county using U.S. Geological Survey 7.5-min maps (i.e.,
were randomly selected from those ponds in the county that were
0.4–40 ha in surface area and that were not used for aquaculture
or as water treatment facilities), and pond owner information
was obtained from tax records. Pond owner surveys were con-
ducted by telephone or by mail (if the pond owner requested).
The survey consisted of 18 questions developed to provide in-
formation regarding physical pond characteristics, pond use,
applied management techniques and goals, owner satisfaction,
information sources, and perceived problems. The overall sur-
vey assessment was considered complete once a minimum of
four surveys were completed in each county.

Field sampling.—Based on the results from the pond owner
survey, we evaluated the three most commonly reported pond
management techniques: fertilization, providing supplemental
pellet feed for Lepomis spp., and stocking threadfin shad as
supplemental prey for largemouth bass. Given this, we defined
five management categories as follows:

1. Unfertilized = owner applied no enhancement techniques.
2. Fertilized = owner fertilized.
3. Fertilized and feeder(s) = owner fertilized and applied sup-
   plemental pellet feed (at least one feeder for every 2–4 ha
   of pond surface).
4. Fertilized and shad = owner fertilized and stocked threadfin
   shad.
5. Fertilized, shad, and feeder(s) = owner fertilized, applied
   supplemental pellet feed (at least one feeder for every 2–4
   ha of pond surface), and stocked threadfin shad.

We originally selected 50 ponds stocked with largemouth
bass and Lepomis spp. for fish collection and assessment based
on surface area (2–16 ha), time of stocking (≥5 years), and
the management techniques that were being applied. We identi-
fied a minimum of five ponds for each management category. Ponds
stocked with other fish species, such as tilapia Oreochromis spp.,
crappies Pomoxis spp., and hybrid sunfish (various crosses of
Lepomis spp.), were not included in the field collections.

Suitable ponds were identified through our telephone surveys
as well as by personnel with the Alabama Division of Wildlife
and Freshwater Fisheries, Alabama Cooperative Extension Sys-
tem, and Alabama Natural Resources Conservation Service. The
final number of replicates totaled 66 and was unbalanced across
the five management categories because the owner descriptions
of the management techniques that we obtained from the survey
did not always match the actual applied management practices.
Selected ponds were each evaluated once, either in fall 2007 or
spring 2008. The sampling period for each management cate-
gory was as follows: category 1 = 5 ponds sampled in the fall
and 11 ponds sampled in the spring; category 2 = 7 in the fall
and 8 in the spring; category 3 = 7 in the fall and 4 in the spring;
category 4 = 8 in the fall and 4 in the spring; and category 5 =
4 in the fall and 8 in the spring.

For each pond, boat-mounted, pulsed-DC electrofishing
(Smith-Root DC electrofisher, 5.0 GPP) was used in three 15-
min transects or until transects overlapped. In order to collect a
representative sample of the fish community in each pond, elec-
trofishing transects were selected to include each of three habitat
types— the dam area, shallow/littoral habitat, and intermediate
depth/offshore habitat. In each pond, we attempted to collect a
minimum of 50 largemouth bass and 100 Lepomis spp., and the
presence of threadfin shad was confirmed for those impound-
ments classified as containing threadfin shad. Each individual
was measured (TL; mm) and weighed (wet weight; g). When
permitted by the pond owner, 10 largemouth bass in each 50-
mm length-group from 100 to 350 mm were placed on ice and
returned to the laboratory for age and growth assessment. All
other fish were returned to the pond.

On the same day as the fish collections, water samples were
collected and taken to the laboratory where we measured the
chlorophyll-a concentration, turbidity, total alkalinity, and hard-
ness. Chlorophyll a was measured by filtering the water using
glass fiber filters. The filters were frozen and later thawed and
the chlorophyll a extracted for 24 hr using 95% ethanol. Flo-
rescence of the extract was read using a Turner Aquafuor fluo-
rometer. Turbidity was measured using a nephelometer (NTU;
HG Scientific, Inc.), and Secchi depth was recorded (0.1 m).

In the laboratory, the sagittal otoliths of largemouth bass were
removed, cleaned, dried, and stored in 10-mL plastic vials. Two
readers independently estimated age from each otolith in whole
mount, and the distances from the focus to each annulus and the
posterior-most end were measured (0.0001 mm). For fish
age 5 or older, otoliths were embedded in two-part epoxy and
sectioned using a low-speed diamond wheel saw (South Bay
Technology Model 650). Back-calculated total length at age to
the last annulus for each fish was estimated using the direct
proportion method (Le Cren 1947). Since pond owners rarely
allowed the harvest of sunfish, otoliths were not available to
permit estimation of the age and growth of bluegills and redbreast
sunfish L. microlophus. We evaluated fish condition, relative
abundance, and size structure for all ponds. Relative weight
(Wr) was calculated for each largemouth bass and Lepomis spp.
collected (Wege and Anderson 1978). The relative abundance of
largemouth bass and Lepomis spp. was calculated for each pond
(CPUE; catch/h). The proportional size distribution (PSD) (for-
merly proportional stock density; Guy et al. 2007) and the PSDs
for preferred (PSD-P) and memorable (PSD-M) sizes were es-
estimated for the largemouth bass and bluegills in each pond. The
values of PSD and PSD- P -M were compared with published
values for indices associated with ponds that are in balance
(sensu Swingle 1950) or that have either overly abundant preda-
tor or prey fish populations (Willis et al. 2010).

Statistical analyses.—A one-way analysis of variance
(ANOVA) was used to examine the differences in CPUE (loge
transformed), Wr, and water quality characteristics (i.e., Sec-
chi depth, turbidity, chlorophyll-a concentration, alkalinity, and
hardness) among management categories (PROC GLM; SAS
2008). Fisher’s least significant difference procedure was used
to test for post hoc differences among means when ANOVA
indicated differences among management categories ($\alpha = 0.05$). Differences in the size structures of largemouth bass and bluegills across management categories were examined using a Kruskal–Wallis test (PROC NPAR1WAY; SAS 2008). Correlation analysis was used to examine the relationships between CPUE and $W_r$, CPUE and mean length at age 2 (MLA-2), $W_r$ and MLA-2, and water quality characteristics and CPUE (PROC CORR; SAS 2008).

Largemouth bass PSD-P and bluegill PSDs were transformed using the logit function (Berkson 1944), namely,

$$ \logit(p) = \log_e \left( \frac{p}{1-p} \right), $$

where $p$ is the probability of a stock size fish being greater than a particular length of interest (e.g., preferred or quality length). Logit-transformed size distribution indices were then compared among management categories using a one-way ANOVA.

The MLA-2s, as estimated from back-calculations from the otolith measurements, were used to characterize largemouth bass growth because some pond owners did not permit collection of largemouth bass longer than 350 mm. Harvesting larger fish would have been necessary to estimate growth in older cohorts. Estimating growth for younger fish was not possible because it was likely that the slower-growing fish in the cohort would not have fully recruited to the electrofishing samples. Differences in largemouth bass growth across management categories were tested by resampling the data and estimating bootstrap means and confidence intervals of MLA-2.

**RESULTS**

**Pond Owner Survey**

Of the 276 randomly selected private-pond owners, 160 in 23 central Alabama counties were contacted by telephone and 135 surveys were completed (Figure 1). Ponds served a wide range of uses, with the most common being recreational fishing (82% of those surveyed), followed by livestock watering (24%) and aesthetics (19%). Thirty-eight percent of the contacts reported that their pond served multiple uses, and 8% reported that their pond provided a source of income by leasing ($n = 6$), aquaculture ($n = 3$), or pay-to-fish operations ($n = 2$).

For those ponds that served as a source of recreational fishing, largemouth bass, *Lepomis* spp., and channel catfish *Ictalurus punctatus* were the three primary fish species stocked. Seventy-four percent of the ponds were managed by their owner, 13% were not managed by anyone, and 7% were managed by private pond consultants. Friends and family (20%), Alabama Cooperative Extension county or regional agents (19%), Alabama Division of Wildlife and Freshwater Fisheries (11%), and Auburn University (11%) were the most commonly reported sources of pond management information, with 16% not using any pond management information resources. While Auburn University and the Alabama Cooperative Extension System are likely the same source of information, these were separated because pond owners are sometimes unfamiliar with this distinction.

The most common management technique applied by pond owners was fertilization (48%). Those respondents that fertilized ($n = 66$) reported doing so based on water clarity ($n = 39$), a time schedule ($n = 21$), at irregular intervals ($n = 4$), or by some other indication/time frame ($n = 2$). No need ($n = 20$), inconvenience ($n = 16$), and cost ($n = 12$) were the primary reasons that the other 52% of pond owners did not fertilize. The next most common management techniques used by pond owners were providing supplemental pellet feed (45%) and stocking supplemental prey for largemouth bass (12%). Those that stocked supplemental prey most often stocked threadfin shad ($n = 5$). Most pond owners (93%) did not keep fish harvest records.

Most respondents (52%) reported that their management strategy was to maintain “general balance” (this was the response provided by survey respondents with no definition offered), 11% managed for “trophy bass,” and 24% reported that they did not have a management strategy. The five most highly ranked pond problems reported by pond owners were slow largemouth bass growth, filamentous algae, beavers or muskrats, poachers, and slow *Lepomis* spp. growth. Fifty-one percent of pond owners had never checked the balance of their pond’s fish community (as per Swingle 1950), and 54% had never checked their pond’s water quality. Seventy-six percent reported that they would have fully recruited to the electrofishing samples. Differences in largemouth bass growth across management categories were tested by resampling the data and estimating bootstrap means and confidence intervals of MLA-2.

**Pond Sampling**

Upon sampling, it was clear that approximately 25% of the owners misclassified the pond management techniques that they actually used (e.g., owners claimed to apply pellet feed but had not purchased feed in years or owned feeders that were obviously long out of commission; owners claimed to fertilize ponds that had actually not been fertilized in decades; or owners claimed to have stocked threadfin shad into ponds that did not contain threadfin shad). In such cases, the ponds were either “extremely happy” or “generally satisfied” with the condition of their pond.
management strategy, more ponds had the combination of largemouth bass PSD-P and bluegill PSD typical of balanced conditions. Logit-transformed largemouth bass PSD-Ps differed among management categories (ANOVA; $F = 3.93$, df = 4, 61, $P = 0.0067$); ponds with management techniques that included threadfin shad had significantly greater occurrences of quality-and preferred-size largemouth bass than did ponds with treatments that did not (Figure 3). Logit-transformed bluegill PSDs did not differ among management categories. Logit-transformed PSD-Ms did not differ among management categories for largemouth bass or bluegills.

**CPUE.**—Electrofishing CPUE differed significantly among management categories for stock- (ANOVA; $F = 2.76$, df = 4, 61, $P = 0.036$), quality- ($F = 6.59$, df = 4, 61, $P = 0.0002$), preferred- ($F = 10.23$, df = 4, 61, $P < 0.0001$), and memorable-size ($F = 4.81$, df = 4, 61, $P = 0.0019$) largemouth bass and for stock- ($F = 6.44$, df = 4, 61, $P = 0.0002$), quality- ($F = 8.51$, df = 4, 61, $P < 0.0001$), preferred- ($F = 5.24$, df = 4, 61, $P = 0.0011$), and memorable-size ($F = 4.74$, df = 4, 61, $P = 0.0022$) bluegills. Ponds with threadfin shad had greater CPUEs of quality-, preferred-, and memorable-size largemouth bass and of stock-size bluegills. The CPUEs of quality-, preferred-, and memorable-size bluegills were significantly lower for unmanaged ponds than those that were managed (Figure 4).

**Growth.**—Monte Carlo simulations of largemouth bass bootstrapped MLA-2 differed among management categories (Figure 5). The unmanaged and fertilized-and-feeder categories had significantly lower MLA-2 than the fertilized, fertilized-and-shad, and fertilized-shad-and-feeder categories (Figure 5).

**Relative weight.**—Largemouth bass mean $W_r$ differed significantly among management categories, with largemouth bass in ponds containing threadfin shad having the highest $W_r$ values (ANOVA; $F = 4.02$, df = 4, 61, $P = 0.0058$, Figure 6). Bluegill mean $W_r$ did not differ among management categories. The mean $W_r$s of bluegills and largemouth bass were not correlated. Largemouth bass mean $W_r$ was positively correlated with largemouth bass MLA-2 when all management categories were combined ($r = 0.64$, df = 50, $P < 0.01$; Figure 7A). When the management categories were examined separately, this relationship remained significant only for fertilized ($r = 0.69$, df = 12, $P = 0.009$) and fertilized-shad-and-feeder categories ($r = 0.77$, df = 8, $P = 0.009$).

The CPUE and mean $W_r$ for stock-size bluegills were not correlated when all management categories were combined. When management categories were examined separately, CPUE and $W_r$ were negatively correlated only for the fertilized-shad-and-feeder management category ($r = -0.59$, df = 8, $P = 0.05$). The log-transformed mean CPUE and mean $W_r$ were positively correlated in the fertilized-shad-and-feeder management category ($r = 0.69$, df = 8, $P = 0.029$).
correlated for preferred-size (≥380-mm) largemouth bass \(r = 0.54, \text{df} = 64, P < 0.0001\) when all management categories were combined (Figure 7B). When examined separately, the relationship was significant only for the fertilized \(r = 0.52, \text{df} = 13, P = 0.05\) and fertilized-and-feeder categories \(r = 0.61, \text{df} = 9, P = 0.05\).

The mean CPUE and MLA-2 of preferred-size largemouth bass were positively correlated \(r = 0.53, \text{df} = 50, P < 0.0001\) when all management categories were combined (Figure 7C). When management categories were examined separately, the relationship remained significant only for the fertilized category \(r = 0.67, \text{df} = 11, P = 0.01\).

**Water Quality Characteristics**

Hardness \(F = 2.8, \text{df} = 4, 61, P = 0.03\), chlorophyll-\(a\) concentration \(F = 3.65, \text{df} = 4, 61, P = 0.0099\), and Secchi depth \(F = 9.15, \text{df} = 4, 61, P < 0.0001\) differed significantly among management strategies, while alkalinity, turbidity, and maximum depth did not. Hardness and chlorophyll-\(a\) were significantly lower and Secchi depth was significantly greater in unmanaged ponds than with other management strategies (Figure 8). The CPUE of stock-size bluegills was positively correlated to alkalinity \(r = 0.33, \text{df} = 64, P = 0.006\) and negatively correlated to Secchi depth \(r = -0.42, \text{df} = 64, P = 0.0005\). Chlorophyll-\(a\) concentration was positively correlated with pond alkalinity \(r = 0.26, \text{df} = 64, P = 0.04\).

**DISCUSSION**

**Pond Owner Survey**

We found that fertilizing, applying pellet feed, and stocking threadfin shad were the three most common pond
management techniques that owners used in an effort to maintain and enhance quality fishing. Most private-pond owners in central Alabama wanted to maintain “generally balanced” largemouth bass and bluegill populations and were “generally satisfied” or “extremely happy” with the condition of their ponds. Similar responses were collected from an Internet survey of Texas pond owners (Masser and Schonrock 2006). Many pond owners failed to use techniques, tools, and information sources that could have been helpful in the proper management of their ponds. For example, nearly all pond owners failed to maintain fish harvest records despite the importance of fish harvest to pond management (Gabelhouse 1987; Coble 1988; Guy and Willis 1990), and less than half of the pond owners had ever checked the water quality in their pond. Because so few owners maintained harvest records, it was impossible for us to quantify harvest. Had we anticipated a lack of harvest records, we could have asked how frequently a pond was fished to obtain an indicator of fishing pressure.

Pond owners had numerous public and private resources from which to gather management information. Some pond owners obtained information from trained professionals (i.e., Cooperative Extension, universities, state management agencies, and private consultants); however, a significant proportion used either “family and friends” (who may not provide science-based pond management information) or no pond management information at all. These responses suggest an ongoing need to inform pond owners and managers about the availability of accurate, reliable, and easily accessible information sources.

**Pond Sampling**

Although most pond owners claimed that they were generally satisfied with the state of their ponds, our field survey indicated that the management goals of most pond owners were not being achieved. The variation in the combined largemouth bass PSD-P versus bluegill PSD both among and within management categories demonstrates that no single management or enhancement strategy is guaranteed to produce good growth and recruitment in fish populations in recreational largemouth bass and bluegill ponds. Most ponds exhibited low largemouth bass PSD-P and moderate to high bluegill PSD, an indication of largemouth bass crowding.

Largemouth bass PSD generally did not indicate populations that were suffering from overcrowding and density-dependent growth because the minimum length for quality-size fish (300 mm) was too small to be a stock-size delimiter for these southeastern U.S. systems. For example, based on the PSDs for largemouth bass, most ponds appeared to be in a balanced or trophy state; but this was obviously not the case when other population characteristics (growth, condition, etc.) were taken into account. We found that largemouth bass PSD-P more accurately represented the condition of largemouth bass population states.
To maintain increased density of largemouth bass larger than the preferred length of 380 mm requires a sufficient biomass of prey fish of appropriate sizes to support the growth of these larger fish.

Our analysis suggests that stocking threadfin shad in conjunction with fertilization has greater potential to improve or maintain largemouth bass population characteristics than the other most common management techniques examined here. The fertilized-and-shad and fertilized-shad-and-feeder categories yielded the highest largemouth bass PSD-Ps and led to higher probabilities of largemouth bass populations with PSD-P $\geq 10$ (i.e., balanced or trophy state) than the other management categories. Ponds with threadfin shad had the greatest electrofishing CPUE of quality-, preferred-, and memorable-size largemouth bass, produced the largemouth bass length frequency distributions most skewed toward large fish, and exhibited some of the highest growth and body conditions of any management strategy we sampled.

Previous research has demonstrated that threadfin shad can have negative effects on sport fishes, including reductions in largemouth bass recruitment through direct competition with larval largemouth bass or indirectly via competition with bluegills (Tharratt 1966; Miller 1971; DeVries et al. 1991). For this reason, pond managers are hesitant to recommend stocking threadfin shad. However, our results did not indicate a decline in largemouth bass or bluegill catch rate when threadfin shad were present, nor did we find any negative effects on bluegill size structure, CPUE, $W_r$, and PSDs, which were all similar across all fertilized and threadfin-shad-enhanced ponds. Given this, we conclude that threadfin shad did not negatively affect bluegills in fertilized ponds. However, we recognize that the ponds we sampled that were stocked with threadfin shad were significantly larger in surface area than the ponds with other management strategies. Threadfin shad are generally recommended for stocking and are more sustainable in larger ponds (Wright and Kraft 2012). This larger pond size is a potential bias in our sampling and may have influenced the population characteristics of largemouth bass and bluegills. A careful study of the effect of pond size on pond dynamics is warranted.

The positive relationships for largemouth bass between CPUE and $W_r$ and between CPUE and MLA-2 indicated that the management techniques increased density while maintaining growth and body condition. Unmanaged ponds yielded length frequency distributions that were more skewed toward small fish than those of any other treatment, as well as having the lowest catch rates of stock-, quality-, and preferred-size bass. This demonstrates the potential impact of fertilization, especially in low-fertility systems. It is also important to note that owners who are willing to invest in enhancement techniques are more likely to perform routine maintenance on their ponds than are owners who are less willing to invest in such techniques. For example, ponds with enhancements may be more likely to have basic management such as weed control and regular harvest.

FIGURE 7. Relationships between (A) largemouth bass back-calculated mean length at age 2 and mean relative weight, (B) the mean log-transformed CPUE of preferred-size largemouth bass and mean relative weight, and (C) the mean log-transformed CPUE of preferred-size largemouth bass and back-calculated mean length at age 2. Each point represents a single pond.
FIGURE 8. Chlorophyll-a concentration, hardness, Secchi depth, and surface area of ponds by management category. Categories with the same letter are not significantly different ($P > 0.05$).

Because bluegill population metrics (length frequency distribution, CPUE, $W_r$, and PSD values) were similar among all fertilized ponds, pellet feeding at the rates examined in our field survey appeared to provide few measurable benefits to bluegills. The probability of the occurrence of trophy-size bluegills ($PSD \geq 60$) tended to be higher in the fertilized-and-feeder category than in ponds that contained threadfin shad, a possible indication that pond owners who chose to enhance their ponds with fertilizer and pellet feeding were more oriented toward bluegill management than those that stocked threadfin shad. This would also help to explain the low CPUE of quality- and preferred-size largemouth bass and the lowest MLA-2 in the management strategy using fertilizer and feed. The increase in bluegill metrics in the fertilized management categories over the unmanaged category provides evidence that fertilization can increase the density of stock-, quality-, and preferred-size bluegills.

The lack of effects of pellet feeding on bluegills may have resulted from variation in the feeding rate. The rate at (kg/ha) and duration over which (months–years) pellet feed is delivered to ponds would certainly affect the magnitude of response of the fish populations. It is also possible that the majority of bluegills sampled (average length, 116 mm) were not able to eat the pellet feed because of gape limitation. Because feeding rates were often unknown and perhaps variable within a pond, our ability to assess the influence of pellet feeding was limited. We do believe that pellet feeding can have positive value to pond owners, if for no other reason than that the feeding attracts bluegills and makes them easier for anglers to catch; this response needs to be quantified, however. A more focused experimental approach in which the feeding rate and duration as well as the age and size structure of the fish populations can be controlled will be necessary to better evaluate the effects of supplemental feeding.

Water Quality and Morphological Characteristics

Unfertilized ponds were broadly different from fertilized ponds in that they had significantly greater Secchi depths (an
indication of lower fertility) than any of the other management types. Secchi depth was the main factor correlated to the probability of whether a pond possessed the fish length distributions characteristic of a balanced pond (i.e., largemouth bass PSD-Ps ≥ 10 and bluegill PSDs ≥ 20). Interestingly, no other water quality or pond morphological characteristic was significantly related to balanced largemouth bass and bluegill communities. When Secchi depth was within the depth recommended by the Alabama Cooperative Extension System (0.46–0.61 m; Wright and Masser 2004), the probability of balance averaged 52%. Fertilization controlled by monitoring Secchi depth is one of the most common and cost-effective management techniques for recreational fishing ponds. Importantly, 71% of the pond owners in this study who maintained Secchi depths between 0.46 and 0.61 m also had their ponds checked for balance, and 64% had water quality checks performed, all indicators of routine quality management.

Management Implications

The phone survey indicated that although pond owners were satisfied with their management efforts, the reality was that the resulting fish population was not meeting their management goals. Additionally, the phone survey provided an indication of the inaccuracy of human memory, demonstrating the importance of record keeping. Survey responses often did not reflect actual pond management.

When assessing largemouth bass populations in recreational fishing ponds, managers should consider using PSD-P rather than PSD, especially in the southeastern USA. PSD clearly did not accurately convey the population state of the largemouth bass in the ponds we sampled. Such indices were developed with northern populations and need to be adjusted for use in warmer climates where fish populations exhibit increased growth. Managers that use PSDs for largemouth bass in warmer climates are at risk of inaccurately assessing their stocks. Although size distribution indices hold tremendous value throughout the USA, their use and interpretation must be adjusted regionally.

Given the variability that we found for bluegill and largemouth bass populations, it is clear that the pond management enhancement techniques of fertilizing, applying pellet feed, and stocking threadfin shad cannot by themselves consistently produce and maintain ideal fish size structure, growth rate, and catch rate in ponds. However, the techniques of fertilizing and stocking threadfin shad did lead to an increased probability of pond owners reaching their pond management goals, which typically includes an increased number and quality of fish caught (Hampton and Lackey 1976). Stocking threadfin shad did not cause evident negative effects on bluegill size and condition indices. Additional techniques are certainly important in managing fishes in ponds, such as consistent and adequate harvest of largemouth bass, the maintenance of water quality, and appropriate aquatic macrophyte control; however, the interaction of these practices with the enhancement techniques from this study requires further assessment. Through better understand-

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Frequency of Strong Year-Classes: Implications on Fishery Dynamics for Three Life History Strategies of Fishes

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ARTICLE

Frequency of Strong Year-Classes: Implications on Fishery Dynamics for Three Life History Strategies of Fishes

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Abstract

Many studies have examined variation in year-class strength and associated density-dependent growth of fishes. Few studies, however, have considered the effects of these factors on fishery quality. We examined how the frequency of strong year-classes affects fish harvest and size structure for three species with varying life histories. We modeled both random and systematic occurrences of strong year-classes for white bass \textit{Morone chrysops} (short-lived species), largemouth bass \textit{Micropterus salmoides} (species with intermediate longevity), and blue catfish \textit{Ictalurus furcatus} (long-lived species). For white bass and largemouth bass, intermediate frequencies of strong year-classes (i.e., every 3–10 years) incrementally reduced harvest but improved the proportional size distribution (PSD) under current fishing regulations. The greatest improvements in PSD with minimal effects on harvest (relative to annual strong year-classes) occurred when strong year-classes were produced every 3 years for white bass and every 5 years for largemouth bass. In contrast, production of strong blue catfish year-classes every 6 years maximized harvest and resulted in a fivefold increase in PSD relative to a strong year-class frequency of every 1–2 years. Greater annual consistency in harvest and PSD for fishes with intermediate and high longevity was achieved when strong year-classes occurred systematically rather than at random. Our results suggest that intermediate frequencies of strong year-class production, relative to species longevity, serve to balance harvest and size structure characteristics. The use of fish stocking or water level manipulations to systematically produce strong year-classes can also improve the consistency of annual harvest and size structure for longer-lived fishes (>10 years).

Year-class strength has been the focus of many studies (e.g., Kramer and Smith 1962; Wahlburg 1972; Mitzner 1991; Sammons et al. 2002; Quist 2007). Past research has identified positive relationships between year-classes and hydrology (e.g., reservoir water levels and inflow). Strong year-classes often occur when rising water levels inundate new spawning and rearing habitat (Aggus and Elliot 1975; Timmons et al. 1980; Miranda et al. 1984; Meals and Miranda 1991), whereas poor year-classes can result when water levels fall below average (DiCenzo and Duval 2002). An understanding of factors regulating year-class strength and quantification of the effects of year-class variability are critical for identifying fish population trends (Quist 2007) and appropriate management actions.

Past studies of year-class variation suggest that both infrequent (i.e., every 10–20 years) and frequent (i.e., annual) strong year-classes influence the abundance and size structure of fish stocks. Infrequent strong year-classes create harvestable stocks that are dependent on fewer cohorts (Colvin 1991). For example, Beam (1983) reported that white crappies \textit{Pomoxis annularis} in Kansas reservoirs were dominated by one year-class, resulting in highly variable harvests. In contrast, consistently strong year-classes result in greater fish abundance but reduced growth. Gabelhouse (1984) reported that largemouth bass \textit{Micropterus salmoides} smaller than quality length (i.e., 300 mm) were abundant in Kansas systems due to consistently high recruitment. Buynak and Mitchell (2002) found that smallmouth bass \textit{Micropterus dolomieu} exhibited poor size structure due to an overabundance of sublegal fish. Because both abundance and size structure contribute to fishery quality (Anderson and Neumann 1996), the results of these prior studies suggest that

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an intermediate frequency of strong year-classes can provide a management approach that balances harvest and size structure.

Reservoir water resources are increasingly restricted due to human population growth (Allen et al. 2008). In addition, climate changes are expected to increase the severity of drought and flood events (Meehl et al. 2004; Stainforth et al. 2005; Allen et al. 2008); hence, the water levels favoring strong year-classes may occur less often. Research efforts to date have quantified year-class variability, but few studies have considered how the frequency of strong year-classes affects fisheries. Keith (1975) recommended systematic reservoir water level increases for producing a strong largemouth bass cohort every 3–5 years. In contrast, Groen and Schroeder (1978) reported an increased relative abundance of white crappies with annual strong year-classes. Such interspecific differences likely relate to variations in life history (e.g., longevity, mortality, and growth) and fishery characteristics (e.g., exploitation rate). Short-lived, highly exploited species may benefit from more frequent strong year-classes, whereas longer-lived species with lower exploitation may sustain quality fisheries even when strong year-classes are less frequent. Species-specific information would aid in determining how often strong year-classes are needed to maintain or enhance recreational fisheries. Therefore, the objective of our study was to examine how the frequency of strong year-classes affects fish harvest and size structure for three species with differing life histories. We modeled (1) random intervals between strong year-classes, with the frequency of strong year-classes mimicking typical environmental control; and (2) systematic (i.e., fixed) intervals between strong year-classes for systems in which water level manipulation or stocking can be used to influence recruitment. Our a priori hypotheses were that (1) an intermediate frequency of strong year-classes would serve to balance population abundance and size structure and (2) systematic strong year-classes would reduce variability, resulting in harvest and population size structure that are more consistent from year to year. Our modeling results can be used to develop management plans that maximize fishery benefits.

**METHODS**

**Model Species**

We selected three sport fishes with contrasting life histories to examine how the frequency of strong year-classes affects fishery characteristics. White bass *Morone chrysops* represented short-lived species, for which typical longevity is less than 5 years (Muoneke 1994; Colvin 2002; Guy et al. 2002; Lovell and Maceina 2002; Willis et al. 2002) and annual mortality is high (≥50%; Muoneke 1994; Colvin 2002; Schultz and Robinson 2002). We used largemouth bass to represent species of intermediate longevity, characterized by a typical life span of up to 10 years (Heidinger 1976; Carlander 1977) and mean annual mortality between 30% and 50% (Allen et al. 2002; Bulak and Crane 2002; Driscoll et al. 2007). Blue catfish *Ictalurus furcatus* represented long-lived fish species, with a life span of up to 15 years and low total annual mortality (<30%; Boxrucker and Kuklinski 2006).

**Model Description**

We developed an age-structured, dynamic-pool model in R software version 2.12.1 to model the effects of the frequency of strong year-classes on fish harvest and proportional size distribution (PSD; Guy et al. 2007). A hypothetical population of each species was created, and starting values for the number of fish in each age-class were set to represent a population size of 100,000 individuals at equilibrium. For each species and each modeled frequency of strong year-classes, 1,000 iterations were conducted over a 100-year chronology. We modeled recruitment ($R$) as

$$R_{t+1} = 100,000 \cdot (1 - S) \cdot \theta,$$

where $S$ is species-specific annual survival and $\theta$ is an exponential population growth function ($e^x$), where $x$ was assigned a bounded, random value corresponding to the occurrence of a weak, average, or strong year-class. Average year-class strength was defined as production that maintained the population near equilibrium (i.e., 61–160% of the number of recruits at equilibrium; $x$ was drawn from a uniform distribution spanning [−0.5, 0.5]). Weak year-classes were defined as 14–61% of average recruitment (i.e., $x$ was drawn from a uniform distribution spanning [−2, −0.05]). Strong year-class production was defined as 160–739% of average production (i.e., $x$ was drawn from a uniform distribution spanning [0.5, 2]). Bounds for weak, average, and strong year-class production were based on the magnitude of variability in year-class strength for these species in five Texas reservoirs as determined by Smith et al. (2009). Random variation in strong year-class frequency was modeled by using a vector of 100 randomly drawn year-class strength values based on the average frequency of strong year-classes simulated. For example, to model the production of a strong year-class occurring every 3 years on average, we randomly assigned 33 strong year-classes within the 100-year vector. During each of the remaining 67 model years, year-class strength was randomly assigned as either weak or average production. To model systematic strong year-classes, we fixed the occurrence of strong year-classes at each desired interval, with the first strong year-class occurring during the first model year. For each species, we modeled strong year-class frequencies at intervals of 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, and 20 years.

To characterize fish growth in relation to the frequency of strong year-classes and density-dependent effects, von Bertalanffy growth curves (VBCs) were fitted to length-at-age data that were obtained from state agency databases and from the literature for multiple populations of each species (Table 1). Average fish growth was defined by the mean of all growth curves for each species; the mean was calculated by fitting a composite VBC to the mean of fitted lengths-at-age from population-specific VBCs. Slow or fast growth rates were
Density-dependent growth was then characterized by using a growth-at-length model. We assigned one of three growth trajectories (slow, average, or fast), depending upon the total trajectories for the three study species (\( t_0 = \) theoretical time [age] at which fish TL is 0; \( K = \) Brody growth coefficient; \( L_\infty = \) maximum [asymptotic] length). Values used in models for slow, average, and fast growth are denoted by asterisks (* = slow; ** = average; *** = fast).

### TABLE 1. The von Bertalanffy growth parameters used to establish density-dependent growth rates for the three study species

<table>
<thead>
<tr>
<th>Water body</th>
<th>( t_0 )</th>
<th>( K )</th>
<th>( L_\infty ) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>White bass</strong></td>
<td></td>
<td></td>
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<td>-0.496</td>
<td>0.593</td>
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<td>Cedar Bluff, KS(^a)</td>
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<td>454.9</td>
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</tr>
<tr>
<td><strong>Average</strong></td>
<td>-0.777</td>
<td>0.471</td>
<td>416.0</td>
</tr>
</tbody>
</table>

### Largemouth bass

<table>
<thead>
<tr>
<th>Water body</th>
<th>( t_0 )</th>
<th>( K )</th>
<th>( L_\infty ) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amistad, TX(^c)</td>
<td>-0.957</td>
<td>0.198</td>
<td>623.3</td>
</tr>
<tr>
<td>Amon G. Carter, TX(^c)</td>
<td>-0.927</td>
<td>0.311</td>
<td>523.5</td>
</tr>
<tr>
<td>Aquilla, TX(^c)</td>
<td>-0.467</td>
<td>0.338</td>
<td>522.1</td>
</tr>
<tr>
<td>Austin, TX(^c)</td>
<td>-1.558</td>
<td>0.216</td>
<td>533.0</td>
</tr>
<tr>
<td>Bastrop, TX(^c)</td>
<td>-0.178</td>
<td>0.729</td>
<td>439.6</td>
</tr>
<tr>
<td>Bellwood, TX(^c)</td>
<td>-0.147</td>
<td>0.599</td>
<td>447.4</td>
</tr>
<tr>
<td>Brownwood, TX(^c)</td>
<td>-0.949</td>
<td>0.326</td>
<td>452.2</td>
</tr>
<tr>
<td>Buchanan, TX(^c)</td>
<td>-0.293</td>
<td>0.517</td>
<td>504.8</td>
</tr>
<tr>
<td>Canyon, TX(^c)</td>
<td>-0.529</td>
<td>0.524</td>
<td>420.6</td>
</tr>
<tr>
<td>Choke Canyon, TX(^c)</td>
<td>-0.540</td>
<td>0.444</td>
<td>516.7</td>
</tr>
<tr>
<td>Coleman City, TX(^c)</td>
<td>-0.511</td>
<td>0.396</td>
<td>495.9</td>
</tr>
<tr>
<td>Fayette, TX(^c,***)</td>
<td>-1.360</td>
<td>0.328</td>
<td>548.8</td>
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### Blue catfish

<table>
<thead>
<tr>
<th>Water body</th>
<th>( t_0 )</th>
<th>( K )</th>
<th>( L_\infty ) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ellsworth, OK(^d)</td>
<td>-0.665</td>
<td>0.063</td>
<td>898.0</td>
</tr>
<tr>
<td>Eufaula, OK(^d)</td>
<td>-2.526</td>
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<tr>
<td>Hugo, OK(^d)</td>
<td>-0.677</td>
<td>0.214</td>
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<tr>
<td>Kaw, OK(^d)</td>
<td>-0.151</td>
<td>0.136</td>
<td>853.0</td>
</tr>
<tr>
<td>Keystone, OK(^d,***)</td>
<td>-0.919</td>
<td>0.133</td>
<td>860.0</td>
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<td>Texoma, TX–OK(^d)</td>
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<td>0.077</td>
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<td>Waurika, OK(^d)</td>
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<td>1,050.0</td>
</tr>
<tr>
<td>Limestone, TX(^c)</td>
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<td>0.242</td>
<td>648.2</td>
</tr>
<tr>
<td>Buchanan, TX(^c)</td>
<td>-0.900</td>
<td>0.171</td>
<td>641.8</td>
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<tr>
<td>J. B. Thomas, TX(^c,***)</td>
<td>-1.335</td>
<td>0.230</td>
<td>315.4</td>
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<tr>
<td>Lewisville, TX(^c)</td>
<td>-3.302</td>
<td>0.068</td>
<td>491.8</td>
</tr>
</tbody>
</table>

**FREQUENCY OF STRONG YEAR-CLASSES**

The von Bertalanffy growth parameters used to establish density-dependent growth rates for the three study species (\( t_0 = \) theoretical time [age] at which fish TL is 0; \( K = \) Brody growth coefficient; \( L_\infty = \) maximum [asymptotic] length). Values used in models for slow, average, and fast growth are denoted by asterisks (* = slow; ** = average; *** = fast).

selected from available population-specific curves to represent growth that was less than or greater than the mean VBC Brody growth coefficient (\( K \)) and maximum (asymptotic) length (\( L_\infty \)). Density-dependent growth was then characterized by using a growth-at-length model. We assigned one of three growth trajectories (slow, average, or fast), depending upon the total trajectories for the three study species (\( t_0 = \) theoretical time [age] at which fish TL is 0; \( K = \) Brody growth coefficient; \( L_\infty = \) maximum [asymptotic] length). Values used in models for slow, average, and fast growth are denoted by asterisks (* = slow; ** = average; *** = fast).
population size in a given model year. Using the size-at-age data from the VBCs, mean size at age was regressed on mean size at (age + 1) to provide a linear representation of growth for each of the three growth trajectories. The appropriate formula for growth was then selected based on the population size in each simulation year. Fast growth was assigned if the total population size fell below 50,000 fish (i.e., <50% of the population at equilibrium); average growth was assigned at abundances ranging from 50,000 to 150,000; and the slow-growth trajectory was assigned when population abundance exceeded 150,000 fish (i.e., >150% of the population at equilibrium).

Annual mortality was assumed to be constant over time and to be equal for all age-classes; the number of age-classes included in the model varied by species. Total annual mortality and fishing mortality estimates were obtained from the literature (Table 2). Maximum ages were derived from literature-reported total mortality rates (Table 2).

### RESULTS

#### Random Year-Class Models

**White bass.**—Under the random modeling scenarios, white bass harvest was greatest with annual strong year-classes and declined exponentially as the frequency of strong year-classes was reduced to an average of every 2–5 years—a decrease in harvest of about 25% (Figure 1). Further reductions in strong year-class production resulted in minimal (i.e., <10%) additional losses in harvest. Annual harvest variability was lowest when strong year-classes occurred annually or infrequently (i.e., frequency of 10 or 20 years on average), whereas harvest variability was greatest when strong year-class production occurred every 2–5 years on average (Figure 1).
In contrast to harvest, white bass PSD was inversely related to the frequency of strong year-classes. The PSD was lowest (PSD = 29) when strong year-classes occurred annually, whereas PSD increased to 67 when strong year-classes occurred every 5 years on average (Figure 1). Further reductions in the frequency of strong year-classes resulted in an additional 15% increase in PSD (PSD = 77). Similar to annual variance in harvest, annual variability in PSD was lowest when strong year-classes occurred every year or when strong year-classes were produced every 10 or 20 years on average (Figure 1).

Largemouth bass.—Largemouth bass harvest for the random model was greatest with annual strong year-classes (Figure 2) and declined 21% when the average frequency of strong year-classes decreased to every 2 years. However, additional reductions in harvest were minimal (range = 0.8–14%) when strong year-classes occurred every 3–20 years on average. Annual harvest variability was lowest when strong year-classes occurred annually or infrequently, whereas variability was considerably greater when strong year-classes were produced every 2–10 years on average (Figure 2).

Blue catfish.—For the random scenarios, blue catfish harvest was lowest when strong year-classes occurred annually and was greatest when strong year-classes were produced every 6 years on average (Figure 3). Harvest remained relatively constant with further reductions in the frequency of strong year-classes. Annual harvest variability was lowest when strong year-classes occurred annually or infrequently, whereas variability was considerably greater when strong year-classes were produced every 2–10 years on average (Figure 3).

In contrast, largemouth bass PSD was lowest (PSD = 40) when strong year-classes occurred annually, and PSD increased nonlinearly as the frequency of strong year-classes declined (Figure 2). The greatest increase (43%) in PSD occurred when the frequency of strong year-class production declined to an average of every 5 years. Further reductions in the frequency of strong year-classes resulted in an additional 12% increase in PSD. Annual variability in PSD was lowest when strong year-classes were produced annually and peaked when strong year-class frequency averaged every 3 years (Figure 2).

Blue catfish.—For the random scenarios, blue catfish harvest was lowest when strong year-classes occurred annually and was greatest when strong year-classes were produced every 6 years on average (Figure 3). Harvest remained relatively constant with further reductions in the frequency of strong year-classes. Annual harvest variability was lowest when strong year-classes occurred annually or infrequently, whereas variability was considerably greater when strong year-classes were produced every 2–10 years on average (Figure 3).

Similar to harvest, blue catfish PSD was also lowest (PSD = 1) with annual strong year-classes. The greatest increases (up to 1,400%) in PSD occurred as the frequency of strong year-classes declined to every 7 years (PSD = 15), and an additional 27% increase in PSD occurred when strong year-class frequency decreased to every 8–20 years (PSD = 19; Figure 3). Annual variance in PSD was also lowest when strong year-classes occurred annually, and variance increased ninefold as the production of strong year-classes declined to an average frequency of every 7 years (Figure 3).
FIGURE 2. Relationships between harvest or proportional size distribution (PSD) index (with associated variances) for largemouth bass and the frequency of strong year-classes under random (left panel) and systematic (right panel) modeling scenarios.

FIGURE 3. Relationships between harvest or proportional size distribution (PSD) index (with associated variances) for blue catfish and the frequency of strong year-classes under random (left panel) and systematic (right panel) modeling scenarios.
Systematic Year-Class Models

White bass.—The response of white bass harvest to systematic strong year-class production was similar to the response in random model simulations (Figure 1). Harvest was greatest with annual strong year-classes and declined exponentially with reduced frequencies of strong year-classes. However, the white bass harvest response to the systematic occurrence of strong year-classes every 2–5 years was slightly greater than harvest under random modeling of the same frequencies. Harvest variance also followed a similar trend. Population size structure and corresponding annual variation under systematic strong year-classes did not differ from those observed in random model simulations (Figure 1).

Largemouth bass.—Harvest of largemouth bass responded differently to systematic strong year-classes in comparison with random model results. Although absolute numbers of fish harvested were comparable and the greatest harvest occurred with annual strong year-classes as observed in the random model, the systematic production of strong year-classes every 4 years resulted in a local maximum in harvest (Figure 2). In addition, for systematic strong year-classes occurring every 2–6 years, the annual harvest variability was 10–59% lower than random model responses (Figure 2). Despite the observed differences in harvest between the random and systematic model scenarios, the differences in PSD were negligible (Figure 2).

Blue catfish.—The harvest of blue catfish under systematic strong year-class scenarios followed trends that were similar to those observed for the random model. Harvest was maximized when strong year-classes occurred every 6 years (Figure 3). For a majority of the strong year-class scenarios modeled, annual variance in harvest was greatly reduced under the systematic model in comparison with the random model. The systematic production of strong year-classes every 2–10 years resulted in an 8–56% reduction in harvest variance relative to random model results for the same frequencies (Figure 3). Similar to our observations for the other species examined, blue catfish population size structure as indexed by PSD was similar between the random and systematic model scenarios. However, as was observed for harvest variance, the PSD variance was considerably reduced under the systematic model (Figure 3).

DISCUSSION

Our modeling results generally supported our hypotheses; relative to annual strong year-classes, moderate frequencies of strong year-classes reduced harvest but improved population size structure for fishes of short and intermediate longevity. In contrast, for a long-lived fish species, moderate frequencies of strong year-classes improved both metrics. In comparison with random models, the systematic production of strong year-classes provided more consistent annual harvest and size structure for the intermediate- and long-lived species; however, this result was not observed for the short-lived species.

Maximization of catch rates and fish size for anglers is a common goal of fisheries managers (Colvin 2004). Walters and Post (1993) suggested that managers may need to seek a compromise between fewer large fish and more abundant small individuals. Our results support their contention. For fishes of short and intermediate longevity, improvements in abundance and size structure were mutually exclusive. Many previous studies have reported that increased fish density lowers individual growth and maximum size due to greater competition (e.g., Bowen et al. 1991; Walters and Post 1993; Lorenzen and Enberg 2001; Pope et al. 2004). Therefore, more frequent production of strong year-classes without compensatory increases in mortality will reduce the growth and size potential of fishes that are subject to density-dependent growth. This observed tradeoff favors management strategies that provide a balance between abundance and size structure. Alternatively, management approaches favoring one metric over the other may be considered based on species-specific life history traits or angler preferences.

Short-lived, smaller-bodied species are unsuitable for trophy production due to their short life expectancy (Muoneke 1994). White bass fisheries tend to be harvest oriented, as evidenced by higher exploitation (47%: Muoneke 1994; 15–35%: Colvin 2002; 21%: Schultz and Robinson 2002) relative to that observed for longer-lived, larger-bodied species, such as largemouth bass (6–15%: Slipke et al. 2003; 18%: Allen et al. 2008) and blue catfish (8–15%: Graham and Deisanti 1999). Therefore,fishery objectives for short-lived species may focus on maximizing the harvest of quality-length individuals. Previous studies evaluating size structure of popular white bass fisheries have reported PSD values greater than 60% in Nebraska (Bauer 2002) and Missouri (Colvin 2002). Our modeling results indicate that similar PSD values could be achieved while minimizing harvest reductions if strong year-classes of white bass occur every 3 years. Our results reinforce the suggestion by Lovell and Maceina (2002) that the production of strong year-classes every 3–4 years is required to sustain white bass fisheries in Alabama reservoirs.

Angler desires for size and trophy potential place a greater importance on longer-lived, larger-bodied fishes, such as largemouth bass (Quinn 1996; Wilde et al. 1998; Driscoll et al. 2007). Wilde and Ditton (1994) and Wilde (1997) reported that harvest-oriented motivations ranked relatively low among largemouth bass anglers, and Quinn (1996) found that catch-and-release rates of harvestable largemouth bass increased between 102% and 250% in recent decades. Increases of more than 50% in catch-and-release rates have also been reported for other longer-lived, larger-bodied species, including the muskellunge Esox masquinongy (Quinn 1996; Margenau and Petchenik 2003) and some salmonids (Quinn 1996). These angler behaviors and motivations suggest that managers should consider an increased focus on quality-size or trophy objectives. In our study, the greatest improvements in largemouth bass size structure with minimal harvest effects were observed when the frequency of strong year-classes was every 5 years. At lower frequencies, further improvements in size structure were minor. For largemouth

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bass and species with similar life histories, management plans that ensure the production of strong year-classes every 5 years may provide the best balance between size structure and harvest.

For blue catfish, a long-lived species, harvest and size structure mutually benefited from reduced frequencies of strong year-classes in comparison with annual strong year-class production. This result may be attributed to the combined effects of density-dependent growth and an interaction of minimum length limits with the comparatively slow growth rates exhibited by long-lived fishes (e.g., the mean $K$ of blue catfish was 0.108, whereas mean $K$ was 0.471 for white bass and 0.369 for largemouth bass). Slow growth rates for blue catfish were exacerbated by density-dependent effects when strong year-classes were produced frequently, thus resulting in reduced harvest and poor size structure as fewer individuals reached the current Texas minimum length limit (304 mm TL). These results suggest that minimum length limits are counterproductive in reservoirs where recruitment is not limiting. Miranda (1999) suggested that for productive southern U.S. reservoirs, regionwide regulations for catfishes (Ictaluridae) should be avoided in favor of system-specific management. Removal of the minimum length limit in Texas systems would allow the harvest of blue catfish smaller than 304 mm and may increase individual growth and improve population size structure of blue catfish. Wilde and Ditton (1999) reported that blue catfish anglers in Texas identified both harvest and trophy potential as important fishing motives. These results indicate a need for fisheries management plans that consider both harvest and size structure to meet angler expectations. Our model suggested that a strong year-class frequency of every 6 years would maximize blue catfish harvest and would increase PSD fivefold relative to the production of strong year-classes every 1–2 years.

Regardless of life history, annual variation in harvest and size structure was lowest when strong year-classes occurred annually or infrequently (i.e., every 20 years). Annual or infrequent strong year-classes would stabilize recruitment (i.e., consistently high or consistently low), whereas intermediate frequencies result in a mix of strong, average, and poor year-classes and hence greater variability. For all three species, our model results suggested that an intermediate frequency of strong year-classes provided the greatest benefits when a balance between harvest and population size structure is desired. However, these intermediate frequencies were also associated with greater variation. Fishery managers must consider tradeoffs between improvements in harvest and size structure and the variability in these metrics. The reduced variability we observed in the systematic models suggested that management plans promoting strong year-classes at fixed intervals would aid in reducing variability. Reservoir water level manipulations, stocking, or other common practices that are used to influence reproductive success could be employed to schedule the production of strong year-classes so as to maximize fishery benefits and reduce annual variation.

Our model assumed that (1) we accurately represented density-dependent growth effects and (2) our results would be robust to changes in a species’ longevity throughout its geographic distribution. Departures from these assumptions could shift the recommendations regarding the frequency of strong year-classes for a given species. Density-dependent growth has been observed for many species; however, uncertainty remains as to the population-level consequences (Walters and Post 1993). Until species-specific relationships are quantified, density-dependent effects on individual growth must be assumed. We used life spans that are typical of southern U.S. populations, whereas northern populations may reach greater maximum ages. For example, Guy et al. (2002) reported that the maximum age of white bass in southern populations was 5 years, while Willis et al. (2002) found white bass as old as age 14 in South Dakota lakes. Such departures from assumptions would alter our recommendations on the frequency of strong year-classes.

Many studies have quantified variation in year-class strength for fish populations (e.g., Kramer and Smith 1962; Shelton et al. 1979; Beam 1983; Sammons et al. 2002; Paukert and Willis 2004). The results of our study further these efforts by quantitatively examining the effects of variability and the associated role of density-dependent growth on fishery quality. Our model results can be used to quantitatively assess tradeoffs between harvest and size structure and to identify the strong year-class frequency that maximizes fishery benefits.

ACKNOWLEDGMENTS

We thank P. Michaeletz and R. Schultz for providing white bass length-at-age data and J. Schlechte for providing valuable input for model development. Constructive comments on earlier versions of this manuscript were given by A. Barkoh, R. Betsill, K. Bodine, D. Buckmeier, M. Driscoll, J. Schlechte, and M. Quist. Funding for this project was provided through Federal Aid in Sport Fish Restoration Program Grant F-22-D to the Texas Parks and Wildlife Department, Inland Fisheries Division.

REFERENCES

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MANAGEMENT BRIEF

Sex at Length of Summer Flounder Landed in the New Jersey Recreational Party Boat Fishery

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Abstract
Female summer flounder Paralichthys dentatus grow faster than males and experience a lower natural mortality rate. Sex-structured assessment models have been developed for other fishes with sexually dimorphic characteristics to better account for population dynamics. Although a desire exists to develop similar assessment techniques for summer flounder, some requisite data are not available, including the sex of fish that are landed in the recreational fishery. Furthermore, summer flounder recreational landings are constrained within harvest limits almost entirely by minimum size restrictions—a management approach that could place much of the recreational fishing mortality on females. To fill a basic but important data requirement to improve the stock assessment of this species while also providing some insight on how current management strategies might impact the sex structure of the population, we collected data on sex and length of summer flounder (n = 4,437) that were landed in the New Jersey recreational fishery in 2009 and 2010. Females dominated the recreational catch in both years (95% female overall). The proportion of landed fish at a given length that were females was greater at lower latitudes and earlier in the summer; the proportion female at length was greater in 2010 than in 2009. Extensive seasonal, annual, and spatial variability evident over such a local scale suggests a highly dynamic sex dependency in the population dynamics of summer flounder and indicates that a more robust data set covering wider geographic and temporal scales will be necessary before sex-specific landings data can be confidently incorporated into an assessment.

The summer flounder Paralichthys dentatus is managed as a single unit from North Carolina to Massachusetts. This species was severely overfished during the mid-1990s (Terceiro 2002), but management measures introduced at that time subsequently placed the fish on a rebuilding program that is nearing a successful conclusion as of this writing (NEFSC 2008; Terceiro 2010, 2011a, 2011b). One of the challenges faced in the management of summer flounder is the sex ratio and sexual dimorphism of the stock. Female summer flounder grow faster than males (Poole 1961; King et al. 2001) and mature at a larger size than males (Able and Kaiser 1994; Pucker et al. 1999). Younger age-classes have sex ratios that are skewed in favor of males (Smith and Daiber 1977; Morse 1981; Bonzek et al. 2009). The male-skewed sex ratio for young fish may result from temperature-dependent differentiation whereby age-0 individuals that are genetically predisposed to be females (XX) develop as males (Ospina-Ávarez and Piferrer 2008; Colburn et al. 2009), a phenomenon that is widely distributed among this group of flatfishes (Goto et al. 1999, 2000; Yamamoto 1999; Luckenbach et al. 2003). In summer flounder, the male-skewed sex ratio at an early age is reversed as the cohort ages, such that older fish are primarily female. This age dependency in sex ratio is interpreted to mean that female summer flounder experience a lower natural mortality rate than males (Mauner and Wong 2011). Population dynamics models that incorporate sex and age structure have been developed (Wang et al. 2005; Su et al. 2011) and implemented (Clarke and Hare 2006) for other sexually dimorphic fishes. For summer flounder, the age dependency in sex ratio suggests that the population’s natural mortality rate is higher than would be inferred from the age of the oldest females (see Chapman and Murphy 1965; Hoenig 1983; NEFSC 2008); this supposition would support the use of a sex-structured model for the stock. However, incorporation of sex-specific parameters into a stock assessment model requires information on the sex of fish that are landed in the recreational and commercial fisheries; such data do not presently exist.

As part of the suite of management measures that attempt to keep the spawning stock biomass above a biomass threshold and near a biomass target, landings in the summer flounder recreational fishery are regulated almost entirely by adjusting the minimum size limits (Bochenek et al. 2010; Powell et al. 2010). Use of this management approach with a fish species
typically results in the catch and release of large numbers of smaller fish (Allen et al. 2009; Veiga et al. 2011), and the summer flounder is no exception (NEFSC 2008; Bochenek et al. 2010). The mortality rate of caught-and-released summer flounder appears to be low, however (Malchoff et al. 2002; Zimmerman and Bochenek 2002; Powell et al. 2011), and mortality is more common among larger animals due to a higher occurrence of deep-hooking (Powell et al. 2011), which is a common outcome in recreational fisheries (Alós et al. 2008, 2009; Veiga et al. 2011). Although high discard of smaller fish is not a trivial concern in the management of summer flounder, a second and possibly more serious concern is the large fraction of recreational fishing mortality that is potentially being directed at the female portion of the summer flounder stock—possibly with serious alterations in population sex ratio, population fecundity, or both. Sex-at-age ratios differing from 1:1 (male : female) may introduce significant challenges to stock sustainability that cannot be resolved by standard modeling approaches (Rago et al. 1998; Brooks et al. 2008; Wilderbuer and Turnock 2009; Su et al. 2011). Unfortunately, no data are available for determining the extent to which summer flounder recreational landings are skewed toward females.

In New Jersey, summer flounder are highly sought by recreational anglers (Bochenek et al. 2010). The fishery is prosecuted along the state’s entire coast. In 2009 and 2010, anglers in New Jersey landed more summer flounder than anglers in any other state in the mid-Atlantic region of the USA (National Marine Fisheries Service, Fisheries Statistics Division, personal communication). To determine the degree to which the sex ratio of landings in the New Jersey recreational fishery is skewed toward females, we implemented a 2-year, statewide data collection program that was focused on the party boat sector of the fishery. The program provides the first data set describing the sex ratio of summer flounder landed in the recreational fishery and documents local spatial and temporal trends in sex at length for these landings. Our results have implications for the current regulatory approach, which restricts landings to only the largest fish in the population and hence potentially directs the recreational catch toward the female portion of the stock.

METHODS

Field sampling program.—Recreational fishing vessels at five ports in New Jersey (Figure 1) were asked to donate summer flounder racks (filleted carcasses) during the 2009 and 2010 recreational fishing seasons. To maximize the number of fish sampled, we chose ports that had the highest number of party boats targeting summer flounder. In 2009, rack collection began on June 22 (4 weeks into the recreational fishing season) and continued until the fishery closed on September 4. In 2010, racks were collected for the entire fishing season (May 29–September 6). Thirteen vessels participated in the program in both years; the vessels ranged in size from 18 to 27 m and ranged in capacity from 49 to 150 passengers.

In 2009 and 2010, observers went to each port once per week to collect racks of all summer flounder that were caught on that day by all participating boats. Boat captains and crews saved the racks in a bin; upon arrival at the dock, the observer collected the racks and recorded the date and the port. In 2010, to increase the number of racks collected, freezers were placed at each port. For the days on which fresh racks were not collected by an observer (i.e., 6 d per week), the personnel of participating boats were asked to deposit all racks in the freezer at the end of fishing trips occurring on those days. The boat personnel placed the racks in large bags that were tagged with the date of capture and the port name before depositing the racks in the freezer. The freezers were emptied once per week when observers arrived to collect fresh racks. Sampling of all fish that were caught during a fishing trip (i.e., instead of collecting a predetermined number of fish at a given length) ensured that a random and representative sample of summer flounder sexes and lengths landed in the recreational fishery was obtained.

Total length was measured on all fish (i.e., from the tip of the snout to the tip of the caudal fin). Sex was determined by macroscopic examination of exposed gonad on the filleted fish carcasses. Over 99% of all fish collected had intact reproductive organs that were readily visible to the naked eye. To verify that TL measurements from frozen and fresh fish were interchangeable, some of the fresh fish racks were measured, frozen for fixed time intervals, and then re-measured after thawing.
RESULTS

Freezing of the summer flounder racks had a negligible impact on fish TLs (Table 1). The change in length after freezing was 0.27 ± 0.49 cm (mean ± SD). The amount of rack shrinkage was dependent on the number of days the rack was frozen, but the results suggested that maximum shrinkage was reached within 3 d (Table 1). As the change in length of frozen racks is trivial in comparison with the length distributions analyzed in this study, all analyses presented hereafter include data from both fresh and frozen racks.

Overall, 4,437 fish were sampled: 1,296 fish in 2009 and 3,141 fish in 2010. Total sample sizes for each port were 1,328 fish at the Atlantic Highlands, 376 fish at Barnegat Light–Point Pleasant, 2,425 fish at Cape May, and 308 fish at Fortescue. On a monthly basis (both years combined), 747 fish were sampled in June, 2,017 were sampled in July, and 1,673 were sampled in August. Female fish vastly outnumbered males (95% of landed fish were female) at all sizes, in both years, and at all ports (Table 2).

The sex ratio of landings was significantly influenced by fish TL (P < 0.0001), port (P < 0.0001), year (P < 0.0001), and month (P = 0.0013; Table 3). There were no significant interactions between TL and any of the main effects. The only significant interaction for main effects was between year and month (P = 0.0001; Table 3). The probability that a summer flounder landed in the recreational fishery was female increased with increasing TL (Figure 2) and was variable in time and space (Figure 3).

Summer flounder that were landed in 2010 were more likely to be female than individuals that were landed in 2009 (P < 0.0001). For fish that were smaller than about 54 cm, more females were landed at a given length in 2010 than in 2009 (Figure 3A). In both years, essentially all of the larger fish landed were females. The probability that a landed summer flounder was female did not vary significantly between July and August (P = 0.1484); however, fish that were caught in June were more likely to be female than fish that were caught in August (P = 0.0004) or July (P = 0.0034). For fish smaller than about 54 cm, the fraction female at length was highest in June and lowest in August (Figure 3B).

The month × year interaction term was significant (P = 0.0001; Table 3). For each of the sampling months, more females were landed in 2010 than in 2009. However, the proportion of landed fish that were males increased over the summer in 2009 but not in 2010 (Table 2). During all three summer months in 2010, 95% or more of the landed fish were females. In contrast, the percentage of landed fish that were female declined during 2009, from 95% in June to 85% in August.

The sex ratio of landed summer flounder did not differ significantly between the two most northerly locations sampled (Atlantic Highlands and Barnegat Light–Point Pleasant; P = 0.4308). The probability that a landed individual was a female was higher at Cape May than at the Atlantic Highlands (P < 0.0001) or Barnegat Light–Point Pleasant (P = 0.0053). Additionally, the likelihood of being female was higher for fish that were landed at Fortescue than for fish landed at any other sampled port, including the Atlantic Highlands (P = 0.0006), Barnegat Light–Point Pleasant (P = 0.0014), and Cape May (P = 0.0107). The probability that a fish landed in the New Jersey recreational fishery was female increased with decreasing latitude (Figure 3C) for fish smaller than about 54 cm, and the degree of change increased with declining size over this latitudinal range such that 45-cm fish landed at the two most northerly ports (Atlantic Highlands and Barnegat Light–Point Pleasant) were more likely to be male than 45-cm fish landed at Cape May. In addition, the Delaware Bay fishery (i.e., landings at Fortescue) was unique in the paucity of landed males at any size—even the minimum landing size (Figure 3C).

Data analysis.—Comparison of sex ratios involved fitting a generalized linear model with a logit-link function and a binomial error distribution (commonly referred to as logistic regression) to the data (Wilson and Hardy 2002). The regression was fitted by use of the LOGISTIC procedure in the Statistical Analysis System version 9.2 (SAS 2008). The probability that a landed fish was female was modeled as the response variable. Main effects included port, year, and month; TL (cm) was included as a covariate. Sex ratio is known to vary with length in summer flounder, so the use of length as a covariate was important to correct for differences in sizes sampled among years, months, and ports. Total sample size was low at the port of Barnegat Light. Data from Barnegat Light were therefore combined with data from the most proximal port, Point Pleasant. All pairwise interaction terms between main effects and between each main effect and the covariate were included in the initial model run. All nonsignificant (P > 0.05) interaction terms were subsequently removed from the final model. For categorical variables, post hoc analysis involved choosing a reference level by using the “REF = ” option so that significant differences (P < 0.05) between levels within that category could be determined via a CONTRAST statement in the Statistical Analysis System (SAS 2008).

### Table 1. Mean and SD of the change in TL of summer flounder racks (filleted carcasses), calculated as the difference between the TL measured when the racks were fresh and the TL measured after the racks were frozen for a set number of days.

<table>
<thead>
<tr>
<th>Days frozen</th>
<th>Number of fish</th>
<th>Mean change in TL (cm)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>76</td>
<td>0.22</td>
<td>0.43</td>
</tr>
<tr>
<td>2</td>
<td>96</td>
<td>0.26</td>
<td>0.55</td>
</tr>
<tr>
<td>4</td>
<td>97</td>
<td>0.29</td>
<td>0.55</td>
</tr>
<tr>
<td>6</td>
<td>61</td>
<td>0.29</td>
<td>0.45</td>
</tr>
<tr>
<td>7</td>
<td>79</td>
<td>0.28</td>
<td>0.45</td>
</tr>
<tr>
<td>Total</td>
<td>409</td>
<td>0.27</td>
<td>0.49</td>
</tr>
</tbody>
</table>
TABLE 2. Counts by sex (females : males) at length of summer flounder that were landed in the New Jersey recreational party boat fishery during summer months in 2009 and 2010 at each port (FO = Fortescue; CM = Cape May; BP = Barnegat Light and Point Pleasant; AH = Atlantic Highlands).

<table>
<thead>
<tr>
<th>TL (cm)</th>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FO</td>
<td>CM</td>
<td>BP</td>
</tr>
<tr>
<td>2009 landings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>44</td>
<td>2:0</td>
<td>1:1</td>
<td>6:5</td>
</tr>
<tr>
<td>45</td>
<td>6:0</td>
<td>8:1</td>
<td>5:0</td>
</tr>
<tr>
<td>46</td>
<td>4:0</td>
<td>10:1</td>
<td>7:0</td>
</tr>
<tr>
<td>47</td>
<td>3:0</td>
<td>9:1</td>
<td>11:0</td>
</tr>
<tr>
<td>48</td>
<td>3:0</td>
<td>8:0</td>
<td>8:0</td>
</tr>
<tr>
<td>49</td>
<td>1:0</td>
<td>4:1</td>
<td>8:0</td>
</tr>
<tr>
<td>50</td>
<td>1:0</td>
<td>1:0</td>
<td>4:0</td>
</tr>
<tr>
<td>51</td>
<td>3:0</td>
<td>2:0</td>
<td>7:0</td>
</tr>
<tr>
<td>52</td>
<td>4:0</td>
<td>2:0</td>
<td>4:0</td>
</tr>
<tr>
<td>53</td>
<td>5:0</td>
<td>4:0</td>
<td>5:0</td>
</tr>
<tr>
<td>54</td>
<td>5:0</td>
<td>2:0</td>
<td>1:0</td>
</tr>
<tr>
<td>55</td>
<td>1:0</td>
<td>1:0</td>
<td>6:0</td>
</tr>
<tr>
<td>56</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>57</td>
<td>2:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>58</td>
<td>2:0</td>
<td>1:0</td>
<td>5:0</td>
</tr>
<tr>
<td>59</td>
<td>2:0</td>
<td>5:0</td>
<td>1:0</td>
</tr>
<tr>
<td>60</td>
<td>1:0</td>
<td>2:0</td>
<td>3:0</td>
</tr>
<tr>
<td>61</td>
<td>1:0</td>
<td>2:0</td>
<td>2:0</td>
</tr>
<tr>
<td>62</td>
<td>1:0</td>
<td>5:0</td>
<td>1:0</td>
</tr>
<tr>
<td>63</td>
<td>3:0</td>
<td>1:0</td>
<td></td>
</tr>
<tr>
<td>64</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>65</td>
<td>1:0</td>
<td>2:0</td>
<td>2:0</td>
</tr>
<tr>
<td>66</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>67</td>
<td>1:0</td>
<td>1:0</td>
<td></td>
</tr>
<tr>
<td>68</td>
<td>1:0</td>
<td>1:0</td>
<td></td>
</tr>
<tr>
<td>69</td>
<td>1:0</td>
<td>1:0</td>
<td></td>
</tr>
<tr>
<td>Monthly total (all ports)</td>
<td>102:5</td>
<td>474:58</td>
<td>561:96</td>
</tr>
</tbody>
</table>

2010 landings

<table>
<thead>
<tr>
<th>TL (cm)</th>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td>44</td>
<td>4:0</td>
<td>4:1</td>
<td>12:0</td>
</tr>
<tr>
<td>45</td>
<td>15:0</td>
<td>31:2</td>
<td>4:1</td>
</tr>
<tr>
<td>46</td>
<td>11:0</td>
<td>43:3</td>
<td>5:2</td>
</tr>
<tr>
<td>47</td>
<td>7:0</td>
<td>39:3</td>
<td>13:0</td>
</tr>
<tr>
<td>48</td>
<td>5:0</td>
<td>37:1</td>
<td>17:1</td>
</tr>
<tr>
<td>49</td>
<td>5:0</td>
<td>35:0</td>
<td>5:0</td>
</tr>
<tr>
<td>50</td>
<td>3:0</td>
<td>41:0</td>
<td>4:0</td>
</tr>
<tr>
<td>51</td>
<td>3:0</td>
<td>26:0</td>
<td>9:0</td>
</tr>
<tr>
<td>52</td>
<td>3:0</td>
<td>22:0</td>
<td>7:0</td>
</tr>
<tr>
<td>53</td>
<td>13:0</td>
<td>3:0</td>
<td>2:0</td>
</tr>
<tr>
<td>54</td>
<td>12:0</td>
<td>2:0</td>
<td>1:0</td>
</tr>
<tr>
<td>55</td>
<td>2:0</td>
<td>10:0</td>
<td>4:0</td>
</tr>
<tr>
<td>56</td>
<td>2:0</td>
<td>9:0</td>
<td>2:0</td>
</tr>
<tr>
<td>57</td>
<td>7:0</td>
<td>3:0</td>
<td>3:0</td>
</tr>
<tr>
<td>58</td>
<td>1:0</td>
<td>4:0</td>
<td>2:0</td>
</tr>
<tr>
<td>59</td>
<td>1:0</td>
<td>4:0</td>
<td>2:0</td>
</tr>
<tr>
<td>60</td>
<td>2:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
</tbody>
</table>
TABLE 2. Continued.

<table>
<thead>
<tr>
<th>TL (cm)</th>
<th>FO</th>
<th>CM</th>
<th>BP</th>
<th>AH</th>
</tr>
</thead>
<tbody>
<tr>
<td>61</td>
<td>1:0</td>
<td>2:0</td>
<td>2:0</td>
<td>1:0</td>
</tr>
<tr>
<td>62</td>
<td>3:0</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>63</td>
<td>2:0</td>
<td>1:0</td>
<td>2:0</td>
<td>1:0</td>
</tr>
<tr>
<td>64</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
<td>1:0</td>
</tr>
<tr>
<td>65</td>
<td>2:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>66</td>
<td>1:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>67</td>
<td>1:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>68</td>
<td>1:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>69</td>
<td>1:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Port total</td>
<td>69:0</td>
<td>349:10</td>
<td>85:4</td>
<td>123:0</td>
</tr>
<tr>
<td>Monthly total (all ports)</td>
<td>626:14</td>
<td>1,462:23</td>
<td>967:49</td>
<td></td>
</tr>
</tbody>
</table>

DISCUSSION

Spatial and Temporal Variability in Sex at Length

The observed spatial and temporal variability in sex at length in this study is likely a phenomenon in the population and is not necessarily unique to the recreational fishery. Morse (1981) found that 89% of 46–50-cm summer flounder caught by a trawl survey in the summer months were female, but the percentage of females in that same size-class fell to 78% during the fall. Other species exhibit similarly variable sex ratios in time and space. A comprehensive examination of the recreational fishery for winter flounder *Pseudopleuronectes americanus* at Long Island, New York, showed that the ratio of female : male landings increased threefold to sixfold for just 1 month out of an 8-month fishing season (Briggs 1965). In European flounder *Platichthys flesus luscus*, the sex ratio of fish that were caught by otter trawl during monthly samplings was skewed toward females in the winter but not during the remainder of the year (Sahin and Gunes 2010). Richards et al. (2008) suggested that sex-specific behavior and movement patterns might explain similar temporal and geographic differences in skewness of the sex ratio for goosefish *Lophius americanus*. Mature spiny dogfish *Squalus acanthias* likewise may exhibit differences in migratory behavior between sexes (Templeman 1984). Sackett et al. (2007) found that barometric pressure, dissolved oxygen, and temperature correlated with emigration of summer flounder from a coastal estuary in the late summer and early fall. It is possible that similar environmental cues could induce sex-specific immigration to the continental shelf and estuaries in the spring and could result in a more highly skewed sex ratio in some regions or during certain times of the year.

Alternatively, latitudinal and annual variability in the sex ratio of summer flounder might be explained by a combination of genetic sex determination, temperature-dependent sex determination, and site fidelity. Summer flounder display homing behavior (Poole 1962; Sackett et al. 2007); thus, genetic and environmental effects in the natal estuary may exert a long-term influence on the local population. The existence of substock structure in mid-Atlantic migratory species would not be unprecedented (Buresch et al. 2006). Luckenbach et al. (2009) reviewed the mechanisms controlling sex determination in flatfishes, with particular emphasis on two species of the genus *Paralichthys*. Olive flounder *Paralichthys olivaceus* and southern flounder *Paralichthys lethostigma* are controlled by an XX/XY system whereby homogametic animals are genetic females and heterogametic animals are genetic males. However, when fish are reared at high or low water temperatures during sexual differentiation, homogametic individuals can differentiate as males (Yamamoto 1999; Luckenbach et al. 2003). Water temperature at differentiation has more recently been shown to influence sex ratio in laboratory-reared summer flounder (Colburn et al. 2009), although empirical evidence for genetic or temperature-dependent sex determination in paralichthyids has yet to be collected in the field. Adult summer flounder spawn offshore in the fall and winter (Smith 1973), and larvae enter estuaries where juvenile development begins (Able et al. 1990; Szedlmayer et al. 1992). The sex determination period in summer flounder occurs when the fish are between 60 and 120 mm (King et al. 2001), coinciding with the known presence of these fish in coastal estuaries (Szedlmayer et al. 1992). Based on the influence of

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**Table 3** Results of a logistic regression model for sex ratio of landed summer flounder, with main effects (port, year, and month), an interaction term (month × year), and a covariate (TL).

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Wald chi-square</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>TL</td>
<td>1</td>
<td>131.4140</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Port</td>
<td>3</td>
<td>41.1543</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>40.9684</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Month</td>
<td>2</td>
<td>13.3142</td>
<td>0.0013</td>
</tr>
<tr>
<td>Month × year</td>
<td>2</td>
<td>17.7429</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
FIGURE 2. Observed (data points) fraction female \( \frac{\text{female}}{\text{female} + \text{male}} \) at length (TL) for summer flounder landed in the New Jersey recreational party boat fishery and model predictions (line) of the probability that a landed fish of a given length was female for all years, months, and ports combined (see Table 3 for model design and statistical results).

temperature on sex ratio and the tendency toward natal estuary fidelity in summer flounder, it is reasonable to expect that natal estuaries will produce year-classes of varying sex ratio and that a latitudinal gradient in the sex ratio of adults will develop as a consequence.

A Fishery Dominated by Female Landings

The observed relationship between sex ratio and TL wherein the fraction female increases with size has been well documented for summer flounder (Smith and Daiber 1977; Morse 1981; Bonzek et al. 2009). Females grow faster than males (Poole 1961; King et al. 2001), and males suffer a higher natural mortality rate than females (Maunder and Wong 2011); the combination of these differences results in a progressively more female-dominated sex ratio with increasing size. Although the steady increase in the proportion female with increasing size is expected, the proportion female at TL observed in our study is higher than previously reported values. Research cruises conducted in the Middle Atlantic Bight from 1974 to 1979 (Morse 1981) indicated that 16% (49/311) of 46–50-cm summer flounder captured via trawling were males and that 8% (11/142) of 51–55-cm individuals were males. More recently, 14% (total \( N = 241 \)) of 45–50-cm summer flounder captured during four inshore trawl surveys (2005–2009; Bonzek et al. 2009) were males, and 5% (total \( N = 142 \)) of 50–55-cm individuals were males. However, among 45–50-cm summer flounder that were landed by the party boat sector of the New Jersey recreational fishery during 2009 and 2010, only 7% (total \( N = 2,942 \)) were males; among 50–55-cm fish, only 0.3% (total \( N = 917 \)) were males. Similarly, otter trawl collections of summer flounder in Delaware Bay during 1966 and 1968 indicated that males were present at lengths of up to 52 cm (Smith and Daiber 1977). Among the 308 Delaware Bay fish that were landed at Fortescue during our study, not a single male was collected.

The difference between the summer flounder sex ratio observed in the New Jersey recreational fishery and sex ratios observed in previous surveys could be explained in several ways: (1) the fishing methods employed by anglers bias landings toward females; (2) the highly female-skewed sex ratio we identified is an accurate representation of the population when and
FIGURE 3. Observed (data points) fraction female (female / (female + male)) at length (TL) for summer flounder landed in the New Jersey recreational party boat fishery and model predictions (lines) of the probability that a landed fish of a given length was female for (A) each year, (B) each month, and (C) each port.
where the recreational fishery took place; or (3) a combination of these. Hook-and-line fishing depends directly on the willingness of a particular fish to attack the bait, whereas otter trawl gear should select male and female fish indiscriminately. Lozan (1992) found that female dab Pleuronectes limanda consumed 73% more food than males of the same size. Female summer flounder grow faster than males (Poole 1961; King et al. 2001), and the energetic costs associated with gamete production in general are higher in females than in males (Hayward and Gillooly 2011). The energy required by females to support fast growth and oogenesis may increase their aggressiveness, thereby increasing the likelihood of their interaction with bait on a fishing line. Similarly female-skewed catches have been documented in king mackerel Scomberomorus cavalla fisheries that use hook-and-line gear (Trent et al. 1987). Furthermore, Claereboudt et al. (2004, 2005) compared fishing methods in the Gulf of Oman fishery for narrowbarred mackerel Scomberomorus commerson and found that significantly more females were caught in regions where hook-and-line fishing was employed than in regions where only drift gill nets were used.

Sex-specific migratory patterns could also explain the low proportion of summer flounder males landed in the recreational fishery. If fewer male summer flounder migrate inshore during the spring, then fewer males would be available to a fishery that takes place primarily inshore during the summer months. In this case, trawl surveys that are carried out offshore or during other periods of the year might show sex ratios that are inappropriate for describing landings in the summer recreational fishery. Supporting information is not yet available for summer flounder; however, Nichol (1998) observed a differential distribution of male and female yellowfin sole Limanda aspera in relation to distance from shore.

Arguments for either sex-specific migration inshore during spring or a bias introduced by recreational fishing practices cannot be fully supported until summer flounder are collected simultaneously by trawling and by hook and line in the same study area. Regardless of whether the more pronounced skewness in sex ratio for the recreational fishery is a product of fishing methods or results from sex-specific movements inshore, a summer flounder fishery with predominately female landings may negatively impact the long-term sustainability of the stock (Buxton 1993; Rago et al. 1998; Alonzo and Mangel 2004; Wilderbuer and Turnock 2009). If fecundity or survivorship increases disproportionately with age or length, as has been observed with other fishes (Chambers and Waiwood 1996; Berkeley et al. 2004) and as can be inferred for summer flounder (see Packer et al. 1999), then landings that are highly skewed toward females could also result in a disproportionate decrease in yearly population fecundity.

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A Comparative and Experimental Evaluation of Performance of Stocked Diploid and Triploid Brook Trout

Phaedra Budy,* Gary P. Thiede, Andrew Dean,1 Devin Olsen, and Gilbert Rowley
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Abstract
Despite numerous negative impacts, nonnative trout are still being stocked to provide economically and socially valuable sport fisheries in western mountain lakes. We evaluated relative performance and potential differences in feeding strategy and competitive ability of triploid versus diploid brook trout Salvelinus fontinalis in alpine lakes, as well as behavioral and performance differences of diploid and triploid brook trout in two controlled experimental settings: behavioral experiments in the laboratory and performance evaluations in ponds. Across lakes, catch per unit effort (CPUE) and relative weight (Wr) were not significantly different between ploidy levels. Mean sizes were also similar between ploidy levels except in two of the larger lakes where diploids attained slightly larger sizes (approximately 20 mm longer). We observed no significant differences between diploids and triploids in diet, diet preference, or trophic structure. Similarly, growth and condition did not differ between ploidy levels in smaller-scale pond experiments, and aggressive behavior did not differ between ploidy levels (fed or unfed fish trials) in the laboratory. Independent of ploidy level, the relative performance of brook trout varied widely among lakes, a pattern that appeared to be a function of lake size or a factor that covaries with lake size such as temperature regime or carrying capacity. In summary, we observed no significant differences in the relative performance of brook trout from either ploidy level across a number of indices, systems, and environmental conditions, nor any indication that one group is more aggressive or a superior competitor than the other. Collectively, these results suggest that triploid brook trout will offer a more risk-averse and promising management opportunity when they are stocked to these lakes and elsewhere to simultaneously meet the needs for the sport fishery and conservation objectives.

The introduction of nonnative species to aquatic ecosystems has had numerous negative impacts, including direct predation on native species (Ruzycki et al. 2003; Pelicice and Agostinho 2009), dramatic changes to community structure (Reissig et al. 2006), altered energy flow (Sousa et al. 2008; Nalepa et al. 2009), and increased pathogen transmission to water bodies and native species (Minchin 2007). Specifically, the introduction of nonnative fishes to historically fishless, alpine lakes has had profound effects, including the downstream dispersal and invasion of streams and lakes that contain native fish populations (Adams et al. 2001; Knapp et al. 2001), shifts in size structure and abundance of zooplankton species (Eby et al. 2006; Latta et al. 2007; Knapp and Sarnelle 2008), and hybridization with native species (Knapp et al. 2001; Dunham et al. 2002). Despite these ubiquitous negative impacts, nonnative fishes are still being stocked to provide and sustain both economically and socially valuable sport fisheries in western mountain lakes (e.g., Halverson 2008).

Reproductively sterile fish may provide a more ecologically risk-averse alternative to stocking fertile fish. Sterility may prevent genetic introgression with native fishes and reduce the risk of creating self-sustaining nonnative populations. Sterilization programs have been successful in closed environments and with nonanadromous fishes (Johnston et al. 1993; Dillon et al. 2000; Kozfkay et al. 2006). Sterility can be induced by several techniques, including the production of triploidy by pressure- or

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heat-triploid fishes are already widely used both in commercial aquaculture and in sport fish hatcheries as an alternative to diploid (i.e., fertile) fish (O’Keefe and Benfey 1999; Hyndman et al. 2003; Koenig and Meyer 2011). Thus, stocking sterile fish in natural lakes may provide a way to balance the interests of native fish conservation with those of sport fishery management (Kozfkay et al. 2006).

Although the sterility of triploid fish provides an ecological advantage, fitness relative to diploid fish can vary greatly among species and environmental conditions, which is an important consideration for establishing viable fisheries. For example, theoretically female triploid fish should have higher growth rates because they demonstrate fewer physiological changes associated with sexual maturation (e.g., inhibited muscle development; Thorgaard and Gall 1979), changes that can result in significant losses in production (Wlasow et al. 2004). Furthermore, female triploid fish should be able to allocate more energy to somatic growth than to reproduction (Hyndman et al. 2003). Higher growth rates of female triploid fishes have been shown for rainbow trout Oncorhynchus mykiss (Suresh and Sheehan 1998; Sheehan et al. 1999) and turbot Psetta maxima (Cal et al. 2006). In contrast, however, Koenig and Meyer (2011) observed no differences in length, weight, or dressed weight between diploid and triploid rainbow trout within a year of being stocked in 13 Idaho reservoirs.

In addition to potential differences in growth rates, triploids may also respond differently to some physiologically stressful environmental conditions (Galbreath et al. 2006). For example, triploid shi drums Umbrina cirrosa demonstrated lesser ability to tolerate stressors relative to diploid shi drums due to larger cell sizes, altered metabolic rates, and an increased sensitivity to elevated water temperatures, all of which lower their competitive ability under suboptimal conditions (Ballarin et al. 2004). In contrast, others have suggested that because triploid fish may experience a lower metabolic rate, they have a greater ability to tolerate lower concentrations of dissolved oxygen and other physical stressors (Stillwell and Benfey 1997). Triploid brook trout Salvelinus fontinalis, Atlantic salmon Salmo salar, and rainbow trout all demonstrated similar stress responses as diploids (Benfey and Biron 2000; Sadler et al. 2000; Maxime 2008), and other studies have observed no difference in critical thermal maxima or swimming velocity between triploid and diploid brook trout (Benfey et al. 1997; Stillwell and Benfey 1997). Nonetheless, if significant, altered performance due to physiological or metabolic differences in triploids could lead to a decrease in growth and increased mortality relative to diploids (Suresh and Sheehan 1998; Hyndman et al. 2003; Atkins and Benfey 2008). Clearly, based on these fitness-related measures alone, the performance of triploids relative to diploids may be highly dependent on environmental conditions such that the capacity for replacing diploids with triploids in popular fisheries remains uncertain (Koenig and Meyer 2011).

In summary, true differences in fitness and behavior between triploid and diploid fish appear to be highly variable, species-specific, and poorly understood in many natural settings. Furthermore, in addition to the factors that may determine the relative differences between diploids and triploids, there are a number of other factors that can influence the stocking success of fishes in general, including fish health, domesticated behavior, fish handling and transport, size at stocking, diet conversion, and habitat and environmental factors in the target water body (see reviews by Cresswell 1981; Cresswell et al. 1982; Kerr 2000). Collectively, these uncertainties highlight the need to evaluate performance of triploid and diploid fish prior to the initiation of a widespread and potentially costly or risky stocking program (Kozfkay et al. 2006).

Although not endemic to the western U.S., brook trout have been stocked throughout the region since the mid-1800s (Tyus et al. 1982). Past stocking has greatly expanded the distribution of brook trout outside their native range such that they are now among the most common salmonids in western streams (MacCrimmon and Campbell 1969; Fuller et al. 1999). Self-sustaining nonnative brook trout populations are widespread and abundant in mountain lakes of Colorado and Wyoming where they are considered nuisance species that threaten populations of the native cutthroat trout O. clarkii via cross-breeding and competition for resources (Hirsch et al. 2006). Nevertheless, brook trout are still currently managed as a game fish stocked for recreational fishing in several states (Ficke et al. 2009).

Due to their popularity among anglers, brook trout have been stocked in Utah lakes for over a century. Other previously stocked species include cutthroat trout, rainbow trout, and Arctic grayling Thymallus arcticus (Sigler and Sigler 1996). As a result of this long stocking history, brook trout have become established in many cold mountain lakes and streams throughout the state, including those in the Uinta Mountain range of northeastern Utah. Presently, approximately 60 lakes in the Uinta Mountains support wild brook trout populations (Carlisle and Hawkins 1998), and more than 100 Uinta Mountain lakes are stocked regularly with brook trout by the Utah Division of Wildlife Resources (UDWR). Uinta Mountain lakes are extremely popular for brook trout fishing and provide an important recreational, cultural, and economic resource to the state of Utah. However, naturally reproducing populations of brook trout have overpopulated many natural lakes, threatening native fish populations. Thus, in recent years UDWR has begun to consider a strategy of stocking only sterile triploid brook trout in an effort to maintain these economically valuable sport fisheries while protecting native cutthroat populations (W. Pearce, UDWR, personal communication).

To assess the effectiveness of a triploid-only management strategy, we evaluated the relative (triploid versus diploid) and overall (independent of ploidy level) performance of stocked brook trout in Uinta Mountain lakes. Specifically, we tested for differences in the relative performance, feeding strategy, and competitive ability of triploid and diploid brook trout stocked...
TABLE 1. Physical conditions, water quality variables, and zooplankton densities for the nine study lakes in the western portion of the Uinta Mountains, Utah. Water quality values are means determined from a vertical profile of each lake during three summer sampling periods in 2008 and 2009 (average of all sampling periods in both years). \( T \) = temperature, DO = dissolved oxygen (range of minimum to maximum), Secchi = Secchi disk depth, Chl \( a \) = chlorophyll \( a \) concentrations.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Elevation (m)</th>
<th>Maximum depth (m)</th>
<th>Mean depth (m)</th>
<th>Surface area (ha)</th>
<th>Volume (m(^3))</th>
<th>( T ) ((^\circ)C)</th>
<th>DO (mg/L)</th>
<th>Secchi (m)</th>
<th>Chl ( a ) ((\mu)g/L)</th>
<th>Zooplankton (number/L)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>2,853</td>
<td>8.5</td>
<td>4.6</td>
<td>9.3</td>
<td>425,551</td>
<td>8.13</td>
<td>0.80–7.53</td>
<td>3.63</td>
<td>46.78</td>
<td>294.8</td>
</tr>
<tr>
<td>Blue</td>
<td>2,950</td>
<td>7.9</td>
<td>3.0</td>
<td>3.2</td>
<td>98,679</td>
<td>7.05</td>
<td>1.10–7.72</td>
<td>2.98</td>
<td>4.58</td>
<td>127.0</td>
</tr>
<tr>
<td>Clegg</td>
<td>3,188</td>
<td>3.7</td>
<td>2.1</td>
<td>2.1</td>
<td>44,035</td>
<td>13.48</td>
<td>2.88–7.67</td>
<td>3.10</td>
<td>6.82</td>
<td>159.2</td>
</tr>
<tr>
<td>Crystal</td>
<td>3,109</td>
<td>3.0</td>
<td>1.4</td>
<td>4.0</td>
<td>54,397</td>
<td>16.85</td>
<td>5.27–7.52</td>
<td>2.28</td>
<td>2.86</td>
<td>216.9</td>
</tr>
<tr>
<td>Haystack</td>
<td>3,030</td>
<td>8.8</td>
<td>3.4</td>
<td>6.9</td>
<td>230,661</td>
<td>7.31</td>
<td>1.37–8.55</td>
<td>3.49</td>
<td>3.11</td>
<td>235.0</td>
</tr>
<tr>
<td>Hoover</td>
<td>3,017</td>
<td>8.5</td>
<td>3.0</td>
<td>7.5</td>
<td>229,427</td>
<td>7.19</td>
<td>0.58–8.68</td>
<td>4.82</td>
<td>15.73</td>
<td>380.4</td>
</tr>
<tr>
<td>Marshall</td>
<td>3,045</td>
<td>11.0</td>
<td>4.6</td>
<td>7.3</td>
<td>333,040</td>
<td>6.95</td>
<td>1.38–10.18</td>
<td>6.25</td>
<td>4.96</td>
<td>187.2</td>
</tr>
<tr>
<td>Ruth</td>
<td>3,152</td>
<td>9.1</td>
<td>3.7</td>
<td>3.9</td>
<td>143,577</td>
<td>7.25</td>
<td>0.63–8.10</td>
<td>3.51</td>
<td>6.76</td>
<td>308.5</td>
</tr>
<tr>
<td>Spectacle</td>
<td>2,969</td>
<td>5.2</td>
<td>1.8</td>
<td>3.8</td>
<td>68,828</td>
<td>11.89</td>
<td>1.48–7.13</td>
<td>2.83</td>
<td>5.41</td>
<td>240.4</td>
</tr>
</tbody>
</table>

in high mountain lakes, and behavioral and performance differences of diploid and triploid brook trout in two controlled settings: behavioral experiments in the laboratory and performance evaluations in ponds.

METHODS

Performance Evaluations in Lakes

Study lakes.—The nine study lakes (Alexander, Blue, Clegg, Crystal, Haystack, Hoover, Marshall, Ruth, and Spectacle lakes) are located along the Mirror Lake corridor of the Uinta Mountains in northeastern Utah (Figure 1; Table 1). We selected these nine lakes from a larger set of high Uinta Mountain lakes because they represented a large range of elevations, lake morphologies, and associated abiotic conditions found in the Uinta range and could be stocked with an equal ratio of uniquely marked (e.g., fin-clipped) triploid and diploid brook trout. Lake elevations range from 2,845 to 3,180 m above sea level, maximum depths range from 3.0 to 10.9 m, mean depths range from 1.4 to 4.6 m, and lake sizes range from 2.1 to 9.3 ha (Table 1). The high elevations of these lakes result in a short summer growing season (late June to mid-October) and long winter season. Deeper lakes in the range usually stratify for a short period of time during midsummer (late July to mid-August) and become mixed again during late August, whereas shallow lakes (\(<\) 5 m maximum depth) typically do not stratify over the summer due to complete solar heating throughout the day.

From 2006 to 2008, UDWR (Kamas State Fish Hatchery) stocked an equal ratio of age-0 (\(~7\) month old) triploid and diploid mixed-sex brook trout in the nine study lakes (Table 2). At the time of stocking, diploids were on average 198 mm total length (TL) and 86 g, and triploids were 209 mm TL and 104 g. Fish were stocked at a quota of approximately 247 fish/ha (100 fish/acre) for brook trout that was adjusted throughout the years based on fish condition (Fulton’s condition factor \([K]\) or relative weight \([W_r]\)) at the time of sampling and angling.

TABLE 2. Annual stocking records for diploid (2N) and triploid (3N) brook trout, stocked by the Northern Region of Utah Division of Wildlife Resources, 2006 – 2008, for nine study lakes in the western portion of the Uinta Mountains, Utah. “Pressure” refers to the angler pressure, where L = light, M = moderate, H = heavy, and VH = very heavy. “Quota” refers to the total number of trout stocked (both ploidy levels), whereas “rate” refers to the stocking quota per hectare of both ploidy levels; quota is matched to a “cycle” that determines the frequency of stocking (e.g., every 1, 2, or 3 years)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Pressure</th>
<th>Quota</th>
<th>Cycle</th>
<th>Rate (number/ha)</th>
<th>2006 2N 3N</th>
<th>2007 2N 3N</th>
<th>2008 2N 3N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>H</td>
<td>2,300</td>
<td>1</td>
<td>247.3</td>
<td>1,113 1,148</td>
<td>1,152 1,150</td>
<td>1,210 1,226</td>
</tr>
<tr>
<td>Blue</td>
<td>M–H</td>
<td>600</td>
<td>3</td>
<td>187.5</td>
<td>305 294</td>
<td>498 498</td>
<td>498 504</td>
</tr>
<tr>
<td>Clegg</td>
<td>M</td>
<td>500</td>
<td>2</td>
<td>238.1</td>
<td>504 504</td>
<td>452 448</td>
<td>454 447</td>
</tr>
<tr>
<td>Crystal</td>
<td>H</td>
<td>1,000</td>
<td>1</td>
<td>250.0</td>
<td>504 504</td>
<td>945 952</td>
<td>948 948</td>
</tr>
<tr>
<td>Haystack</td>
<td>H</td>
<td>900</td>
<td>2</td>
<td>130.4</td>
<td>452 448</td>
<td>903 896</td>
<td>943 950</td>
</tr>
<tr>
<td>Hoover</td>
<td>VH</td>
<td>1,400</td>
<td>1</td>
<td>186.7</td>
<td>945 952</td>
<td>948 948</td>
<td>424 427</td>
</tr>
<tr>
<td>Marshall</td>
<td>H</td>
<td>1,800</td>
<td>2</td>
<td>246.6</td>
<td>252 252</td>
<td>252 252</td>
<td>249 247</td>
</tr>
<tr>
<td>Ruth</td>
<td>H</td>
<td>500</td>
<td>1</td>
<td>128.2</td>
<td>252 252</td>
<td>252 252</td>
<td>249 247</td>
</tr>
<tr>
<td>Spectacle</td>
<td>L</td>
<td>1,400</td>
<td>3</td>
<td>368.4</td>
<td>704 700</td>
<td>704 700</td>
<td>704 700</td>
</tr>
</tbody>
</table>
pressure at lakes along the Mirror Lake Highway. Adjustments to stocking rates have been made by UDWR based on more than 30 years of gill-net surveys and qualitative assessments of fishing pressure (R. Wilson, UDWR, personal communication). Quotas were also matched to a “cycle” that determines the frequency of stocking (e.g., every 1 or 2 years).

All brook trout in this study came from the UDWR Egan Hatchery brood stock and the Owhi strain, which was introduced...
to Utah in 1979 and is the only brook trout strain in the state. Fish stocked in 2006 and 2007 were from the same parents, whereas the 2008 fish were from one year-class younger. Triploids are produced in all UDWR hatcheries by pressure-shocking the eggs (9,500 psi for 4 min). A large number of efficacy fish were retained after stocking to evaluate posttagging and handling mortality, and the mortality rate for these fish was near zero (T. Hallows, UDWR, personal communication). In each year, UDWR randomly samples lots from the different hatcheries for blood testing; the triploid percentage varies between 75% and 100%, depending on the year and hatchery. In 2007 and 2008 the triploid percentage from the Kamas Hatchery was 100%; data for Kamas Hatchery in 2006 are not available. Left and right pelvic fin clips were used to distinguish the diploid and triploid groups, respectively, and all fish stocked during these years were marked.

Relative abundance, size structure, and condition.—In 2008 and 2009, we captured brook trout three times throughout the summer months (early, 1–8 July; middle, 21–28 July; and late, 18–25 August) using experimental monofilament floating gill-nets set overnight. Gill nets consisted of seven 7.6-m panels, each of a different mesh size (ranging from 1.27 to 5.08 cm in 0.635-cm increments), placed in random order throughout the net. Two nets were used per lake. We measured (nearest 1 mm TL) and weighed (mass to nearest 0.1 g) all captured fish to determine population size structure and fish condition. We assessed fish condition using $W_s$, the ratio of the measured weight to the expected weight for a healthy brook trout of the same length (i.e., standard weight). We used the standard weight ($W_s$) equation for brook trout of Hyatt and Hubert (2001) based on TL (mm): $\log_{10} W_s = -5.186 + 3.103 \log_{10} TL$. We calculated the relative abundance of both triploid and diploid brook trout using catch per unit effort (CPUE; fish/h) of gill nets for each sampling period and year.

Statistical analysis: lake performance.—We tested the effects of “ploidy”, “year” and sampling “time” (early, mid, late) on CPUE using a randomized block design with lake as the random blocking factor. “Year” and “time” were fixed-effects factors that were repeated measures on lake. We partitioned residual variance into separate estimates for each sampling time (i.e., variance was heterogeneous for “time”). We log transformed CPUE prior to analysis to better meet assumptions of normality and homogeneity of variance; due to zero values, a small increment was added to each observation prior to transformation. Similarly, we assessed the effects of “ploidy” and “year” on mean $W_s$ using an ANOVA of a randomized block design where “lake” was again the random blocking factor. Both “ploidy” and “year” were fixed-effects factors associated with repeated measures within “lake”. We partitioned residual variance into heterogeneous variances for ploidy level, where the triploid variance was greater than the diploid variance. In addition, we compared the relative size structure and growth of diploid and triploid brook trout based on length-frequency histograms for each ploidy level within and among lakes. We evaluated statistical differences in the length distributions of diploid and triploid brook trout using a Kolmogorov–Smirnov test ($D_{KS}$; Neumann and Allen 2007) across lakes.

Limnology and food availability.—We measured several water quality characteristics during each fish sampling period in all nine lakes and once over the 2009 winter in six lakes (reported in Budy et al. 2011) to identify abiotic factors that potentially limit the performance of brook trout. We measured temperature (°C) and dissolved oxygen (DO; mg/L) profiles at 0.5-m increments from the surface to the bottom of the lake. In addition, we placed temperature loggers in each lake near the bottom (approximately 2 m from the bottom) and approximately midlake depth (approximately 3 m from the surface) with an anchored buoy to continuously record hourly temperatures over a full year. We recorded Secchi disk depth as an index of water transparency at the deepest site. We collected water samples for chlorophyll $a$, as an indicator of phytoplankton biomass, at the midpoint of each lake using an integrated 8-m plastic tube throughout the water column. We placed all collected matter in an opaque bottle until we returned to shore. We filtered a known volume of each sample in the field though a glass-fiber filter, which we then wrapped in aluminum foil and kept frozen until analysis. Chlorophyll $a$ was extracted in the laboratory in a known volume of ethanol for 24 h and then measured with a fluorometer to obtain chlorophyll $a$ concentrations ($\mu$L/L).

To assess pelagic food availability, we collected zooplankton samples from at least one shallow site and one deep site in all lakes during the three summer fish sampling periods and once during the winter period. We performed two vertical tows of the total water column between 10:00 and 16:00 hours with 80- and 500-μm Wisconsin-style zooplankton nets. If the lake was stratified, we took two additional zooplankton tows through the epilimnion. We preserved all samples in Lugol’s solution for later examination. In the laboratory, we enumerated and identified zooplankton to genus and measured 30 individuals per taxa per sample to estimate density and biomass. We calculated zooplankton density for each zooplankter, correcting the number of individuals enumerated by the total water column sampled (number of individuals per liter), and determined individual zooplankton weights using length–weight regressions (McCausley 1984) for an estimate of total biomass.

To assess benthic food availability, we sampled benthic macroinvertebrates using a modified Hess sampler at four randomly selected locations in the littoral zone during the midsummer sampling period in 2008. We pooled all four samples from each lake and identified all invertebrates to order level to obtain estimates of relative abundance (number of each order per square meter) in each lake.

Feeding strategy and competitive ability.—To characterize fish diet and evaluate diet preference and overlap between the two ploidy levels, we removed stomachs from fish and classified prey items as aquatic invertebrates (to order), terrestrial invertebrates (explicitly), fish (to species), or zooplankton (to genera). For zooplankton and invertebrate prey, we weighed
each invertebrate order or zooplankton genus en masse to the nearest 0.001 g blot-dry wet weight. We then calculated the percent wet weight of each prey item for each individual fish.

To determine prey selection (electivity) by each ploidy level, we calculated Chesson’s $\alpha$ (Chesson 1978) as:

$$\alpha = r_i p_i^{-1} \left( \sum r_i p_i^{-1} \right)^{-1},$$

where $r_i$ is the proportion of prey type $i$ in the diet of fish and $p_i$ is the proportion of prey type $i$ in the environment. Random feeding occurs at values of $1/n$ (where $n$ = the number of food items available), with values $<1/n$ indicating avoidance and values $>1/n$ indicating avoidance (Chesson 1978). Due to low fish catches or low abundance of some invertebrate taxa in samples, we determined prey electivity for five of the nine study lakes that had adequate data: Alexander, Blue, Hoover, Ruth, and Spectacle lakes.

In parallel with the electivity analyses, we also compared diet overlap between diploid and triploid brook trout in eight study lakes (all except Clegg Lake) in 2008, 2009, or both using Schoener’s index (D) of diet overlap,

$$D = 1 - 0.5 \sum_{i=1}^{n} |p_{x,i} - p_{y,i}|,$$

where $p_{x,i}$ and $p_{y,i}$ are proportions of prey item $i$ found in $x$ and $y$ populations (e.g., dipsloids and triploids) and $n$ is the total number of prey items. Values of $D$ range from 0 (no overlap) to 1 (complete overlap; Schoener 1970), and biologically significant overlap was defined as any value greater than 0.6. To compensate for different sample sizes in the 2 years and natural variability in the diet overlap analysis (32 diet samples in 2008 and 203 diet samples in 2009), we first combined data by averaging the percent composition of each invertebrate species across sample periods within each lake for each year. We then compared brook trout diet overlap across all lakes in both 2008 and 2009.

We analyzed isotopic signatures of both ploidy levels to assess potential differences in long-term feeding strategies and trophic position. We removed muscle tissue in the field and sent prepared samples to the UC-Davis Stable Isotope Facility, University of California Davis, for natural abundance analyses of $^{13}$C and $^{15}$N. Isotopic signatures are reported in $\delta$-notation, where:

$$\delta^{13}C \text{ or } \delta^{15}N = \left( \frac{R_{sample}}{R_{standard}} - 1 \right) \times 1,000,$$

and where $R$ is the ratio of $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N. The standard for $\delta^{13}$C is PeeDee belemnite and for $\delta^{15}$N is atmospheric nitrogen. We compared $\delta^{13}$C and $\delta^{15}$N of diploid and triploid brook trout from isotope samples pooled across lakes ($n = 53$) using a paired Student’s $t$-test ($\alpha = 0.05$).

**Performance Evaluations in Ponds**

We conducted performance evaluations on age-0 brook trout in five experimental ponds, each of which had a surface area of 500 m$^2$, volume of 1,050 m$^3$, and average depth of 2 m. Ponds were filled in early spring with 10$^\circ$C well water and subsequently inoculated with zooplankton. By late June 2009, the zooplankton community in ponds was well developed; average zooplankton density for all ponds was 36 daphnids/L, 75 ceriodaphnids/L, 43 calanoids/L, and 37 cyclopoids/L, which are densities comparable with those found in the Uinta Mountain study lakes in 2008 (Budy et al. 2011). At the start of the evaluation on 16 June 2009, average Secchi disk depth was 2.2 m (SE = 0.1), surface water temperature was 20.2$^\circ$C (SE = 0.3), and average DO was 10.8 mg/L (SE = 0.7), conditions well suited for brook trout (Raleigh 1982). Temperature loggers were deployed in all ponds in July. Throughout the summer, well water was periodically added to ponds to maintain water levels.

We stocked each pond with 25 diploid and 25 triploid age-0 brook trout (148 d old) supplied by the UDWR Kamas State Fish Hatchery, based roughly on the maximum stocking quota used in the mountain lakes. For this component of the study, only triploids were marked with a pelvic fin clip. At the time of stocking, dipsloids were on average 75 mm TL and 4.5 g, and triploids were 73 mm TL and 4.3 g. At the end of the evaluation (14 October 2009), we sampled all ponds by pulling a 6-mm-mesh seine across the entire pond length four times. We noted length, weight, and ploidy level (based on fin clip) for each captured fish. One week before sampling, we measured abiotic variables that may affect fish performance (e.g., temperature, dissolved oxygen, pH) and collected zooplankton samples in each pond. We evaluated statistical differences for length, weight, and $W_r$ between diploid and triploid brook trout within each pond with paired Student’s $t$-tests ($\alpha = 0.05$).

**Laboratory Behavioral Experiments**

For our behavioral experiments, age-0 diploid and triploid brook trout were supplied by the UDWR Kamas State Fish Hatchery, the same facility that rears and stocks fish into Uinta Mountain lakes. For these experiments, a left pelvic fin clip identified the diploid trout and the triploid trout had no fin clip. Brook trout used in this experiment were spawned on 9 December 2008, hatched around 27 January 2009, and transferred to our experimental facility on 24 June 2009. We housed the two ploidy levels of fish separately in 750-L capacity tanks containing flow-through 10$^\circ$C well water with 25 fish per tank, and fed fish commercially available trout feed daily prior to experiments. In preliminary trials, we determined that two pairs of fish filled the 106-L glass aquarium at a density where individual fish behavior was observable in real time. Fresh well water in each aquarium ranged from 13$^\circ$C to 15$^\circ$C and DO levels never dropped below 5 mg/L during trials.
We analyzed data using the GLIMMIX procedure in SAS (SAS Institute 2005) using a normal distribution and an identity link ($\alpha = 0.05$).

**RESULTS**

**Performance Evaluation in Lakes**

*Relative abundance, size structure, and condition.*—The total catch of all brook trout (triploid, diploid, and no mark) was extremely variable among study lakes (Table 3). We captured the greatest total number of brook trout (marked and unmarked) in Crystal ($n = 249$), Hoover ($n = 290$), and Ruth ($n = 218$) lakes and the lowest number in Clegg ($n = 11$) and Marshall ($n = 89$) lakes (both years combined). In both 2008 and 2009, CPUE of marked fish was greatest in Alexander and Hoover lakes and lowest in Clegg and Marshall lakes (Table 3; Figure 2). Spectacle Lake also demonstrated relatively low CPUE in both years of the study, with no marked fish captured in 2009.

The CPUE did not differ significantly between diploid and triploid brook trout nor did we observe any significant effects of “year” or sampling “time” ($P > 0.06$; Tables 3, 4). Similarly, we observed no significant difference in the mean $W_r$ of diploids versus triploids nor a significant “year” effect ($P > 0.06$; Figures 2, 3; Tables 3, 4). On average, the size distribution of diploid brook trout was skewed toward larger fish compared with triploid brook trout: mean diploid TL = 262.5 mm and mean triploid TL = 241.6 mm ($D_{KS} = 0.24$, $P < 0.05$; Figure 3); however, the actual size difference was quite small ($\sim 20$ mm) and the sample size was large. In some individual lakes (e.g., Alexander Lake), the frequency of larger fish increased from year 1 to year 2 (Figure 3). In all other lakes, the size structure was relatively similar in year 1 and year 2.

**Limnology and food availability.**—In 2008 and 2009, minimum DO levels over the summer months were below the

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<td>49 48</td>
<td>8.9 8.9</td>
<td>3.1 3.4</td>
<td>97.8</td>
<td>99.8</td>
<td>103.8</td>
<td>99.0</td>
<td>201.2</td>
<td>195.7</td>
<td>265.7</td>
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<td>30 11</td>
<td>5.9 3.2</td>
<td>3.5 2.3</td>
<td>120.7</td>
<td>106.8</td>
<td>113.1</td>
<td>99.5</td>
<td>301.4</td>
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<td>317.6</td>
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<td>0.8 1.3</td>
<td>2.2 2.2</td>
<td>127.4</td>
<td>94.5</td>
<td>123.5</td>
<td>131.5</td>
<td>183.2</td>
<td>236.0</td>
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<tr>
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<td>10 0.4</td>
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<td>103.9</td>
<td>96.7</td>
<td>99.5</td>
<td>94.5</td>
<td>201.7</td>
<td>190.6</td>
<td>230.6</td>
<td>217.4</td>
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<tr>
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<td>3 0.4</td>
<td>0.0 3.3</td>
<td>3.3 3.3</td>
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<tr>
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<td>4.3 2.5</td>
<td>99.9</td>
<td>95.1</td>
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<td>97.4</td>
<td>242.5</td>
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### Table 3

Diploid (2N) and triploid (3N) brook trout population information for nine study lakes in the western portion of the Uinta Mountains, Utah, sampled three times each during the summers of 2008 and 2009, including total catch, catch per unit effort (CPUE), mean condition ($W_r$), mean total length (TL), and Schoener’s index (D) of diet overlap (for select lakes). Total catch is for all sampling periods combined in a given year; CPUE, $W_r$, and TL are the average of all sample periods in a year. NA indicates insufficient data were available for computing a given metric.
FIGURE 2. Total catch per unit effort (CPUE) of diploid and triploid brook trout within each lake in year 1 (top left panel) and year 2 (bottom left panel), and average relative weight ($W_r \pm 1$ SD) for diploid and triploid brook trout for each lake during year 1 (top right panel) and year 2 (bottom right panel). No triploid fish were captured in Haystack Lake and Marshall Lake in year 1; one marked fish was captured in Spectacle Lake in year 2.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Number df</th>
<th>Density df</th>
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<th>$P$-value</th>
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<td><strong>CPUE</strong></td>
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<td></td>
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<tr>
<td>Year</td>
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<td>88</td>
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<td>0.80</td>
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<tr>
<td>Time</td>
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<td>88</td>
<td>0.60</td>
<td>0.55</td>
</tr>
<tr>
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<td>2.96</td>
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<tr>
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<td>0.23</td>
</tr>
<tr>
<td>Year $\times$ Ploidy</td>
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<td>88</td>
<td>0.53</td>
<td>0.47</td>
</tr>
<tr>
<td>Time $\times$ Ploidy</td>
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<td>88</td>
<td>0.03</td>
<td>0.97</td>
</tr>
<tr>
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<td>0.93</td>
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<tr>
<td><strong>$W_r$</strong></td>
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<td></td>
<td></td>
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<td>0.57</td>
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<td>0.26</td>
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TABLE 4. Results of statistical analyses of the relative performance of the two strains in lakes for catch per unit effort (CPUE) and condition (relative weight, $W_r$). Results are based on type III tests of fixed effects from randomized block designs; “lake” was the random blocking factor. See text for additional information describing statistical methods.

Winter temperatures in all six lakes sampled were consistently well below the optimal range for trout growth, with temperatures $<4.6^\circ$C throughout the water column of all lakes and mean temperatures ranging from 3.5$^\circ$C to 3.8$^\circ$C. Both winter DO and temperature were correlated with lake surface area and maximum depth ($r^2 = 0.45–0.56$). The small, shallow lake, Spectacle Lake, had the lowest mean DO concentrations and temperatures (minimum, mean, and maximum), and the larger, deeper lakes (Hoover, Haystack, and Marshall lakes) consistently demonstrated higher winter DO concentrations and temperatures.
In 2008, the benthic macroinvertebrate community was dominated by dipterans and amphipods. Total abundance ranged from 95 (Alexander Lake) to 4,686 individuals/m² (Haystack Lake) in 2008. In both years, the zooplankton community was dominated by *Holopedium*, *Daphnia*, and calanoid copepods, although densities of zooplankton were five times greater in 2009 than in 2008. Average chlorophyll \(a\) concentrations (an index of lake productivity) ranged widely from 0.7 to 74.9 μg/L (Table 1).

**Feeding strategy and competitive ability.**—In 2008 we observed biologically significant diet overlap (\(D > 0.6\)) between diploid and triploid brook trout in Alexander Lake (\(D = 0.67\)) and moderate overlap for all other lakes (\(D = 0.50–0.58\)) except Crystal, Haystack, and Marshall lakes (\(D < 0.5\)). In 2009, diet overlap was significant in Ruth Lake (\(D = 0.76\)) and moderate for all other lakes (\(D = 0.42–0.57\)) except Marshall and Spectacle lakes (Table 3). No or extremely low diet overlap was demonstrated in lakes with very small or asymmetric sample sizes.

When we compared diet overlap of the two ploidy levels for all study lakes combined in 2008 and 2009, we observed very high diet overlap between diploid and triploid brook trout in both years (\(D = 0.82\) for 2008 and 0.77 for 2009). Both types of brook trout consumed primarily dipterans, amphipods and isopods, terrestrial invertebrates, and odonates. As zooplankton were only found in stomach samples of triploid fish in two of the lakes (Alexander and Ruth lakes, representing <1% of their diets overall), we did not consider zooplankton in our analyses of prey electivity. In all study lakes, diploid and triploid trout selected odonates and dipterans over other invertebrates based on Chesson’s \(\alpha\). Brook trout avoided Amphipoda, Ephemeroptera, Hemiptera, Isopoda, Mollusca, and Trombidiformes in all lakes where they were found. Oligochaetes were available in the environment of all lakes, yet they were not found in the diets.
of any brook trout, suggesting avoidance or lack of benthic foraging.

Isotopic signatures also indicated significant diet overlap and similar trophic position for both ploidy levels in 2008. Carbon isotopic signatures ($^{13}C$) were not significantly different between diploids ($-24.10 \pm 1.14$ [mean $\pm$ 2 SE]) and triploids ($-24.91 \pm 1.28$) ($t = 0.96, P = 0.35, df = 50$). In contrast, mean $\delta^{15}N$ was significantly higher for diploid trout relative to triploids ($t = 2.01, P = 0.04, df = 50$), although the difference between mean values (diploid: $8.02 \pm 0.51$, triploid: $7.32 \pm 0.46$) is arguably not biologically significant given an assumed trophic fractionation of $3.4\%$ per each trophic level increase (Minagawa and Wada 1984).

**Performance Evaluations in Ponds**

At the end of the performance evaluation period (14 October 2009), temperatures in the ponds ranged from 10.8°C to 11.5°C and DO ranged from 10.3 to 11.7 mg/L, values that are within the optimal range for brook trout growth and survival (Raleigh 1982). Turbidity in ponds was low (0.4–1.6 NTU) and pH ranged from 7.9 to 8.6. Zooplankton abundance was low: average zooplankton densities of ponds were 0.04 daphnids/L, 5.8 ceriodaphnids/L, 1.2 calanoids/L, and 0.05 cyclopoids/L.

Estimated survival at the end of the pond experiment, based on the number of recovered fish in each pond, was significantly better for diploids (mean = 18.4%; range, 0–48%) than for triploids (mean = 13.6%; range, 0–40%) ($t = 3.21, P = 0.03 df = 4$). However, it is important to note that survival event was extremely low for fish from both ploidy levels, indicating the data from this factor should be interpreted with caution. From the four ponds, we captured a total of 23 diploid trout ranging from 127 to 165 mm TL and from 10.5 to 39.6 g, and 17 triploid trout ranging from 119 to 190 mm TL and from 10.5 to 39.6 g, and 17 triploid (Figure 4). Although survival of diploid trout was higher than triploid trout, average $W_r$ was not significantly different between ploidy levels ($t = -0.005, P = 0.50, df = 38$; diploid: $83.4 \pm 10.1$ [mean $\pm$ SE], triploid: $83.5 \pm 7.9$). Similarly, average growth over this 112-d interval was not significantly different between diploids (21.0 g and 67.4 mm TL) and triploids (24.1 g and 72.1 mm TL) ($t = -0.40, P = 0.71, df = 4$).

**Laboratory Behavioral Experiments**

Total lengths and weights of individuals used in behavioral evaluations ranged from 79 to 109 mm and from 6.2 to 12.0 g, respectively, with mean lengths of 93.4 mm for diploids and 95.1 mm for triploids. However, individuals paired within each trial never differed by more than 10 mm. In both the pre- and postfeeding trials, diploids on average performed more attacks than did triploid brook trout, but the variability in number of attacks was extremely high and the differences were not significant (Figure 5). In prefeeding trials, the number of diploid attacks ranged from 0 to 44 (mean $\pm$ SE, 6.7 $\pm$ 4.3), whereas the number of attacks made by triploid trout ranged from 0 to 4 (1.7 $\pm$ 0.4). No attacks from fish from either ploidy level occurred in 2 of the 10 trials. In the postfeeding trials, the number of diploid attacks ranged from 0 to 8 (2.3 $\pm$ 0.7) and the number of triploid attacks ranged from 0 to 5 (1.7 $\pm$ 0.4). Trout attacked conspecifics regardless of ploidy level (i.e., diploids attacked both diploids and triploids and vice versa). In summary, we observed no significant difference between diploid and triploid aggression ($F = 3.36, P = 0.10, df = 9$), no significant period effect for prefeeding versus postfeeding ($F = 1.37, P = 0.26, df = 18$), and no significant interaction effect ($F = 0.05, P = 0.83, df = 18$).

**DISCUSSION**

**Comparisons between Ploidy Levels**

In order to provide a robust test of the potential differences in relative performance between triploid and diploid brook trout, we chose nine lakes for study that covered a large range of lentic conditions found in high mountain lakes. With a few minor
exceptions, we observed very little difference in the relative performance between stocked diploid and triploid brook trout in our study lakes, a result that concurs with previous studies of diploid and triploid performance (E. J. Wagner et al. 2006; Chiasson et al. 2009). Conversely, Koenig et al. (2011) observed marked differences in the performance of diploid and triploid rainbow trout in alpine lakes.

Although we observed no differences in fish condition between stocked triploid and diploid brook trout, diploid brook trout did attain slightly larger average sizes in some lakes. Higher growth rates and size of diploids have been observed in previous studies (Simon et al. 1993), while similarity in size structure of diploid and triploid fish has been noted elsewhere (Xiaoyun et al. 2010; Koenig and Meyer 2011). In some cases the observed differences in size was only for smaller sizes-classes (McGeachy et al. 1995; Chiasson et al. 2009). In our study, diploids attained larger sizes in two large-sized lakes (Marshall and Haystack lakes), but the other lakes showed little difference in size between diploids and triploids. Furthermore, the average difference in size of fish between ploidy levels was small (approximately 20 mm) and is probably undetectable to the average angler. Often, differences in size between diploids and triploids often do no materialize until the onset of sexual maturity. Given that brook trout typically take 3 years to reach maturity (E. Wagner and T. Hallows, UDWR, personal communication), any potential size differences should have been evident in the older trout (i.e., those stocked in 2006), but perhaps not those stocked in 2008. Considering the similarity in size distribution across all sizes of fish and high overwinter mortality overall, the issue of sexual maturation does not appear to have affected the triploid–diploid comparison herein.

Based on observed diet similarities, diet overlap, and trophic position, we did not detect any differences in feeding strategy or evidence for competitive superiority between ploidy levels. Our diet results are novel in that few studies have directly measured the diet composition of trout in mountain lakes or other natural settings. Aquaculture studies support our finding that feeding and diet preferences of diploid and triploid trout are similar (Boulanger 1991; O’Keefe and Benfey 1999). However, in other species others have found evidence of lower performance of triploid versus diploid fish (rainbow trout, Simon et al. 1993; Atlantic salmon, Carter et al. 1994; Cotter et al. 2002) that could have resulted from some undocumented or unknown aspect of feeding ecology.

Similarly, we found similar growth and condition of diploid and triploid brook trout in controlled pond experiments of mixed ploidy levels, despite a wide range of thermal conditions. In our ponds, there was little difference between triploid and diploid trout growth, even when temperatures consistently exceeded 19°C. Previous studies have also found no effect of ploidy on critical thermal maxima (Benfey et al. 1997; Galbreath et al. 2006). In contrast, others have documented increased mortality of triploid brook trout as a result of chronically high temperatures (Hyndman et al. 2003). Despite similarities in growth and condition in pond experiments, average survival of diploids was significantly higher than that of triploids, perhaps due to elevated water temperatures (e.g., conferring an advantage to diploids; Hyndman et al. 2003). Midsummer water temperatures in the ponds occasionally reached 25°C and varied widely, probably as a function of pond seepage (and subsequent topping off with 10°C well water) or algal mat coverage and the resultant shading in some ponds. However, it is important to note that survival in ponds was extremely low overall, such that environmental conditions could be either masking ploidy effects or causing biologically unimportant, yet statistically significant, differences in survival between ploidy groups.

Based on laboratory behavioral experiments, we found no significant difference in aggressive behavior between diploids and triploids in pre- and postfeeding trials. Furthermore, in over one-half of the behavioral trials, no aggressive behavior was recorded, and there appeared to be no inherent difference in brook trout aggression based on ploidy level alone. Although we did find that, on average, diploids performed more attacks than did triploids, this difference was not significant. Statistically, it was just as likely that an aggressive individual was a diploid or triploid fish; aggressive individuals attacked fish from their own ploidy level as often as they attacked the other. In a similarly conducted feeding response trial of triploid and diploid brook trout, only one diploid group (size, 40–58 mm) was dominant over triploids (O’Keefe and Benfey 1999). Furthermore, this dominance difference diminished as the fish grew, and dominance was not observed in groups ranging in size from 99 to 204 mm. In contrast, our results differ from those of Carter et al. (1994) and Garner et al. (2008), who found that triploid trout were less aggressive than diploids.

**FIGURE 5.** Average number of attacks (±1 SE) by diploid and triploid brook trout for behavioral observation trials in aquaria before (pre-) and after (post-) feeding.
Effects of Environmental Conditions on Trout Performance

Independent of ploidy level, the relative performance of brook trout varied widely among lakes, indicating that survival of stocked brook trout in high mountain lakes in general is highly lake-specific (Josephson and Youngs 1996). Larger deeper lakes generally demonstrated high CPUE, while smaller, shallower lakes demonstrated low CPUE (e.g., Clegg and Marshall lakes). Consistently high CPUE in the larger study lakes (Alexander and Hoover lakes) suggest that relative abundance may be influenced by lake size or by a factor that covaries with lake size (e.g., thermal stratification, carrying capacity; Amundsen et al. 2007). Although high CPUE was also observed in the relatively small-sized Crystal Lake, this may be due to overwinter refuge and supplementation from the larger, deeper Washington Lake through a small stream connection available in spring (e.g., Jackson and Zydlewski 2009). In contrast, the large lakes (Alexander and Hoover lakes) in this study are essentially disconnected from additional source populations.

Higher CPUE in larger lakes may be due to differences in the availability of thermal refugia in the summer or winter, or both. In mountain environs, deeper lakes commonly experience thermal stratification that allows coldwater fishes to persist even when surface temperatures approach or exceed upper or lower thermal limits (Jackson and Harvey 1989). In contrast, shallower lakes may never stratify; as a result, elevated temperatures through the full water column may persist throughout the summer. Empirical evidence suggests that temperatures near the upper limit for brook trout may lead to a decrease in growth and increased mortality in triploids (Hyndman et al. 2003; Atkins and Benfey 2008). We observed high temperatures in two of the nine study lakes (Clegg and Crystal lakes), but only near the lake surface. In these lakes, brook trout are likely able to seek out more thermally suitable conditions near the bottom or near stream inlets where temperatures measured seldom reached levels high enough to affect brook trout growth or survival (i.e., 19°C; Hyndman et al. 2003). Thus, it seems more likely that observed differences in CPUE among some lakes are the result of harsh winter conditions, which can be more severe in smaller lakes (Budy et al. 2011). Winter DO levels and temperatures were consistently below the optimal range for brook trout growth in the six lakes sampled, and the small, shallow lakes (e.g., Spectacle Lake) had lower DO and temperatures than did the larger, deeper lakes (e.g., Hoover, Haystack, and Marshall lakes). These severe overwinter conditions occur during a time period when habitat and food are already limited (Bystrom et al. 2006), in part explaining the poor overall condition ($W_i$) of all stocked brook trout in these high mountain lakes.

Although condition was low overall, the condition of brook trout in the large lakes with consistently high CPUE was lower than lakes with low CPUE, indicating a density-dependent effect. In a related study of these same lakes, CPUE, maximum lake depth, and lake area were the top three predictor variables explaining variation in stocked brook trout condition ($W_i$) independent of ploidy level (random forest analysis; Budy et al. 2011; also see Donald and Anderson 1982). Density-dependent effects are common in large oligotrophic lakes, where growth rates are higher at lower densities due to decreased intraspecific competition for limited food resources (Amundsen et al. 2007). Differences in stocking frequency could also account for some of the observed differences in catch rate among lakes. Alexander, Crystal, and Hoover lakes were stocked in all 3 years, whereas Clegg and Marshall lakes were stocked less frequently (twice and once, respectively). However, the small-sized Ruth Lake was stocked in all 3 years but had a much lower CPUE than the larger lakes stocked at the same frequency, suggesting that relative abundance and survival are at least partly a function of lake size, depth, or both.

Management Implications

In summary, we found very few significant differences in performance, feeding strategy, competitive ability, or aggression between diploid and triploid brook trout in both natural and controlled settings at three spatial scales. Our results show that triploid brook trout may provide a valuable management tool that will allow managers to provide a sport fishery in lakes where natural reproduction is not sufficient to maintain the fishery, while simultaneously minimizing the risk of nonnative expansion into other waters and the deleterious effects of negative interspecific interactions on native ecosystems (Knapp et al. 2001; Knapp and Sarnelle 2008). In addition, our findings have important implications for management of triploid brook trout in high mountain lakes in the Uinta Mountains. Large differences in relative performance among lakes calls for a reevaluation of which lakes to stock and at what density and frequency. Strong signals of density dependence indicate these lakes are food or space limited at current stocking densities, suggesting that stocked brook trout, independent of ploidy level, could potentially survive better and attain larger sizes if stocked at lower densities.

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REFERENCES


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ARTICLE

Inferring Adult Status and Trends from Juvenile Density Data for Atlantic Salmon

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Abstract

Typically, juvenile survey data are not used explicitly to determine status, trends, or abundance designations for Atlantic salmon Salmo salar, even though they can be the only source of information for many populations. To determine whether juvenile data can be informative about adult abundance and status in Atlantic salmon, we evaluated the similarities in trends among age-classes for two data-rich populations using a nested log-linear model. We found relatively consistent and significant trends for the age-0, adult and egg time series, but the trends in juvenile density data for older age-classes were less consistent with adult abundance trends. A threshold-based analysis demonstrated that relatively low misclassification rates for adult status relative to a set reference level could be obtained from juvenile density estimates. Together, these results suggest that juvenile density data can be an informative proxy for adult abundance and may be useful as an indicator for large changes in population status relative to reference points. This would make data collection via electrofishing an appropriate monitoring method for fisheries management or conservation programs. However, the validity of the idea that dramatic changes in adult abundance will be mirrored in juvenile data partially depends on the specific age-classes monitored, the survey design, and the timing of density dependence in the population. Using juvenile data as an index would necessitate some prior knowledge of the underlying population dynamics before the method could be applied more generally.

In response to the abundance declines being observed in numerous fish populations (Jonsson et al. 1999; Reynolds et al. 2005), many fisheries management programs have recently expanded to include questions related to conservation or extinction risk (Rice and Legacé 2007). The key questions for fisheries management center on estimating abundance, generally in the context of current status, in order to establish harvest control rules (Botsford et al. 1997). Conversely, conservation concerns often focus on population trends over time and changes in distribution patterns related to overall extinction risk (Dulvy et al. 2004, 2005) or population-level responses to recovery actions (Norris 2004). Given these divergent goals, it becomes acutely important to ensure that the data collected for a given population or species are of sufficient quality to reliably answer questions of interest and that the chosen indicators are robust despite spatial and temporal variability in populations or regions as well as missing data (Holt et al. 2011).

The design of monitoring programs to address questions related to species abundance and trends must balance the potential explanatory power of the data with logistical concerns related to time, cost, and feasibility (Milner et al. 2003). For diadromous fish populations such as Atlantic salmon Salmo salar, one of the most cost-effective and tractable monitoring techniques is electrofishing, whereby juvenile densities are determined at multiple sites for a given river or area (Bohlin et al. 1989; De Leeuw et al. 2007). However, both fisheries management and conservation questions tend to be exclusively defined relative to mature individuals (i.e., adult abundance, distribution, or trends), even in situations where data are collected on multiple life stages (e.g., Rivard and Maguire 1993; Powles 2011). Typically, juvenile abundance or distribution patterns are not explicitly linked to status, trends, or abundance designations, even though they can be the only source of information for a given population. Given that maintaining time- and labor-intensive adult assessments is...
becoming increasingly difficult (Milner et al. 2003), interest in using smaller-scale, widely applicable monitoring methods like electrofishing surveys to track adult abundance, trends, and/or status is likely to increase.

Electrofishing surveys have been used to assess a variety of questions, including those related to the habitat utilization (e.g., Heggennes et al. 1990; Hedger et al. 2005), abundance (e.g., Peterson et al. 2004), distribution (e.g., Tules et al. 2004), or growth and survival (e.g., Evans et al. 1984; Gibson et al. 2008) of juvenile Atlantic salmon as well as multiple species of freshwater fishes. Electrofishing data are commonly incorporated into a larger assessment framework using cohort analyses, which attempt to link juvenile age-class density with smolt production (e.g., Baglinière et al. 2005), egg deposition (e.g., Crozier and Kennedy 1995), or adult abundance (e.g., Niemelä et al. 2005) based on the idea that age-classes are functionally related. However, in the absence of data on mature life stages, the extent to which density data are related to adult abundance is unclear. Before monitoring programs that focus on juvenile data can be used to address fishery management or conservation questions, the validity of juvenile data as an indicator of, or proxy for, adult population status or trends must be established (DeMartini et al. 1989).

Here, we investigate the utility of Atlantic salmon juvenile density data as indicators of both the conservation status of salmon populations and for the status of populations relative to fishery benchmarks. Using data from two populations for which long-term monitoring programs exist, we evaluate (1) whether trends in juvenile density data reflect trends in adult population size (making it an appropriate relative index for changes in adult abundance), (2) whether predictive relationships among adult returns or egg deposition and juvenile density data can be developed (allowing juvenile density data to be used directly to indicate adult abundance relative to fishery reference levels), and (3) whether juvenile data reliably reflect overall population status (i.e., below or above an established reference level) and thus can be used as an indicator of significant changes in population size to inform fisheries management in the absence of adult data. The impact of data standardizations, grouping or splitting juvenile age-classes, variation in life history characteristics, and the robustness of our results to large changes in adult population size are discussed in the context of population monitoring and recovery planning.

METHODS

Study region.—This study considers data collected for the St. Mary’s and LaHave River Atlantic salmon populations in Nova Scotia. These populations are used as indexes for management and assessment purposes for Salmon Fishing Areas 20 and 21, respectively, two regions collectively known as the Southern Upland (Figure 1). Long-term monitoring programs were set up on both rivers, and data on all life stages were collected for a portion of each watershed: the West Branch of the St. Mary’s River (55% of the estimated productive area of the watershed; Amiro et al. 2006) and above a fishway at Morgans Falls on the LaHave River (51% of the estimated productive area of the watershed; Amiro et al. 1996). The commercial fisheries impacting these populations were closed in 1984 (along with the imposition of a ban on the retention of salmon > 63 cm fork length from the recreational fishery), and only catch-and-release angling was permitted from 1998 (Gibson et al. 2009a) until the closure of the recreational fishery in 2010 (DFO 2011).

At present, the wild Atlantic salmon populations in both the St. Mary’s and LaHave rivers are at low population size (DFO 2011; Gibson et al. 2011). In a recent assessment of Atlantic salmon in Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated all populations in the Southern Upland as endangered (COSEWIC 2011). Similarly, the annual assessment of status by the Department of Fisheries and Oceans for the St. Mary’s and LaHave populations determined that the current abundance is well below established reference levels (DFO 2011). The river-specific reference levels used for the assessment of Atlantic salmon populations in the Southern Upland region are termed the conservation requirement (CR). These are calculated as the amount of available habitat in a watershed multiplied by a target egg deposition rate of 2.4 eggs/m² (O’Connell et al. 1997; Marshall et al. 1999). These values are 6.22 and 5.26 million eggs for the LaHave River above Morgans Falls and the West Branch of the St. Mary’s River, respectively. Since 2005, the egg deposition estimates for both the LaHave River above Morgans Falls and the West Branch of the St. Mary’s River have not exceeded 23% of their respective CRs and have been less than 15% in most years (DFO 2011).

Data sources and analyses.—The adult abundance of Atlantic salmon is enumerated at a fishway on the LaHave River which provides access to the area above Morgans Falls, an otherwise impassable barrier (Gibson et al. 2011). The counting facilities are operated for the entire duration of the spawning migration (midspring to late fall) and all individuals are sampled for biological characteristics (Gibson et al. 2009a). From 1984 to 1996, the adult abundance on the West Branch of the St. Mary’s River was estimated from recreational catch data (scaled by the amount of area in the West Branch) and an assumed catch rate of 0.3 (O’Neil et al. 1997). This assumed catch rate is very similar to the long-term average catch rate calculated on the LaHave River from the recreational catch data and the fishery-independent count at Morgans Falls (Amiro and Jefferson 1997). In more recent years (1997–2010), adult abundance was calculated from a mark–recapture seineing experiment and a Peterson estimate (Gibson et al. 2009a). This means that biological information (e.g., spawning history, sex ratios, and size) is only available for the more recent data on the St. Mary’s River. Subsequent egg deposition for the female component of both returning populations was calculated based on the mean length of one-sea-winter and multiple-sea-winter returns in a given year and the length–fecundity relationship developed for Atlantic salmon from the LaHave River (Amiro et al. 1996;
Gibson et al. 2009a). To calculate annual egg and adult densities, we used the estimate of productive habitat area in the West Branch of the St. Mary’s River (2,191,970 m²; O’Neil et al. 1998) or in the LaHave River above Morgans Falls (2,605,200 m²; Amiro et al. 2006).

The mean annual juvenile densities of Atlantic salmon for the West Branch of the St. Mary’s River and the LaHave River above Morgans Falls were determined from electrofishing surveys which followed a random-stratified design for site selection (Amiro et al. 1989; Amiro 1993). Site locations, size (typically 100 m in length), and the potential electrofishing sites in either river were chosen to be representative of all available habitat types, based on the proportion of each habitat type in the river. For later years, all juvenile salmon had a scale sample taken for the purposes of aging, while in earlier years the proportions of the different age-classes were determined from length-frequency distributions (Amiro et al. 2006). Where a sufficient number of juveniles were originally captured, juvenile densities by age-class were calculated using mark–recapture and a Petersen estimate (Schwarz and Seber 1999). For low-density sites (i.e., those where fewer than 25 juveniles of a given age-class were initially captured), the catch of each age-class was multiplied by a mean capture efficiency (for age-0 or age-1 and age-2 fish combined) and scaled by site area to estimate juvenile density (Gibson et al. 2009a). The mean capture efficiencies used in a specific year were averaged from that year’s and the previous year’s individual estimates at mark–recapture sites.

Site selection was not fixed a priori for the electrofishing surveys on the St. Mary’s or LaHave rivers. The locations sampled gradually changed over time in addition to there being variation among years in the number of sites sampled. Each year, between 3 and 9 (out of a total of 30 sites) were electrofished on the West Branch of the St. Mary’s River, and between 2 and 23 (out of a total of 35 sites) on the LaHave River above Morgans Falls. Such variation in sample locations can bias the resulting density estimates if the proportions of high- and low-density sites change annually or systematically over time (Maunder and Punt 2004). Therefore, we used a generalized linear model (GLM) to reduce the overall variation in the time series of estimated age-class densities and to investigate how such variation in sample locations influences the predictive capacity of juvenile data. Following the approach in Gibson et al. (2009b), the mean density of a given age-class was predicted for each year using site and year as factors in the GLM, assuming a Poisson error distribution.
In all cases, the adjusted $R^2$ values for the models using the standardized data were marginally higher, as would be expected if annual estimation error was reduced. Therefore, all of the results that we present are based on the standardized data series. All data were analyzed relative to a specific cohort. For the adult abundance and egg deposition estimate in a given year, the corresponding juvenile densities were lagged by 1 year for age 0, 2 years for age 1, and 3 years for age 2 to account for the time necessary for a juvenile salmon to reach a given age-class.

Trends in the abundance time series were modeled with linear regression using least squares after transformation of the data to the log scale (Venables and Ripley 2002). This log-linear model was nested in that age-class was considered a factor in the analysis. To determine whether the trends in each data series were significant, we estimated separate intercepts and slopes for the different age-classes. To test for significant differences among these slopes, we reparameterized the model to estimate a slope for adults plus deviations from that slope (deviates) for each of the other age-classes (McCullagh and Nelder 1989). The trend analyses were focused on the time period over which all data series were available for the St. Mary’s and LaHave populations (1990–2010) to ensure that the results from the two rivers were directly comparable. Potential predictive relationships between estimated adult abundance or egg deposition (both scaled as a density) and the four juvenile age-classes were investigated using linear models, also treating juvenile age-class as a factor. For both the trends and predictive analyses, it is important to keep in mind that egg deposition or adult abundance is the response variable while juvenile density is the predictor. This means that the axes in the figures are the opposite of those commonly used in salmon stock–recruitment relationships and that the residual values should be interpreted accordingly.

The ability to use juvenile age-class density as an index of status relative to a reference level was investigated using a threshold-based analysis. The goal was to determine whether there is a threshold juvenile density at which egg deposition is accurately predicted to be above the reference level when juvenile density is high and vice versa. There are four potential outcomes in the analysis: (1) egg deposition and juvenile density are both low (true negative), (2) egg deposition is above the reference level when juvenile density is low (false negative), (3) egg deposition and juvenile density are both high (true positive), and (4) egg deposition is below the reference level when juvenile density is high (false positive) (Figure 2A). The analyses found the juvenile density threshold at which the combined number of false positives and false negatives was minimized based on the observed juvenile density data. False positives and false negatives were considered to be equivalent when calculating the overall misclassification rate for a given juvenile density, which meant that different threshold values (i.e., observed juvenile density values) could have the same number of misclassifications, giving multiple potential thresholds for a specific age-class. For the St. Mary’s and LaHave populations, the reference levels chosen were one-half and one-third of the river-specific conservation requirement. This was done because egg deposition in excess of the conservation requirement has rarely been observed on the St. Mary’s River and has never been observed on the LaHave River. Given the overall similarities in these analyses between the two rivers, the St. Mary’s population at one-half the conservation requirement was chosen as a visual representation of the threshold analyses to highlight the differences in the results among age-classes (Figure 2).

RESULTS

For the West Branch of the St. Mary’s River, significant declines were predicted for adults (slope = −0.102), egg deposition (slope = −0.124), and age-0 (slope = −0.120) and age-2 (slope = −0.122) densities, leading to overall decline rate estimates of 88% (95% confidence interval [CI] = 68–98), 93% (80–97), 92% (76–97) and 92% (76–98), respectively, from 1990 to 2010 (Figure 3; Table 1). Only age-1 density did not exhibit a significant declining trend over the time series of data. None of the deviates from the adult slope estimate were significant (indicating greater or lesser decline rates than for adults), although the confidence interval of the predicted decline rate for age 1 encompassed zero (Table 1). For the LaHave River above Morgans Falls, significant declines were predicted for adults (slope = −0.084), egg deposition (slope = −0.057), and age-0 (slope = −0.082) and age-1 (slope = −0.090) densities, leading to overall decline rates of 81% (95% CI = 57–92), 68% (26–86), 81% (55–92), and 83% (58–94), respectively, from 1990 to 2010 (Figure 4; Table 1). For this river, only age-2 density did not show a significantly negative trend over the time series of data and the slope was significantly greater than that estimated for adults (deviate = 0.069, $P = 0.04$; Table 1). This demonstrates that the overall trend in age 2 was not significantly different from zero, and that the magnitude of the trend in age 2 was significantly lower than that estimated for adult abundance.

For both rivers, egg deposition or adult abundance was positively related to each juvenile density age-class based on a nested linear model with no intercept term and separate slopes among age-classes ($P < 0.001$). However, relatively little of the total variability in egg deposition or adult abundance was explained by the nested predictive model. For example, $R = 0.574$ and 0.647 for the St. Mary’s and LaHave Rivers, respectively, for the relationship between juvenile density and egg deposition. Furthermore, individual fits to the older age-classes demonstrated a distinct pattern in the residuals (negative values at low juvenile densities and positive values at high densities), indicating the inappropriateness of a linear functional form. It is worth noting that this residual pattern is consistent with that expected if density-dependent population regulation were affecting the older juvenile age-classes, leading to changes in their survival rate over time (Jonsson et al. 1998; Gibson 2006). Given the issues described above, the nested model was discarded in favor of a simple linear model with no intercept term describing egg deposition or adult abundance (expressed as a density) as a
FIGURE 2. Example results from the threshold analyses conducted to determine the population status for the St. Mary’s River Atlantic salmon population relative to a reference level. Panel (A) depicts a hypothetical scenario to illustrate the four potential outcomes (false positive, false negative, true positive, and true negative) relative to the reference level of one-half the conservation requirement (horizontal dashed line) and the predicted threshold (vertical dashed line). Panels (B)–(D) depict the observed time series of three juvenile life stages (points connected sequentially) relative to observed egg deposition and the point which is predicted to be the threshold (vertical dashed line). Note the differences in the scales of the x-axes.

function of age-0 density. Nearly identical fits were obtained when the regression was used to predict eggs or adults ($R = 0.608$ for adults and $0.758$ for eggs from the St. Mary’s River, and $R = 0.622$ for adults and $0.607$ for eggs from the LaHave River), so we discuss an example using egg density as the response variable. Although both regressions were highly significant ($P < 0.001$), their predictive power was relatively low for both the St. Mary’s ($R = 0.758$) and LaHave ($R = 0.607$) rivers. Additionally, at low age-0 densities, egg density was frequently higher than that predicted by the linear regression and relatively few of the observed data points fell within the 95% confidence intervals predicted for the regressions, particularly for the LaHave River (Figure 5).

Using age-0 density as the predictor of status consistently led to the lowest error rate (i.e., sum of the number of misclassifications) in the threshold analyses for both the St. Mary’s and LaHave rivers. For the St. Mary’s River, the age-0 density data correctly predicted that the population was above one-half or one-third of the conservation requirement in 94% (one misclassification) and 87% (three misclassifications) of the observations, respectively. On the LaHave River, these percentages were 86% (four misclassifications) and 93% (three
TABLE 1. Fits from the nested log-linear model (considering age-class as a factor) to Atlantic salmon abundance or density estimates from populations in the West Branch of the St. Mary’s River and the LaHave River above Morgans Falls. The model was parameterized to determine separate slopes for the different age-classes as well as to estimate a slope for adults plus deviations from that slope for the other age-classes. The significance levels of the individual slope estimates as well as the deviates from the adult slope estimate are shown for all life stages. The decline rate is given for each age-class during the years 1990–2010. Significant values as well as confidence intervals that do not include zero are shown in bold italics.

<table>
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<tr>
<th>River</th>
<th>Life stage</th>
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<th>Decline ratea</th>
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<td></td>
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<td>Age 2</td>
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</table>

*Estimate (%), with 95% confidence interval in parentheses.

FIGURE 3. Adult abundance, egg deposition, and juvenile density (by age-class) for the Atlantic salmon population in the West Branch of the St. Mary’s River. The points represent the available data for each life stage, and the solid lines represent the fits of a log-linear model spanning the years 1990–2010. The dashed lines indicate the 95% confidence intervals for the fits. For the adult abundance and egg deposition estimates in a given year, the corresponding juvenile densities were lagged by 1 year for age 0, 2 years for age 1, and 3 years for age 2.
DISCUSSION

Our analyses show that juvenile density data for Atlantic salmon can be a useful indicator of both the conservation status of populations and the status of salmon populations relative to fishery benchmarks. However, these conclusions are dependent on the specific juvenile age-classes included in the monitoring program relative to the timing of density dependence in the population, the method of data collection, and the availability of existing adult time series that can be used to determine threshold levels. In three types of analyses attempted, age-0 density was the best predictor for egg deposition, the most consistent relative index of trends, and the most consistent indicator of population status relative to a given reference level. Data from the older age-classes were more variable (as detailed in the following two paragraphs), both within and between river systems, even in situations where similar conclusions on trends or thresholds could be drawn. This strongly suggests that monitoring programs focused exclusively on estimating the abundance of older age-classes (i.e., the abundance of parr or smolts) would have limited usefulness for inferring the changes in adult
River and (B) survival may explain the lesser decline rate predicted for age-1 transition between age 0 and age 1 (Gibson 2006), and increasing survival would lead to proportionately larger juvenile populations from a given egg deposition, which would reduce the decline rate for age-0 density. For both rivers, the trends in the two series are still of a similar magnitude and remain highly significant regardless of the time period of data used, indicating that age-0 density has the potential to impact each life stage abundance or status even though such data may be useful for other purposes. Therefore, for population monitoring programs to reliably answer the questions of interest, scientists or managers must make clear decisions about the goals of the monitoring program prior to its implementation.

There are several factors that introduce variability into the functional relationship between adult or egg abundance and the older juvenile age-classes (ages 1 and 2) which have the potential to limit the utility of juvenile density data for inferring the status of Atlantic salmon populations. These include population regulation, variation in life history characteristics, and the compounding effects of environmental variability as individuals’ age. Density-dependent survival is compensatory when it results in reduced population growth rates at high densities and promotes numerical increase of the population at low densities (Rose et al. 2001). As such, juvenile Atlantic salmon survival would be expected to increase as population size declines for the life stages impacted by density dependence. Increases in survival would lead to proportionately larger juvenile populations from a given egg deposition, which would reduce the decline rate observed for the age-classes affected by density dependence. For these populations, density dependence affects the population between age 0 and age 1 (Gibson 2006), and increasing survival may explain the lesser decline rate predicted for age-1 juveniles. On the St. Mary’s River, the predicted decline rate for age-1 juveniles was lower than that predicted for adults (59% versus 88%) and the confidence intervals included zero. For age-2 juveniles, variation in life history characteristics can influence trends because densities in the watershed depend both on age-1 survival and the probability of undergoing smoltification at age 2. In Southern Upland rivers, the majority of age-1 juveniles become smolts at age 2 and emigrate from freshwater to the marine environment (Gibson et al. 2009a). Lower juvenile density has been linked to faster growth in salmonids (Gibson 1993; Milner et al. 2003), and the probability of smolting is largely dependent on juvenile size, with larger juveniles undergoing smoltification at earlier ages (Evans et al. 1984). From 2005 to 2009, the proportion of age-2 smolts estimated from aging scale samples increased from 81% (Amiro et al. 2006) to 97% (Department of Fisheries and Oceans Canada, unpublished data), which could substantially reduce the age-2 density estimated in recent years. It is likely that such a change in age structure contributed to the significant and substantial decline rate predicted for age-2 juveniles in the river.

When evaluating conservation status, two important considerations in using log-linear regression to model trends are evidenced by these data, both of which impact the older age-classes. First, extremely small values at the beginning or end of a data series have high leverage on log-linear model fits, given the distribution of the error structure (Venables and Ripley 2002). For the St. Mary’s River, this means that the age-2 density estimate of 0.02 resulting from the 2006 egg deposition year falls well below the predicted regression fit in log space (i.e., has a very negative residual value). Removing this point from the data series results in a significantly lower prediction of the decline rate for age 2, making it much more similar to the nonsignificant trend in the age-1 series (data not shown). Second, trend analyses are sensitive to the time period of data included, and different decline rates will result from series of varying lengths. The predicted decline rates for the LaHave River are consistently lower than those for the St. Mary’s River from 1990 to 2010. However, if these data are extended to include values from 1980 to the present, not only do the predicted decline rates for eggs and adults increase, (i.e., > 85%), the trend in the age-1 series becomes nonsignificant and the confidence intervals on the decline rate encompass zero. Even so, neither of these issues impacts the comparison between trends in adult abundance and age-0 density. For both rivers, the trends in the two series are still of a similar magnitude and remain highly significant regardless of the time period of data used, indicating that age-0 density is a useful relative index of adult abundance over large changes in population size.

Predictive relationships between egg deposition and juvenile age-class density are difficult to develop due to several factors. First, physical conditions in the river environment (such as hydrology and temperature) and biological variables (such as inter- and intraspecific competition) vary annually (Milner et al. 2003) and have the potential to impact each life stage

![Graphs showing egg deposition as a function of age-0 density in the following year for the Atlantic salmon populations in (A) the West Branch of the St. Mary’s River and (B) the LaHave River above Morgans Falls.](image-url)
TABLE 2. Results from the threshold analysis to determine whether the juvenile density of Atlantic salmon is an appropriate indicator of status relative to a reference level (a fraction of the conservation requirement [CR]) and which juvenile age-class is most useful for prediction. The true-positive (true-negative) values are the numbers of times that egg deposition was correctly predicted to be above (below) the reference level based on observed juvenile densities 1–3 years later. The false-positive (false-negative) values are the numbers of times that egg deposition was incorrectly predicted to be above (below) the reference level based on observed juvenile densities 1–3 years later. The total number of misclassifications, along with the predicted error rate and associated threshold value, are given for each age-class. Instances in which equivalent error rates were predicted from multiple observed juvenile densities are shown in separate rows.

<table>
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<tr>
<th>River</th>
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<th>Reference level</th>
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<th>Correct classifications</th>
<th>Misclassified values</th>
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<th>Error rate</th>
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differently (Gibson 1993). Second, population regulation via density dependence (Jonsson et al. 1998; Milner et al. 2003; Einum and Nislow 2011) introduces nonlinearity into the functional relationship between some or all of the juvenile age-classes and egg deposition, depending on the timing of density-dependent population regulation (Gibson 2006). Third, there is the issue of comparing density estimates collected at a relatively small scale with large-scale abundance estimates scaled by area (Rosenfeld 2003). Here, the randomly stratified study design and data standardization using a GLM was thought to provide a more unbiased estimate of juvenile density over the available freshwater habitats (Gibson et al. 2009b; Carruthers et al. 2011). This should make annual densities more accurately approximate juvenile abundance in the watershed and thus be more directly comparable with estimates of egg deposition. However, recent research using simulated data suggests that site selection and study design cannot compensate for limited monitoring effort (modeled as missing data) in making inferences on population status (Holt et al. 2011). Collectively, both electrofishing surveys sample an extremely small area relative to the total area of the West Branch of the St. Mary’s River and the LaHave River above Morgans Falls, so their ability to approximate true juvenile abundance in the watershed may be limited. Lastly, regression models can be very inaccurate when used to extrapolate outside of the range of the data which generated the relationship (Snee 1977). If the regressions developed here were used for predicting adult abundance in the St. Mary’s and LaHave rivers, they would be most accurate if the populations remained small. Although the predictive relationships confirm that juvenile density is positively related to egg deposition or adult abundance and thus serve as a useful check on the consistency between indices, it is unlikely to be a useful proxy for population size. The fact that relatively few of the observed data fell within the predicted 95% confidence intervals suggests that the linear model would not be useful for making annual predictions of adult population size from juvenile density data, particularly if such predictions were to form the basis of fishery management recommendations like yearly harvest levels. However, high juvenile densities recorded in multiple years could be used as an indicator of potential population increase, one that might warrant the development or reinstitution of an adult monitoring program.
The threshold analyses indicated that there is the potential to use juvenile density data as an indicator of status relative to reference levels or fishery benchmarks (depending on the chosen life stage) and to use the resolution inherent within the data to estimate a threshold value. Thus, it may be possible to apply this analysis to any salmon population for which there are historical time series on juvenile density and adult abundance, but only where the juvenile monitoring program has been continued. For the two rivers investigated in this study, a similar threshold value at a reference level of one-half the conservation requirement was predicted for age-0 density, with an error rate below 15%. Given that the thresholds tested in the analysis are the sorted list of observed densities, the predicted threshold must be one (or more) of the actual densities observed. This means that the predicted threshold value would not be expected to be the same in both rivers unless identical densities had been observed (which was not the case). At one-third of the conservation requirement, the error rate remained below 20% when using age-0 density to determine the threshold but the specific values predicted for the St. Mary’s and LaHave rivers differed substantially. This suggests either that the thresholds are not transferable among river systems such that this type of analysis can only be used on river systems with existing adult abundance data or that threshold predictions become increasingly variable at low population sizes. In terms of the older age-classes, the increase in the number of misclassified values (predominantly false positives) and the concurrent reduction in the number of true positives corroborate previous results suggesting that age-1 and age-2 juvenile densities remain relatively constant over a large range of adult population sizes, as would be expected if the fish were impacted by compensatory density-dependent population regulation (Jonsson et al. 1998; Rose et al. 2001; Milner et al. 2003). The more linear relationship between age-0 density and adult abundance would be expected to be more accurate for predicting status using this type of threshold analysis.

To date, a management paradigm (i.e., the identification of management actions to be undertaken automatically when the population is at a specific level relative to the conservation requirement) has not been explicitly defined for the St. Mary’s and LaHave rivers. Such a definition would warrant choosing a specific reference value for the threshold analysis instead of the somewhat arbitrary one-half and one-third of the conservation requirement that were used here for illustrative purposes. To apply this analysis to other populations, the chosen reference level should be within the range of observed egg deposition values for a given river to ensure that true positive and true negative values have the potential to be observed. This means that the analysis is somewhat limited in that the population must be (or must historically have been) at a size relevant to management questions. Populations that were very small when juvenile and adult data were collected would not have thresholds that could be used to either monitor annual changes in population size relative to harvest control rules or determine conservation status. Conversely, populations that were very large when juvenile and adult data were collected would have threshold values that are too large to be useful for fisheries management or conservation questions. Defining thresholds from populations that have undergone a decline in abundance or that have been fluctuating close to an established reference level like the conservation requirement would be best for this type of analysis.

For the threshold analysis to be useful in the context of fisheries management, decision rules on the acceptable misclassification rate, the risks associated with each type of misclassification, and the management action resulting from different status designations would have to be determined. More precautionary management (Garcia 1994; Hilborn et al. 2001) would likely accept a low overall misclassification rate and seek to minimize the number of false positives in order to reduce the number of times a population would be predicted to be above the reference level based on juvenile data when the adult abundance was actually below it. Giving more weight to a specific type of misclassification (e.g., false positives) would also remove the issue of multiple thresholds being predicted for a specific life stage. If this caveat were applied to the threshold analysis for the St. Mary’s and LaHave Rivers, the predicted thresholds for a reference value of one-half the conservation requirement would become more similar (20.4 fish/100 m² and 19.8 fish/100 m², respectively, for age-0 density).

Overall, age-0 juvenile density data appear to be a useful and economical indicator for a variety of assessment-related questions. The trend analyses suggest that there is the potential to use widespread electrofishing surveys on previously unmonitored systems to gain information on population trajectories, which could then be used to assess both the need for and a population’s response to recovery actions. This would be particularly useful for the Atlantic salmon populations in the Southern Upland region and others that have been designated threatened or endangered by COSEWIC. Before-after-control-impact studies linking population responses to specific recovery actions or threats (Smith et al. 1993; Conquest 2000) are often used to assess the impact of remediation actions on populations. These require data collection at the scale at which the recovery action impacts the population, typically a reach or tributary within a watershed for Atlantic salmon. More large-scale population monitoring can miss population responses because the expected changes in survival over the life cycle of the organism would be small and difficult to isolate (Rosenfeld 2003). However, using trends in juvenile age-class density as an index of trends in adult abundance requires the ability to monitor a life stage before density dependence, so some prior knowledge of the dynamics of the population under study would be required. For the St. Mary’s and LaHave rivers, the threshold analyses indicate that population status relative to reference levels that are set to trigger a specific management action (e.g., the opening or closing of fisheries) could be monitored with limited means over the long term. In this case, age-0 density is thought to be the most reliable indicator of status. However, in the absence of adult data, it is unknown whether the thresholds developed for
the St. Mary’s and LaHave rivers would be transferable to other systems. Furthermore, if these two populations began to increase substantially in size, additional thresholds would need to be developed for higher reference levels (e.g., the conservation requirement), which would necessitate further adult monitoring on the St. Mary’s and LaHave rivers. Despite the applications noted above, the results from the predictive model suggest that by itself monitoring juvenile density on a given river system will not provide answers to questions that rely on knowledge of actual population size, such as the setting of harvest levels. Therefore, juvenile monitoring programs are much more useful in the contexts of population status, threats analysis, and recovery planning than in the traditional context of fisheries management.

While the emphasis in this paper has been on the use of juvenile data to assess the status of Atlantic salmon populations, the analyses can be extended far beyond simple trends or status indicators in situations where there are data on multiple life stages. Incorporating data on multiple life stages for enhanced realism in demographic models provides an explicit description of the population dynamics of the species as well as predictions about extinction risk, population growth, and population size in relation to management actions (Morris et al. 2002; Norris 2004). Additionally, the marine and freshwater components of the life cycle can be analyzed independently to answer questions regarding the main factors limiting population recovery (e.g., Gibson et al. 2009b) and to prioritize remediation actions during recovery planning (e.g., MacGregor et al. 2002). As assessment programs move forward, a clear understanding of the goals, strengths, and limitations of various monitoring options for Atlantic salmon will ensure that the programs remain relevant and maximize the use of available resources for the benefit of populations.

ACKNOWLEDGMENTS

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REFERENCES


Assessing Avian Predation on Juvenile Salmonids using Passive Integrated Transponder Tag Recoveries and Mark-Recapture Methods

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Assessing Avian Predation on Juvenile Salmonids using Passive Integrated Transponder Tag Recoveries and Mark–Recapture Methods

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Abstract
Many populations of coho salmon Oncorhynchus kisutch and steelhead O. mykiss are listed under the U.S. Endangered Species Act. Until recently, the role of avian predation in limiting recovery of coho salmon and steelhead in central California coastal watersheds has been overlooked. We used recoveries of passive integrated transponder (PIT) tags from Año Nuevo Island (ANI), a breeding site for several species of piscivorous seabirds, to estimate predation rates on juvenile salmonids and identify susceptible life stages and species responsible for predation. A total of 34,485 PIT tags were deployed in coho salmon and steelhead in six watersheds in San Mateo and Santa Cruz counties. Tags were deposited on ANI by predators after ingestion of tagged fish. Because tags were not removed...
from the island and were detected on multiple sampling occasions, we were able to use mark–recapture models to generate a corrected minimum predation estimate. We used POPAN, a variation of the Jolly–Seber model, to generate an estimate of gross population abundance, which accounted for tags deposited on the island but not detected during surveys. Detections of 196 tags from surveys conducted between autumn 2006 and spring 2009 were incorporated into the model, producing a gross population estimate of 242 tags (SE = 9.8). Addition of tags detected between autumn 2009 and 2010 to the abundance estimate from POPAN produced a new minimum estimate of 362 tags on ANI. Minimum predation estimates ranged from 0.1% (Soquel Creek) to 4.6% (Waddell Creek) of outmigrating coho salmon and steelhead smolts. Predation was potentially greater given still unquantified deposition of tags off-colony and destruction of tags during digestive processes of predators. Finally, avian predators targeted estuary-reared fish, which contributed disproportionately to adult populations, further impacting imperiled salmon populations.

Pacific salmonids *Oncorhynchus* spp. are commercially valuable but have decreased in number throughout much of their range. Currently many runs in the eastern Pacific Ocean are listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (Gustafson et al. 2007). Decreases often are attributed to the “four-H’s”: overharvest, obstruction of migratory routes by hydropower facilities, habitat degradation, and hatchery propagation (Collis et al. 2001; Good et al. 2007). There is increasing appreciation, however, that additional factors exacerbate salmon declines (e.g., Ruggerone 1986; Good et al. 2007; Sanderson et al. 2009). For example, salmonids are eaten by piscivorous birds, fish, and mammals and are vulnerable to predation during all life history stages (Collis et al. 2001; Weise and Harvey 2005; Wright et al. 2007).

Predation on juvenile salmonids by seabirds has been well documented in large river systems, for example, in the Columbia and Sacramento rivers, and efforts have been made to quantify the extent of avian predation (Ruggerone 1986; Collis et al. 2001; Roby et al. 2003; Major et al. 2005; Good et al. 2007). For example, ring-billed gulls *Larus delawarensis* and California gulls *L. californianus* consumed approximately 10.3% of all juvenile salmonids passing dams on the Yakima River, a tributary of the Columbia River (Major et al. 2005). Juvenile salmonids comprised approximately 75% of the diet of Caspian terns *Sterna caspia* and 50% of the diet of double-crested cormorants *Phalacrocorax auritus* nesting on an artificial dredge-spoil island in the lower Columbia River (Roby et al. 2003). Avian predators ate as many as 4–12 million of the 60–100 million salmonid smolts out-migrating through the Columbia River estuary annually, leading to management actions designed to lessen the effects of predation (Roby et al. 2003; Good et al. 2007). More recently, coded wire tags were used to estimate Caspian tern predation on salmonids originating in the Sacramento–San Joaquin River system (Evans et al. 2011).

In contrast to the body of literature quantifying predation on salmonids by avian species in large river systems, comparable studies in small coastal watersheds in California are lacking from the published literature. Coastal watersheds south of San Francisco Bay, California, provide spawning and rearing habitat for endangered coho salmon *O. kisutch* and steelhead *O. mykiss*. Although diversion of water for human use, degradation of local habitat, and changes in ocean productivity are the major reasons for the continued decrease of Central Coast coho salmon and steelhead (Good et al. 2005), it remains unknown whether predation may be affecting the status of these populations and hindering future recovery. Given the extent of avian predation on salmonids in the Columbia River basin, and associated implications for recovery of federally listed runs, quantifying the magnitude of predation and identifying susceptible life stages was considered a necessary step in understanding factors limiting the recovery of salmonids in California.

Recovery of salmon tags on roosting and breeding sites used by piscivorous birds has increasingly been used to document predation. For example, detection of passive integrated transponders (PIT tags) on seabird colonies was used to document and quantify predation on salmonids by piscivorous birds in the Columbia River basin (Collis et al. 2001; Ryan et al. 2001; Roby et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Although an unknown proportion of tags may be damaged during the digestive process, PIT tags are capable of remaining functional through ingestion of a tagged fish by piscivorous birds and mammals and subsequent defecation or regurgitation at breeding or roosting sites. Since 2002, PIT tags were used to enhance the understanding of population biology and marine survival of coho salmon and steelhead in six watersheds within Santa Cruz and San Mateo counties (e.g., Hayes et al. 2004, 2008, 2011; Bond et al. 2008). In 2006, one of these PIT tags was recovered on Año Nuevo Island (ANI), a seabird and marine mammal breeding colony located in San Mateo County, California (37°6′N, 122°20′W), which prompted the initiation of annual scans for PIT tags on ANI with the objectives of (1) quantifying predation on salmonids by piscivorous birds and marine mammals, (2) identifying life stages most susceptible to predation, and (3) identifying predators responsible for depositing tags on ANI.

Recovery of PIT tags only allows for minimum estimates of predation because (1) an unknown number of tags are deposited away from breeding and roosting areas, (2) some tags may lose function during the process of ingestion and excretion, (3) some tags may lose function after deposition on the island, and (4) not all tags on a colony are detected (Collis et al. 2001; Ryan et al. 2001). We addressed uncertainties from
(3) and (4) by the novel application of mark–recapture statistics to improve our minimum estimate of predation on juvenile salmonids. Mark–recapture approaches generally are applied to generate estimates of population parameters including survival (Lebreton et al. 1992), abundance (Jolly 1965; Seber 1965), and rate of population change (Pradel 1996). Because PIT tags were uniquely numbered, not removed from ANI after detection, and often detected during subsequent trips to the island, it was possible to use mark–recapture statistics to estimate population parameters associated with the population of tags (representing the number of salmonids eaten and deposited by predators) on ANI. We used mark–recapture statistics to create a correction factor to apply to PIT tags detected on ANI between 2006 and 2009 to improve minimum estimates of the number of salmonids eaten by predators using ANI as breeding and resting habitat. Our approach will provide the first steps in understanding the effects of avian predation on ESA-listed coho salmon and steelhead in coastal watersheds near their contemporary southern range extent and may help inform recovery plans for these imperiled populations.

METHODS

Study site.—This study took place in central California and focused on Año Nuevo Island, which provides breeding habitat for several species of piscivorous seabirds and marine mammals. The island is located in close proximity to several watersheds that support coho salmon and steelhead. Año Nuevo Island is 10 ha in size and located 1.6 km off Point Año Nuevo, San Mateo County, California (Figure 1). Piscivorous species that used elevated portions of the island that could be scanned for PIT tags included western gulls \textit{L. occidentalis}, Brandt’s cormorants, and sea lions. Approximate areas used by Brandt’s cormorants (light dashes) and brown pelicans (short and long dash combination) also are shown. [Figure available in color online.]

FIGURE 1. Location of coho salmon and steelhead PIT tags on Año Nuevo Island, by year of detection, 2006–2010. Elevated portions of the island scanned for PIT tags are dark gray, intertidal areas not scanned are light gray, surrounding water is white, and circles represent tag locations. Colors correspond to the year a tag was first detected (white = 2006, yellow = 2007, green = 2008, pink = spring 2009, orange = autumn 2009, blue = spring 2010, purple = autumn 2010). Western gulls (solid lines), and sea lions (heavy dashes) are ubiquitous over areas of the island scanned for PIT tags; approximate areas of greatest density are shown. Approximate areas used by Brandt’s cormorants (light dashes), and brown pelicans (short and long dash combination) also are shown. [Figure available in color online.]
cormorants *P. penicillatus*, pelagic cormorants *P. pelagicus*,
brown pelicans *Pelicanus occidentalis*, California sea lions *Za-
lophus californianus*, and Steller sea lions *Eumetopias jubatus*.

Populations of western gulls and Brandt’s cormorants that breed on
ANI have increased in recent decades. During 1998, an esti-
mated 1,274 western gulls and 664 Brandt’s cormorants bred on
ANI; by 2007, the estimated number of birds breeding on ANI
had reached 2,196 western gulls and 3,660 Brandt’s cormorants
(Point Reyes Bird Observatory [PRBO], unpublished data).

Although gulls and cormorants are present year-round, numbers are
greatest during breeding (spring and early summer), after
which adults disperse. Gulls generally disperse in September and
cormorants in July–August (Pierotti and Amnett 1995;
Wallace and Wallace 1998). Brown pelicans breed in southern
California and Baja California and are present in central
California during the nonbreeding period between June–July
and December (Shields 2002). During the nonbreeding period,
brown pelicans roost on ANI with greatest numbers counted
during July and August except in years when breeding attempts
were unsuccessful, and pelicans arrived on ANI in April or May
(Shields 2002; Thayer and Sydeman 2004; PRBO, unpublished
data). The number of pelicans using ANI varies considerably
among years (PRBO, unpublished data). Steller’s sea lions
breed on ANI and occur in fewer numbers compared with
California sea lions that use ANI for resting habitat during the
nonbreeding season. Although California sea lions are present
on ANI year-round, numbers vary considerably within and
among years (P. Morris, University of California Santa Cruz,
personal communication). For example, the mean number of
California sea lions on ANI during near-monthly aerial surveys
(between May 1997 and September 1998) was 3,145 animals
and ranged from 510 in June 1997 to 5,963 in June 1998 (Weise
2000).

**PIT tag detections.**—Beginning in 2006, we scanned ANI
for PIT tags annually using a portable PIT tag antenna system
modified from the instream PIT tag antenna described by Bond
et al. (2007). The system was capable of detecting 134.2-kHz
full duplex PIT tags (Bond et al. 2007). The portable, pole-
mounted, circular antenna was powered by a 6-V battery and
in a backpack along with a data logger. Tag identity and
time detected were logged for each tag. A portable GPS unit
was carried during each scan of the island beginning in 2007,
allowing GPS coordinates to be assigned to each tag detected.
The GPS positions were logged at 2-s intervals to evaluate the
land area covered and to ensure that coverage of the island was
adequate and consistent among surveys. Deployment histories
of most PIT tags detected on ANI were known, so it was possible
to determine the species, date, and location of initial tagging,
subsequent dates fish were captured (for all watersheds), life
stage at tagging (juvenile or adult), and any detections of fish
by instream PIT tag antennas (Scott Creek only). Surveys for
tags were conducted in late autumn–early winter during 2006,
2007, and 2008 and in spring and late autumn–early winter of
2009 and 2010 (see Table A.1.2 for survey dates).

**Correction factor analysis.**—We applied a modeling frame-
work to improve estimates of predation on juvenile salmonids
obtained from deposition of PIT tags on ANI. We used the
model to generate a correction factor to account for loss of PIT
tags from ANI between sampling events. Tag loss could oc-
cur through erosional processes, tag breakage and loss of tag
function, tag interference, and burial out of range of scanning
antennas (Collis et al. 2001; Ryan et al. 2001). We used the
POPAN (Schwarz and Arnason 1996) formulation of the Jolly–
Seber mark–recapture model for open populations to estimate
the gross population size of tags on ANI, which served as a
corrected estimate of minimum tag deposition on the island.

We selected the POPAN model because PIT tags on ANI represent
a distinct, open population of individual fish with PIT tags that
were eaten by predators and deposited on the island through
regurgitation or defecation. Additionally, the estimates of gross
recruitment produced by POPAN allowed us to account for tags
deposited on the island that were subsequently lost through
physical tag loss or tag breakage before the next sampling in-
terval (Arnason and Schwarz 2002). Modeling was conducted
within the framework of Program MARK version 5.1 (White
and Burnham 1999), and model notation followed Arnason
and Schwarz (2002).

Key assumptions of the POPAN model are: (1) tags are re-
tained throughout the experiment and are read properly; (2)
sampling is instantaneous relative to the study period; (3) catch-
ability and survival of marked and unmarked individuals are
homogeneous; and (4) the study area did not change in size
during the course of the study (Lebreton et al. 1992; Arnason
and Schwarz 2002). Locations of tags were mapped after each
survey of the island, so areas of the island with high tag depo-
sition were known. All areas of the island were allocated equal
effort during surveys regardless of tag densities to avoid biases
associated with heterogeneous catchability (Lebreton et al.

Four fundamental parameters were generated using POPAN:
(1) survival (*φ*), interpreted as the probability that a tag initially
deposited at ANI was not lost from the island or destroyed be-
tween sampling at time *i* and time *i* + 1 (given that the tag was
in the population and available to be detected); (2) probability of
capture (*p*), interpreted as the probability of detecting a given
tag during a complete scan of the island at time *i*; (3) super-
population size (**N**), which was the pool of all tags deposited
on ANI (total net recruitment, Arnason and Schwarz 2002); and
(4) proportion of tags from the superpopulation that entered the
island population (*b*), after time *i* that survived to time *i* + 1
(Arnason and Schwarz 2002). In addition, four other parame-
ters of interest were derived from the fundamental parameters:
(1) gross recruitment (**B**), which accounts for tags that entered
the population after time *i* but were lost from the population
before the next sampling interval at time *i* + 1; (2) net births
(**B**), defined as the number of tags that entered the population
after time *i* and survived to time *i* + 1; (3) abundance at time
*i* (**N**); and (4) total gross population size (**N**), which includes
FIGURE 2. PIT tags detected on Ano Nuevo Island by watershed of origin, salmonid species, and year first detected between 2006 and 2010. Tags from Soquel, San Lorenzo, Gazos, and Waddell watersheds were from steelhead only.

RESULTS

Between autumn 2006 and autumn 2010, we detected 316 unique PIT tags on ANI (Figure 1) out of 34,485 wild and hatchery coho salmon and steelhead tagged in five watersheds in Santa Cruz County (Waddell, Scott, San Lorenzo, Soquel, and Aptos) and one watershed in San Mateo County (Gazos) (Table A.1.1). It was possible to determine the identity of 312 of the PIT tags detected on ANI using known deployment history data (Figure 2). Four tags were from salmonids (all steelhead from Scott Creek) that were last handled as adults (mean fork length [FL], 40.3 cm; SD = 2.4); however, the majority of tags detected were from juvenile steelhead (88%; 273 out of 312). Only 11% of the tags detected on ANI were from juvenile coho salmon. Tagging effort for juvenile coho salmon was extremely variable during the years encompassed by this study, whereas tagging effort was more consistent for steelhead. Because of the variation in tagging effort and the low recovery rate of PIT tags from coho salmon on ANI (35 tags), detections of tags from coho salmon and steelhead were combined and analyzed together for generating the correction factor.

Tags detected were from salmonids originating in five of the six watersheds where PIT tags were deployed (Figure 2). Although PIT tags were deployed in Apts Creek, no tags from this watershed were detected on the island. The greatest number of PIT tags on ANI (n = 226) were from fish that originated in Scott Creek (Figure 2). For this watershed, we identified the species,
Steelhead of wild origin were tagged in the upper watershed (UWS) upstream from the estuary influence, or in estuary habitat.

The majority of tags detected during all years (approximately 90%) on ANI were located in an area of the south terrace used by western gulls for breeding (Figure 1). Approximately 7% of tags were located in areas used by Brandt’s cormorants for breeding, but these areas also were used by western gulls and sea lions (P. Morris, University of California at Santa Cruz, personal communication). The remaining 3% of tags were detected in an area used by western gulls and brown pelicans. California sea lions are ubiquitous over areas of the island scanned for PIT tags; thus, they also use the north and south terraces of ANI where tags were found (P. Morris, personal communication).

Correction Factor Analysis

Complete scans of ANI were conducted during autumn 2006, 2007, and 2008 and spring 2009. The areas surveyed during autumn 2009 and spring and autumn 2010 were not comparable with previous scans of the island. In autumn 2009 we experienced an equipment failure that resulted in a nonquantifiable loss of sensitivity. During spring 2010 the area surveyed was reduced physically to prevent disturbance of cormorants and sea lions, whereas effort was increased during autumn 2010 as part of an associated study. Consequently, data collected in autumn 2009, spring 2010, and autumn 2010 were not included in the estimation of tag abundance using POPAN (as this would underestimate abundance and associated parameters, Arnason and Schwarz 2002). We ran the model with tags detected in the reduced area of the island scanned during spring 2010 (using detections from 2006 to spring 2009, and spring and autumn 2010). However, data were too sparse to test model goodness of fit, and the estimated tag abundance differed from the original model (2006 to spring 2009 for the entire island) by less than 1%. We therefore chose to use the original model (2006 to spring 2009 for the entire island) to generate our corrected minimum estimate of predation.

Tag detections from complete surveys (autumn 2006, 2007, and 2008 and spring 2009; all detections: n = 358, unique tags: n = 196) were incorporated into the POPAN model (Schwarz and Arnason 1996). The unequal sampling intervals created by sampling in autumn (2006, 2007, and 2008) and spring (2009) were accounted for within the Program MARK framework, so estimates of survival rates are presented on a per-time basis. The goodness-of-fit test indicated lack of overall model fit ($\chi^2 = 14.5$, $P = 0.006$). The assumption of homogeneous capture probability was met (Test 2C.2, Table A.2.1); therefore, the lack of model fit stemmed from overdispersion or failure to meet the assumption of homogeneous survival. The assumption of homogeneous survival had two components: (1) the probability that an individual alive at occasion i was seen again was independent of whether it was marked on or before occasion i, and (2) timing of subsequent detections of individuals was independent of whether they were marked on or before occasion i. Component (1) of the assumption of homogeneous survival was met (Test 3.SR2 and 3, Table A.2.1); however, component (2) was not met (Test 3.Sm2, Table A.2.1) because a great number of individuals (18) were detected during all four surveys of ANI (see Appendix 2 for a discussion of how this was determined). Although it was not possible to determine whether lack of fit stemmed from heterogeneity of survival or overdispersion, the variance inflation factor ($\hat{\epsilon}$) for our model was 3.6, indicating that model structure was reasonably adequate (Lebreton et al. 1992). To account for overdispersion, therefore, we applied the variance inflation factor of 3.6 to the resulting model set (Lebreton et al. 1992).

The model that best fit the data (i.e., received the lowest QAIC, score) had constant probability of survival and probability of capture and time-variant probability of entry (Table 1, Model A). Based on comparison of the QAIC, weights, support for this model was 6.2 times greater than the next best model (Table 1, Model B). Probability of survival ($\Phi$) was 0.8578 (95% confidence interval [CI], 0.6504–0.9513), probability of capture ($p$) was 0.6436 (95% CI, 0.4715–0.7853), and the superpopulation size ($N$) was 233.29 (Table 2). Because the best-fit model predicted constant capture ($p$) and survival ($\Phi$), all fundamental and derived parameters were estimable (Schwarz and Arnason 1996). Although it was not possible to directly measure efficiency of PIT tag scanning equipment, the constant probability of capture indicated that scanning effort and PIT tag antenna...
efficiency were relatively consistent among surveys. The difference between gross recruitment (\(B_i^*\)) and net recruitment (\(B_i\)) provides an estimate of tags that were deposited on ANI between sampling events but were lost from the tag population before they could be detected, and ranged from two to four tags (Table 3). Gross population size (\(N_i^*\)) was 242 PIT tags (SE = 9.8; Table 3). This means that although only 196 tags were detected on the island between 2006 and spring 2009, 242 tags were probably deposited on the island through spring 2009. When added to the raw number of tags detected between autumn 2009 and autumn 2010 (120 tags), our corrected, minimum estimate of deposition on ANI was 362 tagged fish.

To apply our correction factor to individual watersheds, we multiplied the new corrected estimate of tag deposition (362 tags) by the percentage of tags detected on the island for each watershed (Table 4). This approach was taken because the number of tags detected on ANI from fish tagged in Scott Creek (\(n = 226\)) was 2.5 times greater than the number of tags recovered from all other watersheds combined (\(n = 89\)); therefore, data were too sparse to run the POPAN model with data grouped by watershed. By applying this correction factor, there was no increase in the number of fish originating from the San Lorenzo watershed and Soquel Creek in the ANI tag population (Figure 3). New estimates of total tags originating from Scott Creek (260), Gazos Creek (22), and Waddell Creek (72) were obtained when the correction factor was applied, increasing the minimum predation rates for these watersheds to 0.94% for Scott Creek, 2.9% for Gazos Creek, and 4.6% for Waddell Creek (Figure 4).

### Table 1. Comparison of candidate POPAN models used to estimate abundance, survival, recapture, and entry parameters for salmonid PIT tags on Ano Nuevo Island (2006–Spring 2009). AIC\(_c\) = Akaike’s information criterion adjusted for small sample sizes, \(\Delta\text{AIC}\_c\) = difference in AIC between the AIC\(_c\) for a given model and the AIC\(_c\) for the best-fit model, AIC\(_c\) weight = Akaike weight indicating the relative support for a model based on AIC\(_c\), \(\Phi_i\) = probability of survival, \(p_i\) = probability of capture, \(b_i\) = probability of entry, \(t\) = time, NA = not applicable. Numerical convergence was not reached for models G and H.

<table>
<thead>
<tr>
<th>Model identification</th>
<th>Model</th>
<th>AIC(_c)</th>
<th>(\Delta\text{AIC}_c)</th>
<th>AIC(_c) weight</th>
<th>Number of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>136.27</td>
<td>0</td>
<td>0.81</td>
<td>6</td>
</tr>
<tr>
<td>B</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>139.90</td>
<td>3.64</td>
<td>0.13</td>
<td>8</td>
</tr>
<tr>
<td>C</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>141.93</td>
<td>5.66</td>
<td>0.05</td>
<td>9</td>
</tr>
<tr>
<td>D</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>145.85</td>
<td>9.58</td>
<td>0.01</td>
<td>11</td>
</tr>
<tr>
<td>E</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>22,629.92</td>
<td>22,493.65</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>F</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>22,631.51</td>
<td>22,495.24</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>G</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>H</td>
<td>(\Phi(\cdot)p(\cdot)b(\cdot))</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

### Table 2. Estimates of real parameters from the best fit model \([\Phi(\cdot)p(\cdot)b(\cdot)\)]\). \(\Phi = \text{probability of survival, } p = \text{capture probability, } b_i = \text{probability of entry, } N = \text{superpopulation size. Estimates for each parameter are presented with associated standard error (SE) and upper and lower 95% confidence limits (CL).}

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>Lower 95% CL</th>
<th>Upper 95% CL</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Phi)</td>
<td>0.8578</td>
<td>0.0732</td>
<td>0.6504</td>
<td>0.9513</td>
</tr>
<tr>
<td>(p)</td>
<td>0.6436</td>
<td>0.0825</td>
<td>0.4715</td>
<td>0.7853</td>
</tr>
<tr>
<td>(b_1)</td>
<td>0.2327</td>
<td>0.0936</td>
<td>0.0978</td>
<td>0.4588</td>
</tr>
<tr>
<td>(b_2)</td>
<td>0.1185</td>
<td>0.0805</td>
<td>0.0288</td>
<td>0.3786</td>
</tr>
<tr>
<td>(b_3)</td>
<td>0.2562</td>
<td>0.0795</td>
<td>0.1320</td>
<td>0.4383</td>
</tr>
<tr>
<td>(N)</td>
<td>233.2914</td>
<td>18.0445</td>
<td>197.9241</td>
<td>268.6587</td>
</tr>
</tbody>
</table>

### Table 3. Estimates of derived parameters from the best fit model \([\Phi(\cdot)p(\cdot)b(\cdot)\)]. \(\Phi = \text{probability of survival, } p = \text{capture probability, } b_i = \text{probability of entry. \(N_i^*\)} = \text{abundance of tags in the island population during each survey, Gross population size (\(N_i^*\)} = \text{all tags deposited on the island including tags deposited but lost from the island before sampling. Estimates for each parameter are presented with associated standard error (SE) and upper and lower 95% confidence limits (CL).}

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>Lower 95% CL</th>
<th>Upper 95% CL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gross births ((B_i^*))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006–2007</td>
<td>58.5</td>
<td>12.5</td>
<td>34.1</td>
<td>83.0</td>
</tr>
<tr>
<td>2007–2008</td>
<td>29.8</td>
<td>10.6</td>
<td>8.95</td>
<td>50.7</td>
</tr>
<tr>
<td>2008–Spring 2009</td>
<td>62.1</td>
<td>11.2</td>
<td>40.2</td>
<td>84.0</td>
</tr>
<tr>
<td>Net births ((B_i))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006–2007</td>
<td>54.3</td>
<td>11.4</td>
<td>32.0</td>
<td>76.6</td>
</tr>
<tr>
<td>2007–2008</td>
<td>27.7</td>
<td>9.7</td>
<td>8.6</td>
<td>46.7</td>
</tr>
<tr>
<td>2008–Spring 2009</td>
<td>59.8</td>
<td>10.8</td>
<td>38.6</td>
<td>80.9</td>
</tr>
<tr>
<td>(B_i^* - B_i)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006–2007</td>
<td>4.3</td>
<td>1.1</td>
<td>2.1</td>
<td>6.4</td>
</tr>
<tr>
<td>2007–2008</td>
<td>2.1</td>
<td>0.9</td>
<td>0.4</td>
<td>4.0</td>
</tr>
<tr>
<td>2008–Spring 2009</td>
<td>2.3</td>
<td>0.4</td>
<td>1.6</td>
<td>3.1</td>
</tr>
<tr>
<td>Abundance ((N_i))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>91.6</td>
<td>12.0</td>
<td>68.0</td>
<td>115.2</td>
</tr>
<tr>
<td>2007</td>
<td>132.8</td>
<td>12.1</td>
<td>109.1</td>
<td>156.5</td>
</tr>
<tr>
<td>2008</td>
<td>141.6</td>
<td>11.8</td>
<td>118.5</td>
<td>164.7</td>
</tr>
<tr>
<td>Spring 2009</td>
<td>190.9</td>
<td>13.9</td>
<td>163.7</td>
<td>218.2</td>
</tr>
<tr>
<td>Gross population size ((N_i^*))</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>242.1</td>
<td>9.8</td>
<td>222.8</td>
<td>261.3</td>
</tr>
</tbody>
</table>
TABLE 4. Corrected estimates of PIT tags deposited on Año Nuevo Island (ANI) by watershed of origin. Number of tags recovered on ANI from five central California watersheds between 2006 and Autumn 2010 are presented as: (1) total number and (2) percentage of total number of tags detected on ANI, (3) the number of tags deployed per watershed, and (4) the percentage of tags recovered on ANI relative to the number deployed in each watershed and all watersheds combined (deposition rate). NA = not applicable.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Number of tags recovered on ANI</th>
<th>Percentage of total recovered on ANI (%)</th>
<th>Number of tags deployed</th>
<th>Deposition rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All combined</td>
<td>316</td>
<td>0.92</td>
<td>34,485</td>
<td>0.92</td>
</tr>
<tr>
<td>Waddell</td>
<td>63</td>
<td>19.9</td>
<td>1,576</td>
<td>4.00</td>
</tr>
<tr>
<td>Gazos</td>
<td>19</td>
<td>6.0</td>
<td>762</td>
<td>2.49</td>
</tr>
<tr>
<td>Scott</td>
<td>226</td>
<td>71.5</td>
<td>27,570</td>
<td>0.82</td>
</tr>
<tr>
<td>San Lorenzo</td>
<td>1</td>
<td>0.3</td>
<td>401</td>
<td>0.25</td>
</tr>
<tr>
<td>Soquel</td>
<td>3</td>
<td>0.9</td>
<td>4,176</td>
<td>0.07</td>
</tr>
<tr>
<td>Unidentified</td>
<td>4</td>
<td>1.3</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

DISCUSSION

We improved our minimum estimates of juvenile coho salmon and steelhead mortality from predation through a novel use of the POPAN formulation of the Jolly–Seber model (Jolly 1965; Seber 1965; Schwarz and Arnason 1996). During four complete scans of ANI conducted between autumn 2006 and spring 2009, use of the POPAN model to correct for tags deposited on the island but not detected during surveys resulted in an estimate of 242 tags deposited during the same period. This was an increase of 23% from the 196 tags that were physically detected on the island. By adding the number of tags detected during surveys conducted in autumn 2009 and 2010 and spring 2010 (120 tags), we obtained a new, minimum estimate of 362 PIT tags on ANI.

This estimate of 362 tags still represents a minimum estimate of predation. For instance, the estimate does not account for a still unknown proportion of tags that were deposited away from ANI or that lost function during the process of ingestion and excretion (Collis et al. 2001; Ryan et al. 2001). Further, we were unable to use the POPAN method to calculate a corrected minimum estimate of predation when survey area was not consistent (autumn 2009 and 2010, spring 2009). Inclusion of these years would violate a key assumption of the model, resulting in an under- or overestimate of tag deposition (Arnason and Schwarz 2002). The estimate of 362 tags does not account for gross recruitment between sampling intervals after spring 2009. That is, we were unable to determine how many tags were deposited on ANI but were lost before sampling occurred during autumn 2009 or spring and autumn 2010 (Schwarz et al. 1993; Arnason and Schwarz 2002).

During years when effort and equipment performance was consistent, however, the mark–recapture approach we employed worked particularly well at ANI, where tags were not removed because of the clay-like substrate and risk of disturbance to seabirds and marine mammals. This method can be applied to future scans of ANI provided that effort and equipment performance are consistent among surveys. Although the corrected minimum estimates of predation we generated are applicable only to the system studied, the method we employed could be used in similar systems where PIT tags (or other individually unique tags that persist through digestion and excretion by predators) (1) are not removed from an area used frequently by predators, (2) are readily resighted, and (3) effort is consistent among surveys. Use of the POPAN model to generate a corrected minimum estimate of tag deposition and abundance on the island allowed us to account for tags that lost function after deposition on the island and tags that were not detected (due to tag breakage, signal interference, or burial out of the range of detection equipment), which have been cited as some of the common problems with using PIT tag recoveries to quantify predation on salmonids (Collis et al. 2001; Ryan et al. 2001).
The area of ANI where tags were most concentrated was within areas of the island heavily used by western gulls for breeding (Figure 1). Sea lions also use these areas; however, numbers vary greatly, and greatest abundance generally does not overlap in time with salmonid availability (Figure 5). Although some tags were located in areas used by Brandt’s cormorants, these areas also were used by western gulls and California sea lions (P. Morris, personal communication). Brown pelicans roosted on the south terrace and central island in low numbers; the greatest numbers of brown pelicans roosted on the north terrace (P. Morris, personal communication), which is where the fewest tags were found (Figure 1).

Presence of tags from adult steelhead (mean FL > 400 mm) implies at least some deposition of tags by California sea lions. Western gulls, Brandt’s cormorants, and brown pelicans eat small schooling fish (Pierotti and Annett 1995; Wallace and Wallace 1998; Shields 2002). Fish eaten by Brandt’s cormorants breeding on southeast Farallon Island ranged from 4 to 200 mm total length (TL) (Boekelheide et al. 1990); brown pelicans in California and Mexico took similarly sized prey (range, 85–172 mm TL; Shields 2002). Sea lions were the only predator that used elevated portions of ANI where tags were found and were large enough to eat adult-sized salmonids. Steller sea lions were present on ANI; however, numbers were extremely low compared with numbers of California sea lions, so the probability of a Steller sea lion depositing a PIT tag on the island was believed to be extremely low (P. Morris, personal communication). Alternatively, gulls could have ingested PIT tags while scavenging a dead, PIT-tagged adult salmonid, but the probability of this occurring was extremely low because very few dead adult salmonids occurred in areas where they could be scavenged by gulls, and the occurrence of PIT tagged adults in these areas was even lower.

Several predators may be depositing PIT tags on ANI; however, we believe western gulls are responsible for the majority of tag deposition. The area of ANI where the most PIT tags were found was used by western gulls and California sea lions. Although recovery of some PIT tags deployed in adult steelhead indicates predation by sea lions, PIT tags have not been identified during diet analysis of California sea lions on ANI. Beginning in 2001, fecal samples (scats) collected from ANI were used to determine prey eaten by California sea lions. No PIT tags were found in fecal samples from California sea lions despite a large number of samples processed (100–150 per year between 2001–2007 and 371 between 2008 and 2011; M. Weise, Marine Mammals and Biological Oceanography Program, Office of Naval Research, personnel communication). If sea lions accounted for appreciable deposition of tags on ANI, we would expect that PIT tags would have been identified in at least some scat samples. Therefore it is unlikely that sea lions were responsible for deposition of the majority of tags in areas of ANI where western gulls and sea lions overlap. Of the predators that use areas of ANI where tags were located, western gulls were the only species visually observed eating juvenile salmonids during 198 h of observations conducted at the mouths of Scott and Waddell creeks as part of an associated study (Frechette 2010). Observed predation on juvenile salmonids by gulls occurred in freshwater before ocean entry (Frechette 2010). Recovery of archival temperature loggers deployed on juvenile salmonids also indicated predation occurred in freshwater (Hayes et al. 2012). The only predators that used ANI and were observed on the beach or in the estuary at Scott or Waddell creeks were western gulls and brown pelicans. Neither western gulls nor pelicans were observed upstream of bridges that cross Scott and Waddell creeks, approximately 100–200 m from where these creeks enter the ocean (D. Frechette, unpublished data). Therefore predation most probably occurred in the most downstream portion of the estuary or immediately after salmonids entered the ocean. Because the estuary is too shallow to support the plunge-diving foraging methods employed by brown pelicans, any predation by pelicans would have occurred after fish had entered the ocean. As discussed previously, few tags have been detected in the area of the island most heavily used by roosting brown pelicans (the north terrace), so it is still unlikely that PIT tags were deposited on ANI by pelicans. Unlike gulls and cormorants, however, brown pelicans do not cast
pellets (Shields 2002), so predation on juvenile salmonids could go unnoticed if tags were destroyed in the process of digestion. Western gulls have been observed bathing, loafing, and drinking water at all six watersheds where PIT tags were deployed in coho salmon and steelhead (Table A.1.1); however, the majority of PIT tags on ANI were from fish tagged in the three watersheds in closest proximity to the island (Waddell, Gazos, and Scott creeks). Recoveries of PIT tags on ANI only are indicative of predation by the population of western gulls using ANI as a roosting and breeding site. Gulls eating salmonids at watersheds at greater distances from ANI (e.g., San Lorenzo, Soquel, and Aptos) may not use ANI for breeding and roosting and probably deposit tags elsewhere, resulting in an underestimation of total predation on central California salmonids. Although no PIT tags were deployed in Gazos and Aptos creeks or the San Lorenzo River during the years when sampling was conducted on ANI, we still feel it was appropriate to apply the correction factor to these watersheds to improve minimum estimates of predation because tags from all watersheds, regardless of year of deployment, were incorporated in the model.

The majority of PIT tags on ANI originated in steelhead (89%). In the Columbia River basin, consumption of steelhead by Caspian terns was greater than expected based on their availability relative to other salmonids, which may represent selectivity by terns for the larger, more energy-dense steelhead compared with other salmonids (Collis et al. 2001; Ryan et al. 2003; Antolos et al. 2005). In central California, however, tagging efforts have focused on the more abundant steelhead, so interpretation of the relative susceptibility of coho salmon and steelhead must be approached with caution. Work is ongoing to further examine relative susceptibility of juvenile salmonids to predation (A.-M. K. Osterback, unpublished data). It was possible, however, to draw some conclusions of relative susceptibility of juvenile steelhead to predation from Scott Creek, where the greatest tagging effort has occurred. Steelhead tagged in the Scott Creek estuary represented a greater proportion of wild-reared steelhead on ANI than fish tagged upstream of estuary influence (Figure 3). These estuary-reared steelhead have the life history strategy with greatest effects on population persistence in coastal watersheds in central California (Bond et al. 2008; Hayes et al. 2011).

Watersheds in the central California study area experience a unique hydrodynamic regime. Rainfall occurs predominantly during winter. During dry summers, deposition of beach sand creates a sandbar across creek mouths, blocking the estuaries from the ocean and causing formation of freshwater lagoons, typically during summer and autumn (Shapovalov and Taft 1954). Whereas coho salmon generally migrate directly to sea each spring as smolts, steelhead in some central California watersheds have alternative life history strategies that take advantage of seasonally forming freshwater lagoons. While some steelhead smolts complete their spring migration to the ocean, many pause in the lagoon where they spend several months during the summer (Bond et al. 2008) before migrating back upstream for the winter and performing a second downstream migration the following spring, ultimately entering the ocean a year later (Hayes et al. 2011). Lagoon-reared steelhead undergoing the second migration are greater in size (FL > 150 mm) than steelhead completing a first downstream migration (FL < 150 mm) (Bond et al. 2008; Hayes et al. 2011). Bond et al. (2008) documented increased smolt-to-adult survival for juvenile steelhead that reared in the Scott Creek lagoon. Although larger lagoon-reared fish comprised approximately 95.5% of returning adults, they only were 8–48% of the estimated number of spring out-migrants (Bond et al. 2008). Conversely, smaller juvenile steelhead that migrated directly to sea comprised only 4.5% of the returning adult steelhead population but were the majority of spring out-migrants (Bond et al. 2008; Hayes et al. 2011). Because all PIT-tagging in the Scott Creek estuary occurred during the lagoon period, tags on ANI from estuary-reared steelhead represent fish that reared in the lagoon (S. A. Hayes and D. Frechette, unpublished data). Tags from lagoon-reared steelhead comprised 70% (93 of 133) of tags from wild-origin steelhead that originated in Scott Creek and were detected on ANI during our study period. Our results indicated, therefore, that western gulls breeding on ANI predominantly ate lagoon-reared steelhead, which contribute disproportionately to the returning adult population thereby exacerbating population declines for this ESA-listed species.

Considerable effort has been expended to estimate avian predation on salmonid smolts migrating out of the Columbia River system, with particular emphasis placed on breeding colonies of Caspian terns. Predation rates on juvenile salmonids by Caspian terns have been estimated for tern colonies throughout the Columbia River basin using recovery of PIT tags (Roby et al. 2003; Antolos et al. 2005; Maranto et al. 2010). Not surprisingly, our corrected estimate of predation by western gulls breeding on ANI (0.92% of tagged salmonids) was less than the estimate of predation reported for a substantially larger Caspian tern colony on Rice Island in the Columbia River estuary. Based on recovery of PIT tags on Rice Island, Caspian terns ate 4.4% (95% CI, 4.2–4.6%) of salmonids that entered the Columbia River estuary during 1998. Caspian terns on Rice Island, however, were more numerous (8,766 breeding pairs) than were western gulls on ANI (mean = 1,019 breeding pairs between 1998 and 2007; PRBO, unpublished data). Our estimate was more comparable with the estimated percentage of salmonids eaten by terns nesting in two smaller colonies upstream of the Columbia River estuary. During 2001, Crescent Island (located in the mid-Columbia River basin approximately 510 km upstream from the river mouth) supported 664 pairs of Caspian terns, which ate 1.4% of the salmonids originating in the upper Columbia River (Antolos et al. 2005). In the upper Columbia River basin, 202–323 pairs of Caspian terns nesting at Pot holes Reservoir ate between 0.03% and 0.38% of PIT-tagged salmonids (coho salmon, Chinook salmon O. tshawytscha, and steelhead combined) during the years 2003, 2005, and 2006 (Maranto et al. 2010).
In addition to colony size, avian foraging strategy may also explain differences in predation rates observed between Caspian tern colonies on the Columbia River and the western gull colony on ANI. Caspian terns and glaucous-winged gull L. glaucescens × western gull hybrids breeding on Rice Island had very different diets, despite breeding in the same location. On Rice Island, the diet of Caspian terns consisted of 74% salmonids (by mass). Glaucous-winged × western gull hybrids had a more diverse diet composed of only 11% salmonids (Collis et al. 2002). Juvenile salmonids migrating out of central California watersheds were probably buffered from predation by the generalist diet of western gulls, contributing to the lower predation rate observed for ANI (0.92%) compared with that observed for the Caspian tern colony at Crescent Island (1.4%, Antolos et al. 2005). Additionally, the Columbia River system is orders of magnitude larger than watersheds in central California; thus, species diversity and abundance of salmonids in the Columbia River basin is far greater than in small central California watersheds, and salmonids occur in the Columbia River basin year-round. In central California coastal streams, coho salmon and steelhead are only available to avian predators during part of the year (Figure 5). Increased abundance, species diversity, and overlap between avian predators and salmonid prey may allow Caspian terns and other avian predators in the Columbia River basin to specialize on salmonids in ways that are not possible in small coastal watersheds in central California, resulting in greater levels of predation observed in the substantially larger Columbia River basin.

Further, predation rates at Rice Island reported by Roby et al. (2003) were based on the estimated number of salmonids that entered the Columbia River estuary and were available to Caspian terns nesting on the island. Fish that did not survive in-river migration to the estuary were not included in calculation of predation rates (Roby et al. 2003). We were not able to separate mortality of juvenile salmonids occurring upstream from the estuary from predation occurring immediately before or after ocean entry. Our predation estimate was based simply on the proportion of tags detected on ANI relative to total tags deployed. We expect that our estimate of tag deposition would increase if we could account for this as-yet undocumented in-river mortality. Such in-river mortality may result from density-dependent effects or predation by species of birds that occur in the upper watershed (for example, common mergansers Mergus merganser or belted kingfishers Ceryle alcyon). Roby et al. (2003) demonstrated that use of a bioenergetics modeling approach to estimate predation rates produced greater estimates than use of PIT tag recoveries (Roby et al. 2003). Bioenergetics models generate estimates of total consumption of salmonids by a breeding colony of birds, whereas PIT tag recoveries represent minimum estimates of predation, as described previously (Collis et al. 2001; Ryan et al. 2001; Roby et al. 2003). Using a bioenergetics approach, Roby et al. (2003) estimated that 13% (95% CI, 9.31–16.9%) of salmonids that entered the Columbia River estuary were eaten by Caspian terns breeding on Rice Island during 1998, which was greater than double the percentage estimated using PIT tag recoveries. Application of a comparable bioenergetics technique may further improve our estimate of the impacts on central California salmonids by western gulls breeding on ANI.

Although our novel use of a mark–recapture model allowed us to create a corrected estimate of predation for threatened and endangered coho salmon and steelhead along the central California coast, it remains a minimum estimate. However, based on application of this correction factor, we estimated that minimum predation on salmonids by western gulls breeding on ANI was between 1% (Scott Creek) and 4.6% (Waddell Creek) of juveniles. This previously undocumented degree of predation on juvenile salmonids in central California was greater than expected, especially considering that recoveries of intact PIT tags from ANI were indicative of predation predominantly by one age-class (adults) of one species (western gulls) at one breeding site (ANI). Further, the majority of PIT tags that originated from Scott Creek and were detected on ANI were from estuary-reared steelhead, which comprise the majority of returning adults (Bond et al. 2008). Predation on juvenile steelhead by western gulls, therefore, may be particularly detrimental to Central Coast steelhead. The levels of predation presented in this paper indicate that predation may be one factor limiting recovery of these species in central California and warrants further attention as populations of salmonids continue to decrease.

**ACKNOWLEDGMENTS**

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APPENDIX 1: SUPPLEMENTAL SAMPLING INFORMATION

TABLE A.1.1. Number of coho salmon and steelhead smolt PIT tags deployed in each watershed during each year and distance from Año Nuevo Island (ANI). County is given in parentheses; SCC = Santa Cruz County, SMC = San Mateo County.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Distance from ANI (km)</th>
<th>Year</th>
<th>Number of tags deployed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gazos (SMC)</td>
<td>6.6</td>
<td>2003</td>
<td>150</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004</td>
<td>289</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
<td>323</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>762</strong></td>
</tr>
<tr>
<td>Waddell (SCC)</td>
<td>5.5</td>
<td>2006</td>
<td>159</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2008</td>
<td>720</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2009</td>
<td>697</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>1,576</strong></td>
</tr>
<tr>
<td>Scott (SCC)</td>
<td>12.0</td>
<td>2003</td>
<td>2263</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004</td>
<td>2359</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
<td>1512</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2006</td>
<td>3585</td>
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<tr>
<td></td>
<td></td>
<td>2007</td>
<td>2807</td>
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<td></td>
<td></td>
<td>2008</td>
<td>3877</td>
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<td></td>
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<td>2009</td>
<td>7173</td>
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<td></td>
<td></td>
<td>2010</td>
<td>3907</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2011</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>27,570</strong></td>
</tr>
<tr>
<td>San Lorenzo (SCC)</td>
<td>33.0</td>
<td>2004</td>
<td>140</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
<td>261</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>401</strong></td>
</tr>
</tbody>
</table>

TABLE A.1.2. Date of trips (month/day/year) made to Año Nuevo Island to scan for coho salmon and steelhead smolt PIT tags (2006–2010). Surveys included in the POPAN model are in bold text.

<table>
<thead>
<tr>
<th>Season scan completed</th>
<th>Date of trips</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn 2006</td>
<td>11/16/2006</td>
</tr>
<tr>
<td></td>
<td>1/24/2007</td>
</tr>
<tr>
<td>Autumn 2007</td>
<td>9/24/2007</td>
</tr>
<tr>
<td>Autumn 2008</td>
<td>9/10/2008</td>
</tr>
<tr>
<td></td>
<td>10/7/2008</td>
</tr>
<tr>
<td></td>
<td>10/27/2008</td>
</tr>
<tr>
<td></td>
<td>11/17/2008</td>
</tr>
<tr>
<td></td>
<td>12/29/2008</td>
</tr>
<tr>
<td>Spring 2009</td>
<td>4/21/2009</td>
</tr>
<tr>
<td></td>
<td>5/1/2009</td>
</tr>
<tr>
<td></td>
<td>12/29/2009</td>
</tr>
<tr>
<td>Spring 2010</td>
<td>3/22/2010</td>
</tr>
<tr>
<td></td>
<td>4/14/2010</td>
</tr>
<tr>
<td></td>
<td>4/28/2010</td>
</tr>
<tr>
<td>Autumn 2010</td>
<td>9/7/2011</td>
</tr>
<tr>
<td></td>
<td>11/30/2011</td>
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<tr>
<td></td>
<td>12/31/2011</td>
</tr>
<tr>
<td></td>
<td>1/27/2012</td>
</tr>
</tbody>
</table>
TABLE A.2.1. Goodness-of-fit test statistics (Burnham et al. 1987) for the fully time-dependent POPAN model \( [\Phi(t)p(t)b(t)] \). Test 3 relates to the assumption of homogeneous survival; Test 2 relates to the assumption of homogeneous capture.

<table>
<thead>
<tr>
<th>Test</th>
<th>Component</th>
<th>( \chi^2 )</th>
<th>df</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>3.SR2</td>
<td>2.17</td>
<td>1</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>3.SR3</td>
<td>1.91</td>
<td>1</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>3.Sm2</td>
<td>10.04</td>
<td>1</td>
<td>0.001</td>
</tr>
<tr>
<td>2</td>
<td>2.c2</td>
<td>0.39</td>
<td>1</td>
<td>0.53</td>
</tr>
</tbody>
</table>

APPENDIX 2: SUPPLEMENTAL STATISTICAL AND MODELING INFORMATION

Unlike animals, PIT tags have the ability to last indefinitely. It was suspected that failure to meet component (2) (see text) of the assumption of homogeneous survival resulted from the great number of individuals that were detected on all sampling occasions \( (n = 18) \). To test whether lack of model fit stemmed from having a high number of individuals detected during all surveys, we decreased the number of individuals detected during all sampling occasions in steps of two individuals, then reran the POPAN model and tested for goodness of fit using Program RELEASE (Burnham et al. 1987) within the Program MARK framework (White and Burnham 1999). When the number of individuals detected during all four surveys was set at 10, the assumption of homogeneous survival was met (Test 3.Sm2, Table A.2.2) and the \( \chi^2 \) goodness-of-fit test indicated that the model fit the data \( (\chi^2 = 7.15, P = 0.1281) \). Estimates of parameters \( (\Phi_i, p_i, N) \) from model sets based on the original data set and the data set with the reduced number of individuals were similar so we used the model set derived from the original data to estimate the parameters of interest \( (\Phi_i, p_i, N, B_i^*, B_i, N_i, \text{and } N^*) \).

TABLE A.2.2. Goodness-of-fit test statistics (Burnham et al. 1987) for the fully time-dependent POPAN model \( [\Phi(t)p(t)b(t)] \) for the case in which the number of tags detected during all four surveys was set at 10 individuals. Test 3 relates to the assumption of homogeneous survival; Test 2 relates to the assumption of homogeneous capture.

<table>
<thead>
<tr>
<th>Test</th>
<th>Test component</th>
<th>( \chi^2 )</th>
<th>df</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>3.SR2</td>
<td>0.95</td>
<td>1</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>3.SR3</td>
<td>0.85</td>
<td>1</td>
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<tr>
<td></td>
<td>3.Sm2</td>
<td>4.85</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>2</td>
<td>2.c2</td>
<td>0.86</td>
<td>1</td>
<td>0.35</td>
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</table>