North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.818080

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Length–Length and Width–Length Conversion of Longnose Skate and Big Skate Off the Pacific Coast: Implications for the Choice of Alternative Measurement Units in Fisheries Stock Assessment

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Abstract

Most traditional fisheries models have size or stage–age relationships as their foundation. Two long-established metrics used are FL and TL. Body length measurements are linked to age, maturity, and fecundity. Obtaining FL or TL measurements are not always convenient, especially for larger fish (>100 cm TL). Two skate species, Longnose Skate Raja rhina and Big Skate R. binoculata, were collected from commercial fishery landings along the coast of Washington State and length–length or width–length conversions were investigated for four metrics of size: TL, tail only length (TOL), interspiracular width (ISW), and interorbital width (IOW). Relationships between TL and alternative measures were examined using model II regression analyses and confirmed a strong linear relationship in all cases ($R^2 > 0.94$). It is likely that both TL and TOL measures have errors due to worn-off tail portions; conversely, the ISW is nonlaborious and convenient to obtain. The ISW metric has a smaller coefficient of variation compared with IOW if we assume that both metrics have the same distribution of measurement errors. We recommend ISW as the preferred alternative metric in the assessment of large skate. The ISW will probably yield measurements that are equivalent, or potentially superior, to traditional metrics because the measurement is taken from body parts devoid of worn-off portions.

Size dimensions of fish are crucial for age and growth studies because they are linked to key biological parameters such as fecundity, growth rate, attainment of sexual maturity, and maximum size (Moran and Burton 1990; Mollet and Cailliet 1996; Francis 2006). Length is the preferred way to identify “size” because it can be quantified quickly and cheaply (Kara and Bayhan 2008). The preferred length metric used in fisheries management is TL because it is taken from the longest longitudinal axis on the fish and as Francis (2006) conveys, “it is naturally the best index of size.” Another traditional metric is FL, which is generally applied in cases where TL is unreliable due to differential wearing of distal tail elements. Bagenal (1978) revealed that TL is a fundamental measurement used to set management controls, whereas FL is the preferred method in fisheries studies because it is more accurate for biological analyses. However, due to the diversity of field conditions under which biologists must often take measurements, neither TL nor FL are always the most logistically feasible metric to obtain. For example, measurement of TL or FL is difficult to accomplish for the Narrowbarred Mackerel Scomberomorus commerson because they reach lengths just under 2 m. Biologists eliminated the difficulties associated with the collection of length data for the Narrowbarred Mackerel by

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Received December 30, 2011; accepted June 13, 2013
Published online September 6, 2013
using an alternative length method, which involved the measure
of fish heads (Cheng and Mackie 2006).

Various partial length measures have been deployed in
field sampling regimes and are reliable, repeatable, and af-
firm tight linear relationships to TL, making them recommend-
able for use in fisheries science (Moran and Burton 1990).
An alternative length–width metric can yield measurements
equivalent, or potentially superior, to traditional metrics. Many
biologists have applied length–length or width–length relation-
ships in the stock assessment of fish and marine invertebrates
(Ricker 1973; Kara and Bayhan 2008). Alternative length or
width measurements can easily be transformed directly to TL
for use in fisheries management through a simple conversion
equation.

Skate (Rajidae) are known for their large size. For example,
the Common Skate Dipturus batis, or Blue Skate, is known
to reach a TL of 250 cm (Dulvy et al. 2000; Ebert et al.
2008). During the past decade, market demand has increased
for skate worldwide, creating the need to manage skate stocks
more closely. In response, Washington Department of Fish and
Wildlife (WDFW) biologists increased sampling efforts to sup-
port better science for management and stock assessment of
skate. Data WDFW collects are used to assess stocks managed
by the Pacific Fishery Management Council for fisheries off
the coasts of Washington, Oregon, and California. Efforts to
ensure representative sampling have been thwarted because of
the large size of skate and associated risk of injury to field staff
from handling. Obtaining representative TL measurements
is further compromised because skate frequently are landed dam-
aged (e.g., abraded or missing snouts and tails). This paper
investigates three alternative metrics of Longnose Skate Raja
rhina and Big Skate R. binoculata: (1) tail only length, (2)
tail only length (TOL)—from the fold
of the pelvic fin to the tip of the tail; (c) interspiracular
width (ISW)—from the cartilage knob of one spiracle to the
cartilage knob of the other spiracle, measured across the top
of the head (Figure 1); and (d) interorbital width (IOW)—the
distance between the nearest edges of the eyes, measured
across the top of the head, from the outer side of the ridgeline
of one eye to the outer side of the ridgeline of the other eye
(Figure 2). All TL and TOL measurements (to the nearest
centimeter) were taken with a meter stick. All ISW and IOW

FIGURE 1. Interspiracular width (ISW) measurement technique on a Long-
nose Skate: ISW was measured across the top of the head, from the cartilage
knob of one spiracle to the cartilage knob of the other spiracle, using vernier
calipers. Skate specimens were collected from September 2008 to March 2010.
Fishing grounds were approximately 29–61 km offshore from the Washington
outer coast.

METhODS

Data collection.—All measurements were taken at the fish
buyer’s facility during vessel offloading. Skate were positioned
ventral side down and the following measurements were taken:
(a) TL—from the tip of the snout to the tip of the tail, with
the tail straightened and aligned with the anterior–posterior
axis of the body; (b) tail only length (TOL)—from the fold
of the pelvic fin to the tip of the tail; (c) interspiracular
width (ISW)—from the cartilage knob of one spiracle to the
cartilage knob of the other spiracle, measured across the top
of the head (Figure 1); and (d) interorbital width (IOW)—the
distance between the nearest edges of the eyes, measured
across the top of the head, from the outer side of the ridgeline
of one eye to the outer side of the ridgeline of the other eye
(Figure 2). All TL and TOL measurements (to the nearest
centimeter) were taken with a meter stick. All ISW and IOW

FIGURE 2. Interorbital width (IOW) measurement technique on a Longnose
Skate: IOW was measured from the outer side of the ridgeline of one eye to the
outer side of the ridgeline of the other eye using vernier calipers.
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variables is one with the same physical units. Additionally, we used the major axis regression, which produces unbiased slope estimates and accurate confidence intervals (Jolicoeur 1990).

The determination of the best out of the three paired metrics: (1) TL–TOL, (2) TL–ISW, and (3) TL–IOW, was done by comparing the estimated coefficient of determination ($R^2$). The probability of differences between sexes with regard to fish length–length or width–length conversions was taken into consideration via our comparison of the 95% CIs of estimated coefficients of model II regression. We further investigated two commonly used allometric relationships for the possibility of differences between sexes, second-order polynomial and power equations, against simple linear equations with Akaike information criteria (AIC) and Bayesian information criteria (BIC) (Akaike 1974; Schwarz 1978). We followed the recommendation of Kuha (2004) to use both the AIC and BIC for locating a favorable model. Using AIC alone may lead to overparameterization, while using BIC may lead to underparameterization (Cheng and Lawrence 2004).

RESULTS

Longnose Skate and Big Skate specimens were collected from September 2008 to March 2010. Fishing grounds were approximately 29–61 km offshore from the Washington outer coast, ranging from Cape Alava (48° 09' 53 N) to the most southern point of Grays Canyon (46° 51' 59 N). All skate in this study were caught by commercial groundfish bottom-trawl gear. Longnose Skate were caught between 91 and 732 m depth and most Big Skate were caught between 38 and 161 m depth. A total of 295 Longnose Skate were collected: 173 females (41–141 cm TL) and 122 males (15–125 cm TL). A total of 179 Big Skate were collected: 82 females (60–180 cm TL) and 97 males (38–131 cm TL). The minimum-to-maximum size ranges for Longnose Skate and Big Skate collected in this study were similar to those reported by Ebert et al. (2008).

Skate with imperfections (i.e., missing a portion of its tail) were encountered and included in our random sampling scheme. The TL and TOL measurements, with such imperfections, will increase process errors. The ISW and IOW measures are less affected by worn-off body portions and, therefore, can be considered as alternative metrics. The errors of length–length and width–length conversion increase with the length–width measurement, as observed in both skate species. This is due to individual growth variation, which increases with time or length.

We fitted model II regressions (major axis) with the response variable, TL, and all possible predictor variables, TOL, ISW, and IOW; males and females were considered separately (Tables 1, 2). The observed and predicted model II regression values are plotted in Figures 3, 4. The estimated slopes of all length–length and width–length conversions for both species are significant ($P < 0.05$) because they are outside the slope 95% CIs estimated for the opposite sex; e.g., the estimated TOL slope of 2.735 is outside the 95% CI (2.896–3.048). The estimated intercepts of all length–length and width–length conversions of both species are significant ($P < 0.05$), except the estimated IOW intercept for both sexes of Big Skate. We conclude that there is a difference between female and male length–length and width–length conversions for both species of skate.

It is unlikely that standard errors of fit can be obtained directly from model II regressions. Instead, we used standard errors of fit for the least-squares linear regression to estimate the information criteria (Table 3). In the length–length and width–length allometric study, the preferred model from both AIC and BIC is the linear equation for female Longnose Skate and Big Skate. For male Longnose Skate and Big Skate, the preferred models are the power equation (BIC) and the second-order polynomial equation (AIC). The reason for this inconsistency between male

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Sex</th>
<th>Estimated intercept (limits of 95% CI)</th>
<th>Estimated slope (limits of 95% CI)</th>
<th>Estimated correlation</th>
<th>Estimated coefficient of determination ($R^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOL</td>
<td>Female</td>
<td>-15.901 (−19.437, −12.564)</td>
<td>3.110 (3.013, 3.212)</td>
<td>0.978</td>
<td>0.957</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>-10.852 (−14.451, −7.474)</td>
<td>2.906 (2.805, 3.012)</td>
<td>0.981</td>
<td>0.963</td>
</tr>
<tr>
<td>ISW</td>
<td>Female</td>
<td>7.048 (4.539, 9.416)</td>
<td>12.538 (12.186, 12.911)</td>
<td>0.982</td>
<td>0.965</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>3.521 (1.129, 5.785)</td>
<td>13.172 (12.816, 13.549)</td>
<td>0.988</td>
<td>0.977</td>
</tr>
<tr>
<td>IOW</td>
<td>Female</td>
<td>13.820 (10.857, 16.573)</td>
<td>16.346 (15.765, 16.971)</td>
<td>0.972</td>
<td>0.944</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>10.437 (7.736, 12.961)</td>
<td>17.078 (16.517, 17.679)</td>
<td>0.983</td>
<td>0.967</td>
</tr>
</tbody>
</table>
TABLE 2. Summary of the model II regression results for Big Skate, separated by sex, with the response variable TL and predictor variables: tail only length (TOL), interspiracular width (ISW), and interorbital width (IOW). Values in bold italic text are significant.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Sex</th>
<th>Estimated intercept (limits of 95% CI)</th>
<th>Estimated slope (limits of 95% CI)</th>
<th>Estimated correlation</th>
<th>Estimated coefficient of determination ($R^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOL</td>
<td>Female</td>
<td>-10.714 (-13.547, -8.007)</td>
<td>2.970 (2.896, 3.048)</td>
<td>0.976</td>
<td>0.952</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>-5.343 (-9.711, -1.290)</td>
<td>2.735 (2.622, 2.855)</td>
<td>0.979</td>
<td>0.958</td>
</tr>
<tr>
<td>ISW</td>
<td>Female</td>
<td>12.111 (9.274, 14.774)</td>
<td>9.761 (9.458, 10.834)</td>
<td>0.990</td>
<td>0.980</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>3.824 (-0.495, 7.767)</td>
<td>10.927 (10.447, 11.454)</td>
<td>0.975</td>
<td>0.952</td>
</tr>
<tr>
<td>IOW</td>
<td>Female</td>
<td>7.145 (3.587, 10.448)</td>
<td>14.498 (13.971, 15.066)</td>
<td>0.986</td>
<td>0.972</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>6.567 (3.438, 9.486)</td>
<td>15.179 (14.669, 15.725)</td>
<td>0.986</td>
<td>0.971</td>
</tr>
</tbody>
</table>

skate is unknown. For the TL and IOW relationship, the preferred model for the male Longnose Skate is the power equation from both AIC and BIC. The preferred model for the male Big Skate is the linear equation from both AIC and BIC.

DISCUSSION

Previous studies conducted on skate have routinely used TL as the conventional metric of size, followed by common metrics such as disk length (pectoral or pelvic) and disk width.
LENGTH–LENGTH AND WIDTH–LENGTH CONVERSION IN TWO SKATE

(Francis et al. 2001; Francis 2006; Arkhipkin et al. 2008; Ebert et al. 2008). This study’s overarching goal led us to exclude these common metrics. Taking size metrics from features like disk length (pectoral or pelvic) and disk width would require more handling of the fish than was desired and would not have improved sampler efficiency and safety. Additionally, Francis (2006) stated that disk widths for batoids have higher variability than other measurement methods and are not a recommended choice for quantification of size.

A variety of metrics are used in field studies and therefore corresponding conversion equations from one metric to another are equally numerous. We concur with Pol et al. (2011) that proper documentation of a conversion equation is crucial for accurate analyses when comparing historical data or for

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Equation</th>
<th>AIC</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Skate</td>
<td>Male</td>
<td>Linear</td>
<td>571.62</td>
<td>579.34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Second-order polynomial</td>
<td>569.02</td>
<td>579.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>569.69</td>
<td>577.42</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Linear</td>
<td>497.094</td>
<td>490.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Second-order polynomial</td>
<td>502.22</td>
<td>492.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>501.87</td>
<td>494.65</td>
</tr>
<tr>
<td>Longnose Skate</td>
<td>Male</td>
<td>Linear</td>
<td>650.14</td>
<td>658.55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Second-order polynomial</td>
<td>641.20</td>
<td>652.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>643.64</td>
<td>652.05</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Linear</td>
<td>943.58</td>
<td>953.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Second-order polynomial</td>
<td>945.22</td>
<td>957.84</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Exponential</td>
<td>943.76</td>
<td>953.22</td>
</tr>
</tbody>
</table>
cross-comparison studies. Appropriate equations are necessary for combining different data sets of the same fish species processed differently (e.g., live, dead, or frozen) to adjust for the length differences between the environmental conditions encountered (Buchheister and Wilson 2005). We measured skate that were dead, held on ice, and stored for up to 4 d. Therefore, results presented in our study may not apply to live skate sampled, for example, during tagging studies.

The most limiting factor for measuring skate is the commonly used tool, the meter stick, because it is often shorter than the specimen being measured. We expect to see larger measurement errors for skate that exceed 1 m TL. The reason for different and larger measurement errors is due to the need to divide the measurement of these skate into two steps, with a corresponding potential increase in measurement error. Conversely, the use of vernier calipers is sufficient for measuring ISW and IOW: its scale goes to 20 cm, and the largest width encountered was 16.4 cm. A distinct advantage in using vernier calipers is that they are not subject to wear, as opposed to the meter stick, which over time will exhibit worn ends that eventually become sizeable enough to cause measurement inaccuracies.

Body condition is important to consider when taking length measurements. Reliable data cannot be obtained for age and growth studies when body condition of the fish is poor. A skate’s body is often damaged by natural conditions; this can be attributed to a skate’s behavior, such as using their snout to dig in the mud or sand to obtain bivalve mollusks (Wettstein 2010). As a result, outer edges of the body are more susceptible to wear than are the inner portions. Furthermore, the thoracic vertebrae from the dorsum area can be easily stretched apart during handling and this can alter its TL. The ISW and IOW measurements are taken on stiff structures whereas TL and FL measurements are taken on jointed structures. The use of the ISW metric can reduce the bias in both the construction of length-frequency distributions and growth curves with age data.

The estimation of measurement errors or the bias induced by the measurement errors was not conducted. This would have required an extensive study of the precision of measurement reproducibility, for which we did not have the funds or staff available. Rather, we assumed similar measurement errors exist as both response and predictor variables. Naturally, TL and TOL are ideal metrics for stock assessment because they have a lower CV (SD/mean). The descending order of CV follows the same pattern as the magnitude of each metric: TL, TOL, ISW, and IOW. We favor using the statistical approach of simple linear regression relationships for use in fisheries management, although in some cases the use of allometric forms may fit better, because it is easy to convert from one measurement to another, and all estimated \( R^2 \) values are over 0.94. Furthermore, we applied the model II regression method to avoid the bias caused by inverse prediction of the estimated linear regression. In our analysis, we found the length and width conversions of all size measurements tested were adequate by model II regression. For length-frequency compositions, we recommend the ISW metric because it is reliable and data are easy to collect.

ACKNOWLEDGMENTS

We thank Lorna Wargo for her assistance in the start-up and ongoing support of this research and for constructive comments on the manuscript. Our appreciation goes out to Farron Wallace and Barbara McClellan for their helpful discussions. We also thank Dayv Lowry and Corey Niles for providing many useful suggestions to this manuscript. We are grateful to the editors and reviewer for constructive comments on the early version of the manuscript. Our gratitude goes to the workers at Washington Crab Producers Incorporation for providing access to skate and for their support in this research.

REFERENCES


Use of Laparoscopy for Sex Identification of Asp Aspius aspius

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Published online: 08 Oct 2013.

To cite this article: Bahram Falahatkar & Mohammad H. Tolouei Gilani (2013) Use of Laparoscopy for Sex Identification of Asp Aspius aspius, North American Journal of Fisheries Management, 33:5, 894-899, DOI: 10.1080/02755947.2013.818083

To link to this article: http://dx.doi.org/10.1080/02755947.2013.818083
MANAGEMENT BRIEF

Use of Laparoscopy for Sex Identification of Asp Aspius aspius

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Mohammad H. Tolutei Gilani
Aquaculture Department, Fisheries General Directory of Guilan, Bandar Anzali, Guilan, Iran

Abstract

Asp Aspius aspius is an endangered rheophilic cyprinid species. This study describes a laparoscopic technique for Asp sex identification that also permits observations of the gonads. Seventeen fish (790–3,020 g, 41.4–73.6 cm TL, age 2–5) were examined using a laparoscope for gender determination. The cystoscope sheath was inserted into the body cavity through a small (0.9–1 cm) incision in the left flank, after which the gonads were visualized using a monitor. All fish but one were correctly sexed using this procedure in a minimal amount of time. Histological preparations showed the gonads to be at different stages of maturity in both sexes. This study demonstrated that laparoscopy can be used as an effective and minimally invasive diagnostic technique for sex identification and maturity stage determination in Asp that are under propagation and used for stock rehabilitation.

Gender must be identified in studies of controlled reproduction, reproductive behavior, spawning activity, and sex ratio. Unfortunately, most teleost fishes lack external sexual characteristics for sex identification. This deficiency has necessitated the development of practical procedures to enable sex identification via internal inspection of the gonads. Sexing of fish that lack obvious external sexual dimorphism, or in which external sex characters have yet to be developed, has typically required the use of expensive techniques such as hormone radioimmunoassay or invasive techniques such as biopsy and subsequent histology, or both (Falahatkar et al. 2013). These techniques are time and labor intensive because the fish need to be maintained individually and handling them can be stressful, as indicated by circulating cortisol levels that increase with stressor exposure time (Falahatkar and Poursaeid 2013). Fortunately, noninvasive techniques for sexing by means of ultrasonography and endoscopy have been developed for a number of fish species (Wildhaber et al. 2005, 2007; Macri et al. 2011).

The Asp Aspius aspius is a freshwater, rheophilic, cyprinid species that occurs widely in eastern Europe and some parts of Asia, including the Caspian Sea basin (Kottelat and Freyhof 2007). Males become reproductively mature after 3 to 4 years, and females from 4 to 5 years (Froese and Pauly 2013). Spawning in nature occurs between March and May, depending on when the water temperature reaches 5–12°C (Targońska et al. 2008). Asp lay sticky grey-green eggs on the bottom gravel or on submerged plants (Freyhof and Kottelat 2008). Absolute fecundity in Asp varies with fish size, age, and feeding conditions, and ranges between 19,000 eggs (for a 35.8-cm-SL female: Bashunova 1980) and 324,800 (for a 64.3-cm-SL female: Kompowski and Neja 2004).

Due to environmental changes, local populations of Asp are currently endangered (Targońska et al. 2008); some locations in southern parts of the Caspian Sea basin no longer support Asp. Decreases in some European Union regions have also occurred because of pollution and overfishing. Thus, finding and catching this rare species in natural water bodies can be difficult (Targońska et al. 2010). Consequently, developing methods to culture juvenile Asp for stocking into natural environments is of interest.

One emphasis in hatcheries is to control reproduction and optimize rearing of the species (Kucharczyk 2002; Wojda 2004; Targońska et al. 2008), but starting hatchery production requires obtaining high quality broodfish, which are in low abundance (Peňáž 1996; Penczak and Kruk 2000; Kujawa et al. 2006). Historically, Asp broodstocks were collected in nature from rivers, lakes, and reservoir habitats. However, rearing this fish in

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Received March 26, 2013; accepted June 13, 2013
Published online September 6, 2013
earthen ponds used for Chinese carps would facilitate obtaining large numbers of Asp for hatchery culture (Targóńska et al. 2008). Asp reproduction under such culture conditions is only possible using hormonal stimulation (Targóńska et al. 2008, 2010, 2011).

Knowing the sex of individual fish is critical for aquaculture or conservation management where sex ratio determinations and reproductive potential are being considered. However, determining sex while minimizing handling and disruption of the fish’s ongoing activities can be a challenge. For Asp, finding a fast, reliable, and easy method to determine sex is complicated because they lack obvious external sex characters. Thus, the objective of the present research was to test the utility and accuracy of laparoscopy for sexing Asp.

**METHODS**

*Fish and holding conditions.*—Asp for broodstock were caught in winter 2006 from the reservoir behind the Aras Dam (West Azarbaijan province, northwestern Iran) and then transported to the Dr. Yousefpour Fish Hatchery Center, Siahkal, Guilan, Iran, where they were held in an earthen pond (600 m² surface area) during the winter season and fed with baitfish, Common Carp *Cyprinus carpio* fingerlings. Ten females and seven males were used in the study (see Table 1). In October 2007, after a year in captivity, they were transferred to 4-m³ circular fiberglass tanks for attempted sex identification. The age of the fish was determined by counting the annuli on scales taken from beneath the fish’s dorsal fin.

*Laparoscopy.*—To examine the gonads, a laparoscope system (Lut GmbH, Denzlingen, Germany) was used following the procedures of Falahatkar et al. (2011). In brief, the laparoscope consisted of a 7.5-mm-diameter and 22-cm-long cystoscope sheath with the end bevelled at a 30° angle. An internal canal allowed the internal organs to be rinsed with sterile, physiological saline solution for clear observation. A light transmission optic fiber attached to a halogen cold-light source and a video camera connected to a 35.56-cm color television monitor (Atlas Company, Mashhad, Iran; Figure 1a) enabled image capture. The system allowed us to view the fish’s internal organs and save selected images.

Fish were fasted for at least 2 d before undergoing the sex identification procedure. Each fish was anesthetized in a plastic container (30 L) containing a 120-mg/L solution of tricaine methanesulfonate (MS-222; Sigma, St. Louis, Missouri). To view the abdominal cavity and examine the gonads, a lengthwise incision (9–10 mm) was made in the body wall with a sterile scalpel (Figure 2) through which the cystoscope sheath could be inserted (Figure 1b). The incision was then opened with a trocar (Unimax, Hsin Tien, Taipei) to allow entry into the abdomen cavity. On completion, the incision was closed with a simple suture (0.3 mm diameter silk; Figure 3) and disinfected with povidone-iodine solution (Kishmedifarm, Kish, Iran) and a chloramphenicol spray (Afagh, Tehran, Iran), after which the fish was injected with 1 mL of 10% oxytetracycline antibiotic (Razak, Tehran, Iran) (Falahatkar et al. 2011). Lastly, the fish

![Figure 1](https://example.com/figure1.png)

**FIGURE 1.** (a) Laparoscopic set-up for sex identification of Asp. Laparoscopy arrangement: Mo = monitor, Tr = trocar, LS = light source, VT = V-transfer, Cy = cystoscope. (b) An anesthetized female Asp under laparoscopic examination through an abdominal incision. (c, d) Laparoscopic view of an Asp’s ovaries. [Figure available in color online.]
were individually tagged (plastic PIT tag) and placed into clean freshwater to recover. Times to anesthesia and recovery were recorded for each fish according to the fish’s behavior.

**Sex determination.**—For all but one fish, designating sex was made possible based on viewing structures similar to those described previously by Wildhaber et al. (2007): oocytes (Figure 1c, d), ovarian folds, and testicular lobes. After the procedure, the incision site was monitored for 1 month until healing was completed.

One male required a gonadal tissue biopsy and subsequent microscopic histological examination to verify sex. For this, a 2.5-cm incision in the abdomen was made to permit direct inspection and then gonad biopsy sampling using forceps. Biopsy samples were fixed in Bouin’s solution for at least 24 h, dehydrated in a 70–96% graded ethanol series, and then embedded in paraffin. Serial sections, 5 µm thick, were stained with hematoxylin–eosin (H&E) for histological assays (Shelton et al. 1995; Ismail et al. 2011). To quantify stage of gonadal development, we used the six-category classification scheme of Morrison (1990).

### TABLE 1. Mean (range) in weight, TL, and age of male and female Asp before sex identification via laparoscopy. The results of all between-sex t-tests were not significantly different (P > 0.05).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Weight (g)</th>
<th>TL (cm)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male (n = 7)</td>
<td>1,257 (1,060–1,590)</td>
<td>53.1 (50.6–58.7)</td>
<td>3.3 (2–5)</td>
</tr>
<tr>
<td>Female (n = 10)</td>
<td>1,746 (790–3,020)</td>
<td>57.4 (41.4–73.6)</td>
<td>3.5 (2–5)</td>
</tr>
<tr>
<td>P-value for between-sex comparison</td>
<td>0.122</td>
<td>0.279</td>
<td>0.642</td>
</tr>
</tbody>
</table>

**Statistical analysis.**—Homogeneity of variances was verified by Levene’s test (Zar 1999). Then, independent-sample t-tests were used to compare weight, TL, age, and times to anesthesia, and recovery times between males and females at a significance level of P < 0.05. All procedures were carried out using SPSS 13.0 software (SPSS, Chicago, Illinois). Data throughout the text are presented as mean ± SE.

### RESULTS

There were no significant differences in the mean weights, TLs, and ages of female and male Asp (Table 1). Time of anesthesia did not differ between males (mean = 190 s) and females (mean = 228 s) (P = 0.310; Figure 4); time to recovery also did not differ significantly (P = 0.391) between males (mean = 128 s) and females (mean = 158 s).

Sex determination with the laparoscopic method was completed in less than 1 min. The testes of males were easily visualized via laparoscopy; of seven males, four were staged as prespermating and two as spermatizing. Thus, 87.5% of males were correctly identified solely through laparoscopy. The remaining fish was smaller than the others (1,060 g), and the histological assay identified it as male. Histology also confirmed the sexing of the remaining males.
For the 10 females, 100% were correctly identified to sex via laparoscopy. Histologically, the oocytes of six females were in the stage IV migratory nucleus phase of development (Figure 5) and the other four fish were previtellogenic. All determinations were confirmed by histological examination.

Visual examination of the fish immediately and 30 d after laparoscopy revealed minimal hemorrhaging related to the procedures (Figure 6). No mortality occurred due to the procedure.

**DISCUSSION**

Of the 17 Asp specimens we examined, 94.1% \((n = 16)\) were accurately sexed using laparoscopy. Thus, laparoscopy through a small incision in the abdomen appears to be an effective tool to view Asp gonads for sexing. The lack of surgical trauma or hemorrhage after the procedures and the successful completion of all attempts were noteworthy. Generally, the efficiency of the laparoscopy for sex identification in Asp was comparable with that of other similar studies in chondrosteans and teleosts (Ortenburger et al. 1996; Wildhaber et al. 2005, 2007; Hurvitz et al. 2007; Falahatkar et al. 2011; Macri et al. 2011).

Several noninvasive or minimally invasive approaches have been developed to identify sex and stage of gonadal development in different fish species. Sonography (Martin et al. 1983; Bonar et al. 1989; Mattson 1991; Shield et al. 1993; Blythe et al. 1994; Karlsen and Holm 1994; Martin-Robichaud and Rommens 2001; Will et al. 2002; Evans et al. 2004; Bryan et al. 2005; Whiteman et al. 2005) and endoscopy (Driscoll 1969; Moccia et al. 1984; Ortenburger et al. 1996; Wildhaber et al. 2005, 2007; Falahatkar et al. 2011) have both proven practical for sex identification and maturity staging in fishes, and neither method apparently poses harm to the fish’s reproductive organs. All 17 of the Asp we examined survived after examination of their gonads via laparoscopy, and there was no delayed mortality after 1 month. Studies on sturgeons similarly show 100% survival after endoscopy (Hernandez-Divers et al. 2004; Falahatkar et al. 2011; Matsche et al. 2011). Thus, this method appears to be amendable to fishes of both small (e.g., Asp) and large (e.g., acipenserids) size.

While some fish display external morphological characters indicative of sex, the male Asp are indistinguishable from the females, although males are usually smaller than females at first maturity. In many fish that are held as broodstock during the reproductive season, a routine activity to sex the fish is to look for abdominal distension and perform abdominal massage during the final maturity stage.

Although the gonads of many fishes have been examined via laparoscopy, both the advantages and disadvantages of this method need to be recognized. Laparoscopy is useful for sexing and maturity staging, is apparently safe for the ovaries and testes, and can be used in either laboratory or field settings. However, the price of the equipment and instruments is high (around US$10,000). In addition, when identifying the sex of previtellogenic females and prespermatogenic males, gonad biopsy and histology may be an additional requirement. Histological processing is difficult in the field and does not provide “instant” results. However, histology may be required for females if greater precision in maturity staging is required.

One of the main problems with controlled reproduction and hormonal stimulation in captive propagation is sexing and determining the stage of gonadal maturation (Ortenburger et al. 1996). Histological analyses combined with circulating sex steroid determinations are the “gold standard” for evaluating sex and stage of maturity. However, these methods are time-consuming and costly procedures. Histological sampling of the gonads may require performing an invasive and thus risky procedure (e.g., surgery, caesarean section, catheterization of the oviduct). For aquaculturists, laparoscopy represents a practical visualization tool for sex identification that can be adapted for field application. Even though laparoscopy requires familiarity with fish anatomy and experience in distinguishing gonads at
the differing stages of maturity, laparoscopy yields immediate information regarding sex and maturity stage without the need of a large incision, risk to internal organs, or excess stress to the fish. As such this technique may hold promise for use on threatened and endangered fish species in propagation and production programs.

ACKNOWLEDGMENTS
The authors gratefully acknowledge I. Efaptcha, B. Mehnatkhah, and Z. Arzbo for their help in obtaining the fish and for caring them before, during, and after examination. We also thank two anonymous reviewers for useful comments on this manuscript.

REFERENCES
Kucharczyk, D. 2002. [Controlled reproduction and androgenesis of chosen cyprinid fish species]. University of Warmia and Mazury, Olsztyn, Poland. (In Polish.)


Impacts of Aging Error on Walleye Management in the Winnebago System

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Published online: 08 Oct 2013.

To link to this article: http://dx.doi.org/10.1080/02755947.2013.815667

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Impacts of Aging Error on Walleye Management in the Winnebago System

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Abstract
The age data used to manage Walleye Sander vitreus fisheries are not always accurate, as otoliths typically provide more accurate age estimates for larger, older Walleyes than dorsal spines. We assessed the impacts that the aging error associated with the use of dorsal spines has on the estimated age distribution, growth and mortality rates, and yield per recruit for Walleyes in the Winnebago system, Wisconsin. Age distributions derived from otolith age estimates more accurately portrayed variable recruitment than those derived from dorsal spine age estimates. The mean estimates of instantaneous total annual mortality developed from sex-specific catch curves were greater when dorsal spine age estimates were used (0.515 for males, 0.493 for females) than when otolith age estimates were (0.349 for males, 0.396 for females), with most of the differences being observed in natural mortality estimates. The von Bertalanffy growth models were not significantly different, but the yield-per-recruit models (which rely heavily on von Bertalanffy model parameters) incorporating spine age data produced average yield estimates 50–70% lower than the models developed from otolith ages. The yield-per-recruit models derived from spine-determined ages also resulted in lower recommendations as to the age and size of fish for maximum yield at all exploitation levels than the models developed from otolith age data. The mean dorsal spine and otolith age estimates were similar for male Walleyes <457 mm and female Walleyes <508 mm, but for larger fish otoliths yielded significantly older ages than spines. Given the economic and social impacts of the Winnebago system Walleye fishery, we recommend exclusive use of otoliths to obtain the most accurate estimates of fish age, growth, mortality, and yield. In populations in which the sacrifice of large quantities of fish is not acceptable, we recommend using spines to estimate the ages of smaller fish (males <457 mm, females <508 mm) and otoliths to estimate the ages of fish larger than these critical lengths.

Aging error associated with underestimating the ages of older fish reduces the accuracy of estimated rates of growth, mortality, and recruitment (Bradford 1991; Mertz and Myers 1997). These three rates have the greatest impact on the dynamics of a fish stock and are used extensively in population dynamics models, including catch-at-age models and cohort analyses, which are becoming more commonly used in fisheries management and research (Ricker 1975; Beverton 1987; Maceina et al. 1998). Model results are only as accurate as the data that are input into them, underlining the critical importance of collecting accurate age data for producing reliable and meaningful results (Mertz and Myers 1997).

Walleyes Sander vitreus are one of the most popular and actively managed recreational and commercial freshwater game fish species in North America, and extensive research has been conducted to determine the relationships between Walleye age estimates derived from various structures, including scales, spines, fin rays, vertebrae, cleithra, and otoliths. The majority of these studies have concluded that Walleye age estimates from otoliths are the most precise and likely the most accurate, while age estimates from nonlethal structures (scales, spines, and fin rays) typically agree with otolith age estimates for fish up to a certain age and size but underestimate the ages of larger, older fish relative to otolith ages (Campbell and...
If fisheries managers could identify the critical size at which nonlethal structures begin to underestimate fish ages for Walleyes, a sampling protocol could be developed using nonlethal structures to accurately estimate the ages of smaller fish and otoliths to accurately assign ages to larger fish. For example, Kocovsky and Carlone (2000) recommended the use of scales to age Walleyes <500 mm in Pymatuning Sanctuary, Pennsylvania, while otoliths were used to more accurately estimate the ages of Walleyes >500 mm. To date, no study published in the peer-reviewed literature has identified these critical lengths for Walleye age estimates derived from dorsal spines and otoliths.

The Winnebago system Walleye fishery is nationally recognized, and accurate age data are required to estimate and track mortality rates for the effective management of the fishery. Age estimates from known-age Walleyes collected from the Winnebago System showed that dorsal spines underestimated the age of Walleyes age 7 and older, while age estimates from otoliths were accurate for Walleyes up to at least age 10, with strong corroboratory evidence that these age estimates were accurate for all ages of Walleyes (Wisconsin Department of Natural Resources [WDNR], unpublished data). Due to the size of the Winnebago System (the largest inland lake in Wisconsin) its high Walleye abundance, the sacrifice of Walleyes for age estimation is tolerated by the educated and engaged general public. However, there are other populations within the state for whom the sacrifice of large numbers of fish for age estimation is not possible or acceptable. Our objectives were (1) to determine the impact that the aging error inherent in dorsal spine age assignments has on estimates of age distribution, somatic growth rates, mortality, and yield per recruit and (2) to design a sampling protocol for collecting age structures that would provide relatively accurate age estimates for Walleyes while minimizing the number of fish that would have to be euthanized.

METHODS

Study area.—The Winnebago system is a large, shallow, eutrophic ecosystem in east-central Wisconsin composed of Lake Winnebago and three smaller lakes (Butte des Morts, Winneconne, and Poygan) that collectively comprise 668 km² of surface water. The upper Fox River and the Wolf River (along with their major tributaries) flow into the lakes, draining a 15,540-km² watershed. The floodplain of the lower 60 km of the upper Fox River and the lower 200 km of the Wolf River upstream of the lakes contain an extensive network of old channels, oxbows, and bottomland forest and marsh which in most years carry spring floodwaters over wet meadows, providing spawning habitat for Walleyes. Walleyes are abundant in the Winnebago system and are the primary focus of a high-profile, year-round recreational fishery that has an annual regional economic impact of $234 million (Cook and Neiswender 2007).

Fish collection.—Adult Walleyes were collected during April spawning assessments (2009–2011) on the upper Fox and Wolf rivers via electrofishing using a standard Wisconsin-style boom shocker with pulsed DC (25% duty cycle, 50 pulses per second, conductivities of 330–370 µS/cm, typically producing an electrical field of 100 V at 5 A or less). In addition to electrofishing, fyke nets (19-mm bar mesh) were set in spawning marshes during the 2011 spawning assessments. Sex and reproductive stage (ripe for males; green (hard), ripe, or spent for females) were determined for all captured fish based on extrusion of gametes. The TL of all fish was measured to the nearest 0.1 in, and the first 50 fish at each spawning location were weighed to the nearest 0.02 lb (length and weight measurements were recorded in English units and later converted to metric units). Random samples of adult male Walleyes were euthanized to obtain a representative age sample for each 12.7-mm size-class (8–16 fish per class, with greater sampling of larger size-classes to account for the greater age variability at greater lengths). Age assignments from otoliths and dorsal spines were independently used to estimate the age, somatic growth, mortality, and yield per recruit of adult male Walleyes. Estimates of these population characteristics were compared to assess the impacts of underestimating fish age with dorsal spines on the management of male Walleyes in the Winnebago system. All Walleyes that were not euthanized for otolith collection were marked with Floy anchor tags (FD-94) using a Floy Mark II tagging gun (Floy Tag and Manufacturing, Inc.) equipped with a 33-mm needle. Tags were inserted at an acute angle into the base of the left posterior dorsal fin, similar to the methods described by Guy et al. (1996). Special care was taken to ensure that tags were inserted behind pterygiophores and then properly seated by gently tugging on the tag. Each tag contained a unique number sequence and the address of the Wisconsin DNR in Oshkosh. Tag returns from angler-harvested Walleyes were used to estimate annual exploitation rates (u) of adult Walleyes (1993–2011) using the equation

\[ u = \frac{(N_C/0.5)/(N_T)}{0.5} \times 100, \]

where \( N_C \) is the number of tagged fish reported by anglers as harvested, \( N_T \) is the total number of fish tagged during spawning assessments conducted that spring, and 0.5 represents the 50% tag return rate by anglers (a standard value used as part of the Winnebago Walleye management program that has been vetted over time, 1989–2011; WDNR, unpublished data).

The Winnebago system hosts over 65 Walleye tournaments annually, which provide an opportunity to collect otoliths and dorsal spines from mortalities of fish >381 mm (most Winnebago system Walleye tournaments impose a 381-mm size limit). Two tournaments were monitored in June 2009, while three tournaments were monitored in June 2010. After weigh-in, Walleyes were deemed releasable or unreleasable by WDNR personnel and all unreleasable fish were measured and weighed as previously described. Sex and maturity were also determined.
for all unreleasable fish based on color, shape, and development of the gonads. Dorsal spines and otoliths were removed from a random sample of female Walleye mortalities as previously described. As with those for male Walleyes, these age estimates were used to compare the age, growth, mortality, and yield per recruit of female Walleyes and to assess the impacts of aging error on the management of female Walleyes in the Winnebago system.

Fish age estimation from calcified structures.—The second or third dorsal spine was removed as close as possible with surgical nail nippers, placed in a sample envelope, and allowed to air dry for a minimum of 2 weeks. Excess dry tissue was removed before cutting 0.30–0.50-mm sections with a Buehler Isomet low-speed saw using glycerol as a blade lubricant. Sections were aged (without knowledge of sex and size under 25–56 mm) with a Buehler Isomet low-speed saw using glycerol as a blade lubricant. Sections were aged (without knowledge of sex and size) using a Meiji microscope under 25–45× magnification and dark field transmitted light. To maintain consistency between past and present aging techniques and criteria for annuli enumeration, all age estimates were made by the same reader who has aged all Walleye spines collected from the Winnebago system since 1989.

Otoliths were extracted and placed in perforated vials to minimize breakage and air dry for a minimum of 30 d. Otoliths were then embedded in Epo-Quick two-part epoxy for a minimum of 24 h before 0.30–0.40-mm sections were cut using a South Bay Technology low-speed diamond wheel saw (Model 650) with water as a blade lubricant. Cross sections were aged by a reader with 4 years of experience aging otoliths. Age was estimated without knowledge of sex and size under 25–56× magnification with an Olympus SZX7 stereomicroscope and bright field transmitted light. Isopropyl alcohol (50%) was used to help clear sections, but no polishing was done.

Data analysis.—Due to sexually dimorphic growth, data from male and female Walleyes were analyzed independently. Male length and age data from April spawning assessments and female length and age data from June tournament monitoring were incorporated into sex-specific age–length keys to assign ages to all adult Walleyes that were sampled during April spawning assessments (Robson and Chapman 1961). Due to the high-profile nature of the spring fishery and the high value placed on adult female Walleyes by the public, we were unable to euthanize adequate sample sizes of mature female Walleyes during April spawning assessments. Therefore, we used age structures removed from female Walleyes sampled within length-classes during June tournament monitoring and incorporated these age data into age–length keys to assign ages to adult female Walleyes captured during April spawning assessments. The age assignments derived from structure- and sex-specific age–length keys were used to estimate both the age distributions of the spawning stock and the mean length at age of fish within the sample, as outlined by Bettoli and Miranda (2001). Mean length at age data from individual spawning assessments (2009–2011) were averaged to establish a mean length at each age-class for adult male and female Walleyes sampled during the 3-year period. Mean lengths at age 1 and age 2 were derived from empirical data collected during night electrofishing surveys conducted on Lake Winnebago in October 2008–2010. The von Bertalanffy growth model (von Bertalanffy 1938),

\[ L_t = L_\infty \cdot (1 - e^{-K(t-t_0)}) \]

where \( L_t \) is the length at time \( t \), \( L_\infty \) is the asymptotic length (model parameter), \( K \) is Brody’s growth coefficient (model parameter), and \( t_0 \) is the time of zero length or fertilization (model parameter), was fit to mean length-at-age data to estimate \( L_\infty \), \( K \), and \( t_0 \) for male and female Walleyes (a total of four growth models were constructed, one based on otolith age estimates and one on dorsal spine age estimates for each sex). Asymptotic 95% confidence intervals were estimated for the three model parameters using the PROC NLIN procedure available in SAS. Likelihood ratio tests were used to determine whether the von Bertalanffy growth models for male and female Walleyes were significantly different (\( P \leq 0.05 \)) and whether the growth models derived from otolith age estimates were significantly different from those derived from dorsal spine age estimates.

The parameters from the von Bertalanffy models for male and female Walleyes derived from spine and otolith age data were used to develop four yield-per-recruit (YPR) models of the form

\[ Y_t/N_0 = F \cdot e^{-M(t-t_0)} \cdot W_\infty \cdot (1/Z - (3e^{-K(t-t_0)}/Z + K) + (3e^{-2K(t-t_0)}/Z + 2K) - (e^{-3K(t-t_0)}/Z + 3K)) \]

where \( Y_t \) is the yield per recruit, \( N_0 \) is the number of fish that recruit to the population (set to 1 to eliminate it from equation), \( F \) is the instantaneous fishing mortality (treated as a variable), \( M \) is natural mortality (treated as constant), \( t_0 \) is the age of recruitment to the fishery, \( W_\infty \) is the weight at \( L_\infty \) derived from the von Bertalanffy models and weight–length models for summer male and female Walleyes from the Winnebago system in 2009–2011 (WDNR, unpublished data), and \( Z \) is total mortality \((F + M)\). These models were run at instantaneous fishing mortality rates \((F)\) ranging from 0 to 1.0 so as to include the mean annual exploitation estimates \((u)\) for male and female Walleyes during 1993–2011; they were also run at ages ranging from 1 to 20 to allow evaluation of the impact of aging error on predicted yields derived by the hypothetical size limits derived using spine versus otolith length–at–age data for the range of ages of each sex observed in the fishery. The impact of spine versus otolith age data on the mean yields predicted by YPR models was evaluated for male and female Walleyes. The YPR model estimates for males age 1–10 at an \( F \) of 0.185 \((u \approx 14.7\%)\) and females age 1–12 at an \( F \) of 0.285 \((u \approx 22.6\%)\) were averaged for both the spine and otolith age models and compared. The maximum ages selected for this analysis were the ages at which male and female Walleyes were beginning to approach their
average asymptotic lengths in the Winnebago system (526 and 665 mm; WDNR, unpublished data).

Sex-specific catch curves were developed from both dorsal spine and otolith age assignments for all adult fish sampled during spring spawning assessments. The first ages represented in the catch curves were 4 for male Walleyes and 5 for female Walleyes (the ages at which >85% of male Walleyes and >95% of female Walleyes are mature; WDNR, unpublished data). A linear regression from each catch curve yielded the slope of the line of best fit through the descending limb of the catch curve, from which the rates of instantaneous total annual mortality (\( Z \)) were estimated as the negative values of the slopes of the lines of best fit. Rates of conditional total annual mortality (\( A \)) were then calculated from the equation

\[
A = 1 - e^{-Z}.
\]

Rates of instantaneous fishing mortality were estimated from the mean rates of conditional total annual mortality and instantaneous annual mortality using the Baranov catch equation (Ricker 1975),

\[
F = \mu(Z/A),
\]

where \( \mu \) is the mean estimate of exploitation from angler tag returns. Instantaneous natural mortality rates (\( M \)) were estimated by subtracting the estimated values for \( F \) from those for \( Z \).

Mean dorsal spine and otolith age estimates from 25.4-mm length-classes were calculated from adult male age data collected during April spawning assessments (2009–2011) and female age data collected during June tournament monitoring (2009–2010) to determine the lengths at which dorsal spines began to underestimate fish age relative to the ages derived from otoliths. Fishery managers do not positively know the age of fish when they handle them during surveys; therefore, it is important to determine the length at which age estimates from otoliths and nonlethal structures deviate. Dorsal spine age estimates were considered to underestimate fish age if the mean spine age estimate was not within the 95% confidence interval around the mean otolith age estimate for that length-class.

RESULTS

Age was determined for 668 male Walleyes and 537 female Walleyes. The adult male and female stocks were dominated by fish age 10 and younger (>89% of the adult population in all years) based on age data from both dorsal spines and otoliths, but there was poor agreement between the age-class strengths estimated from the two structures (Tables 1–2; Figure 1). For example, the 2001 year-class (age-8 fish in 2009 and age-9 fish in 2010) was estimated to compose >20% of the adult stock in both 2009 and 2010 based on otolith age assignments, while that same year-class was significantly smaller in both years based on dorsal spine age estimates (Tables 1–2; Figure 1). Older age-classes were detected from the otolith age estimates each year that were not detected with the dorsal spine age estimates. With otoliths the oldest males were estimated to be 18 years of age in 2009, 19 in 2010, and 20 in 2011; with dorsal spines, however, the oldest males were estimated to be 14 in 2009, 15 in 2010, and 16 in 2011.

Likelihood ratio tests detected a significant difference in the otolith-based von Bertalanffy growth model parameters between male and female Walleyes (\( F = 30.5; \text{df} = 3, 29; P < 0.001 \) (Figure 2) but were unable to detect a significant difference between otolith- and dorsal spine–based von Bertalanffy growth models for male (\( F = 0.35; \text{df} = 3, 33; P = 0.79 \)) and female Walleyes (\( F = 0.93; \text{df} = 3, 29; P = 0.44 \)) (Figure 3). Although no significant difference was found between the growth models derived from dorsal spine and otolith age estimates for either sex, fish were projected to attain greater asymptotic lengths when dorsal spine age estimates were used for the models (Figure 3).

Yield-per-recruit modeling showed that the average yields of Walleyes up to their asymptotic ages (age 10 [which corresponds to 526 mm] for males and age 12 [665 mm] for females) at the long-term average instantaneous fishing mortality rates (0.185 for males and 0.285 for females) were 73.0% (SD = 9.5%) less for males and 49.8% (10.8%) less for females when the models incorporated spine ages rather than otolith ages. The
FIGURE 1. Age distributions of adult (A) male and (B) female Walleyes sampled during April 2010 spawning assessments in the Winnebago system, based on dorsal spines and otoliths.
TABLE 2. Age composition (percent) of adult female Walleyes in the Winnebago system derived from otolith and dorsal spine age estimates, 2009–2010.

<table>
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The model derived from spine age data indicated that at an annual $u$ of 14.7% the maximum yield per recruit of male Walleyes (70 g) would be attained by implementing a 300-mm minimum size limit (msl) at age 2; by contrast, the model derived from otolith age data indicated that a higher yield (183 g) would be attained with a 399-mm msl at age 3. Models run for females found similar results: the model derived from spine age data indicated that at an annual $u$ of 22.6% the maximum yield per recruit (362 g) would be attained by implementing a 460-mm msl at age 4, while the model derived from otolith age data indicated that a higher yield (632 g) would be attained with a 500-mm msl at age 5.

The mean estimates of instantaneous total annual mortality derived from the catch curves were higher for both males and females when based on dorsal spine age estimates rather than otolith age estimates. The mean estimate for adult males was 0.515 (range = 0.388–0.639, SD = 0.126; $N = 3$) with dorsal spine age data and 0.349 (range = 0.249–0.411, SD = 0.087; $N = 3$) with otolith age data; the estimates for adult females were 0.427 in 2009 and 0.557 in 2010 (mean = 0.493) with dorsal spine age data and 0.346 in 2009 and 0.446 in 2010 (mean =
0.396) with otolith age data. Although the mean estimates of Z based on dorsal spine age estimates were consistently higher than the estimates derived from otolith-based estimates, the small sample size (N = 3 for males and 2 for females) limited our ability to statistically compare spine- and otolith-age-based catch curves.

The mean annual estimates of adult exploitation based on 1993–2011 tag return data are 14.7% (range = 7.1–23.0%, SD = 0.054; N = 19) for adult males and 22.6% (range = 5.4–32.9%, SD = 0.077; N = 19) for adult females (WDNR, unpublished data). The estimates of instantaneous fishing mortality were very similar when using dorsal spine (0.19 for males and 0.29 for females) and otolith age estimates (0.17 for males and 0.27 for females), while the estimates of instantaneous natural mortality were higher with dorsal spines (0.32 for males and 0.20 for females) than with otoliths (0.17 for males and 0.12 for females).

The mean dorsal spine and otolith age estimates were similar for males <457 mm and females <508 mm (Figure 4).

However, the mean dorsal spine age estimates were significantly lower than the mean otolith age estimates for male and female Walleyes larger than these critical lengths, at which the 95% confidence intervals did not overlap (Figure 4).

**DISCUSSION**

The use of otoliths—and thus more accurate age data—has greatly advanced understanding of the population dynamics of the Walleye population in the Winnebago system. Otolith age estimates have allowed older year-classes of Walleyes to be observed that were not represented when using age estimates derived from nonlethal structures. Priegel (1969) reported a maximum longevity of 8 years for Walleyes in the Winnebago system using scales, whereas longevity was perceived to be 16 years with the dorsal spine age data included in this study. The use of otoliths for age estimation has shown that the Walleyes in the Winnebago system can reach at least age 20.

The detection of these older age-classes leads to estimates of instantaneous total annual mortality and natural mortality that are lower than previous estimates. The total annual mortality and natural mortality estimates derived from catch curves based on otoliths were lower than those based on dorsal spines for the male and female Walleyes sampled in every year of this study. These results are important, as fishing mortality and natural mortality are believed to be compensatory risks of death for certain species, i.e., natural mortality rates decrease as fishing mortality rates increase (Allen et al. 1998). Therefore, by overestimating natural mortality rates, managers may incorrectly perceive that harvest can be increased, which could lead to overharvest (Lai and Gunderson 1987; Rien and Beamesderfer 1994; Reeves 2003). Leaman and Nagtegaal (1987) estimated much lower instantaneous natural mortality rates, and thus substantial reductions in total allowable catch, for Yellowtail Rockfish *Sebastes flavidus* when using age estimates derived from sectioned otoliths (0.07) than when using otolith surface readings (0.25). Similarly, underestimating the age of snappers (*Lutjanus* spp.) caused overestimates of natural mortality rates, and the population would have been overfished if the inflated estimates of natural mortality had been applied to the snapper management program (Newman et al. 2000). The greater the aging error, the less accurate the mortality estimates are, underscoring the importance of using accurate age data to estimate mortality rates that in turn are used to make critical management decisions. Given the economic and social importance of the Walleye population in the Winnebago system, it is imperative to collect data that are as accurate as possible in order to accurately track the mortality rates of this population through time.

There are many factors that can affect mortality, such as variable recruitment, exploitation, prey abundance, and thermal regimes (Kocovsky and Carline 2001). As strong and weak year-classes move through a fishery, they affect the trajectory of the catch curves and thus the mortality estimates. Due to the inherent variability in the estimated rates of mortality within populations, it is imperative to collect accurate age data for an
extended period of time to fully understand the mortality dynamics of a fish population (Kooce et al. 1977; Kocovsky and Carline 2001). This study includes 3 years of otolith age data for males and 2 years for females, and otolith age estimates will continue to be used to track annual mortality through time to better observe how year-class strength affects mortality estimates. More years of paired age data collection (dorsal spines and otoliths) would provide more statistical power to detect differences between catch curves developed with age data from the two aging structures.

Given that year-class strength can affect the mortality estimates derived from catch curves, it is important to accurately assign fish to age-classes. In this study, we demonstrated that age distributions derived from otolith age estimates accurately portrayed the variable recruitment of Walleyes in the Winnebago system, with each generation containing multiple strong year-classes that collectively compose the majority of the adult stock. Due to the relatively high fishing mortality rates exerted on the Winnebago system Walleye fishery, especially on females, the robustness of the population is dependent on these regular strong year-classes. By underestimating age with dorsal spines, fish from abundant year-classes were mistakenly assigned to adjacent weaker and younger years, which in turn reduced estimates of interannual variability in recruitment. Bradford (1991) further described this process and stated that underestimating fish age through the use of unvalidated aging techniques can affect recruitment estimates and severely hinder studies to assess the environmental influences on recruitment.

The mean age estimates from dorsal spines and otoliths were very similar for adult males <457 mm and adult females <508 mm, but dorsal spines yielded significantly lower age estimates than otoliths for fish larger than these critical lengths. Kocovsky and Carline (2000) observed similar results in Pymatuning Sanctuary, where scales yielded relatively accurate age estimates for Walleyes <500 mm but otoliths were required to accurately estimate the ages of fish >500 mm. The results from our study can be used to develop an age sampling protocol in which dorsal spines are used to estimate the ages of smaller Walleyes (females <508 mm and males <457 mm) with relative accuracy but otoliths are required to accurately estimate the ages of larger fish.

Underestimating the ages of larger Walleyes by using dorsal spines had little impact on the von Bertalanffy growth models for both sexes. Most of the somatic growth among the Walleyes inhabiting the Winnebago system has already occurred by age 7, the age at which dorsal spines begin to underestimate age. Similar results were reported by Kocovsky and Carline (2001) for Walleyes in Pymatuning Sanctuary, where fish attained approximately 67% of their terminal length before reaching maturity and grew very slowly following maturity. These results demonstrate that most fish growth has taken place by the age at which nonlethal structures begin to underestimate fish age, such that the growth models were relatively unaffected by aging error. Therefore, the use of dorsal spines to estimate growth rates and von Bertalanffy growth model parameters is acceptable in scenarios where the sacrifice of fish is not possible and yield-per-recruit models are not utilized.

Spine- versus otolith-specific von Bertalanffy model parameters were used along with structure-specific estimates of natural mortality to examine the yield estimates for male and female Walleyes at various exploitation levels through sex- and structure-specific yield-per-recruit models. Despite our failure to find differences between von Bertalanffy models based on spine ages as opposed to otolith ages, yield-per-recruit modeling showed that the minimum size limits to maximize yield inferred from model results based on spine age data would be lower (implying younger ages) for both male and female Walleyes than with otolith age–based models. Also, the yield at any age or size was estimated to be much lower using models based on spine age data. The importance of these findings (assuming that otolith-derived ages are accurate) is that the type of aging error exhibited by spines, i.e., underestimating age after maturity or attainment of a certain size, would likely move a fisheries manager’s decision on a minimum size limit to fish that are too small to maximize yield. This phenomenon could have serious ramifications for a fishery, especially if it is managed for maximum sustainable yield, as often is the case in commercial fisheries.

In any assessment, the ultimate use and application of age data need to be considered when determining which aging structure should be used to estimate fish age. Although age estimates derived from scales and dorsal spines are likely inaccurate to varying degrees, they may be acceptable for indicating general trends in age and growth for young, fast-growing fish populations. Such fish are typically more accurately aged because their annuli are easier to identify (Erickson 1979; Belanger and Hogler 1982; Frie et al. 1989). However, otoliths should be used to estimate fish age when populations contain a large percentage of older fish and age data are used to estimate mortality or growth rates used to set harvest regulations. Based on the results from this study, otoliths will be exclusively used to estimate the age of Walleyes in the Winnebago system, as this species is the primary focus of a sport fishery in this system, which annually contributes $234 million to the local economy and receives national recognition (Cook and Neiswender 2007).

Collecting and utilizing accurate age data are critical to the efficiency and effectiveness of any fisheries management program, as any aging error inherent in scale and dorsal spine age estimates reduces the accuracy of the estimated rates of growth, mortality, recruitment, and yield (Bradford 1991; Mertz and Myers 1997). Effective management hinges on the accurate estimation of growth, mortality, and recruitment, which are the driving forces behind the population dynamics of a fish stock, while yield-per-recruit estimates are often used by managers to set size limits in both commercial and recreational fisheries for Walleyes and many other species. Collecting only spines from Walleyes to derive age estimates is not recommended due to the inaccurate and misleading results from models utilizing spine age data and the erroneous management decisions that
ACKNOWLEDGMENTS

We thank the Oshkosh fisheries management staff of the Wisconsin Department of Natural Resources for collecting the data that were included in this analysis. We also thank Jack O’Brien and Eli Felts for their efforts and expertise with age estimation and Robert Stelzer, Greg Adler, and Jonathan Hansen for providing critical reviews of the manuscript. This research was made possible by an education grant from Walleyes for providing critical reviews of the manuscript. This research estimation and Robert Stelzer, Greg Adler, and Jonathan Hansen O’Brien and Eli Felts for their efforts and expertise with age data that were included in this analysis. We also thank Jack

REFERENCES


Erickson, C. M. 1979. Age differences among three hard tissue structures observed in fish populations experiencing various levels of exploitation. Manitoba Department of Natural Resources, Report 79-77, Winnipeg.


North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 08 Oct 2013.

To cite this article: Ryan P. Koenigs , Ronald M. Bruch & Kendall K. Kamke (2013) Impacts of Anchor Tag Loss on Walleye Management in the Winnebago System, North American Journal of Fisheries Management, 33:5, 909-916, DOI: 10.1080/02755947.2013.815671

To link to this article: http://dx.doi.org/10.1080/02755947.2013.815671

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Impacts of Anchor Tag Loss on Walleye Management in the Winnebago System

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Abstract
Rates of tag loss should be estimated and accounted for when using mark–recapture surveys and angler tag returns to estimate fish population abundance and exploitation rates. Walleyes *Sander vitreus* sampled during April 2010 spawning assessments conducted in the Winnebago system, Wisconsin, were marked with anchor tags and upper caudal fin clips to estimate tag loss rates during three time intervals: 0–11 d posttagging, 0–90 d posttagging, and 1 year posttagging. Tag loss was negligible (<0.5%) within the first 11 d but increased to 4.7% within the first 90 d and to 21.9% after 1 year. After we corrected for the tag loss occurring within the first 90 d, estimates of population abundance decreased 4.3% for females and 4.4% for males, while estimates of exploitation increased 4.9% for both sexes. Accounting for 21.9% annual tag loss led to more severe decreases in the estimates of population abundance (20.0% for females and 21.2% for males) and increases in the estimates of exploitation (28.0% for both sexes) than not accounting for any tag loss. Higher exploitation rates resulted in higher estimates of fishing mortality and lower estimates of natural mortality. When used in yield-per-recruit models, the estimated natural mortality rates derived from exploitation rates that accounted for tag loss resulted in higher yields through the implementation of larger minimum length limits to maximize yield. We recommend that managers evaluate the effectiveness of their tagging operations by estimating tag loss and assessing the potential impacts of quantified loss on management metrics. We also caution against the application of population models without an accurate estimate of tag loss and the associated impacts on estimates of population abundance and exploitation and, in turn, fishing and natural mortality rates.

Fish tagging and marking techniques are utilized by fisheries managers to determine population characteristics, including abundance, exploitation, movement, somatic growth, and mortality (Guy et al. 1996; Pegg et al. 1996). External tags such as anchor tags, Carlin tags, and jaw tags have commonly been used due to their easy detection during recapture by anglers and fisheries personnel, but these tags are often shed following tagging. Tag loss studies have been conducted on many species of fish and have yielded extremely variable results (Ebener and Copes 1982; Franzin and McFarlane 1987; Muoneke 1992; Hartman and Janney 2006). For example, Pierce and Tomcko (1993) observed 1.8% annual loss of anchor tags in Northern Pike *Esox lucius*, while Hartman and Janney (2006) observed 57.1% loss of anchor tags after 403 d in Largemouth Bass *Micropterus salmoides*. Estimated rates of tag loss for Walleye *Sander vitreus* have been variable as well, depending on tag type and water type. Annual jaw tag loss ranged from 23% to 50% in Lake Erie (Isermann and Knight 2005) and from 12.5% to 27.8% in Escanaba Lake, Wisconsin (Newman and Hoff 1998). Walleyes in Kabetogama Lake, Minnesota, shed Carlin tags at an annual rate of 24.2% (Kallemeyn 1989). Weeks and Hansen (2009) reported mean annual anchor tag loss rates of 2.9% for Walleyes inhabiting the Manitowish Chain, Wisconsin, which, to our knowledge, is the only estimate of anchor tag loss for Walleyes reported in the peer-reviewed literature.

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Received May 22, 2013; accepted June 11, 2013
Published online September 23, 2013

© American Fisheries Society 2013
ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2013.815671
Not accounting for tag loss leads to overestimation of population abundance and underestimation of exploitation rates (Ebener and Copes 1982; Kallemeyn 1989; Isermann and Knight 2005). Kallemeyn (1989) reported that estimates of Walleye population size decreased by approximately 8.5% after accounting for 24.2% tag loss rates, and Isermann and Knight (2005) documented exploitation rates that were 25–59% higher after accounting for tag loss. Ebener and Copes (1982) calculated exploitation and fishing mortality rates that were 17% higher after accounting for tag loss, and these increases led to a 40% increase in yield-per-recruit model outputs. These studies all underscore the importance not only of determining tag loss rates within populations but also of correcting for tag loss in deriving estimates of the population metrics that are used to manage exploited fisheries.

The Winnebago system, Wisconsin, is home to a renowned Walleye population that is the primary focus of a high-profile, year-round recreational fishery that has an annual regional economic impact of $234 million (Cook and Neiswender 2007). Since 1989, the Wisconsin Department of Natural Resources (WDNR) has been using Floy anchor tags (FD-94) to mark Walleyes spawning in the extensive network of old channels, oxbows, bottomland forest, and marshes on the upper Fox and Wolf rivers within the Winnebago system. Tag returns from anglers fishing the Winnebago system are used to estimate rates of exploitation, and data collected during two recapture events (June Walleye tournaments and spawning stock assessments in the following year) are used to estimate population abundance. Our objectives were (1) to estimate tag loss over three time periods posttagging (within the first 11 d, within the first 90 d [between the time of tagging and summer Walleye tournaments], and after 1 year) and (2) to examine the impacts of tag loss on estimates of population abundance, exploitation, fishing and natural mortality, and yield per recruit.

**METHODS**

**Tag loss.**—Walleyes were captured on the upper Fox and Wolf rivers from March 23 to April 1, 2010, using a standard Wisconsin-style electrofishing unit with pulsed direct current (25% duty cycle, 50 pulses per second, conductivities of 330–370 µS/cm, typically producing an electrical field of 100 V at 5 A or less). Captured fish were observed for the presence of Floy anchor tags (FD-94; Floy Tag and Manufacturing Inc.), and all fish tagged prior to 2010 (as determined by the tag number) were treated as recaptures and released after their tag number, TL to the nearest 2.5 mm, and sex (as determined by extrusion of gametes) were recorded. All untagged Walleyes were marked with Floy anchor tags (FD-94) using a Floy Mark II tagging gun equipped with a 33-mm needle. Tags were inserted at an acute angle into the base of the posterior dorsal fin on the left side of the body, as described by Guy et al. (1996). Special care was taken to ensure that tags were inserted behind pterygiophores and then properly seated by gently tugging on the tags after insertion. All newly tagged fish were secondarily marked by removal of the upper lobe of the caudal fin at a 90° angle to the fin rays. All Walleyes captured during Winnebago system assessments are measured in TL to the tip of the upper lobe of the caudal fin, so Walleyes with missing or partially regenerated fin rays would be identified as fish that had been tagged and had their upper caudal fin clipped in 2010 (Guy et al. 1996). Any nontagged fish encountered throughout the study that exhibited key characteristics indicating that the upper caudal fin had been clipped was identified as a fish that had shed its anchor tag.

Three Walleye recapture periods were included in the study: initial tag loss (0–11 d posttagging), tag loss occurring before and during summer tournaments (0–90 d posttagging), and tag loss occurring within the first year following tagging (annual tag loss). Initial tag loss was determined during the 2010 spawning assessments. Tag loss occurring up to June tournaments was determined during three catch–hold–release Walleye tournaments. All three tournaments were held on the Winnebago system during consecutive weekends in June 2010, and each tournament was treated as a replicate to establish confidence intervals for the mean tag loss rates observed during this time period. Annual tag loss was evaluated during spawning assessments conducted on the upper Fox and Wolf rivers in April 2011. In addition to electrofishing, fyke nets (1 m high, 19-mm-bar mesh) were also used to capture Walleyes during 2011 spawning assessments. Similar methods were used to evaluate tag loss during all three time periods. All fish were observed for the presence or absence of upper caudal clips, and the presence/absence of a tag was recorded for fish missing the upper lobe of their caudal fin. Captured Walleyes that had been fin-clipped but had shed their tags were secondarily marked by removing the sixth dorsal spine in April 2010, the ninth dorsal spine in June 2010, and the lower lobe of the caudal fin in April 2011. This indicated that tag loss had already been documented for that fish during that time period, and if the fish was captured again within the specific period, it would not be counted as a tag loss an additional time. Data collected during the April 2011 spawning assessments were separated between the two gear types to assess whether either gear was contributing to tag loss. The probability of tag loss ($R_{TL}$) for each individual period was calculated using the equation

$$R_{TL} = N_L/N_C,$$

where $N_L$ represents the number of clipped fish that had shed their tag and $N_C$ represents the total number of fish observed with fin clips.

**Management implications.**—Mark data from the March–April spawning assessments, together with capture and recapture data from June Walleye tournament monitoring, were used to estimate population abundances (1993–2012). Walleyes are typically randomly dispersed throughout the Winnebago system by June after being marked during the March–April spawning assessments and moving back downstream following release (WDNR, unpublished data). Walleyes caught by anglers...
in catch–hold–release tournaments in June were observed for the presence/absence of tags. Tournaments have traditionally imposed a 381-mm minimum size limit; therefore, the WDNR estimates the abundance of male and female Walleyes ≥381 mm and only fish originally marked at lengths ≥381 mm were included in the marked sample. Sex–specific annual adult population densities for 1994–2012 (1993 was not included because no marked fish were recaptured that year) were also estimated using recapture data collected during the stock assessments 1 year posttagging. The number of marked fish estimated to be present in the population during recapture sampling events was the number of fish tagged the previous year minus natural mortality (15.8% for males and 11.4% for females; WDNR, unpublished data) and harvest since tagging. Harvest estimates for marked fish were calculated based on angler tag returns assuming a 50% tag return rate by anglers (a standard value used as part of the Winnebago Walleye management program that has been vetted over time [1993–2012; WDNR, unpublished data]). Population abundance was estimated using the Chapman variation of the Petersen estimator (Ricker 1975), i.e.,

\[ N = (M + 1)(C + 1)/(R + 1), \]

where \( M \) represents the number of fish marked, \( C \) the catch or the total number of Walleyes in the recapture sample, and \( R \) the number of recaptured marks in the recapture sample. Population estimates adjusted for tag loss were calculated as described in Seber (1982):

\[ N = \pm (M + 1)(C + 1)/(R/(1 - R_{TL}) + 1). \]

Mark data from the March–April spawning stock assessments, in combination with angler tag return data, were used to estimate exploitation rates for adult male and female Walleyes (1993–2012) using three different tag return rates (25, 50, and 75%) with and without incorporating the tag loss occurring within the first 90 d and the first year posttagging. Exploitation estimates \((u)\) not incorporating tag loss were calculated using the equation

\[ u = (N_H/T_R)/(N_T), \]

where \( N_H \) represents the number of tagged fish reported by anglers as harvested, \( T_R \) represents the tag reporting rate, and \( N_T \) represents the total number of fish tagged. Exploitation estimates incorporating tag loss were calculated using the equation

\[ u = (N_H/T_R)/(N_T[1 - R_{TL}]). \]

The mean instantaneous total annual mortality rates \((Z)\) were estimated to be 0.396 for adult female Walleyes and 0.349 for adult male Walleyes in the Winnebago system (WDNR, unpublished data). The rates of instantaneous fishing mortality \((F)\) were estimated from the mean rates of instantaneous annual mortality, conditional total annual mortality \((A, or 1-e^{-Z})\), and \(u\) based on a 50% tag reporting rate using the Baranov catch equation (Ricker 1975):

\[ F = u(Z/A). \]

Fishing mortality rates were calculated for both male and female Walleyes at 0.47, and 21.9% tag loss rates. Instantaneous natural mortality rates \((M)\) were estimated by subtracting the estimated values of \(F\) from those of \(Z\).

Yield-per-recruit (YPR) models were built in Excel to assess the impacts of tag loss on YPR estimates using the equation

\[ Y_t/N_0 = F \cdot e^{-M(t-t_0)} \cdot W_{\infty} \cdot (1/Z - (3e^{-K(t-t_0)}/Z + K) + (3e^{-2K(t-t_0)}/Z + 2K) - (e^{-3K(t-t_0)}/Z + 3K)); \]

\[ N_0 = \text{the number that recruit to the population (set to 1 to eliminate it from equation)}; \]
\[ t_r = \text{age of recruitment to the fishery}; \]
\[ t_0 = \text{a constant from von Bertalanffy length–age models (WDNR, unpublished)}; \]
\[ W_{\infty} = \text{weight at infinite length} (L_{\infty}) \text{ derived from von Bertalanffy length–age models and weight–length models for summer male and female Walleyes from the Winnebago system, 2009–2011 (WDNR, unpublished)}; \]
\[ K = \text{a constant from von Bertalanffy length–age models (WDNR, unpublished).} \]

These models were run for 31–34 different values of \(F\) ranging from 0 to 1.0 and three (constant) values of \(M\) based on the three tag loss scenarios (0, 4.7, and 21.9% tag loss) for both male and female Walleyes aged 1–20. These models demonstrated the impacts of tag loss on predicted yields and the hypothetical size limits needed to maximize yield. Model estimates of yield at set total instantaneous mortality rates for fish up to an age at which the asymptotic length is approached (0.349 for males aged 1–10 [526 mm] and 0.396 for females aged 1–12 [665 mm]; WDNR, unpublished data) were averaged for each of the models incorporating the three tag loss rates.

**RESULTS**

**Initial Tag Loss (0–11 d Posttagging)**

A total of 10,553 Walleyes were Floy tagged and upper caudal fin–clipped during 2010 spawning assessments on the upper Fox and Wolf rivers; males ranged from 292 to 592 mm \((n = 9,007; \text{mean} = 424 \text{ mm}; \text{SD} = 1.56)\) and females from 391 to 734 mm \((n = 1,546; \text{mean} = 531 \text{ mm}; \text{SD} = 2.53)\). During the 2010 assessments, 887 fish that had been marked and caudal fin–clipped in the same year were recaptured, 2 of which had shed their tags, resulting in a 0.2% tag loss during the period 0–11 d posttagging.
Tag Loss 0–90 d Posttagging

A total of 3,896 Walleyes were observed during monitoring of three June Walleye tournaments (1,345 at tournament 1, 1,257 at tournament 2, and 1,294 at tournament 3; Table 1). During these three tournaments, 65 Walleyes were observed with upper caudal fin clips, 3 of which had shed their anchor tags (Table 1). All three fish that had shed their tags exhibited fresh, bright red tagging scars where the tag had been inserted. The mean tag loss rate between the three tournaments was 4.7% (SD = 0.008; 95% confidence interval = 3.8–5.6%).

Tag Loss 1 Year Posttagging

Some regeneration of the top lobe of the caudal fin occurred by 1 year posttagging, but the clips were still clearly discernible, as regenerated rays were distorted at a different angle from the original fin rays (Figure 1). A distinct line of scar tissue along the original removal cut was also observed that could be felt between the fingers along the area between the original and regenerated rays of the caudal fin (Figure 1). A total of 161 individual Walleyes with caudal fin clips were collected during electrofishing surveys conducted in April 2011, of which 38 had shed their tags (23.6% tag loss). An additional 154 individual Walleyes with caudal fin clips were collected during fyke net surveys conducted in April 2011, of which 31 had shed their tags (20.1% tag loss). The mean tag loss rate among the two gear types was 21.9% (SD = 0.02).

Management Implications

Two recapture periods (June tournament monitoring and spawning assessments 1 year posttagging) were used to estimate population abundance during this study, which allowed the impacts of varying tag loss rates on population estimates to be evaluated. Accounting for the 4.7% tag loss that took place within the first 90 d (using June tournament monitoring as the recapture sample) resulted in population abundance estimates for 1993–2012 that were on average 4.4% lower for males and 4.3% lower for females. Mean abundance estimates assuming 0% tag loss were 197,681 males ≥381 mm (range = 30,945–853,885; SD = 181,406) and 309,406 females ≥381 mm (range = 89,750–707,249, SD = 182,996), excluding the year 2000 due to tag loss in tournaments 1–3 (Table 1). During these three tournaments, 65 Walleyes were observed with upper caudal fin clips, 3 of which had shed their anchor tags (Table 1). All three fish that had shed their tags exhibited fresh, bright red tagging scars where the tag had been inserted. The mean tag loss rate between the three tournaments was 4.7% (n = 3; SD = 0.008; 95% confidence interval = 3.8–5.6%).

TABLE 1. Number of Walleyes observed, number with clipped caudal fins (N_C), number with clipped caudal fins that had shed their tags (N_L), rate of tag loss in tournaments 1–3 (R_TL) held in the Winnebago system in June 2010. The mean tag loss between tournaments was 4.7% (SD = 0.008; CI = 3.8–5.6%).

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FIGURE 1. Photo of a Walleye with a caudal fin clipped in April 2010 that was recaptured in April 2011 on the Wolf River showing tissue regeneration (note the distinct line between the original and regenerated fin tissues). [Figure available in color online.]

R values of 0 or 1. Mean abundance estimates incorporating the 4.7% tag loss were 196,816 males ≥381 mm (range = 29,573–820,177, SD = 175,507) and 296,575 females ≥381 mm (range = 85,784–677,991, SD = 176,316), excluding the years 1999, 2000, 2006, and 2011 due to R values of 0 or 1.

The population abundance estimates for 1994–2012 using tag returns 1 year posttagging and incorporating a 21.9% annual tag loss rate for adult Walleyes were on average 21.2% lower for males and 20.0% lower for females than estimates developed without accounting for annual tag loss. Mean abundance estimates assuming 0% tag loss were 261,015 (range = 88,351–707,249, SD = 182,996), excluding the year 2000 due to R values of 0 or 1. Mean abundance estimates incorporating the 21.9% tag loss were 205,371 (range = 74,436–649,341, SD = 132,720) for males and 62,111 (range = 20,130–120,592, SD = 28,908) for females, again excluding 1995 and 1998–2002 due to R values of 0 or 1.

Mean exploitation estimates for adult male Walleyes in 1993–2012 assuming 0% tag loss were 28.0% (range = 8.0–43.9%, SD = 10.1%) at 25% angler tag reporting, 14.0% (range = 4.0–21.9%, SD = 5.0%) at 50% reporting, and 9.3% (range = 2.7–14.6%, SD = 3.4%) at 75% reporting, all lower than the estimates incorporating the 4.7% tag loss observed within the first 90 d posttagging (29.4% [range = 8.4–46.0%, SD = 10.6%], 14.7% [range = 4.2–23.0%, SD = 5.3%], and 9.8% [range = 2.8–15.3%, SD = 3.5%] at the 25, 50, and 75% angler tag reporting rates, respectively) and the 21.9% annual tag loss (35.9% [range = 10.3–56.2%, SD = 12.9%], 17.9% [range = 5.1–28.1%, SD = 6.5%], and 12.0% [range = 3.4–18.7%, SD = 4.3%], respectively). Similar results were observed for adult female Walleyes (Tables 2–4). Accounting for the 4.7% tag loss resulted in a 4.9% proportional increase in exploitation.
### Table 2: Number of fish tagged in each year ($N_T$), number of the tagged fish reported by anglers as harvested within 1 year posttagging ($N_H$), and corresponding estimates of exploitation ($u$) based on 25, 50, and 75% angler tag reporting rates for adult female Walleyes in the Winnebago system, 1993–2012, assuming 0% tag loss.

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### Table 3: Number of fish tagged in each year ($N_T$), number of the tagged fish reported by anglers as harvested within 1 year posttagging ($N_H$), and corresponding exploitation estimates ($u$) based on 25, 50, and 75% angler tag reporting rates for adult female Walleyes in the Winnebago system, 1993–2012, accounting for the 4.7% tag loss 90 d posttagging.

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Estimates over estimates not accounting for tag loss, while accounting for the 21.9% tag loss resulted in a 28.0% proportional increase in exploitation estimates for both sexes.

The estimates of $Z$ derived from otolith-driven catch curves (2009–2011) for Walleyes in the Winnebago system were 0.396 for females and 0.349 for males (WDNR, unpublished data). Assuming 0% tag loss, estimates of $F$ were 0.166 for males and 0.246 for females, while those for $M$ were 0.183 for males and 0.150 for females. Accounting for the 4.7% tag loss, exploitation rates were higher and in turn $F$ increased to 0.174 for males and 0.258 for females, causing a decrease in estimates of $M$ (to 0.175 for males and 0.138 for females). Accounting for the 21.9% annual tag loss led to even larger increases in estimated exploitation and even higher values of $F$ (0.212 for males and 0.315 for females) and lower values of $M$ (0.137 for males and 0.081 for females).

Yield-per-recruit modeling produced average yields of Walleyes in the Winnebago system up to their asymptotic age and size at average 2009–2011 instantaneous total annual mortality rates for each sex that were 10.0% (SD = 2.8%) higher for males and 13.0% (SD = 5.0%) higher for females when the models incorporated the 4.7% tag loss than they did when they did not incorporate any tag loss. Average yields were 67.3% (SD = 17.8%) higher for males and 102.6% (SD = 38.1%) higher for females when the models incorporated the 21.9% annual tag loss than when they did not incorporate any tag loss.

The YPR model derived from the data assuming 0% tag loss predicted that a maximum yield of 160 g per recruit for male Walleyes (annual $u = 14.0\%$) would be attained by implementing a 400-mm minimum size limit (msl) at age 3, while the model incorporating the 4.7% tag loss (annual $u = 14.7\%$) predicted a maximum yield of 174 g per recruit at that msl. The model derived from the data incorporating the 21.9% annual tag loss (annual $u = 17.9\%$) predicted a maximum yield of 248 g per recruit with implementation of a 409-mm msl at age 4. The models run for females showed similar results, with those assuming 0% tag loss ($u = 20.3\%$) and 4.7% tag loss ($u = 21.3\%$) predicting maximum yields per recruit of 505 and 563 g, respectively, with the implementation of a 500-mm msl at age 5, while the model incorporating annual tag loss of 21.9%...
Both time periods (5% shedding at week 6 and 19% shedding posttagging) observed better retention of FD-67F tags during *Salvelinus fontinalis* anchor tags increased shedding rates up to 88% in Brook Trout (Muoneke 1992). Improper tag attachment and failure to anchor the T-bar anchor increased shedding rates during the initial tag loss (Davis and Reid 1982; Muoneke 1992; Fabrizio et al. 1996). The Oshkosh fisheries management crew of the WDNR has tagged 145,000 Walleyes during spawning assessments conducted from 1993 to 2012, and all personnel tagging fish in this study were experienced, consistently inserting each tag and then tugging on it to properly seat the T-bar.

The 4.7% mean tag loss rate that we observed during the first 90 d posttagging is comparable to the loss rates reported in other studies over similar time periods. Pegg et al. (1996) determined that 4.4% of the Saugers *Sander canadensis* that were double-tagged on the lower Tennessee River had shed their tags after a 5-month period, and researchers on Mille Lacs in Minnesota concluded that 4.3% of the double-tagged Walleyes collected 31–90 d posttagging had shed one of their tags (Schwarz 2008). Walleyes in the St. Louis River exhibited a 7.5% loss of anchor tags within the first 65 d posttagging (Osborn et al. 1991).

Reported estimates of anchor tag loss from Walleyes after the first year posttagging have been quite variable. Weeks and Hansen (2009) reported a mean annual tag loss rate of 2.9% for Walleyes tagged with anchor tags in the Manitowish Chain, while Osborn et al. (1991) reported higher loss rates of 7.0–17.9% after 1 year for Walleyes in the St. Louis River. Further, Schwarz (2008) reported that 28.5% of the double-tagged Walleyes on Mille Lacs had shed an anchor tag within the first 271–360 d posttagging, and another study from Minnesota (on the Woman Lake Chain) estimated 49–56% loss of anchor tags after 1 year (S. M. Shroyer, Minnesota DNR, personal communication). Although our results fall well within the range of annual tag loss reported in these other studies, there remains considerable variation among estimates of anchor tag loss from different Walleye populations and tagging operations, reinforcing the importance of estimating tag loss for the populations being studied.

There are numerous factors that likely contribute to long-term tag loss and variability in tag retention, including algal growth on the tag, snagging of tags, fish behavior, and equipment failure (Muoneke 1992). The growth of filamentous algae on the tubing of tags is commonly suspected to contribute to tag loss (Carline and Brynildson 1972; Ebener and Copes 1982; Muoneke 1992). Algal growth may increase water drag on the tag, promoting irritation of adjacent tissue and increasing the prevalence of tag loss (Ebener and Copes 1982). Carline and Brynildson (1972) reported the growth of filamentous algae over time on Floy anchor tags placed in Brook Trout and noted that such growth may reduce the usefulness of similar tags in nutrient-rich waters.

### Table 4. Number of fish tagged in each year ($N_T$), number of the tagged fish reported by anglers as harvested within 1 year posttagging ($N_H$), and corresponding exploitation estimates ($\mu$) based on 25, 50, and 75% angler tag reporting rates for adult female Walleyes in the Winnebago system, 1993–2012, accounting for the 21.9% annual tag loss.

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($\mu = 26.0\%$) predicted a higher maximum yield per recruit of 964 g with the implementation of a 559-mm msl at age 7.

**DISCUSSION**

Although the initial loss of T-bar anchor tags from Walleyes can be negligible, the number and percentage of tags shed increases over time—up to 21.9% after 1 year in the Winnebago system. The loss of tags can have a significant impact on metrics developed from tag return data if tag loss is not accounted for, and the application of unadjusted metrics in a management program can lead to management actions that are ineffective or possibly detrimental to the Walleye stock or fishery.

Improper tag attachment and failure to anchor the T-bar anchor between pterygiophores are the most common causes of initial tag loss (Muoneke 1992). Improper attachment of Floy anchor tags increased shedding rates up to 88% in Brook Trout *Salvelinus fontinalis* (Keller 1971). Greeneland and Bryan (1974) studied the loss rates of two different models of Floy anchor tags in Channel Catfish *Ictalurus punctatus* at 6 weeks and 12 weeks posttagging and observed better retention of FD-67F tags during both time periods (5% shedding at week 6 and 19% shedding at week 12 versus 70% shedding by week 6 and 90% by week 12 with FD-67 tags). They attributed the different loss rates to the fact that FD-67F tags had longer tag anchors that could more effectively be inserted behind the interneural spines of the dorsal fin. Our results indicate that initial tag loss (0–11 d posttagging) was negligible (<0.3%), suggesting that the tags were rarely shed due to improper tag attachment or failure to engage between interneural bones. Prior experience with tagging fish may increase proper placement of the T-bar anchor, in turn minimizing the amount of initial tag loss (Davis and Reid 1982; Muoneke 1992; Fabrizio et al. 1996).
The Winnebago system is eutrophic, and tags from recaptured Walleyes that were at large for a year or more were usually coated with filamentous algae and occasionally Zebra Mussels *Dreissena polymorpha*.

Long-term tag loss due to entanglement in sampling nets has been reported for various fish species, e.g., gill nets used to sample White Suckers *Catostomus commersonii*, Lake Trout *Salvelinus namaycush*, and Lake Whitefish *Coregonus clupeaformis* (Ebener and Copes 1982; Franzin and McFarlane 1987; Fabrizio et al. 1996). Although Newman and Hoff (1998) documented higher rates of jaw tag loss in Walleyes that were captured in fyke nets than those observed in creel surveys, entanglement in fyke nets likely did not contribute to tag loss in this study, as our estimated tag loss rate for fish captured in fyke nets was actually lower than that for fish captured with electrofishing. Granted, small-mesh dip nets (∼12-mm bar) were used to capture Walleyes during electrofishing surveys on the Winnebago system; however, we have never seen a Floy tag entangled in a dip net used during electrofishing in over 20 years of sampling.

Fish behavior can influence tag shedding as well. As fish move, anchor tags tend to vibrate and wobble back and forth, creating an open wound that could promote tag loss. Tag spinning could also be exacerbated by algae coating the tags (Muoneke 1992; Fabrizio et al. 1996). Adult Walleyes in the Winnebago system utilize open water pelagic and littoral vegetated habitats during the course of the year and make long annual spawning migrations (up to 201 km upstream), which could contribute to tag loss via spinning or snagging. Tag failure can also contribute to tag loss. For example, the plastic tubing on a Floy tag may harden, become brittle, and eventually break (Muoneke 1992). Malfunction of tags has also been observed when the cement bond between the vinyl tube and the nylon shaft breaks (Tranquill and Childers 1982). Previously tagged Walleyes in the Winnebago system are frequently observed with only the tub from the nylon shaft of the tag remaining, while the remainder of the nylon shaft and the sheath containing the tag information are lost; this is thought to be the result of tag spinning over time, causing the nylon shaft to break below the vinyl tube. The three fish observed at June tournaments that had shed their tags had distinct wounds where the tags had been inserted in the spring, but none of them contained tag nubs. However, several tag nubs were observed on Walleyes that had shed their tags by 1 year posttagging, suggesting that tag failure is likely contributing more to long-term tag loss than tag loss within the first few months.

Although understanding the tag loss that occurs during the first 90 d is most important to Walleye management on the Winnebago system, estimates of shorter- or longer-term tag loss may be more important to other Walleye management programs. Assessing the tag loss occurring over three time periods allowed us to estimate three temporal tag loss rates and provide insight into how rates might change over the course of a year. Initial tag loss was negligible (<0.5%) and would have had little impact on the population metrics developed from tagging data (population abundance, exploitation, etc.). However, tag loss increases over time and has a greater impact on these metrics as it does so. This was observed in our study, where accounting for the 21.9% annual tag loss had far greater impacts on estimates of population abundance, exploitation, and YPR than the 4.7% tag loss seen after 90 d. For example, with our use of spring marking and early summer tournament recapture data to estimate the abundance of Walleyes in the Winnebago system, the time between marking and recapture was relatively short, which reduced the amount of harvest, natural mortality, and tag loss impacting the number of marks at large during the recapture effort, thus reducing the impact of tag loss on the population metrics estimated with these data. We observed 4.7% tag loss over this period, which decreased our population estimates by 4.3%. These results are similar to those reported by Kallemeyn (1989), who documented an 8.5% decrease in abundance after correcting for tag loss. Collecting recapture data after a longer period, such as the 1-year period in our study, increases the impact of natural and fishing mortality on the number of marks at large during recapture sampling. Our results showing an increasing tag loss rate up to at least a year emphasizes the importance of assessing a tag loss rate for the specific period between marking and recapture efforts for individual studies and then incorporating that tag loss into calculations of population metrics developed from the tagging data. If we had not accounted for our observed 21.9% annual tag loss, we would have overestimated our population size by more than 20%. This type of overestimation could lead to significant overfishing of a fish stock if managers were using population estimates to set harvest quotas or calculating total allowable catch for that population.

Not accounting for tag loss can also lead to overfishing due to the underestimation of exploitation. The greater the tag loss rate, the greater the underestimation of exploitation rates. Our estimated exploitation rates were 4.9% higher when we accounted for the 4.7% tag loss and 28.0% higher when we accounted for the 21.9% tag loss. These results are comparable to other studies that reported estimates of Walleye exploitation increasing by 25–59% after accounting for tag loss (Kallemeyn 1989; Isermann and Knight 2005).

Accurate estimation of exploitation is essential to the effective management of a fishery, as exploitation data are used to parcel total annual mortality into fishing and natural mortality. By assuming 0% tag loss, managers are underestimating exploitation and fishing mortality rates and thus overestimating natural mortality rates. Fishing and natural mortality rates are generally accepted to be compensatory risks of death for certain fish species, i.e., natural mortality decreases as fishing mortality increases (Allen et al. 1998). By overestimating natural mortality, managers might believe that exploitation and fishing mortality can be increased, thereby leading to overfishing of the stock. For example, overestimates of natural mortality rates for three red snappers (the Crimson Snapper *Lutjanus erythropterus*,
Malabar Snapper *L. malabaricus*, and Emperor Snapper *L. sebae* would have led to overfishing if the inflated estimates of natural mortality were applied to the red snapper management program (Newman et al. 2000).

Inaccurate estimates of natural and fishing mortality rates also affect the accuracy of YPR models. Although incorporating our lower 90-d tag loss value (4.7%) into male and female Walleye YPR models suggested implementation of the same minimum size limits to maximize yield per recruit for both sexes, accounting for the higher tag loss (21.9%) led to greater differences between fishing mortality rates within the two models, producing substantially different model outputs. Maximum YPR outputs were 67.3–102.6% higher when the higher fishing mortality due to accounting for higher tag loss values resulted in lower estimates of natural mortality. The models also recommended higher minimum size limits to attain maximum yields. Ebener and Copes (1982) reported similar results, in which equilibrium yield per recruit estimates for Lake Whitefish in Lake Michigan increased 40% after accounting for 11.1% tag loss after 1 year and 20.5% tag loss after 2 years. Yield-per-recruit models are becoming more common in fisheries management programs through wider use of programs such as FAST (Fishery Analyses and Simulation Tools; Slipke and Maceina 2006), making it imperative to incorporate data that are as accurate as possible into these models to support effective management decision making.

We recommend that managers evaluate the effectiveness of their tagging operations and use of tagging data by estimating tag loss and assessing the impacts of tag loss on the metrics they are calculating and using to make management decisions. Lower levels of tag loss may not significantly affect the estimates of metrics derived from mark–recapture studies, but high levels of tag loss can negatively affect the accuracy of population data and should be accounted for. We also recommend that tag loss be accounted for in the parameters and values used in population models to minimize the impacts on estimates of population abundance and exploitation and, in turn, fishing and natural mortality rates.

**ACKNOWLEDGMENTS**

We thank the Oshkosh fisheries management staff of the Wisconsin Department of Natural Resources for collecting the data that were included in this analysis. We also thank Robert Stelzer and Greg Adler for providing critical reviews of the manuscript. This research was made possible by an education grant from Walleyes for Tomorrow, while the technical work was funded by the Federal Aid in Sport Fish Restoration Program.

**REFERENCES**


Impact of Reservoir Elevation during the Spawning Season on the Distribution of Bull Trout Redds

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.818081

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MANAGEMENT BRIEF

Impact of Reservoir Elevation during the Spawning Season on the Distribution of Bull Trout Redds

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Abstract

Adfluvial Bull Trout Salvelinus confluentus reside in Chester Morse Lake (CML), a major reservoir in the City of Seattle water supply system on the central west slope of the Cascade mountain range, Washington. Annual surveys over a 12-year period (2000–2011) were used to investigate the spatial distribution of adfluvial Bull Trout redds in river systems of CML relative to reservoir elevation. Because reservoir elevations were lower in the spawning season than during the incubation period, some redds placed in river reaches near the reservoir were vulnerable to cumulative effects from impending inundation as reservoir levels increased and as fine sediments settled across gravel substrates. Higher average elevation of CML during the peak period of spawning caused significantly lower percentages of Bull Trout redds in lowermost river reaches, where fluctuating water levels could adversely affect incubating eggs ($R^2 = 0.73$). Annually, the proportion of redds distributed within habitat reaches where inundation, as indicated by mean CML elevation during the incubation period, could affect them, varied from 1% to 18%. However, a greater proportion of annual Bull Trout redds (10–68%) fell within the maximum reservoir elevation during the incubation period. These results suggest that maintaining moderate reservoir elevations during the spawning season and holding the reservoir near this elevation through the incubation period can lower the effect on incubating Bull Trout redds. The implications for water level management to benefit adfluvial Bull Trout derived from this data set could also be applicable in similar systems, especially where knowledge of temporal and spatial distribution of salmonid spawning is available.

The quality of spawning habitat for salmonids in fluvial systems depends upon many variables, including water velocity (Hinch et al. 2002), substrate size (Reiser et al. 1997; Wissmar and Craig 2004), streambed mobility (Montgomery et al. 1999), and the exchange of upwelling groundwater from hyporheic zones (Baxter and Hauer 2000). For adfluvial salmonid populations, spawning habitat immediately upstream of reservoirs can be affected by water management strategies as well as by natural lacustrine processes (Leonetti 1997). As fish move upstream from lakes or reservoirs, the lacustrine edge effects near the confluence of rivers diminish, and riverine spawning habitats are affected to a greater extent by natural riverine processes.

The management of reservoir systems requires an adaptive approach to management of water supply to both meet societal needs (i.e., for municipal, industrial, and agricultural purposes) and conserve important biological resources. Because reservoirs are managed for the extraction of resources, environmental conditions experienced by fish populations often differ from those in a natural lake system. For example, dam construction increase water elevations from natural lake levels, and the timing of drawdown often differs from that in a natural regime. River habitat immediately upstream of reservoirs can be affected as water elevations increase and backwatering occurs in the lowest reaches of the river, reducing flow velocities and depositing a layer of sediment over gravels. This transitional zone between the reservoir and the river system provides spawning habitat for fish in some reservoir systems and consequently requires attention by water managers. Numerous studies document that higher levels of sediment at egg incubation sites lead to greater egg mortality (Lapointe et al. 2004; Kock et al. 2006; Fudge et al. 2008). Determining the relative impact of such reservoir effects on the annual population of redds first requires documentation of redd distribution in the river network. Managers can then assess the extent and timing of water elevation changes that occur prespawning, during the spawning season, and postspawning to predict any effects on fish.

Adfluvial Bull Trout Salvelinus confluentus are found in several reservoir and lake systems in the western United States (e.g., Fraley and Shepard 1989; Beauchamp and Van Tassell 2001; Monnot et al. 2008). Listed as threatened under the U.S. Endangered Species Act (USFWS 2004), Bull Trout are fall spawners, typically selecting spawning sites upstream of lake and...
reservoir habitat (Brenkman et al. 2001; Dunham et al. 2001). Redd count surveys provide a consistent and repeatable method for assessing population trends of Bull Trout (Fraley and Shepard 1989; Rieman and McIntyre 1996; Rieman and Myers 1997; Dunham et al. 2001; Al-Chokhachy et al. 2005) and generate data that can be used to assess the spatial distribution of redds (Dunham et al. 2001). Documenting how management activities (e.g., reservoir water elevations) affect the annual distribution of Bull Trout redds upstream of reservoir systems provides water managers an opportunity to assess current operational protocols and refine those strategies to better protect and conserve threatened species such as Bull Trout.

The goal of this study was to determine the spatial distribution of Bull Trout redds in tributaries of Chester Morse Lake (CML) relative to reservoir elevations by documenting redd site locations in multiple consecutive years (2000–2011). Specific objectives included (1) defining the spatial distribution of Bull Trout redds, (2) investigating the relationship between Bull Trout redd distribution and reservoir elevation during the spawning season, and (3) evaluating the proportion of Bull Trout redds potentially affected by inundation when reservoir elevations fluctuated during the incubation period. The data collected and analyzed over 12 spawning seasons provide water managers a basis to evaluate strategies for minimizing the proportion of redds that could be spawned within the zones affected by reservoir operations.

STUDY AREA

Chester Morse Lake is located in the Cedar River Municipal Watershed (CRMW), approximately 55 km east of Seattle, Washington (Figure 1). The City of Seattle owns the entire hydrographic basin of the upper Cedar River upstream of CML and manages the area under a federal Habitat Conservation Plan (City of Seattle 2000). Management of the watershed complies with the federal Endangered Species Act, while supplying drinking water and a small amount of hydroelectric power to the City of Seattle. In addition, water levels (i.e., reservoir elevation) are managed to provide instream flows and limited flood control downstream in the Cedar River. Before its use as a municipal water supply, CML was a natural lake system (formerly Cedar Lake) with an outlet elevation of 467.1 m above mean sea level. Construction of the Masonry Dam in 1915 raised the capacity of the lake to a maximum of 478.7 m, although water levels are typically maintained below 477.1 m.
The Bull Trout population is genetically isolated by a natural fall downstream of the Masonry Dam, and fish spawn in core river habitats upstream of the reservoir system (Figure 1). The only other fish species present in the lake and its tributaries are native Pygmy Whitefish Prosopium coulterii and Shorthead Sculpin Cottus confusus and introduced Rainbow Trout Oncorhynchus mykiss. The Bull Trout population appears to primarily express an adfluvial life history, given that no conclusive evidence of a resident life history strategy for Bull Trout has been found in the CML system (Mesa et al. 2008; E. J. Connor and colleagues, 2001 report prepared for the City of Seattle, on CML fisheries; Seattle Public Utilities [SPU], unpublished data).

The Cedar and Rex rivers, the two major tributaries to CML, provide the majority of Bull Trout spawning habitat. The amount of mainstem habitat available to Bull Trout in the Cedar and Rex rivers totals approximately 24 and 6 km, respectively. Rack Creek provides some spawning and rearing habitat for Bull Trout (0.6 km) and flows directly into CML with a gradient of approximately 5–7%. When reservoir elevations are relatively low (<473.0 m), there is no surface connection between Rack Creek and CML, and Bull Trout cannot access spawning habitat for a portion of the spawning season in these years. Investigations of other small tributaries feeding into the reservoir show no use or only minimal use by Bull Trout for spawning or rearing.

Habitat in the Cedar and Rex rivers upstream of CML to an elevation of 475.5 m (Seattle datum 1,560 ft) is within the areas affected by winter and spring reservoir fluctuations. A water elevation of 472.4 m (Seattle datum 1,550 ft) is typically maintained during fall to create a flood pocket for fall rain and is referred to here as a “low” reservoir elevation. An elevation of 474.0 m (Seattle datum 1,555 ft) is an “intermediate” reservoir level during fall to winter, and the current high operating level is 476.4 m (Seattle datum 1,563 ft). Until 2003, 475.5 m (Seattle datum 1,560 ft) was the traditional maximum (“high”) operating level. The deltas of the Cedar and Rex rivers were formed by depositional processes, modified through erosion of delta surfaces by channel migration, and have been subject to variable fill and drawdown regimes since the early 1900s.

Chester Morse Lake reaches seasonal low elevations at the beginning of the Bull Trout spawning season (mid-September to early October); during that period, the elevation has fluctuated between 467.9 and 473.0 m over the last 20 years (USGS real-time gauge 12115900). Seasonal water elevations in CML have been determined by many factors, including municipal water demand, instream flow requirements throughout the summer, drought or flood events, and the amount of water stored from snowmelt runoff the previous spring. Reservoir high water levels are achieved in late spring (approximately June 1), inundating the lowest reaches of the Cedar and Rex rivers and depositing a fine layer of sediment over spawning gravels such that the deepest layers are located nearest the reservoir. Reservoir water levels drop throughout the summer and often reach a minimum level coinciding with the beginning of the Bull Trout spawning season in fall (approximately October); at that time, fine sediments are flushed from interstitial spaces, exposing gravel that may become inundated during the incubation period as the reservoir refills.

METHODS

Spawning surveys.—Bull Trout spawning surveys were conducted from 2000 to 2011 in the mainstem Cedar and Rex rivers, in several associated tributaries and floodplain channels, and in tributaries feeding directly into CML. Spawning surveys were initiated in late September of each year and continued until late December or early January. A team of two surveyors walked the stream and thoroughly searched for Bull Trout redds in the core spawning zones (0–4.0 km upstream CML). Although spawning surveys upstream of the core spawning zones were less frequent, we conducted surveys at least once during the peak of the season (approximately October 15–November 15) to document Bull Trout spawning activity; we returned later in the season if snow did not block access. Surveyors carefully watched streamflow and rainfall predictions to ensure that upstream reaches were surveyed before formation of any freshets that would make locating redds difficult. The numbers of all redds documented throughout the season were combined for analysis.

Unbiased sampling techniques are required to assess temporal and spatial variation of redd distributions over time (Dunham et al. 2001). Research indicates that use of experienced surveyors minimizes observer error in redd count data collection, especially in migratory populations such as this one (Muhlfeld et al. 2006; Howell and Sankovich 2012). To reduce potential bias in counts among surveyors, we calibrated the observer counts and used the same group of observers to conduct all surveys. These precautions allowed us to reasonably assume that surveys were conducted in the same manner each year, while acknowledging that some redds may have been omitted or falsely identified.

Each redd site was marked with a 15 cm × 20 cm cloth bag (www.brasspack.com) on which the date and the number of redds counted were recorded. The bag was filled with rocks and placed at the downstream end of each redd. This mark prevented double counting of redds through the spawning season, especially in areas of high aggregation (Dunham et al. 2001). In addition, superimposition events were identified when the bag was buried in the material of any redd spawning during subsequent weeks. The spatial location for each redd was documented with a handheld global positioning system (GPS) unit or by referencing preexisting station-flagging along the bank in some reaches.

Data from a 0.3-m topographic survey conducted on the Cedar and Rex rivers in 2002 were used to assess the spatial distribution of redds versus reservoir elevation (SPU, unpublished data). These data were available in ArcGIS and processed with existing topographic information to develop contour maps of the river corridor. Using these contours, we estimated the
extent of inundation with each 0.3-m rise in lake elevation for all rivers where redds were documented. Redd locations collected during spawning surveys were plotted on the elevation map to determine the percentage of Bull Trout redds falling within each band of inundation. We were unable to survey several reaches upstream of the core spawning zones on a weekly basis, so the likelihood of missing redds in these zones is greater than that in reaches surveyed weekly. However, repeat surveys over the last two decades have indicated that few fish spawn upstream of the core spawning zones.

Statistical analysis.—The annual average reservoir elevation was calculated for the peak of the Bull Trout spawning season (USGS gauge 12115900). The peak period of the spawning season was defined by the dates when the middle 50% of all redds for the year was documented (25% before and 25% after the mean spawn date). The mean and maximum reservoir elevations were also calculated for the incubation period, defined as December 1 through February 28. The end of February is when the earliest fry have been observed in these river systems (SPU, unpublished data).

A regression analysis was performed to determine whether the average water elevation of CML during the peak of the spawning season explained a significant amount of variation in the percent of annual Bull Trout redds downstream of three management threshold elevations (472.4 m, 474.0 m, and 475.5 m) on the Cedar and Rex rivers. A normality test indicated no data transformation was needed, and Cook’s distance test showed no unusual observations (Di < 1.0). Finally, we performed an analysis of variance (ANOVA) to test the significance of the regression for each elevation. All statistical analyses were conducted with SigmaPlot statistical software.

RESULTS

Bull Trout Redd Counts

Annual Bull Trout redd counts ranged from 236 to 587 over the 12-year spawning period (2000–2011) and were highly variable (Figure 2). Despite interannual variation in total counts, the majority of redds (70–85% of the total annual counts) were documented in the Cedar River system (Table 1). The Rex River maintained the second highest percentage of redds, ranging widely from 11% to 26% of the annual total Bull Trout redds in the CML basin. Rack Creek typically supported fewer than 6% of the annual redd count.

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</table>

Spatial Distribution of Bull Trout Redds

Bull trout in the Cedar and Rex rivers did not migrate long distances from CML to spawn. Ninety percent of Bull Trout redds in the Cedar River system were found within 3.5 km of the reservoir (measured from CML elevation of 470.4 m) between years 2000 and 2011 (3,476 of a total 3,843 redds; Figure 3). However, the presence of a few Bull Trout redds (n = 30) documented approximately 10.5 km upstream of CML on the Cedar River during the 2005–2011 spawning seasons indicated that Bull Trout did use upstream reaches, albeit in much lower densities than elsewhere. Similarly, 91% of all Bull Trout redds documented in the Rex River system from 2000 to 2011 were located within 2.0 km of CML (949 of a total 1,038 redds). Redd locations in Rack Creek were distributed throughout the stream from its confluence with CML to an apparent barrier created by large boulders 0.6 km from CML.

The annual distribution of redd sites relative to CML indicated that density-dependent effects related to increased competition for habitat in years with more abundant Bull Trout populations did not affect the reach of river wherein Bull Trout redds were located (Figure 4). In years with higher redd counts (e.g., 2004 or 2010), Bull Trout spawned in the same habitat reaches upstream of CML as in low redd count years. While the mean distance of redd location differed significantly between years (ANOVA: F(11, 3,800) = 27.0, P < 0.001), Bull Trout were
Distribution of Bull Trout Redds Relative to Chester Morse Lake Elevation

The proportion of Bull Trout redds distributed downstream of 472.2 m (typical fall low elevation) varied but was always less than 29% of the total redd count in any year (Figure 5). The proportion of redds recorded downstream of 474.0 m ranged from 10% to 49% (Table 2), and redds counts downstream of 475.5 m ranged from 28% to 67% of the annual total. In 9 of the 12 years, at least 40% of all redds were found downstream of 475.5 m lake elevation.

A significant amount of variation in the percentage of Bull Trout redds located downstream of the three management elevations can be attributed to the average elevation of CML during the peak of the spawning run (472.4 m: $R^2 = 0.73$, $F = 26.6$, $P < 0.001$; 474.0 m: $R^2 = 0.71$, $F = 24.2$, $P < 0.001$; 475.5 m: $R^2 = 0.55$, $F = 12.1$, $P < 0.01$). During 2002, considered a drought year, the average elevation of CML was only 469.1 m, and the highest proportion of Bull Trout redds was located in the zone downstream of 472.4 m elevation. In contrast, during 2001 and 2010, less than 2% of all redds fell within this zone, and the average lake elevation during the peak of the run was held much higher (473.0 and 472.7 m, respectively).

Bull Trout Redd Inundation

The spatial distribution of Bull Trout redds was compared relative to the distribution of reservoir elevations during the incubation period (mean and maximum; Table 3; Figure 6). Reservoir elevations were higher during incubation than during the spawning season in all years except 2001 (0.3 m lower) and 2007 (same elevation).

The percentage of redds affected by inundation at the mean reservoir elevation during the incubation period ranged from 1% (2000) to 18% (2002). Rain events in several years (e.g., January 2008) caused short-term increases in reservoir elevations, but in most cases the reservoir elevation returned to prestorm levels. The percentage of redds located downstream of the maximum reservoir elevation during the incubation, that is, those that potentially were affected by inundation, was as high as 68% (2002 and 2008; Table 3).
TABLE 2  Percentage of Bull Trout redds documented downstream of three management elevations on Chester Morse Lake (CML; low = 472.4 m, intermediate = 474.0 m, and high = 475.5), date range for the peak spawning period, and mean reservoir elevation (m) during the peak of the spawning period (2000–2011).

<table>
<thead>
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<th>Year</th>
<th>472.4 m</th>
<th>474.0 m</th>
<th>475.5 m</th>
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<th>Mean reservoir elevation during peak spawning period (m)</th>
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DISCUSSION

The quality of redd incubation sites varies, depending on factors such as adequate water flow, oxygen delivery, and waste removal (Peterson and Quinn 1996; Curry and MacNeill 2004). In reservoir systems, the management of water elevations is an additional consideration that affects spawning and incubation habitat in the lowermost tributary reaches upstream of the reservoir. Documenting the spatial distribution of Bull Trout redds provided the means to estimate potential reservoir effects on incubating Bull Trout redds. Some of the Bull Trout redds that spawned in the lowermost reaches of tributaries upstream of the reservoir each year were at risk of negative effects from inundation as the reservoir refilled and sediment was deposited over redd sites. Evaluating the distribution of redds from 12 spawning seasons, under different reservoir regimes, gave us the ability to examine potential effects on incubation of Bull Trout redds and provided a basis for recommendations on reservoir management during the Bull Trout spawning season and incubation period.

Adfluvial Bull Trout migrate to spawning sites each fall; however, the length of this migration varies widely among populations. For example, adfluvial Bull Trout in Flathead Lake, Montana, migrate as far as 250 km to spawning grounds (Fraley

TABLE 3  Mean CML elevation during the peak of the spawning season (time period when middle 50% of annual redds was documented), mean and maximum CML elevation during the incubation period (December 1–February 28) with the percent of Bull Trout redds inundated at each level in the Cedar and Rex rivers combined (2000–2011).

<table>
<thead>
<tr>
<th>Spawning year</th>
<th>Mean CML elevation (spawn)</th>
<th>Mean CML elevation (incubation)</th>
<th>Percent redds inundated at mean incubation elevation</th>
<th>Maximum CML elevation (incubation)</th>
<th>Percent redds inundated at maximum incubation elevation</th>
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<td>474.8</td>
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</table>
and Shepard 1989), while adfluvial Bull Trout in Lake Cushman, Washington, migrate 6 km or less (Brenkman et al. 2001). We found that the majority of Bull Trout redds were located immediately upstream of CML, in the first 3.5 km on the Cedar River and the first 2.0 km on the Rex River. While we did not enumerate the annual spawner population, we think it logical to expect that in years with higher redd counts the density of spawning Bull Trout was also higher. Despite the concentration of redds within the core spawning zones, habitat did not appear to be limiting for Bull Trout; although Bull Trout did cluster redd sites within certain reaches, we observed few superimposition events. While density-dependent effects on distribution have been observed in other spawning populations (Isaak and Thurow 2006), Bull Trout redd distribution remained clustered in similar reaches in years with both high and low redd counts.

We did not collect physical data to examine differences in habitat in close proximity to the reservoir versus habitat further upstream, but several possibilities exist to explain why Bull Trout redds are concentrated in these lower reaches. First, the habitat where redds were consistently documented in the highest densities had a gradient of less than 1.5%, consistent with Bull Trout selection of low-gradient reaches in other populations (Fraley and Shepard 1989). Beyond these reaches, both gradient and substrate size increase (SPU, unpublished data), potentially creating less suitable habitat (flow and gravel composition) for spawning. Second, floodplain channel habitat is relatively abundant at approximately 2.5 km upstream of CML. The spawning habitat type in these channels differs from that in main-stem channels. The observed concentration of redds at this distance in all study years probably correlates with the diversity and quantity of habitat available to Bull Trout. Finally, we have documented tagged Bull Trout that make multiple trips between CML and river habitat during a single spawning season (Barnett and Paige 2013). Such behavior during the spawning season may increase the likelihood of Bull Trout spawning immediately upstream of the reservoir because the fish seek spawning habitat and partners while making relatively short, multiple movements between the river and reservoir. The concentration of redds immediately upstream of CML suggests that management strategies designed to minimize the number of redds within the lowest reaches of the rivers may be advantageous to this population.

The distribution of Bull Trout redds was affected by fluctuating reservoir elevations during the spawning season. Because water levels began rising in the reservoir after the spawning season, the redds that spawned within 1.8 km of CML probably became inundated during incubation. The average elevation of CML during the peak of the spawning season was a significant factor affecting the distribution of redds upstream of the reservoir. While the percentage of redds downstream of the typical water level in fall (472.4 m elevation) was always less than one-third of the annual redd population, these redds, as well as those located within reservoir management zones (<475.5 m), were vulnerable to inundation during the incubation period. In years where the mean reservoir elevation during the peak period of spawning was higher (e.g., 2009–2011), Bull Trout moved further upstream to spawn and the proportion of redds at risk of inundation was reduced.

Many studies have documented the negative effects on salmonid redds of increased sedimentation resulting from reduced flow velocity (e.g., Curry and MacNeill 2004; Lapointe et al. 2004; Kock et al. 2006; Fudge et al. 2008). The mechanisms for a lower survival rate included reduction in flow, thus causing lower oxygen concentrations, or entombment of embryos as sediment covered the emergence area. Shepard et al. (1984) found that when gravels were comprised of greater than 30% find sediment (<6.4 mm), significant mortality of Bull Trout eggs or alevin resulted and suggested that entombment could be the cause of mortality. We did not attempt to quantify mortality of Bull Trout eggs or alevin; in some cases, it is possible that local geomorphic processes create enough groundwater flow to keep eggs oxygenated despite backwatering from rising reservoir elevations. The risk of entombment, as observed in tributaries of the Flathead Lake system (Shepard et al. 1984), is indeed present and deserves further study. Curry and MacNeill (2004) documented that increased sediment at redds sites caused greater mortality when it occurred late in development. These studies suggest that the timing of increased sediment at redd sites during incubation should be considered in a management strategy.

Bull Trout are adapted for life in unpredictable mountain watershed streams and are a relatively long-lived iteroparous species (McPhear and Baxter 1996). It is possible that the CML Bull Trout population, which evolved in a natural lake system but over the last century has been exposed to reservoir management, has developed strategies to reduce mortality and may be able to tolerate occasional years with increased inundation.
Management of reservoir elevations, whenever possible, to inhibit Bull Trout from spawning within 2.0 km of the reservoir (at an elevation of 470.4 m) may foster greater survival of an annual cohort by reducing the number of inundated redds. However, maintaining the reservoir at the lowest possible elevation could create a deeper thermocline during late summer months (Wells and Wells 2012), potentially affecting redd survival through other trophic levels in the reservoir. Our data indicate that when the reservoir elevation was held higher than 472.4 m elevation before and during the peak of the Bull Trout spawning season, less than 5% of the annual redd population was spawned below this elevation. As a potential, highly effective management tool to reduce mortality of Bull Trout eggs due to adverse effects of increased sedimentation, we suggest that whenever possible, reservoir levels during early summer drawdown period be managed so as to effectively reduce the possibility of extremely low reservoir elevations in fall.

Although we did not quantify this observation, in years during which the reservoir is maintained at a higher elevation (>475.5) for a longer period of time during spring and summer, we have noted the presence of a thicker layer of sediment on gravels during the early spawning season within the area of potential inundation. Our spawning surveys show that in such cases Bull Trout move upstream of these reaches with heavy sediment loads before spawning. Because the first elevated streamflow of the season typically flushes sediments off the spawning grounds, holding the reservoir higher in the spring in an effort to increase sediment loads in the lowest reaches of the river must also be accompanied by a moderate reservoir level during the spawning season. Additionally, evaluation of reservoir elevations during the spawning season allows managers to predict the proportion of redds that could be inundated during incubation. Delaying spring refill of the reservoir until at least March 1 would reduce the duration of inundation on incubating Bull Trout redds and potentially reduce mortality of eggs.

Collecting a long-term data set examining the spatial distribution of Bull Trout redds upstream of CML allowed us to gain valuable insight into the interactions between seasonal reservoir levels, Bull Trout spawning behavior, and resulting potential effects on egg survival from spawning through emergence of fry. The results of this study demonstrate that adjusting reservoir levels to encourage fish to seek spawning sites further upriver could be an effective management tool for reducing spawning in habitat expected to be subsequently inundated by rising reservoir levels. This study also demonstrates, especially for adfluvial Bull Trout populations in reservoirs, that water management strategies must consider not only how reservoir elevations affect Bull Trout spawning behavior, but more importantly how these and subsequent reservoir elevations will affect the conditions of redd site habitats, the incubation process, and ultimately, survival through emergence. Such considerations are important in the protection, conservation, and management of adfluvial Bull Trout populations in reservoir systems.

ACKNOWLEDGMENTS

We thank Kyle Meier, Jamie Thompson, Amy Reichenbach, David Chapin, Sally Nickelson, Bill Richards, Janis Hill, Mark Joseyn, Jeff Shellberg, Nathan Haase, Mark Joselyn, and Rick Sugg for help collecting data. Comments provided by David Chapin, Matt Groce, and three anonymous reviewers greatly improved earlier versions of this manuscript. This study was funded by Seattle Public Utilities under the Cedar River Watershed Habitat Conservation Plan guided by Jim Erckmann (SPU retired) and Tim Romanski (U.S. Fish and Wildlife Service).

REFERENCES


North American Journal of Fisheries Management

Self-Regulation of the Okanagan Lake Kokanee Recreational Fishery: Dynamic Angler Effort Response to Varying Fish Abundance and Productivity

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Published online: 08 Oct 2013.


To link to this article:  http://dx.doi.org/10.1080/02755947.2013.818082

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Self-Regulation of the Okanagan Lake Kokanee Recreational Fishery: Dynamic Angler Effort Response to Varying Fish Abundance and Productivity

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Abstract
The fishery for kokanee Oncorhynchus nerka in Okanagan Lake, British Columbia, exemplifies three common issues in the management of recreational fisheries: time-varying stock–recruit parameters, mixed stocks within a single fishing area, and open-access fishing effort. The aggregate kokanee stock (consisting of stream-spawning and shore-spawning stocks) declined 50-fold between 1971 and 1998 and then partially recovered in the most recent decade. This contrast in fish abundance provides an opportunity to gain insights into the predator–prey dynamics of anglers and fish in an open-access sport fishery. Structural variations in the Ricker stock–recruit function were fitted to the time series of spawner escapements and fishery data to estimate the relative role of nonstationary stock–recruit parameters versus angler harvest in the observed time series. The optimal model structures selected by Akaike’s information criterion suggested that kokanee dynamics were driven by external factors (e.g., lake nutrient concentration or opossum shrimp Mysis diluviana abundance) as opposed to fishery harvest. The functional response of angler catch rates to fish abundance was well predicted by a type I function (i.e., no density dependence in catchability). Conversely, the angler effort numerical response to variation in kokanee density was sigmoid, with a steep transition at an average catch rate between 1 and 2 fish/d. The interaction of angler response functions with fish recruitment dynamics led to an open-access recreational fishery that never harvested the lower-productivity (stream-spawning) stock to a level below the optimal escapement abundance, despite dramatic declines in stock productivity (i.e., recruits per spawner at low abundance) over time. Standard management reactions to declining fish abundance (successive reductions in daily bag limits) were largely ineffective in altering harvest rate or effort dynamics. Our results show that the Okanagan Lake kokanee fishery was self-regulating over a large range in fish densities and that the declines in kokanee abundance resulted from time-varying stock productivity rather than from overharvest.

Ensuring the sustainability of open-access recreational fisheries requires an understanding of the dynamic interaction between angler harvest and fish abundance. These dynamics can generally be described by predator–prey theory (Johnson and Carpenter 1994), requiring a production function for the prey (harvested fish), which is represented by the stock–recruit function within fisheries literature, and a predation component that is represented by angler harvest. Predation is generally described as two response functions: a functional response and a numerical response (Gotelli 1998). In recreational fisheries, the functional response is the catch rate as a function of fish density, and the numerical (or aggregational) response describes how angler effort changes in response to fluctuations in fish density. Predator–prey theory shows that understanding the form of both response

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Received January 15, 2013; accepted June 17, 2013
Published online September 23, 2013

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functions will dictate the stability of the fish–angler dynamics (Gotelli 1998; Walters and Martell 2004). Ultimately, the fishery will only be sustainable (i.e., not recruitment overfished) if the response functions result in fishing harvest that is less than the surplus production over the range of stock abundances below the stock density of maximum production (Walters and Martell 2004). Thus, recreational fisheries managers must clearly understand the numerical response of angler effort and the functional response of angler catch rates to fish abundance and how these responses can be adjusted toward desired ends given the underlying fish recruitment dynamics.

The importance of and challenges for estimating stock–recruit functions, especially stock productivity (i.e., recruits per spawner as spawner abundance approaches zero), are well recognized in fisheries management literature (Walters and Martell 2004). Two key challenges that are potentially encountered when estimating stock–recruit functions for recreational fisheries management targets are (1) the stock–recruit parameters may be changing over time, which will cause the target harvest and escapement to vary; and (2) there is often more than one stock within a single fishing area, and the stocks can have different stock–recruit parameters and fishery management targets (optimal harvest rate and escapement). The first challenge recognizes that variation in fish abundance can be a consequence of either environmental changes (i.e., regime shifts) or effects of the fishery. If time-invariant stock–recruit parameters are estimated for fish stocks, as is often the case, then the estimated impact of fishery harvest may be inaccurate. Alternatively, stock–recruit parameters can be allowed to vary over time either as a function of suspected environmental drivers (van Deurs et al. 2009) or by nonmechanistic estimation methods (e.g., Peterman et al. 2003; Chaput et al. 2005). Capturing time-varying recruitment in this way is an important step towards developing management approaches that are robust to varying environments (Walters and Parma 1996). Similarly, knowledge of the variation in recruitment parameters among different stocks within a mixed-stock fishery is critical to understanding the impacts of different harvest strategies. Open-access recreational fisheries may attract a high abundance of anglers based on the numbers of fish in the stock aggregate, thereby imposing harvest rates that are excessive for the weak (lower-productivity) stock(s) within the aggregate. Thus, both time-varying production parameters and mixed-stock fisheries may require precautionary approaches to harvest management that may be difficult to implement effectively in open-access fisheries where harvest mortality is driven by angler effort and is not controlled directly.

There is a growing recognition that the angler effort response to fish abundance is the key process dictating whether a recreational fishery will be sustainable (Post et al. 2002, 2008; Johnston et al. 2010; Schueller et al. 2012; Allen et al. 2013). Unlike the typical predator–prey systems that have been used to develop ecological theory, angler abundance is not constrained to reproductive rates dependent on prey density. Thus, the numerical (aggregational in this context) response of anglers is decoupled from any single fish population, and in open-access fisheries the total effort is limited only by the number of anglers who choose to fish a particular stock. The effort response may be very elastic due to a large pool of potential anglers, alternative fishing and recreational opportunities, and the absence of barriers to entering or leaving the fishery. Furthermore, managers influence total effort and catch only indirectly, through regulations that alter the behavior or effectiveness of individual anglers. These characteristics suggest that recreational angler–fish interactions could lead to potentially unstable systems, and documented examples of collapse through overharvest indicate that open-access recreational fisheries are not intrinsically self-regulating (Post et al. 2002; Sullivan 2003; Erisman et al. 2011). Modeling of recreational fisheries also confirms that recruitment overfishing is possible, although whether a fishery is likely to collapse is entirely dependent on the effort response function (Schueller et al. 2012; Allen et al. 2013). Ideally, recreational fishery managers would design a management control system that is self-regulating—a system in which management regulations force fishing effort and harvest to respond to variations in fish abundance in ways that stabilize the population without additional intervention by the manager. However, understanding the nature of the response of angling effort to fish abundance and the factors that determine this response will be necessary to devise management controls that ensure the sustainability of open-access fisheries.

In general, it is expected that angler effort is positively correlated with fish abundance; however, the effort response function could take on several general forms. Effort response functions have previously been modeled as linear (Cox et al. 2003; Post and Parkinson 2012), saturating (Beard et al. 2003; Cowley et al. 2003), or sigmoid (Post et al. 2003; Allen et al. 2013). A growing number of studies has documented the observed angler effort as a function of fish abundance (e.g., Moring 1985; Johnston and Carpenter 1994; Rienman and Maiolie 1995; Post et al. 2008; Schueller et al. 2012); however, high variability or a lack of contrast in data limits the inference of the underlying function shape. The aggregate effort response to variations in fish abundance will depend on the decisions of individual fishers to participate in the fishery, which is a complex function of angler motivations, perceptions, and the heterogeneity in these factors (Johnston et al. 2010). When a large proportion of the potential fishers share common perceptions of the fishery and common motivations to fish, abrupt transitions in effort may occur at fish abundance levels that cross thresholds of angler expectations. The position of such transitions in the effort response relative to expected surplus production for that stock size (determined by a stock–recruit function) will dictate the sustainability of a recreational fishery (Walters and Martell 2004).

Here, we examine the angling effort dynamics and sustainability of a fishery for kokanee Oncorhynchus nerka (lacus-trine Sockeye Salmon) in which fish abundance has fluctuated over 50-fold. The example incorporates three common issues in fisheries management: time-varying stock productivity, mixed
stocks, and open-access fishing effort. We fitted alternate models to the observed fish–angler dynamics on Okanagan Lake, British Columbia, over a 40-year time period to (1) test for potential temporal variation in stock–recruit parameters; (2) describe the functional and numerical responses of anglers to variation in fish abundance; (3) determine the efficiency of standard management reactions to declining fish abundance (successive reductions in daily bag limits); and (4) determine whether the fishery is self-regulating. Such examples of open-access recreational fisheries may be informative in identifying the conditions and management controls that promote self-regulation of harvest rates. The observed responses of the fishery to large variations in fish abundance provide considerable insight into the form of the anglers’ functional and numerical responses to prey abundance and the factors that may shape these responses.

METHODS

Study site.—Okanagan Lake (49°45′20″N, 119°43′45″W) in south-central British Columbia is a large (351 km²), natural lake that formerly supported important fisheries for kokanee and trophy Rainbow Trout Oncorhynchus mykiss, producing about 80,000 angler-days of effort per year. A series of small cities and towns along the 135-km length of the lake provides a large pool of potential anglers, and the lake also attracts significant numbers of visitors from other regions. Okanagan Lake has undergone dramatic changes in productivity, kokanee abundance, and angler use over the last 45 years. The lake experienced localized anthropogenic eutrophication throughout the 1960s, which led to stringent controls that reduced phosphorus inputs from treated sewage effluent by 95% over the period between the early 1970s and the mid-1990s (Jensen and Epp 2002). Mean epilimnetic total phosphorus concentrations in the lake fluctuated in a declining trend from about 7 µg P/L to 5 µg P/L over the same period (see Appendix Table A.1). Omnivorous opossum shrimp Mysis diluviana were introduced into Okanagan Lake by provincial biologists during 1966 in an attempt to improve kokanee forage. Thus, the subsequent build-up of mysid abundance to a large established population over the next decades (Vidmanic 2008) coincided with the period of declining nutrient inputs and likely reduced the standing crop of the zooplankton species that form the kokanee’s diet (Nesler and Bergersen 1991; Andrusak and Sebastian 2000). Okanagan Lake has 18 spawning tributaries for spawners in 2010 and 2011 indicated that over 85% correct assignment could be achieved using this method.

Spawner escapements for the STR and SH stocks have been estimated (almost) continuously from 1978 onward and were estimated sporadically prior to 1978 (Table A.1). Data collected prior to 1978 were not used in our stock–recruit analyses. However, the 1971 datum is noteworthy because a counting fence on the principal spawning stream provided a very accurate enumeration of the high STR escapement. Subsequent STR escapements were determined from peak counts that were obtained from standardized periodic visual surveys throughout the spawning period. The STR escapement is estimated as 1.5 × peak count for each stream based on data from three kokanee spawning channels in southern British Columbia (Andrusak and Sebastian 2000). Okanagan Lake has 18 spawning tributaries that are regularly enumerated; however, on average, 60% of the run is derived from a single large stream (Mission Creek), and 90% of the run is concentrated within six key spawning streams. The SH escapement is estimated as the peak count of SH spawners observed during periodic visual surveys, without any expansion factor (Andrusak and Sebastian 2000), and may be underestimated. Overall, the spawner census methods have been consistent and have thoroughly covered known spawning locations throughout the time series, thus accurately reflecting population dynamics. There has been no method to verify absolute abundance, so these estimates are conservative. Kokanee abundance was expressed as the number of fish per hectare based on the lake surface area corresponding to depths greater than 20 m (i.e., 24,800 ha), which are typically habitable by kokanee.

The Ricker stock–recruit function is generally used for kokanee and Sockeye Salmon (e.g., Martell et al. 2008) and provides more conservative estimates of stock productivity than
Beverton–Holt (Walters and Martell 2004). We estimated the production parameters for each kokanee stock by using the logarithmic form of the Ricker stock–recruit relationship, which was modified to account for the stocking of STR-origin fish during part of the time-series:

\[
\log_e \left( \frac{R_t}{S_t} \right) = a - b \cdot S_t + \delta \cdot F_t + \epsilon_t,
\]

(1)

where \( R_t \) refers to the total recruits (primarily age 3; age range = 2–5) produced from the spawners \( S_t \) in brood year \( t \); \( a \) is stock productivity (in logarithmic units); \( b \) measures the density dependence of the stock productivity index, \( \log_e (R_t/S_t) \); \( F_t \) is the number of stocked fry added from brood year \( t \); \( \delta \) is the effect of fry on the productivity index; and \( \epsilon_t \) is normally distributed process error with a mean of zero and a variance of \( \sigma^2 \). Recruits included both spawners and fish that were killed by the fishery (see below). Fry of STR origin were stocked during 8 years, and STR eyed eggs were stocked during 2 years. We converted eggs to fry-equivalents by using the egg-to-fry survival rate (54%) measured in egg baskets within regional streams (Long 2007). The data used in the analyses are given in Table A.1. Because both of the kokanee stocks share a common rearing environment, we also considered models that shared a common \( b \)-value.

The changes in nutrient loading to the lake and the build-up of the mysid population make it likely that kokanee stock–recruit parameters varied through time (Nesler and Bergerson 1991; Ashley et al. 1997; Schindler et al. 2010). Therefore, we considered two model forms that allowed time variation in the stock–recruit parameters. The first time-varying model modified the process error to include an autocorrelation term:

\[
e_t^* = \theta \cdot e_{t-1:2:3} + \omega_t,
\]

(2)

where \( e \) is the average residual across both stocks averaged for the previous 3 years; \( \theta \) is the autocorrelation coefficient; and \( \omega \) represents the random and independent normally distributed residual errors. Smoothing over 3 years was done to match the 4-year life cycle of kokanee, to allow all three previous cohorts to influence the production dynamics, and to prevent shorter time-scale fluctuations from influencing parameter estimates. We also modeled time variation in kokanee production parameters by using epilimnetic phosphorus concentration as a time-varying environmental covariate. The time-varying stock productivity parameter \( (a_t) \) was modeled as

\[
a_t = a + \rho \cdot I_t,
\]

(3)

where \( I_t \) is an index of epilimnetic phosphorus concentration and \( \rho \) is a measure of the effect of \( I_t \) on stock productivity. The index of phosphorus concentration \( (P_t) \) was defined as the 5-year moving average of the spring (April) epilimnetic phosphorus anomaly relative to the all-year \( (N = 34) \) mean concentration \( (\mu_p) \),

\[
I_t = \frac{1}{t+4} \sum_{t=1}^{t+4} (P_t - \mu_p) / \mu_p.
\]

(4)

We used a 5-year moving average to reduce the effects of observation error and because it encompassed the entire kokanee life cycle from brood year to returning adult. We also considered the analogous case where \( b \) varied temporally with the index of nutrient concentration. We compared model performance by using Akaike’s information criterion corrected for small-sample bias (AIC\(_c\); Burnham and Anderson 2002).

To assess the consequences of the observed harvest regime, the parameters of the Ricker stock–recruit relation were related to two common management benchmarks (Schneute and Kronlund 1996; Martell et al. 2008): the spawner escapement at maximum sustainable yield (\( S_{MSY} \)) and the exploitation rate at MSY (\( u_{MSY} \)),

\[
a = u_{MSY} - \log e(1 - u_{MSY})
\]

(5)

and

\[
S_{MSY} = u_{MSY} / b.
\]

(6)

Effort dynamics and harvest.—Effort and catch data for the recreational fishery have been collected continuously since 1978 by using boat counts from fixed-wing aircraft and simultaneous creel sampling at major boat access points throughout the year; shore-based angling is not effective for targeting kokanee (a pelagic species). Exit creels consistently obtained information on catch, retention, fish size, and duration of fishing, but target species was only recorded after the kokanee decline. Sampling was stratified by month, day type (weekdays, weekends, and holiday weekends), and time period within days (<1000, 1000–1200, 1200–1400, 1400–1600, and >1600 hours). The intensity of sampling has varied through time; a single mid-day flight replaced the within-day counts as information on fishing patterns accumulated, and there were fewer counts and the occasional omission of some monthly strata as available resources varied. Several additional strata were imposed in the analysis of these data: a special event category (derby or free fishing days; or no event) and a weather categorization with five levels from good to poor. A detailed discussion of the effort and harvest estimation is given by Askey (2008). The data were summarized in linear additive models for boat counts and catch per unit effort (CPUE):

\[
\log_e (\text{boat count}) = \beta_0 + \beta_1 \cdot \text{time of day} + \beta_2 \cdot \text{day type} + \beta_3 \cdot \text{month} + \beta_4 \cdot \text{year} + \beta_5 \cdot \text{event} + \beta_6 \cdot \text{weather category} + \omega
\]

(7)
and

\[
\log_e(\text{CPUE}_{\text{year/month}}) = \beta_0 + (\beta_1 \cdot \text{year}) + (\beta_2 \cdot \text{month}) + \omega, \\
\]

(8)

where \(\beta_0\) is the intercept, \(\beta_1 - \beta_6\) are coefficients for associated categorical variables, and \(\omega\) is a normally distributed error term. The AIC\(_c\) was used to evaluate the retention of effect terms within the models. These models were used to predict boat counts and CPUE for periods in which data were missing (unsampled strata); the interpolated data are given in Table A.1. Instantaneous boat counts were converted to daily rod-hours by integrating over all time-of-day strata and multiplying by the average number of rods per boat from the exit creels. Daily catch was estimated from the daily effort estimates (equation 7) and monthly CPUE (equation 8) and was summed over the May–September kokanee fishing season to an annual total catch. A postrelease mortality rate of 30\% was applied to the released portion of the catch based on a range of values for other similar species as presented by Bartholomew and Bohnsack (2005). Kokanee-specific postrelease mortality rates are not available in the literature, but species characteristics (e.g., significant scale loss during handling and soft mouth tissue) suggest that release mortality for kokanee could be higher than that of more commonly studied salmonids.

We summarized the relationship between angler effort and the abundance of age-3 kokanee that were vulnerable to the fishery by fitting a sigmoid response function to our data:

\[
\text{Effort} = E_{\text{min}} + \frac{(E_{\text{max}} - E_{\text{min}})}{[1 + e^{-c(NV-v)}]}, \\
\]

(9)

where \(NV\) is the number of recruits that are fully vulnerable to the fishery; \(c\) and \(d\) are shape parameters, \(E_{\text{min}}\) is minimum effort, and \(E_{\text{max}}\) is asymptotic maximum effort. Inclusion of \(E_{\text{min}}\) is necessary because the Rainbow Trout fishery involves some bycatch of kokanee even when the kokanee fishery is closed. It is necessary to specify the number of fully vulnerable recruits (as opposed to total recruits) because the vulnerability of kokanee to sport fisheries depends strongly on fish size (Rieman and Maiolie 1995). The STR and SH recruits differ in their average sizes, but there is an overlap in size distributions, so the direct allocation of surveyed angler catch to stock is not possible. Unequal vulnerability between stocks should manifest in catch rates that will vary not only by overall abundance but also by relative stock proportions. We allowed for the potential of unequal vulnerability between stocks by estimating the vulnerability \((v)\) of the smaller-bodied SH fish relative to STR fish given observed stock-specific escapements \((S_{\text{STR}}\) and \(S_{\text{SH}}\)) but aggregate catch and catch rates. This was done as a two-step process; first, we partitioned the aggregate catch \((C)\) into the individual stocks for a given value of \(v\),

\[
C_{\text{STR,}t} = u_t \cdot \frac{S_{\text{STR},t}}{(1 - u_t)} \quad \text{and} \quad C_{\text{SH,}t} = u_t \cdot v \cdot \frac{S_{\text{SH},t}}{(1 - u_t v)}, \\
\]

(10)

where \(u_t\) is the annual exploitation rate of fully vulnerable STR fish, and the product \(u_t \cdot v\) is the exploitation rate on SH fish. Second, the time series of \(u_t\) were adjusted as nuisance parameters (minimized sums of squared residuals) so that the observed time series of total catch and predicted total catch \((C_{\text{STR,}t} + C_{\text{SH,}t})\) were equivalent for a given value of \(v\). This process allowed for estimation of the number of fully vulnerable fish that were available to anglers \((NV)\) prior to harvest:

\[
NV_t = \frac{S_{\text{STR},t}}{(1 - u_t)} + \frac{v \cdot S_{\text{SH},t}}{(1 - u_t v)}. \\
\]

(11)

The \(v\)-dependent \(NV\) values could then be compared with the observed catch rates (May–September average) under an assumption of constant catchability \((q)\) in the standard fisheries equation:

\[
\text{CPUE}_t = q \cdot NV_t. \\
\]

(12)

The value of \(v\) that produced the best-fit relationship between \(NV\) and CPUE was used as a most likely value for \(v\). Because this estimate of relative vulnerability is indirect, it is potentially confounded with differences in observation efficiency between STR and SH spawner counting methods as well as any temporal trends in target species and fish sizes. As an alternative hypothesis to the estimated \(v\), we also considered the case of equal vulnerability \((v = 1.0)\).

Exploitation rate is expected to be a function of \(q\) and angler effort \((E)\) as

\[
u_t = 1 - e^{-q \cdot E}. \\
\]

(13)

However, fishing regulations aimed at conserving dwindling stocks (e.g., decreased bag limits) could decrease effort if anglers prefer not to fish for a lower allowable catch or if anglers end their trips more quickly as they catch their limit. On the other hand, if anglers chose to fish a fixed amount of time (after having invested time mobilizing their boats, gear, etc.), then bag limits could decrease the efficiency of a unit of angler effort (i.e., \(q\)) since fewer fish would be retained in a day’s fishing. We fitted this relationship to the harvest and effort data to investigate whether management actions had impacted \(q\).

The effort response to vulnerable kokanee density and the series of relationships for calculating stock-specific catch make it possible to assess the sustainability of the fishery under current regulations by comparing catch to surplus production as a function of stock size. Surplus production (recruits minus spawners) for a given stock size was estimated from the most parsimonious stock–recruit model structure based on equation (1), and catch
TABLE 1. Comparison of alternative model structures based on the Ricker stock–recruit model for Okanagan Lake kokanee. Akaike’s information criterion corrected for small-sample bias (AICc) was used for model selection (ΔAICc = 0 indicates the most parsimonious model, determined separately for the stream-spawning ecotype [STR], the shore-spawning ecotype [SH], and the stock aggregate). Models with ΔAICc less than 2 are highly plausible; models with ΔAICc less than 5 have some support (Richards 2005). Catch and recruitment were estimated using a relative vulnerability of 0.15 for the SH fish ($R^2$ = coefficient of determination; $K$ = number of model parameters; $S_{MSY}$ = spawners per ha at maximum sustainable yield (MSY); $u_{MSY}$ = optimum annual exploitation rate; $b$ = Ricker density dependence parameter; $ρ_a$ = lake productivity impacts on stock productivity; $ρ_b$ = lake productivity impacts on density dependence; $θ_a$ and $θ_b$ = impacts of autocorrelation of residuals on stock productivity and density dependence, respectively; $δ_a$ = stocking adjustment for years during which stocking of STR fry occurred). See Methods for the equation forms of the models.

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<th>$u_{MSY}$</th>
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RESULTS

The reconstructed time series of kokanee spawner escapements, angler effort, catch, and harvest for Okanagan Lake between 1978 and 2011 is given in Table A.1. The general trend in aggregate kokanee abundance in Okanagan Lake is a pronounced (50-fold) decline from 1971 to the late 1990s, followed by a moderate recovery (Figure 1). The key changes to the lake environment over the period of decline were an increasing abundance of mysids after their introduction in 1966 and a decrease in nutrient loading from sewage treatment upgrades starting in 1972 and continuing through the 1990s (Jensen and Epp 2002). The increase in kokanee abundance seen from 2000 onward was driven by the SH stock; the STR stock remains at low abundance. Angler effort and catches were relatively constant throughout the mid-1970s to mid-1980s period and then declined rapidly until the fishery was closed in 1995. The limited re-opening of the fishery after 2005 has not generated significant angler effort or catch.

The observed fluctuations in spawner abundances were large relative to angler catch (Figure 1), suggesting that factors other than the fishery could be forcing the dynamics of the kokanee stocks over the time series. Our model selection analyses supported this qualitative observation, and stock–recruitment models that incorporated time trends in the Ricker parameters were more parsimonious than those with time-invariant parameters (Table 1). The best-performing models for each stock individually and for the stock aggregate were those with temporal autocorrelation in the residuals of either the stock productivity...
parameter $a$ or the density-dependence parameter $b$. The observed time variation in the stock-recruit parameters could not be directly attributed to nutrient concentrations over the time series because models that incorporated the nutrient index as a covariate performed poorly relative to other models. Time variation in the Ricker $a$-parameter was strongly supported for the STR stock because the AIC$_c$ difference ($\Delta$AIC$_c$) exceeded 5.2 for all other models. Time variation in stock-recruit parameters was more ambiguous for the SH stock. Although the best-performing model was that with autocorrelation in $b$, both the time-invariant Ricker model and the model with autocorrelation in $a$ had some support ($\Delta$AIC$_c < 2.5$). Thus, while it seems likely that the productivity of the SH stock was changing through time, the basis of that change was not clear. However, it was clear that the fishery was not driving SH stock abundance, and this was confirmed by the analysis of relative vulnerability to angling.

The abundance of kokanee detected by anglers (through their catch rates) may differ from the total abundance of kokanee in the lake if individual stocks have different vulnerabilities to angling. The observed time series of catch rates on Okanagan Lake suggested that the SH stock had a low vulnerability relative to the STR stock given the corresponding stock-specific escapements and aggregate catch. The maximum likelihood estimate of $\nu$ was 0.15. However, similar fit to the data could be achieved for all $\nu$-values less than 0.3 (Figure 2). The implied sevenfold difference in relative vulnerabilities of the two stocks is consistent with size-vulnerability data for kokanee in Idaho lakes (Rieman and Maiolie 1995), which predict a fivefold difference in vulnerability between SH and STR fish from the difference in average spawner size of the two Okanagan Lake stocks. The stock-specific vulnerability information suggests that the fishery effort and catch are driven by STR abundance.

The variation in angler effort and catch rates seen over the 40-year time series (Figure 3A, B) can be understood by examining the components of the functional and numeric responses to variations in the abundance of vulnerable kokanee (Figure 3C, E). Observed angling effort was relatively constant between 1971 and 1987 but then underwent a sharp increase followed by a rapid and continuous decline until the fishery was closed (Figure 3A). The sharp peak in angler effort (1988) coincided with the capture of the world-record kokanee (at that time) from Okanagan Lake, and publicity around that event may have influenced effort. The Rainbow Trout fishery continued to attract low effort throughout the closure of the kokanee fishery, and there was no notable impact of re-opening the kokanee fishery on effort in recent years. Kokanee CPUE declined continuously over the time series prior to the closure of the kokanee fishery (Figure 3B). The decline in CPUE did not result from density-dependent changes in $q$. CPUE was proportional to the abundance of vulnerable kokanee (i.e., type I functional response; Figure 3C). The strong positive correlation between CPUE and abundance holds regardless of the $\nu$-value used to assess the abundance of vulnerable fish (Figure 2). The $q$ for fully vulnerable kokanee was $0.074 \pm 0.004$ ha swept/rod-hour (mean $\pm$ SD) at a $\nu$-value of 0.15. Unlike catch rates, angling effort was not simply proportional to fish abundance or catch rates. Effort was relatively constant at CPUE values greater than about 0.4 fish/rod-hour, declined rapidly at lower levels of CPUE, and stabilized (at very low effort) for CPUEs below about 0.2 fish/rod-hour (Figure 3D). The response of angling effort to the abundance of vulnerable kokanee prior to the limited re-opening of the fishery was best described by a sigmoid relationship (Figure 3E); again, this was true whether a $\nu$-value of 0.15 or 1.0 was used to determine the abundance of vulnerable fish. However, when $\nu$ was equal to 1.0, the effort response was much more gradual (not shown) than the steep transition shown in Figure 3E. The continued monitoring of effort during the closure of the kokanee fishery provides important data on the residual Rainbow Trout effort when kokanee abundance was minimal (i.e., $E_{min}$). Recent data from the re-opened kokanee fishery fell on or near the trend line; however, these recent data primarily represent the low-vulnerability SH stock. The coefficients of the best-fit ($R^2 = 0.63$) sigmoid relation (equation 9) were as follows: $E_{min}$ was 1.25 rod-hours/ha, $E_{max}$ was 7.27 rod-hours/ha, $c$ was 2.91, and $d$ was 2.92 vulnerable fish/ha.

Reductions in daily bag limits had little impact on angler effort dynamics or harvest. In response to declining kokanee abundance, fisheries managers attempted to lower exploitation rates by decreasing bag limits over the same period. Changes in the bag limit may influence harvest rates either by repelling angler effort (changing the numerical response to a given fish abundance) or by decreasing fishing efficiency (fewer fish per angler trip). However, there was no indication that the numerical response was impacted by bag limits (Figure 3D, E). Furthermore, harvest rates were well predicted ($R^2 = 0.90$) by the standard fisheries model (equation 13) assuming a constant
Angling effort for kokanee in Okanagan Lake was relatively constant between 1971 and 1987 but then underwent a sharp increase followed by a rapid and continuous decline; (B) catch per unit effort (CPUE) declined continuously from 1971 until the kokanee fishery was closed in 1995; (C) CPUE varied linearly with the abundance of vulnerable kokanee ($R^2 = 0.87, P < 0.001$), implying a constant catchability coefficient; (D) angling effort was invariant at CPUEs above about 0.4 fish/rod-hour but declined linearly with decreasing CPUE between 0.4 and 0.2 fish/rod-hour and stabilized at a low value thereafter (these CPUE values correspond to 2 and 1 fish/rod-day at the average trip duration of 4.5 h); and (E) the best-fitting angling effort response to the abundance of vulnerable kokanee was sigmoid and accounted for 63% of the variance. The functional and numerical responses (solid lines) shown in panels C and E do not include the data from the postclosure, limited-opening fishery, but the postclosure data nevertheless fall along the fitted relations. [Figure available in color online.]

Thus, reductions in the daily bag limit from 25 fish to 15, 10, and 5 fish had no clear effect on exploitation rates. It is notable that exploitation rates were lower than expected from equation (13) when effort levels were less than about 6 rod-hours/ha (Figure 4). These data all occurred during the period of low kokanee abundance (and low effort) after 1991 and could be an artifact of the voluntary switching of target species due to a lack of vulnerable fish (i.e., low catch rates) rather than...
FIGURE 4. Annual exploitation rate on vulnerable kokanee varied with total angling effort given the expected relation (equation 12; solid line), accounting for 90% of the variance. The estimated catchability was 0.072 ha swept/rod-hour, but observed exploitation rates were below predicted values at low effort. [Figure available in color online.]

FIGURE 5. Throughout most of the decline in kokanee abundance (except during 1987 and 1988), the angler catch did not exceed the available stream-spawning stock (STR) surplus (recruits – spawner abundance at maximum sustainable yield [SaMSY]) estimated from the time-varying stock productivity model (model 4 in Table 1). The fishery on the STR stock (which was more vulnerable than the shore-spawning stock) did not reduce the stock below SaMSY during the period of decline and low abundance immediately prior to the kokanee fishery’s closure. The fishery was closed from 1995 to 2005, and the catch since the fishery’s re-opening is barely visible on the graph (0.05 fish/ha in 2006; 0.03 fish/ha in 2007).

Incorporating the angler effort response (Figure 3E) with the stock productivity dynamics suggested that, in general, the aggregate kokanee fishery would be self-regulating and sustainable over large fluctuations in the abundance of vulnerable kokanee under conditions of both high and low productivity. The specific predictions for the weak stock (STR) under conditions of relatively high SH stock abundance (3 × STR), low vulnerability of SH fish (ν = 0.15), and three levels of productivity are presented in Figure 6. The intersections of the harvest and production functions are generally stable equilibria to the right of the production dome for low and high productivities. However, catch is expected to exceed the surplus production at MSY over a narrow range of productivity (i.e., where 0.6 < e* < 0.9 for the model 4 parameterization of Table 1). Thus, the rapid transition of the effort response has the potential to lead to a slightly suboptimal (overfished) equilibrium at certain specific levels of productivity and relative stock abundance. The series of conditions needed for the weak STR stock to be overharvested are (1) the SH stock is at high relative abundance (≥3 × STR abundance), (2) relative vulnerability of SH fish is low (ν ≤ 0.15), and (3) aggregate stock productivity is about 2.5 times the all-time average (i.e., RSY [the number of recruits produced at the MSY spawner abundance] is in the range of the rapid effort response). However, the observed time series tends to show an inverse relationship between the relative abundance of SH kokanee and overall productivity, so the narrow

representing an impact of bag restrictions. Unfortunately, target species was not recorded throughout the time series, so this hypothesis could not be tested directly.

In the Okanagan Lake mixed-stock kokanee fishery, the STR stock is clearly the “weak” stock that is more susceptible to overharvest given a constant harvest rate across stocks. All of the recruitment models indicated that density-dependent effects were greater for the STR stock than for the SH stock and that sustainable harvest rates were lower for the STR stock (Table 1). Furthermore, the vulnerability analyses outlined above indicated that harvest was not constant across stocks and that STR fish comprised the bulk of the sport fishery harvest. Thus, vulnerability analysis for the fishery should focus on STR fish, and the optimal model structure (model 4 in Table 1) suggested that uMSY and SMSY varied considerably through time. The harvest rate on the STR stock (when ν = 0.15) averaged 47% (range = 32–69%) during 1978–1990 but was only 13–18% during the period of sharp decline in kokanee abundance beginning in 1990. The observed harvest rates for the STR stock exceeded the equilibrium-predicted uMSY only throughout the late period of rapid decline immediately prior to the fishery closure in 1995. However, the kokanee stocks were not overharvested during the decline because the continual downgrading of production potential in that period meant that the observed escapement always exceeded the SaMSY (Figure 5). Thus, the temporal trends in the Ricker parameters suggest that the lake’s productive capacity was rapidly downgrading and that anglers had no additional detrimental impact (i.e., the fished cohorts still produced progeny over lake capacity).
conditions required for overfishing have not been observed to date.

DISCUSSION
The biological sustainability of a recreational fishery is influenced by the productive capacity of the fish stock (life history characteristics and rearing environment), the functional and numerical responses of anglers to variations in fishing quality, and management regulations that may modify these response functions. The interaction of these factors within the Okanagan Lake kokanee fishery resulted in a fishery that was biologically sustainable over a wide variation in fish abundance, although the social and economic benefits derived from the fishery declined considerably as angling effort responded to the long-term decrease in fish productivity.

The large changes in abundance of the kokanee stock aggregate over the last 40 years resulted from time variation in productivity of the two ecotypes rather than from overharvest. The mechanisms causing the long-term decline were not identifiable in the stock–recruit analysis and may differ for the two stocks. It is expected that long-term changes in phosphorus loading will influence kokanee production, as seen in whole-lake nutrient manipulations in nearby Kootenay Lake (Ashley et al. 1997). However, models based on a time-varying index of epilimnial phosphorus concentration performed poorly in comparison with nonmechanistic (but time-varying) models. There are several possible reasons for this poor performance, despite the underlying plausibility of the mechanism. First, measured epilimnial phosphorus concentrations may not correlate well with bioavailability; in the Kootenay Lake experiments, the measured phosphorus concentrations were poorly correlated with the known loadings, presumably because of rapid biological uptake (Schindler et al. 2010). Second, the food web relationships that mediate the transfer of nutrients to kokanee are complex and have varied through time as the abundance of M. diluviana has varied (Schindler et al. 2012). Third, factors other than nutrients (e.g., temperature regimes or disease) could drive recruitment variation among years by altering growth or survival. The alternative approach of modeling autocorrelation in residuals from the stock–recruit relation provided the great advantage of fitting data series where multiple unknown and uncontrollable factors may limit production. In the present situation, the nonmechanistic autocorrelation models were much better descriptors of the time changes in production than were the mechanistic models, as is often the case (Walters and Martell 2004).

The best-performing stock–recruit model for the STR ecotype indicated that stock productivity (recruits per spawner at very low spawner abundance) had declined through time. None of the other models was a plausible alternative for this stock. In contrast, the most likely model for the SH ecotype indicated time variation in the $b$-parameter, but a model with time-varying stock productivity and a time-invariant model also had some support. Despite the common rearing environment for the STR and SH kokanee stocks, the spatial separation of their spawning sites may have resulted in divergent recruitment dynamics if bottlenecks to production occurred primarily at the egg-to-fry stage. In addition to environmental variation that is common to both stocks, the stock-specific spawning habitats would be differentially impacted by environmental factors, such as tributary inflow regimes or lake level fluctuations during egg incubation; descriptors of the time variation in production might therefore vary between the two stocks. In any event, the time-varying stock productivity experienced by the more vulnerable STR stock resulted in large decreases in sustainable exploitation rates for that stock between 1970 and 1990, which resulted in harvest rates exceeding equilibrium $u_{MSY}$ values through the period of decline. However, since stock productivity was in continual decline, recruitment was overshooting the current $S_{MSY}$ during that period and recruitment overfishing did not occur during the decline (although there was a brief spike in effort and some overharvest in 1987–1988 prior to the decline). If stock productivity had rebounded (thereby increasing $S_{MSY}$) at some point in the early 1990s, then recruitment overfishing could have occurred and delayed recovery of the STR stock, which primarily supported the sport fishery. The much-lower vulnerability of the smaller-sized but more abundant SH stock resulted in the dynamics of that stock being much less affected by harvest. It also meant that CPUE, which controlled angling effort below a threshold of about 2 fish/rod-day, was partially decoupled from the abundance and productivity of the stock aggregate, which remained capable of sustaining the fishery even at very low levels of stock productivity (Figure 6). During periods of low stock productivity and low abundance, most of the surplus production provided by the SH stock is not perceived by anglers, who start leaving the fishery when their CPUE falls below expectations for fish of that size. In effect, the effort dynamics of the fishery are primarily regulated only by the abundance of the vulnerable STR fish.

![FIGURE 6. Surplus production for the kokanee stock aggregate exceeds the angler harvest over most expected densities of vulnerable kokanee under conditions of low (gray line), medium (dashed gray line), and high production (dashed black line) in Okanagan Lake. The intersections of the catch (solid black line) and surplus production functions are stable equilibria, so overharvest at fish densities above these points will not cause continuous declines in abundance.](image-url)
The elasticity of recreational angling effort to variation in the abundance of vulnerable fish is an essential component of fishery sustainability. Previous work on British Columbia Rainbow Trout fisheries indicates that angler effort is highly elastic to fish abundance at a given site because anglers can easily move between alternate angling opportunities (Cox et al. 2003; Parkinson 2004; Post et al. 2008). In the Rainbow Trout fishery, it was found that anglers place a premium on fish size when trading off fish size and catch rates in their perceptions of angling quality (Parkinson et al. 2004; Askey et al. 2013). Thus, fisheries that target small fish must generate high catch rates to meet anglers’ expectations from regional norms (i.e., to attract effort away from alternate sites). Kokanee are small fish, and the size at maturity in natural kokanee populations (e.g., McGurk 2000) is often near the lower limits of acceptability to anglers (about 20 cm FL). If fish abundance and catch rates decrease, anglers may quickly lose interest in angling for small-bodied fish that provide low consumptive value unless multiple individuals are harvested.

The decision of individual anglers to participate in the fishery based on expected and realized catch rates appeared to play a large role in Okanagan Lake effort trends. The regional norm for retained CPUE of 25-cm fish in Rainbow Trout lakes within the southern interior of British Columbia is approximately 0.5 fish/rod-hour (Parkinson et al. 2004; Askey et al. 2013). Rainbow Trout lakes represent the highest use fishery in the interior of British Columbia and provide the most likely alternative fishery for kokanee anglers. The observed abrupt decrease in effort coincided with the decline in average retained CPUE below the size-specific regional mean for Rainbow Trout. These data suggest that for the majority of anglers, decreased fish abundance led to catch rates that were well below the anglers’ expectations based on the regional norm for kokanee-sized fish; this caused many of the anglers either to leave the Okanagan Lake fishery completely or to switch their target species to Rainbow Trout lakes represent the highest use fishery in the interior of British Columbia and provide the most likely alternative fishery for kokanee anglers.

The linkage between angler effort and catch rates (realized versus expected) as highlighted above is a consequence of anglers’ motivations and satisfaction with the fishing experience. Thus, the observed sigmoidal effort response function may be consistent with human dimensions research (Arlinghaus 2006) segregating the factors that motivate fishing (predominantly non-catch-related factors) and the factors that lead to satisfaction with the fishing experience (strongly catch-related factors). The observed $E_{\text{min}}$ over a range of low kokanee abundance values is at least partially representative of anglers who are motivated by non-catch-related factors (e.g., relaxation and a desire for time in the outdoors). However, as satisfaction with the experience increases (catch rates meet or exceed expectations), anglers are expected to make decisions to allocate more personal time into the fishery as well as to share information on their success with other anglers, leading to the transition in the effort response. The observed upper limit to angler effort ($E_{\text{max}}$) is consistent with the view that the marginal utility to anglers for catch rates decreases above a certain point (e.g., Johnston et al. 2010). However, there are several alternative mechanisms that may produce the observed effort asymptote. Rieman and Maiolie (1995) suggested that effort decreased at high kokanee densities due to density-dependent decreases in fish size. Although our analysis did indicate the importance of fish size for catch rates and effort, the variation in size was caused by stock composition (i.e., the relative abundances of STR fish versus SH fish). Since we accounted for this variation in our metric of vulnerable kokanee (i.e., $NV$ is correlated with more STR fish and a higher average size), it does not explain the saturating form of the effort response. Full utilization of the available pool of angler effort (e.g., a finite pool of anglers) could also produce an asymptote. This seems unlikely, both because effort peaked in the late 1980s at levels well above the asymptote and because the fishery could attract effort from a very large pool of potential anglers from major population centers with easy access to the lake as well as from the large population scattered in communities along the lake.

The shape of the observed effort function has important implications for recreational fisheries management. The sharp transition in angler effort suggests that fisheries managers can drastically alter the benefits of the Okanagan Lake kokanee fishery if management actions lead to changes in vulnerable fish abundance between 3 and 5 fish/ha or changes in catch rates between 0.2 and 0.5 fish/rod-hour. Over these ranges of abundance and catch rate, there is almost an order of magnitude change in angler effort. Conversely, action to enhance the fishery above an abundance of 5 fish/ha or above a CPUE of 0.5 fish/rod-hour would have no incremental benefit to angler effort (and associated societal benefits). Similar results were reported by Rieman and Maiolie (1995), with a steep transition in effort response occurring at low kokanee densities. Therefore, although fisheries for dispersed and small-bodied species like kokanee may not pose high sustainability risks, management interventions may greatly alter associated fishery values. In the specific case of Okanagan Lake, variations in the abundance of vulnerable kokanee can cause effort to vary between 31,000 and 181,000 angler-hours/year (Figure 3), which is near the full range of effort levels observed in all of the lake years presented by Rieman and Maiolie (1995). Although past attempts to manage harvest rates by use of bag limits were ineffective on Okanagan Lake, targeted management actions to increase the abundance of vulnerable kokanee from their current low value by increasing the relative proportion of STR fish in Okanagan Lake (e.g., STR stocking or habitat enhancement) could have substantial impacts on the fishery.

Past management regulations had little impact on this fishery. Management regulations often attempt to constrain harvest mortality to sustainable levels or to distribute catch more equitably by imposing daily bag limits, reducing gear efficiency, or
limiting effort via time or area closures. The bag limit was reduced successively from 25 fish/d to 15, 10, and 5 fish/d as kokanee abundance declined, but these changes in the bag limit had no impact on angling effort (Figure 3D), $u$ (Figure 4), or $q$ (Figure 3C) because the bag limit was always far higher than average catch rates in the fishery and because the declines in abundance were primarily driven by changes in productivity rather than by overharvest. A change in the bag limit from 2 fish/d to 5 fish/d in the re-opened fishery similarly had no impact on effort (Figure 3A). None of the regulatory changes altered the relative vulnerability of the two stocks, so harvest principally affected the more vulnerable STR stock. Although managers recognized that the faster growth and larger age-3 size of the STR stock resulted in its earlier recruitment, longer exposure, and greater vulnerability to the fishery, there are few practical mechanisms short of closure that could direct harvest away from the more vulnerable stock in this mixed-stock fishery.

Examination of the Okanagan Lake kokanee fishery provides several insights concerning general features of open-access fisheries that influence self-regulation. First, stock-recruit relationships—and thus the productivities of fished stocks—are not time invariant. Time trends in productivity, such as the rather extreme example provided here, are a common feature of fisheries (Walters and Parma 1996; Peterman et al. 2003). How best to detect and manage for directional trends in productivity of recreational fisheries has rarely been considered except in retrospective analyses of fishery collapses, such as the Okanagan Lake kokanee fishery. Walters and Martell (2004) suggested that effort towards developing management strategies that are robust to regime shifts is a more prudent approach than attempting to predict regime shifts. Management approaches that are relevant for recreational fisheries with open-access effort and with temporally varying productivity have yet to be examined. Second, the data suggest that anglers use regional norms for size-specific CPUE to assess whether to allocate effort to a fishery. Knowledge of these norms would likely aid managers in assessing the status of individual fisheries. More generally, the management of open-access fisheries would benefit from a better understanding of how angler expectations (e.g., CPUE) compare with sustainability benchmarks (e.g., $S_{MST}$). If anglers are willing to fish to (size-specific) catch rates that would imply a fish abundance below a sustainable level (i.e., a regional norm in which the acceptable CPUE is less than $S_{MST}$), then management interventions must occur. Conversely, if angler expectations are above conservation thresholds for fish abundance, as in Okanagan Lake, then the population is inherently self-regulating. Sorting out this interaction between angler perceptions and fish productive capacity will require a landscape-level approach to understanding anglers (Lester et al. 2003; Post and Parkinson 2012) and the consideration of fish life history (Johnston et al., in press). Third, anglers’ responses to perceived fishing quality seem to be asymmetric: effort allocation is (1) sensitive to realized size-specific CPUE that is below expectations but (2) insensitive to fishing quality that is moderately above expectations. Thus, management activities that maintain a baseline fishing quality may be more effective than those providing exceptional fishing quality. Fourth, heterogeneity in the effectiveness of individual anglers is narrowed at low stock abundance and may lead to rapid changes in effort as perceived fishing quality crosses a threshold value that becomes common to a larger proportion of the anglers. More generally, the segmentation of anglers into distinct groups with different skill levels and motivations may influence the effort dynamics of a fishery, as has been argued by others (Johnston et al. 2010). Understanding the composition of the anglers and their likely responses to variation in metrics of fishing quality may allow managers to better respond to variations in fish production. Collective results for the Okanagan Lake kokanee fishery indicate that some recreational fisheries may be resilient to recruitment overfishing, but further understanding of approaches for maximizing the social components that are absent from commercial fisheries (Johnston et al. 2010) is required.

**ACKNOWLEDGMENTS**

We thank the many field crews who collected the data for this study over the last 40 years, especially Jason Webster, who has provided consistency for the most recent 15 years of the time series. We are grateful to Chris Bull, Chris Houston, Bruce Shepherd, Steve Matthews, and Andrew Wilson for maintaining the data collection as a priority project throughout the period. We also thank the British Columbia Fisheries Branch and the Habitat Conservation Trust Fund for their long-term financial support of the data collection.

**REFERENCES**


TABLE A.1. Spawner escapement and catch data for the Okanagan Lake kokanee fishery, 1971–2011. Catch is allocated between stream-spawning (STR) and shore-spawning (SH) stocks by using a relative vulnerability of 0.15 for SH fish. Values that were interpolated when effort data were not available are shown in bold italics. The kokanee fishery was closed between 1995 and 2005 (gray-shaded area), but the Rainbow Trout fishery maintained low levels of angler effort throughout the closure (TP = epilimnetic [0–10-m] total phosphorus concentration; CPUE = catch per unit effort; HPUE = harvest per unit effort).

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Kokanee fishery closed
Predicting Paddlefish Roe Yields Using an Extension of the Beverton-Holt Equilibrium Yield-per-Recruit Model

Michael E. Colvin a, Phillip W. Bettoli b & George D. Scholten c

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.820242
ARTICLE

Predicting Paddlefish Roe Yields Using an Extension of the Beverton–Holt Equilibrium Yield-per-Recruit Model

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Abstract

Equilibrium yield models predict the total biomass removed from an exploited stock; however, traditional yield models must be modified to simulate roe yields because a linear relationship between age (or length) and mature ovary weight does not typically exist. We extended the traditional Beverton–Holt equilibrium yield model to predict roe yields of Paddlefish *Polyodon spathula* in Kentucky Lake, Tennessee–Kentucky, as a function of varying conditional fishing mortality rates (10–70%), conditional natural mortality rates (cm; 9% and 18%), and four minimum size limits ranging from 864 to 1,016 mm eye-to-fork length. These results were then compared to a biomass-based yield assessment. Analysis of roe yields indicated the potential for growth overfishing at lower exploitation rates and smaller minimum length limits than were suggested by the biomass-based assessment. Patterns of biomass and roe yields in relation to exploitation rates were similar regardless of the simulated value of cm, thus indicating that the results were insensitive to changes in cm. Our results also suggested that higher minimum length limits would increase roe yield and reduce the potential for growth overfishing and recruitment overfishing at the simulated cm values. Biomass-based equilibrium yield assessments are commonly used to assess the effects of harvest on other caviar-based fisheries; however, our analysis demonstrates that such assessments likely underestimate the probability and severity of growth overfishing when roe is targeted. Therefore, equilibrium roe yield-per-recruit models should also be considered to guide the management process for caviar-producing fish species.

Biologists have modeled fishery yields for decades, and the advent of software such as the Fisheries Analysis and Modeling Simulator (FAMS, previously known as FAST; Slipke and Maceina 2010) has encouraged the use of yield models in freshwater fisheries. Data requirements for yield models (e.g., the Beverton–Holt equilibrium yield model; Beverton and Holt 1957) are straightforward (although perhaps difficult to obtain) and include estimates of fishing mortality and natural mortality, length-at-age data, and weight-at-length data. Predicted yield is typically expressed in terms of biomass, or the weight of fish that are removed from an exploited stock.

Traditional yield models are not applicable when a fishery targets roe for caviar because of interactions among ovary weight, sexual maturity, age, and length and because the harvest of sexually immature fish does not contribute to roe yields. For example, the relationship between eye-to-fork length (EFL) and ovary weight for Paddlefish *Polyodon spathula* differs markedly between mature and immature females (e.g., Scholten...
and Bettoli 2005). Specifically, a Paddlefish of any length or maturity status has a body weight; however, only mature female Paddlefish have ovarian weights that contribute to roe harvests. Additionally, ovary weights of mature Paddlefish will vary by more than an order of magnitude among larger individuals (Jennings 2000), whereas the total body weight of similar-length mature fish is much less variable over a wide size range. Variation in ovary weight at a specified length or age is due in part to the nonlinear (e.g., sigmoidal) pattern of population sexual maturation, resulting in only the largest age-classes and size-classes reaching 100% maturity. Therefore, roe yield of an exploited population is the result of interactions among ovary weight, sexual maturity, and size, which cannot be described as a simple linear function of biomass yield.

In Tennessee and elsewhere, interest in modeling the roe yields of Paddlefish is high for several reasons. First, commercial fisheries for Paddlefish are usually managed to maximize roe yields rather than flesh yields (Bettoli et al. 2007; Quinn 2009; Scholten 2009). Second, Paddlefish are enduring increased harvest pressure with the decline of Eurasian sturgeon stocks (e.g., Beluga Huso huso), and there are widespread concerns that Paddlefish stocks are being overfished in some locales (Quinn 2009). Scholten and Bettoli (2005) modeled Paddlefish yield per recruit in Kentucky Lake, Tennessee–Kentucky, and concluded that this stock was experiencing modest growth overfishing (i.e., fish were being harvested at an average size less than the size that maximizes yield) in terms of biomass. The implication of this result was that the stock also likely suffered from growth overfishing in terms of roe yield, but the traditional Beverton–Holt yield-per-recruit model could not be used to directly assess the degree to which roe yields might be improved if recruitment to the fishery was delayed by raising the minimum size limits. Another reason for investigating whether roe yields could be increased by reducing fishing mortality is the high roe prices received by commercial fishers in Tennessee during recent years (i.e., US$165–220 per kilogram wholesale between 2008 and 2011; E. Ganus, Tennessee Wildlife Resources Agency, personal communication). The Paddlefish caviar trade represents an important source of revenue in small river communities of rural Tennessee, and maximizing economic value is important to politicians and to the fishing industry. Finally, management of Paddlefish roe fisheries in Tennessee has become a contentious issue in recent years. For instance, a bill was introduced in 2011 by the Tennessee legislature to set seasons and length limits on Paddlefish, and a lawsuit claiming mismanagement of Paddlefish in Tennessee was filed by a fishing industry trade group against the Tennessee Wildlife Resources Commission.

For species that are commercially exploited for caviar, the modeling of yields based on total biomass is a common practice (e.g., Rieman and Beamesderfer 1990; Quist et al. 2002; Colombo et al. 2007); however, we are unaware of any previous attempt to simulate the effects of fishing mortality and harvest regulations on roe yields. In this study, we modified the traditional Beverton–Holt equilibrium yield model to predict biomass yield accounting for sex-dependent growth and roe yield under varying exploitation rates, natural mortality rates, and minimum size limits for the Paddlefish fishery in Kentucky Lake, which was previously analyzed by Scholten and Bettoli (2005). We then used the model to compare equilibrium biomass and roe yields and to assess the potential for growth overfishing in terms of roe yields. Finally, we used the roe yield model to calculate spawning potential ratios (SPRs) and to assess the potential for recruitment overfishing in the Kentucky Lake Paddlefish fishery.

METHODS

Study Area

Kentucky Lake is a mainstream impoundment of the Tennessee River, located in western Tennessee and Kentucky (37.01° N, 88.27° W). Impounded in 1944 by Kentucky Dam at Tennessee River kilometer 35, this 296-km-long reservoir is a eutrophic impoundment that covers 64,870 ha at full pool. Water discharged from Pickwick Dam (the upstream boundary of the lake at Tennessee River kilometer 331) flows north through Kentucky Lake. Tennessee was one of six states that allowed the commercial harvest of Paddlefish for their roe beginning in 2006 (Bettoli et al. 2009). Those states currently remain open to commercial harvest, and an additional fishery has opened in Mississippi. The current minimum length limit for Paddlefish harvested in the Kentucky Lake system is 914 mm EFL. Kentucky Lake has traditionally provided most of the Tennessee Paddlefish roe destined for domestic and international markets, although in recent years export permits have been denied by the U.S. Fish and Wildlife Service (USFWS) Office of Scientific Authority over concerns that the stock was being overfished (M. Maltese, USFWS, personal communication).

Data Collection

A complete description of field collections and sample processing was provided by Scholten and Bettoli (2005). In summary, most Paddlefish were collected between September 2003 and May 2004 by using horizontal experimental gill nets. The mesh size in the six panels of each net ranged from 89- to 203-mm bar measure. Additional data from Paddlefish captured by commercial fishers were obtained from 15 November 2003 to 23 April 2004. The EFL (mm), weight (nearest 0.25 kg), sex, and maturity status were recorded for each Paddlefish. Sex and maturity were determined by examining the gonads. Females with partially developed or immature ova (usually white or mottled) were categorized as immature. Females were classified as mature if their ovaries contained large (2–3-mm diameter), dark eggs (Bronte and Johnson 1985). Ovaries were excised from all females and were weighed to the nearest 0.1 g. Dentary bones of at least five Paddlefish per 25-mm EFL group were removed for use in age estimation. Ages were then assigned to unaged fish by using an age–length key. Fish collected during these efforts were used to parameterize the yield models detailed below.
Yield Model Construction

Flesh and roe yields were calculated by extending the basic yield model, where yield (either biomass or roe) is calculated by multiplying the number and average weight of fish material captured (Everhart and Youngs 1953; Beverton and Holt 1957; Ricker 1975; Die et al. 1988). Total yield can be calculated by integrating the sum of the sex-specific product of the number of fish captured and mean weight from the age (t) at which a fish of sex i is recruited to the fishery to the maximum fish age. Formally, total yield (accounting for sex-specific growth) is calculated by evaluating the integral

\[
\text{Yield} = \sum_{i=1}^{2} \int_{t_{i}}^{t_{i}} \left[ C(t)W(t) \right] dt,
\]

where \( t_{i} \) is maximum fish age, \( C(t) \) is a function predicting the age-specific number of fish of sex \( i \) that were caught, \( W(t) \) is an age-dependent function predicting the mean weight of harvested material (i.e., biomass or roe) for fish of sex \( i \), and \( dt \) is the change in age. The yield equation requires two sex-specific functions relating the number (i.e., catch at age) and weight (i.e., weight at age) of fish at age \( t \) (Die et al. 1988).

Catch at age.—Our model assumes that commercial harvest of Paddlefish does not discriminate between maturity stage or sex. The only reliable method for determining sex and sexual maturity is visual inspection of sex and sexual maturity status (Ricker 1975). Therefore, length (EFL) was converted to age for integration. This was accomplished by assuming that sex-specific von Bertalanffy growth functions (VBGFs) adequately describe fish length (EFL) as a function of age and sex:

\[
\text{EFL}(t) = \text{EFL}_{\infty,i} \left[ 1 - e^{-k_i(t-t_0)} \right].
\]

Specifically, the above VBGF equation predicts length based on age, where EFL is in millimeters, \( \text{EFL}_{\infty,i} \) is the asymptotic EFL, \( k_i \) is the Brody growth coefficient, \( t \) is age, \( t_0 \) is the theoretical age at a length of zero, and \( i \) indexes sex (Ricker 1975).

Weight-at-Age Functions

Fish weight at age.—Sex-specific parameter estimates for the EFL–weight relationship were estimated using field data. Fish weight at length was estimated by fitting the standard equation that describes the allometric scaling of weight with length (i.e., \( W = aL^b \), where \( L = \text{length} \)) and then allowing the \( a \) and \( b \)-parameters to vary for males and females. Fish weight at EFL was then calculated as

\[
W_{\text{fish}}(t_i) = a_i \cdot \text{EFL}(t_i)^b,
\]

where \( a_i \) and \( b_i \) are sex-specific parameters of the EFL–weight relationship, and \( \text{EFL}(t_i) \) is the sex-specific VBGF.

Roe weight-at-age.—Calculation of roe weight at age required a roe weight-at-age function (for females only) that accounted for age-dependent sexual maturity and ovary weight as

\[
W_{\text{roe}}(t_i) = \text{mat}(t_i) \cdot \text{ow}(t_i),
\]

where \( \text{mat}(t) \) and \( \text{ow}(t) \) are age-dependent functions predicting the mature fraction and the ovary weight, respectively, of female Paddlefish. Paddlefish females (n = 357) collected from Kentucky Lake were used to develop the predictive relationships for maturity and ovary weight (detailed below).

Maturity at eye-to-fork length.—Maturity was associated with EFL, and a small fraction of female Paddlefish became sexually mature at age 8 (Table 1; Figure 1). A general linear model assuming a binomial distribution was used to predict maturity as a function of EFL (Gelman and Hill 2007). Specifically, the general linear model predicted the proportion of sexually mature females as a function of EFL:

\[
\text{mat}(\text{EFL}) = \left[ e^{(\beta_0+\beta_1 \cdot \text{EFL})} / [1 + e^{(\beta_0+\beta_1 \cdot \text{EFL})}] \right].
\]

A chi-square test was used to assess model goodness of fit, where failure to reject the null hypothesis (i.e., \( P > 0.05 \)) indicated an adequate fit to the data.

Ovary weight at eye-to-fork length.—Ovary weight was modeled as a function of sexual maturity status and EFL. Specifically, mean ovary weight at EFL accounting for maturity status was predicted by fitting the equation:

\[
\log_e(\text{OW}) = \beta_0 + \beta_1 \cdot \text{Mature} + \beta_2 \cdot \log_e(\text{EFL}) + \beta_3 \cdot [\log_e(\text{EFL}) \cdot \text{Mature}],
\]

where OW is ovary weight, \( \beta_0 \) is the intercept, \( \beta_1 \) is the effect of whether a female is mature, \( \beta_2 \) accounts for the effect of EFL on ovary weight, and \( \beta_3 \) accounts for the interaction of whether
TABLE 1. Maturity (%), mean eye-to-fork length (EFL; mm), mean body weight (kg), and mature ovary weight (kg) for each age-class of female Paddlefish collected from Kentucky Lake, Kentucky–Tennessee, by use of experimental and commercial gill nets, 2003–2004.

<table>
<thead>
<tr>
<th>Age</th>
<th>Number</th>
<th>Percent mature</th>
<th>EFL Mean</th>
<th>EFL SE</th>
<th>Weight Mean</th>
<th>Weight SE</th>
<th>Mature ovary weight Mean</th>
<th>Mature ovary weight SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>3</td>
<td>0</td>
<td>510</td>
<td>7.5</td>
<td>1.50</td>
<td>0.06</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>0</td>
<td>552</td>
<td>17.4</td>
<td>2.27</td>
<td>0.11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>0</td>
<td>661</td>
<td>11.9</td>
<td>4.76</td>
<td>0.39</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>16</td>
<td>0</td>
<td>731</td>
<td>14.9</td>
<td>6.12</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>58</td>
<td>0</td>
<td>821</td>
<td>6.4</td>
<td>9.17</td>
<td>0.27</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>65</td>
<td>0</td>
<td>862</td>
<td>7.8</td>
<td>10.99</td>
<td>0.38</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>99</td>
<td>16</td>
<td>932</td>
<td>6.2</td>
<td>14.27</td>
<td>0.33</td>
<td>2.26</td>
<td>0.07</td>
</tr>
<tr>
<td>9</td>
<td>49</td>
<td>51</td>
<td>969</td>
<td>7.1</td>
<td>15.67</td>
<td>0.48</td>
<td>2.09</td>
<td>0.04</td>
</tr>
<tr>
<td>10</td>
<td>38</td>
<td>92</td>
<td>1,006</td>
<td>8.6</td>
<td>17.55</td>
<td>0.65</td>
<td>2.34</td>
<td>0.02</td>
</tr>
<tr>
<td>11</td>
<td>8</td>
<td>88</td>
<td>1,045</td>
<td>21.1</td>
<td>20.04</td>
<td>1.58</td>
<td>2.17</td>
<td>0.24</td>
</tr>
<tr>
<td>12</td>
<td>1</td>
<td>100</td>
<td>1,020</td>
<td></td>
<td></td>
<td></td>
<td>16.50</td>
<td>2.79</td>
</tr>
</tbody>
</table>

A female is mature on the estimate of $\beta_2$. The model used to estimate ovary weight for sexually mature fish was simplified to account for interactions and was used in subsequent yield analysis.

**Full equilibrium yield models.—**Fish and roe yields were calculated by substituting catch-at-age and roe weight-at-age functions into the base yield equation (equation 1) as:

$$Y_{\text{fish}} = \sum_{i=1}^{2} \int_{t_{r,i}}^{t_{\lambda,i}} \left( F \cdot R_i \cdot e^{-(M-F)(t-t_{r,i})} \right) \cdot a_i \left[ EFL_{\infty,i} \left[ 1 - e^{-(M-F)(t-t_{r,i})} \right] \right] \cdot dt,$$

and

$$Y_{\text{roe}} = \int_{t_{r,1}}^{t_{\lambda,1}} \left( F \cdot R_1 \cdot e^{-(M-F)(t-t_{r,1})} \right) \cdot \frac{e^{[\beta_0 F + \beta_1 EFL_{\infty,1} [1 - e^{-(M-F)(t-t_{r,1})}]]} \cdot 1 + e^{[\beta_0 F + \beta_1 EFL_{\infty,1} [1 - e^{-(M-F)(t-t_{r,1})}]]}}{\left[ 1 + e^{[\beta_0 F + \beta_1 EFL_{\infty,1} [1 - e^{-(M-F)(t-t_{r,1})}]]} \right]} \cdot dt,$$

where the parameters and variables are as previously described.

Full models incorporating the parameter estimates and variables used in subsequent equilibrium yield analysis are presented in Tables 2 and 3.

**Simulation of Equilibrium Yield**

Four minimum EFL limits were used to simulate flesh and roe yields: 864 mm (historic [pre-2005] limit), 914 mm (current limit), 965 mm, and 1,014 mm EFL. Minimum length limits were converted to age by solving the VBGF, and the ages were used as values of $t_{r,i}$ for sex $i$ given the sex-specific VBGF. A maximum age ($t_{\lambda}$ of 21 years was used in the previous analysis of Kentucky Lake Paddlefish (Scholten and Bettoli 2005). To maintain consistency with previous analyses of North American
TABLE 2. Parameterized versions of the in-text equations required to simulate biomass and roe yield for the Paddlefish population in Kentucky Lake. See Table 3 for definitions of parameters and variables.

<table>
<thead>
<tr>
<th>Equation number</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females (i = 1)</strong></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>EFL(t) = 1.279[1 − e^{−0.14(t + 1.29)}]</td>
</tr>
<tr>
<td>4</td>
<td>W_{fish}(t) = e^{−20.1 \cdot EFL(t)0.327}</td>
</tr>
<tr>
<td>6</td>
<td>\text{mat}(EFL) = \frac{e^{(e^{−27.78 + 0.028 \cdot EFL}) \cdot [1 + e^{(−27.78 + 0.028 \cdot EFL)}]}}{1}</td>
</tr>
<tr>
<td>7</td>
<td>\log_e(OW) = −50.7 + [37.2 \cdot \text{Mature}] + [3.0529 \cdot \log_e(EFL)] + {−5.1 \cdot \log_e(EFL) \cdot \text{Mature}}</td>
</tr>
<tr>
<td><strong>Males (i = 2)</strong></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>EFL(t) = 898[1 − e^{−0.38(t + 0.33)}]</td>
</tr>
<tr>
<td>4</td>
<td>W_{fish}(t) = e^{−14.5 \cdot EFL(t)2.472}</td>
</tr>
</tbody>
</table>

Equilibrium yield equations

\begin{align*}
Y_{fish} & = \int_{t_{r,1}}^{t_{M,1}} \left\{ F_{t,1} \cdot R_1 \cdot e^{−(M \cdot 8.3)} \cdot e^{−(M + F_{t,1}) \cdot (−8.3)} \cdot e^{−20.1 \cdot 1.279[1 − e^{−0.14(t + 1.29)}]3.327} \cdot dt \\
& + \int_{t_{r,2}}^{t_{M,2}} \left\{ F_{t,2} \cdot R_2 \cdot e^{−(M \cdot 6.7)} \cdot e^{−(M + F_{t,2}) \cdot (−6.7)} \cdot e^{−14.5 \cdot 898[1 − e^{−0.38(t + 0.33)}]2.472} \cdot dt \right\}
\end{align*}

\begin{align*}
Y_{roe} & = \int_{t_{r,1}}^{t_{M,1}} \left\{ F \cdot R_1 \cdot e^{−(M \cdot t_{r,1})} \cdot e^{−(M + F)(t_{r,1})} \cdot \frac{e^{−27.78 + 0.028(1279[1 − e^{−0.14(t + 1.29)}]0.529)}}{1 + e^{27.78 + 0.028(1279[1 − e^{−0.14(t + 1.29)}]0.529)}} \cdot 0.0000014[1, 279[1 − e^{−0.14(t + 1.29)}]3.0529] \right\} \cdot dt
\end{align*}

Paddlefish natural mortality was less than 9% in a sub-pond on the Cumberland River, Tennessee, where fishing was prohibited (Boone and Timmons 1995); furthermore, Timmons and Hughbanks (2000) suggested that natural mortality was low (~8%) for Paddlefish in Kentucky Lake. Previous yield analysis of the Kentucky Lake population by Scholten and Bettoli (2005) used a conditional natural mortality rate (cm) of 8%. However, cm should be slightly higher than natural mortality if any fishing is occurring; therefore, a cm of 9% was used in this analysis. Additional simulations were evaluated for a cm of 18% to assess the sensitivity of results to uncertainty in natural mortality rates. This higher cm falls within the range (13–20%) we estimated by using multiple natural mortality estimators (Hoenig 1983; Peterson and Wroblewski 1984; Jensen 1996; Quinn and Deriso 1999) and an assumed maximum age of 21, and it represents a probable maximum natural mortality rate given the lowest observed total mortality rate from a previous study of this population (22%; Timmons and Hughbanks 2000). Natural mortality rates were assumed to be the same for male and female Paddlefish. Values of cm were converted to M.

The current analysis assumed 1,000 age-0 recruits (R) to the population, which is a common assumption in equilibrium yield models and was used in the previous analysis by Scholten and Bettoli (2005). The analysis by Scholten and Bettoli (2005) used a sex ratio of 1.0:1.5 (male : female); therefore, the female fraction of age-0 fish that recruited to the population was 0.6, while the male fraction was 0.4 (i.e., R1 = 600 female recruits; R2 = 400 male recruits). Overall results did not differ for varying sex ratios, and therefore we report results for the 1:0:1.5 ratio.

Yields were simulated for conditional fishing mortalities (cf) increasing from 0.1 to 0.7. Values of cf were first converted to F, and annual survival was calculated for each combination of F and M. Exploitation rates (i) were then calculated and used in graphical analysis of yield to maintain consistency with previous yield modeling of Paddlefish in Kentucky Lake. Growth over-fishing was illustrated in graphical analysis as a dome-shaped relationship between yield and exploitation.

**Solving the Yield Model Equations**

Equation (8) can be solved by using the Jones (1957) method, whereas a straightforward analytical or approximate solution to equation (9) is unavailable, thus requiring numerical integration. Therefore, in this analysis, total equilibrium yield (biomass or roe) was calculated by numerically integrating equations (8) and
(9) from \( t_{r,j} \) to \( t_2 \) using the integrate function in R software (R Development Core Team 2010) for all combinations of \( F \) and \( M \).

**Spawning Potential Ratio**

Spawning potential ratios based on fecundity are frequently used in combination with yield modeling to evaluate the potential for recruitment overfishing. Given that roe yield of gravid females was being modeled, the amount of mature ovary biomass left after harvest (i.e., potential spawning biomass) was used to calculate the SPR. Specifically, spawning stock potential (SSP) was calculated by simply modifying equation (9) to calculate the amount of mature ovary biomass at age \( t \) via removal of the first \( F \)-parameter as

\[
\text{SSP} = \int_{b,1}^{t_1} \left[ R_1 \cdot e^{-(M \cdot t_{r,1})} \cdot e^{-(M+F)\left( t-t_{r,1} \right)} \right. \\
\left. + e^{[\beta_0+\beta_1 \cdot \text{EFL}(t) \cdot t_1]} \cdot \left[ a_{\text{ovary}} \cdot \text{EFL}(t)^{b_{\text{ovary}}} \right] \right] dt. \quad (10)
\]

Equation (10) is a continuous analog to the discrete approximation used to calculate SSP as provided by Goodyear (1993). The SPR was then calculated as

\[
\text{SPR} = \frac{\text{SSP}_{\text{fished}}}{\text{SSP}_{\text{unfished}}}, \quad (11)
\]

where \( \text{SSP}_{\text{fished}} \) and \( \text{SSP}_{\text{unfished}} \) are the spawning stock potentials for \( F > 0 \) and \( F = 0 \), respectively. The SPRs resulting from equation (11) were similar to values calculated in FAMS by using the method of Goodyear (1993). All statistical and simulation analyses were conducted in R (R Development Core Team 2010). Code to reproduce the yield and SPR analyses is available upon request from the corresponding author.

**RESULTS**

**Simulated Yields**

**Biomass yield.**—Biomass (i.e., flesh) yield per 1,000 recruits varied among minimum length limits and between the two \( cm \) levels (Figure 2). In general, biomass yield increased with \( u \) for all length limits and both \( cm \) values, with maximum yields occurring at or near the largest modeled values of \( u \); thus, there was little evidence for growth overfishing (Table 4; Figure 2). Biomass yield was maximized at a high exploitation level (\( u \sim 61\% \)) for the 864-mm minimum length limit and the \( cm \) of 9%. Yield increased across the range of simulated \( u \)-values for the 864-mm minimum length limit when \( cm \) was 18%. Regardless of the \( cm \) level, yield increased with increasing \( u \) for the 914-, 965-, and 1,016-mm minimum length limits. A decrease in biomass yield was apparent when the minimum length limit increased from the 864-mm historic limit; this result was due to differences in growth and the underlying sex-specific VBGF parameters. Specifically, the EFL\(_{\text{sc}} \) parameter for the male VBGF was 894 mm; therefore, minimum length limits that exceed this

<table>
<thead>
<tr>
<th>( cm ) (%) limit (mm)</th>
<th>Biomass(_{\text{max}} )</th>
<th>Roe(_{\text{max}} )</th>
<th>SPR(_{30} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 864</td>
<td>61</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>9 914</td>
<td>70</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>9 965</td>
<td>70</td>
<td>24</td>
<td>22</td>
</tr>
<tr>
<td>9 1,016</td>
<td>70</td>
<td>37</td>
<td>31</td>
</tr>
<tr>
<td>18 864</td>
<td>70</td>
<td>17</td>
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<tr>
<td>18 914</td>
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<td>23</td>
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</tr>
<tr>
<td>18 965</td>
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<td>29</td>
</tr>
<tr>
<td>18 1,016</td>
<td>70</td>
<td>70</td>
<td>50</td>
</tr>
</tbody>
</table>

EFL will protect male Paddlefish from harvest and will reduce overall biomass yield.

**Roe yields.**—Roe yields per 1,000 recruits varied more dramatically than biomass yields among minimum length limits at both of the simulated \( cm \) levels (Figure 2). Roe yield increased to a maximum with increasing \( u \), followed by a decrease in yield for all minimum length limits when \( cm \) was 9%. Simulated roe yields exhibited similar patterns when \( cm \) was 18%, with yields increasing to a maximum at intermediate values of \( u \), followed by yield decreases for all but the largest length limit (Table 4). Specifically, roe yields were maximized at \( u \) levels ranging from 14% to 27% for a \( cm \) of 9% and at \( u \) levels from 17% to 70% for a \( cm \) of 18%. Growth overfishing in terms of roe yields was apparent under both of the \( cm \) scenarios at the historic and current minimum length limits when \( u \) exceeded modest levels (i.e., 14–37% for \( cm = 9% \); 17–36% for \( cm = 18% \)).

**Spawning Potential Ratio**

The SPR varied among the four minimum length limits and between the two levels of \( cm \) (Figure 2). Patterns of decreasing SPR with increasing \( u \) were similar between the \( cm \) levels; however, decreases in SPR were more rapid when \( cm \) was equal to 9%. A narrow range of \( u \)-values maintained SPR above 0.2–0.3, which was recommended by Goodyear (1993) as an SPR threshold for most fish populations and was previously used in the analysis by Scholten and Bettoli (2005). Results indicated the potential for recruitment overfishing when low levels of \( u \) were exceeded, especially with liberal minimum length limits, regardless of the simulated \( cm \) level (Table 4). In particular, the \( u \)-value that produced an SPR of 30% (SPR\(_{30} \)) increased from 15% to 31% with increasing minimum length limit for a \( cm \) of 9%. Exploitation rates that generated SPR\(_{30} \) were higher for a \( cm \) value of 18%, increasing from 17% to 50% with increasing minimum length limit. When viewed in conjunction with
roeyield simulations, the potential for growth overfishing (in terms of roe yield) and for recruitment overfishing was minimized with higher minimum length limits, regardless of the $cm$ level.

**DISCUSSION**

This study extended the Beverton–Holt equilibrium yield model to evaluate biomass yields given sex-dependent growth as well as roe yield, which is increasingly important considering...
the number of previous studies that have used biomass-based equilibrium yield models in assessments of caviar-producing fishes. Biomass-based yield assessments are currently used to assess fishing impacts on caviar-producing fish stocks because of the perceived risks of overfishing due to increased caviar demand (e.g., Quist et al. 2002; Kennedy and Sutton 2007; Koch et al. 2009; Leone et al. 2012). Generally, these types of studies conclude that growth overfishing occurs at low minimum length limits, providing justification for higher minimum length limits. For example, Koch et al. (2009) showed that a 685-mm length limit was needed to prevent growth overfishing for several populations of Shovelnose Sturgeon Scaphirhynchus platorynchus in the Upper Mississippi River. A recent study of Paddlefish in Arkansas suggested that growth overfishing may occur with an 833-mm length limit (Leone et al. 2012). However, the results of the present study indicate that biomass-based yield assessments are likely to underestimate the potential for and the severity of growth overfishing when roe is being targeted, even if sex-dependent growth is accounted for in the biomass yield model.

Discrepancies between the effect of varying u and minimum length limits on biomass and roe yields reflect the interactions of maturity, sex ratio, and ovary weight. Roe yields increased with minimum length limit for both of the cm levels simulated. This result reflects the effect of larger minimum length limits delaying recruitment of younger, immature fish to the fishery, thereby allowing them to become larger and increasing their likelihood of being sexually mature at harvest. Consequently, roe yield increases, as more harvested females are likely to be gravid with larger ovaries.

Given the declines in European stocks of caviar-producing acipenseriform fishes and the high market value for roe (Birstein 1993), equilibrium yield-per-recruit analyses will likely continue to be an important tool for assessing and managing fisheries associated with caviar-producing species. The present analysis provides a method for evaluating equilibrium roe yield given a stock-specific maturation schedule and ovary weights. Females in the Kentucky Lake Paddlefish population are believed to spawn every year once they reach sexual maturity (Scholten and Bettoli 2005). However, the spawning of females every other year (or up to every 3 years) has been noted in other Paddlefish and sturgeon populations (Quist et al. 2002). The effect of variable spawning frequency on the generalization of our methods to other caviar-producing species is uncertain; however, this has not precluded SPR analyses (i.e., which account for the number of females spawning annually by age-class) from being used for those populations (e.g., Quist et al. 2002; Koch et al. 2009). Given that the models for roe yield and SPR are related, our approach to modeling roe yields can likely be generalized to fishes with variable spawning frequency and is at least better than biomass-based yield assessments; however, this topic requires further research.

Identification and implementation of harvest strategies that reduce the likelihood of both growth overfishing and recruitment overfishing would help to ensure a sustainable fishery for Paddlefish roe. However, it is difficult to perfectly manage the fishery, especially if fishing effort, harvest, or realized u is associated with uncontrollable environmental factors (i.e., partial harvest control). Specifically, Scholten and Bettoli (2005) observed a threefold increase in the number of harvested Paddlefish with increases in the number of fishable days on Kentucky Lake (i.e., days with mean Pickwick Dam discharge < 850 m³/s). Pickwick Dam is operated to provide flood control, navigation, and power production and cannot be operated to manage harvest by limiting fishable days; therefore, regulations that are robust to variation in u and that can maximize yields are desirable. For example, relative to the other minimum length limits evaluated in our analysis, the largest length limit (1,016 mm) provided the most protection from growth overfishing and recruitment overfishing while also maximizing roe yield across a broad range of u-values and cm levels.

Paddlefish fisheries target roe because of lucrative roe prices that greatly exceed the value of flesh. However, Paddlefish flesh can also be sold to provide additional revenue (Scholten and Bettoli 2005). Therefore, analysis of both flesh and roe yields may be important for management of the fishery to minimize economic consequences, which is of concern in the rural areas where commercial fishers reside. Specifically, the effect of varying length limits and u on the potential economic yield of the Kentucky Lake Paddlefish fishery could be evaluated as the sum of the estimated economic yields of roe and flesh. For example, assuming market prices of $220 per kilogram for roe and $1.10 per kilogram for flesh, the equilibrium yields presented in Figure 2 can be combined into a single monetary value (Figure 3). For the Kentucky Lake fishery, economic yield is largely a function of roe yield since the market price for roe is about 200 times that of flesh. Therefore, the economic yield plots in Figure 3 do not vary greatly from the patterns in roe yield depicted in

FIGURE 3. Potential economic yield of combined roe and flesh of Paddlefish harvested under four minimum eye-to-fork length limits (mm) at two levels of conditional natural mortality (cm) and over a range of exploitation rates in Kentucky Lake. Predictions are based on 1,000 recruits and assume that fishers receive wholesale prices of US$1.10 per kilogram for flesh and $220 per kilogram for roe.
Figure 2. However, this illustration can potentially be useful in the management of mixed-tissue fisheries, especially if the ratio of flesh price to roe price changes, which may be the case if farm-raised Paddlefish can provide a reliable source of caviar (Mims 2001). Mixed-tissue fisheries are not limited to caviar-producing Paddlefish or sturgeon species; roe markets also exist for several marine and freshwater fishes, such as herrings Clupea spp., mullets (e.g., Striped Mullet Mugil cephalus), Alaskan Wall-eye Pollock Gadus chalcogrammus, and several salmon species (e.g., Oncorhynchus spp.). Additionally, this type of analysis could also be extended to other commercially harvested species, such as Goosefish Lophius americanus or cods Gadus spp., that support a market for flesh and liver.

Although the highest minimum length limit (1,016 mm) produced the greatest roe yields and economic returns at most of the modeled -values, there are at least three reasons why it will be difficult to achieve an increased length limit for Paddlefish in Kentucky Lake. First, after previously embracing a plan to gradually increase the minimum length limit from 864 mm (historical) to 965 mm, the commercial fishing industry in Tennessee subsequently lobbied to abandon that management action and to hold the limit at 914 mm EFL. It is unlikely that the industry will suddenly reverse course and embrace a higher minimum length limit. Secondly, raising the minimum length limit will likely increase the bycatch of sublegal Paddlefish, potentially leading to an increase in discard mortality. Lastly, Tennessee fishermen have recently been allowed to check captured fish for roe by using a large-bore needle and syringe prior to harvest—a practice that is viewed as a conservation measure among fishermen (Scholten 2009). Returning non-roe-producing Paddlefish back into the population was not accounted for in our model. However, this practice should increase roe yield and reduce the potential for growth overfishing and recruitment overfishing over the simulated range of minimum length limits and -values, assuming there is no bycatch or discard mortality. Although most of the released Paddlefish will survive at cool water temperatures, discard mortality can exceed 70% with the warm temperatures that typically occur at the end of the fishing season (Bettoli and Scholten 2006). The prevalence among fishermen of checking Paddlefish for roe and the effects of discard mortality on yield dynamics are uncertain and will require further research.

Greater flexibility and biological realism in underlying weight-at-age functions can be evaluated by using numerical integration to predict yield. Historically, evaluation of integrals was limited to analytical solutions or approximations. The best example of this was the original analytical solution for the equilibrium yield model presented by Beverton and Holt (1957). This solution could predict equilibrium yield, but it required the unrealistic assumption of isometric scaling of fish weight with length. Using an incomplete beta function, Jones (1957) provided an approximation to the equilibrium yield function that allowed allometric scaling of weight with length, thus conferring increased biological realism to equilibrium yield predictions. Numerical integration can be used to evaluate very complex biomass and yield dynamics, representing increased biological realism for which analytical solutions or approximations likely do not exist. Specifically, this approach can potentially accommodate variable rates of natural mortality and fishing mortality or fishery recruitment (e.g., knife edge or continuous). The improved biological realism afforded by the use of numerical integration to solve the equilibrium roe yield model provided a better understanding of potential growth overfishing in this mixed-tissue fishery.

ACKNOWLEDGMENTS

Principal funding for the field collections of Paddlefish in Kentucky Lake was provided by the U.S. Geological Survey, acting on the recommendation of the USFWS Office of Scientific Authority. The Tennessee Cooperative Fishery Research Unit is jointly supported by the U.S. Geological Survey, Tennessee Technological University, and the Tennessee Wildlife Resources Agency. The manuscript was improved by critical reviews from Craig Paukert, Andre Punt, and three anonymous reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES


PREDICTION OF PADDLEFISH ROE YIELDS

fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120.


Slipke, J. W., and M. J. Maceina. 2010. Fishery analysis and modeling simulator (FAMS 1.0). Auburn University, Department of Fisheries and Allied Aquaculture, Auburn, Alabama.

North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.820243

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Evaluation of an Alternative Technique for Attaching External Transmitters to Blue Catfish

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Abstract
Attaching telemetry transmitters to catfishes (family Ictaluridae) has historically been problematic. Current attachment techniques produce low retention rates or high mortality, or cause altered physiological or behavioral effects. We investigated an alternative attachment technique during three experiments in which external transmitters were fastened to the supraoccipital bone of Blue Catfish Ictalurus furcatus. We hypothesized that attaching a transmitter to the skeletal structure would improve retention rates and minimize negative health effects. In a 2-month pilot study, retention was 100% (N = 20; TL range = 435–638 mm) and fish appeared to be in excellent condition. However, in a subsequent laboratory experiment, retention was poor (41.7% at 2 months and 0% at 6 months; N = 24; TL range = 600–995 mm), which may be attributed to excessive handling during the experiment. The attachment technique was also field tested as part of a larger telemetry study. Fifty Blue Catfish (TL range = 600–995 mm) were tagged and monitored for up to 17 months in Lake Buchanan, Texas. Retention in the field was 40% at 6 months and 19% at 12 months, which was comparable to current free-floating internal transmitter retention rates. Although our procedure produces lower retention than internal transmitters fastened to the pectoral girdle (60–93% annual retention), we believe this modified attachment procedure has future utility despite our mixed results. Our procedure avoids negative health effects (i.e., transmitters absorbed in the intestine or stomach or passed through the body wall) associated with both internal and external transmitter attachment techniques severely limit the efficacy of telemetry studies on catfishes (Siegwarth and Pitlo 1999; Grist 2002). For example, Siegwarth and Pitlo (1999) observed 80% mortality over a 3-week period for Channel Catfish Ictalurus punctatus fitted with external, “saddle-style” transmitters. These issues associated with both internal and external transmitter attachment techniques severely limit the efficacy of telemetry studies on catfishes. Identifying new or improved transmitter attachment techniques for catfishes is essential so that future telemetry studies can provide both representative and cost-effective data.

Telemetry is often used to study movement, habitat selection, and other life history characteristics of fishes (Winter 1996). These studies are expensive and usually entail long-term evaluations (e.g., greater than 12 months). Successful telemetry projects rely on multiple important assumptions, including (1) transmitters do not affect fish behavior or physiology, (2) transmitters remain attached, and (3) fish fitted with transmitters do not experience increased mortality. Any violation of these assumptions may cause erroneous or unrepresentative data collection or a premature end to an expensive project (Jepsen 2002).

Both internal and external transmitter attachment techniques have been employed on catfishes, each with limited success. Channel Catfish Ictalurus punctatus and Blue Catfish I. furcatus are well known to expel free-floating internal transmitters (up to 70% annually) through the surgical incision (Marty and Summerfelt 1986), or by encapsulating them in the stomach or intestine and passing them through the digestive tract (i.e., transintestinal expulsion; Summerfelt and Mosier 1984; Marty and Summerfelt 1986; Holbrook et al. 2012). To circumvent these issues, researchers recommend securing internal transmitters to the pectoral girdle (Siegwarth and Pitlo 1999). However, Holbrook et al. (2012) found that when using this modified procedure, transmitters can still enter the digestive tract or pass through the body wall, causing unacceptable health effects in up to 40% of tagged fish. Externally mounted transmitters also produce high mortality rates or cause deleterious effects (e.g., excessive abrasion and infection) on catfishes (Siegwarth and Pitlo 1999; Grist 2002). For example, Siegwarth and Pitlo (1999) observed 80% mortality over a 3-week period for Channel Catfish fitted with external, “saddle-style” transmitters. These issues associated with both internal and external transmitter attachment techniques severely limit the efficacy of telemetry studies on catfishes. Identifying new or improved transmitter attachment techniques for catfishes is essential so that future telemetry studies can provide both representative and cost-effective data.

Holbrook et al. (2012) recommended identifying a secure external attachment method that would not alter behavior or physical condition. We hypothesized that attachment of a transmitter to the skeletal structure would produce higher retention

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Received March 12, 2013; accepted June 20, 2013
Published online September 23, 2013
rates and avoid negative health effects (see Holbrook et al. 2012) associated with current available methods. Attaching hardware (e.g., plates and screws) to bone is common practice in veterinary medicine (Yovich et al. 1985; Smith et al. 1989; Rodgerson et al. 2001) and may provide a practical approach for securing telemetry tags to Blue Catfish. Therefore, we investigated tag retention associated with external transmitters attached to the supraoccipital bone of Blue Catfish.

METHODS
Our alternative telemetry attachment technique was evaluated during a series of experiments. We conducted an initial 2-month pilot study in a laboratory pond to evaluate the practicality of the attachment procedure. We then conducted a long-term (i.e., 6-month) laboratory pond evaluation as well as an evaluation of the technique in the field. Blue Catfish used in the pond experiments were collected from Lake Buchanan and Choke Canyon Reservoir, Texas, in autumn 2010 with low-frequency electrofishing and jug lines (Schmitt and Shoup 2013). Collected fish were transported to Heart of the Hills Fisheries Science Center (HOH; Mountain Home, Texas) in hauling tanks equipped with oxygen diffusers and filled with a 1% solution of NaCl. Upon arrival, fish were held for a minimum of 28 d in a 0.24-ha earthen pond (maximum depth = 2.2 m) until tagging was conducted. Fish used in the field evaluation were collected from Lake Buchanan with jug lines, tagged, and immediately released.

Tag description and attachment procedure.—Blue Catfish used in the pond experiments were randomly selected and fitted with dummy transmitters constructed of epoxy resin resembling the shape, size, and weight of commonly used, commercially available ultrasonic transmitters. We used three sizes of dummy transmitters, specific to fish weight, to ensure transmitters were < 2% of the fish weight (Winter 1996). Fish less than 800 g were fitted with a 5.5-g dummy transmitter (small; 47 mm long × 11 mm in diameter), fish 800–1,399 g were fitted with a 16-g dummy transmitter (medium; 38 mm long × 15 mm in diameter), and fish greater than 1,399 g were fitted with a 28-g dummy transmitter (large; 63 mm long × 16 mm in diameter). A hole was drilled through one end of each transmitter, and a stainless steel wire (about 1-mm diameter and 80 mm in length) was passed through the hole. Both ends of the wire were then inserted into stainless steel tubing (about 5-mm diameter and 38 mm in length), and the tube was crimped. The end of the tubing opposite the tag was flattened and two, 3-mm holes were drilled through the flattened surface.

Prior to transmitter attachment, each fish was placed in a wood cradle and draped with a damp, dark towel to cover its eyes. Tagging was then conducted by two individuals: one person holding the fish while the other applied the tag. An incision was made through the dorsal surface immediately posterior to the cranium to expose the supraoccipital bone (a small, postcranial bone along the dorsal midline; Figure 1). Two pilot holes (1.6-mm drill bit size) were drilled into the bone, and the tag was fastened to the bone with stainless steel screws (#6 × 10 mm in length for small tags and #4 × 13 mm in length for medium and large tags). Dummy transmitters were individually numbered for identification purposes; each fish also received a T-bar anchor tag (47 mm in length × 2 mm in diameter; Floy FD-94; Floy Tag and Manufacturing, Seattle, Washington) inserted near the caudal peduncle or below the dorsal fin between the pterygiophores, and a PIT tag (2.1 mm in diameter × 8.5 mm in length; Model TXP148511B; Biomark, Boise, Idaho) injected into the dorsal musculature immediately posterior to the dorsal fin of each fish (Guy et al. 1996; Daugherty and Buckmeier 2009). All tagging was administered by the same individual for each experiment. During our study, there were no approved anesthetics by the U.S. Food and Drug Administration (FDA) for immediate fish release; therefore, we did not use anesthesia.

Pilot study evaluation.—In November 2009, 20 Blue Catfish (TL range = 435–638 mm) were collected from the holding pond and moved to one of two 6,777-L indoor holding tanks for a minimum of 4 d to recover from handling stress. After the recovery period, all fish were dipped in a 3% solution of NaCl (3–5 s) to minimize the potential for bacterial infection; measured (TL [mm]); fitted with the appropriate transmitter, T-bar, and PIT tag; and immediately transferred to a 0.24-ha
earthen laboratory pond. Fish were fed a diet of juvenile Koi Carp (*Cyprinus carpio*) (hereafter, Koi) ad libitum and monitored for 2 months. Two months posttagging, the pond was drained and fish were collected and examined for the presence or absence of the dummy transmitter. Mortality was also monitored and recorded, and these fish were removed from retention analysis.

**Long-term laboratory pond evaluation.**—Beginning September 2011, 24 Blue Catfish (TL range = 392–892 mm) were harvested from the laboratory pond with capture techniques commonly used by fisheries managers (i.e., low-frequency electrofishing and hook-and-line methods) and fitted with transmitters. Collection and tagging procedures mimicked realistic field tagging methodologies (i.e., fish collection, tagging, holding, and release) in efforts to reproduce typical field tagging conditions. During the tagging process, fish were measured (TL [mm]), dipped in a 3% bath of NaCl, and fitted with tags (i.e., dummy transmitters, T-bars, and PITs). To minimize risk of potential infection, all surgical equipment, tagging supplies, and the surgery location was sterilized in Betadine and all personnel wore latex gloves. After tagging, fish were immediately released into an adjacent pond and held for 6 months on an ad libitum diet of Koi. The perimeter of the pond was visually checked daily for dead fish, and the pond was drained every 2 months to record retention. At each draining, all fish were measured, evaluated for the presence of a dummy tag, and released. Missing fish were recorded as mortalities and excluded from retention analysis.

**Field evaluation.**—In addition to the laboratory pond evaluations, tag retention was field tested as part of a larger study that examined seasonal movement of Blue Catfish in Lake Buchanan, Texas. From February 2010 through June 2011, 51 Blue Catfish (TL range = 600–995 mm) were collected from the reservoir with hook and line or electrofishing, and fitted with 36-month Sonotronics CT-05-36-E ultrasonic transmitters. Tags were fastened externally to the supraoccipital bone with procedures established during the laboratory pond evaluations. After tagging fish were held in a live well for 5–15 min to recover from handling and tagging, and then released at the capture location.

Fish were monitored until June 2012 by manual tracking and with an array of Sonotronics submersible underwater receivers (SURs) deployed at 25–30 locations throughout the upper reservoir and main-stem Colorado River, Texas. A detailed description of the SUR array can be found in Betsill (2012). Receiver data were processed with SURsoftDPC (Sonotronics) software and verified for accurate detections. Monthly field tag retention was assessed and compared with monthly retention observed in the laboratory.

**Data analysis.**—Retention in the pilot study was expressed by reporting the percent of fish retaining tags after 2 months. In the laboratory experiment, we used regression analyses to model monthly retention rates. We tested a series of nonlinear models to identify the model that best fit the data without undue complexity (Freund and Hartman 2002). Fit was assessed by looking for evidence of a high R-square and nonrandom patterns within regression residuals. To allow for comparison between laboratory pond and field results, we selected a curve whose functional form fit both sets of data. Regression analyses were conducted with the Dynamic Fit Wizard in SigmaPlot (SigmaPlot 2008). We fixed the intercept to 1.0 because initially, all fish were tagged. Despite the lack of control fish, mortality was also anecdotal examined in both experiments by calculating the percent of fish surviving at the completion of each experiment. Health was examined qualitatively by observation and categorized as excellent (no skin lesions or deterioration, healthy fins, and no obvious weight loss) or poor (skin lesions or deterioration present, reddening of fins, or signs of weight loss).

In the field evaluation, tag retention was evaluated by calculating the number of days fish were active and reported as the percent of tagged fish that retained tags in monthly (i.e., 30-d) intervals. To determine if fish were active, detections were sorted by date and time in the database. Fish were considered active when detections (by date and time) were noncontinuous (i.e., detections were spaced ≥ 5 min apart) and considered inactive if fish were missing or when all remaining detections were < 5 min apart. Non-tag-related mortality and migration patterns were unknown; therefore, our estimates should be considered minimum retention rates. Retention estimates were adjusted with the Kaplan–Meier procedure (Cox and Oakes 1984; Bendock and Alexandersdottir 1993) to account for the removal of fish reported harvested and then assessed with the regression techniques used in the laboratory pond experiment.

**RESULTS**

**Pilot Study**

In the 2-month pilot evaluation, we observed 100% tag retention and no mortality. Although fish weights were not recorded, our observations suggested fish health was excellent. We observed no skin lesions or infection, no visible signs of weight loss, and tag sites were healed at 2 months posttagging.

**Lab Experiment**

About 64% of fish retained tags in the first month, but by 6 months, all fish expelled transmitters (Figure 2). We found that a two-parameter, exponential decay model (Predicted retention = 1.0099 e[−0.4643 month]) provided a reasonable model of tag retention across time (\( F_{1,2} = 357.57, P < 0.01, R^2 = 0.99; \) Figure 2). Similar to the pilot study, no signs of skin lesions, body deterioration, or infection were apparent during any month. Three fish were not recovered during the second draining and were therefore considered mortalities. Total mortality at 6 months was 12.5%.

**Field Evaluation**

Transmitter retention was significantly related to month \( (F_{3.9} = 145.79, P < 0.01) \) and was higher than the laboratory retention estimate (Figure 2). Although 50% of fish expelled
Attaching transmitters to catfish is problematic because most available procedures produce high mortality, low retention, or altered behavior effects (Summerfelt and Mosier 1984; Siegwarth and Pitlo 1999; Grist 2002; Holbrook et al. 2012). We attempted to develop a new transmitter attachment method that could circumvent these issues. Tag retention in our laboratory pond evaluations showed mixed results that ranged from 0% to 100%; however, the field evaluation produced results comparable to other available methods. Despite modest retention rates, this attachment method appears to be at least as effective as most alternative attachment options, yet we believe it is also less invasive (e.g., no surgery in the abdominal cavity or abrasion caused by saddle-style external transmitter mounts). In its current form, this attachment technique could be used as a comparable surrogate for currently employed techniques. However, further modification of our attachment design may produce an attachment procedure that is even more effective than all other available methods.

Retention rates observed in the pilot and laboratory experiment were quite variable, despite the difference in duration. Although the pilot study was only conducted for 2 months, results were compelling: the 100% retention strongly suggested this technique was a viable option for providing acceptable retention rates. We are unaware of any studies that observed higher telemetry tag retention 2 months posttagging with an alternative method. Unfortunately, we observed differing results at the 2-month interval in the subsequent experiment. The reason for our contrasting results is unclear; however, we speculate that high expulsion in the long-term laboratory experiment may be attributed to elevated stress and subsequent infection associated with confinement in the hatchery pond. Stoskopf (1993) reported that excessive handling, transport, and confinement can depress the immune system in catfishes, increasing susceptibility to infection. Thus, confinement in our hatchery pond, coupled with excessive handling, may have promoted bacterial infection. Because catfish notoriously expel transmitters in response to infection (Summerfelt and Mosier 1984), we presume that some tag loss observed in the long-term laboratory pond evaluation may be attributable to infection (possible weakening of the bone). Handling was minimized and retention was higher in our pilot and field evaluations, providing further support for this rationale. Biologists may be able to circumvent these issues by using anesthesia to reduce fish stress during the transmitter attachment procedure. During our study, there were no approved anesthetics for immediate release of fish; however, the FDA has since authorized the use of AQUI-S 20E (AQUI-S, New Zealand) for sedating and immediately releasing freshwater fish.

We suspect much of the tag expulsion was caused by the posterior screw splitting the supraoccipital bone. During each pond draining (long-term laboratory experiment), we routinely observed tags missing the posterior screw. The posterior end of the supraoccipital bone is much smaller and more fragile than the anterior end, which likely caused the bone to break when fitted with a screw. Once split, the rear screw could fall out causing the tag to spin freely, ultimately extracting the remaining anterior screw. Using smaller screws or an alternative attachment device, such as a single bone rivet, may eliminate this issue. Bone rivets would prevent extraction caused from reverse spinning and would eliminate the need for the second screw. Although attaching hardware (e.g., plates and screws) to bone is common (Yovich et al. 1985; Smith et al. 1989; Rodgerson et al. 2001), the attaching surface must be large and strong enough to retain the hardware. Thus, selecting a larger, alternative bone such as the frontal bone (a skull bone located dorsally, anterior to the supraoccipital bone) may significantly improve retention rates. We suspect these recommended modifications, would create an attachment procedure that will produce retention rates superior to all other methods. Therefore, we recommend future research focus on identifying an alternative skeletal structure that is larger than the supraoccipital bone.

Field retention estimates were modest (at least 40% for the first 6 months) and probably underestimated considerably because unknown emigration and mortality rates likely caused us to underestimate retention. For example, tracking efforts (SURs and manual) did not always cover all available habitats (e.g., lower reservoir, and the upper Colorado River); therefore, some tagged fish could have migrated out of the study area and gone undetected. Nonmobile fish could not be accurately verified as an expulsion, mortality, or sedentary, but had to be
were conservatively regarded as expelled. Other sources of mortality were unknown and also likely decreased the tagged population size. For example, we verified that at least seven tagged fish (14% of the tagged population) were harvested. However, total harvest could not be quantified because tag reporting rates were unknown. Typical reporting rates of a voluntary tag return system range from 24% to 85% (Nichols et al. 1991; Miranda et al. 2002; Meyer et al. 2012); therefore, it is likely that some of our tagged fish were harvested and not reported. If this occurred, retention estimates could have been increased; however, we chose to conservatively estimate retention by excluding any unknown harvest estimates.

We feel this attachment technique has future utility, even if our procedures are not modified. First, we believe the retention rates observed in the field probably most represent actual retention rates. Catfish are not confined, less stressed, and probably able to minimize abrasion to the tag or attachment (e.g., minimize objects hitting the tag) when in natural environments compared with artificial laboratory settings. Second, our attachment procedure offers some advantages over other, currently available attachment options. Our field retention rates are comparable to free-floating internal transmitters (30–50% annually; Summerfelt and Mosier 1984; Holbrook et al. 2012); however, our procedure eliminates risks associated with surgery in the abdominal cavity. Tying internal transmitters to the pectoral girdle will produce the highest known retention (60–93% annually; Siegwarth and Pitlo 1999; Holbrook et al. 2012), but this option typically creates unacceptable health effects (e.g., tags absorbed into the intestine or stomach or pushed through the body wall while remaining fixed to pectoral girdle; Holbrook et al. 2012). In these situations, advantages of higher retention are offset by altered behavior effects. Alternative external attachments, such as a saddle-style, typically result in elevated mortality (i.e., 48–80% in 128 d; Siegwarth and Pitlo 1999; Grist 2002), which could result in fewer experimental fish after 1 year than our method.

Although retention rates for our attachment procedure are comparable to other methods, its effects on fish behavior are unknown and may warrant further investigation before implementing this technique. At the conclusion of each laboratory experiment, mortality was low and all fish appeared to be healthy (no obvious signs of weight loss or body deterioration), suggesting the transmitter as well as any possible bone deterioration (e.g., the supraoccipital bone splitting) had limited effects on behavior (e.g., foraging, growth, swimming speed, etc.) However, these data may not adequately describe how behavior will be affected in natural environments. Future evaluations should systematically examine behavior and also determine the appropriate transmitter attributes (e.g., determine if the 2% transmitter: fish weight ratio is appropriate).

Currently, no tag attachment method is completely reliable or effective for Blue Catfish. Many researchers (Summerfelt and Mosier 1984; Marty and Summerfelt 1986; Siegwarth and Pitlo 1999; Grist 2002; Jepsen et al. 2002; Holbrook et al. 2012) have investigated methods to improve telemetry tag retention rates on catfish but have had minimal success. We believe our work provides an alternative approach that is at least comparable to other methods and suggests a potential future direction (i.e., attaching transmitters to the skeletal structure) in developing improved telemetry attachment procedures for catfishes. We recognize that, in its current form, our method does not produce retention rates higher than other available methods. However, our method produces comparable retention rates while minimizing known health effects and surgical risks associated with the other methods. However, slight modifications to our procedure may create a superior transmitter attachment method and improve the efficacy of future catfish telemetry studies.

ACKNOWLEDGMENTS

We thank the many Texas Parks and Wildlife Department employees that assisted with data collection. Editorial comments by staff at Heart of the Hills Fisheries Science Center improved this manuscript. Funding for this project was provided through Federal Aid in Sport Fish Restoration Project F-231-R-1 to the Texas Parks and Wildlife Department.

REFERENCES


North American Journal of Fisheries Management

Development of a Stock–Recruitment Model and Assessment of Biological Reference Points for the Lake Erie Walleye Fishery

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.822442

PLEASE SCROLL DOWN FOR ARTICLE
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Abstract
We developed an updated stock–recruitment relationship for Lake Erie Walleye Sander vitreus using the Akaike information criterion model selection approach. Our best stock–recruitment relationship was a Ricker spawner–recruit function to which spring warming rate was added as an environmental variable, and this regression model explained 39% of the variability in Walleye recruitment over the 1978 through 2006 year-classes. Thus, most of the variability in Lake Erie Walleye recruitment appeared to be attributable to factors other than spawning stock size and spring warming rate. The abundance of age-0 Gizzard Shad Dorosoma cepedianum, which was an important term in previous models, may still be an important factor for Walleye recruitment, but poorer ability to monitor Gizzard Shad since the late 1990s could have led to that term failing to appear in our best model. Secondly, we used numerical simulation to demonstrate how to use the stock recruitment relationship to characterize the population dynamics (such as stable age structure, carrying capacity, and maximum sustainable yield) and some biological reference points (such as fishing rates at different important biomass or harvest levels) for an age-structured population in a deterministic way.

Recruitment is a primary driver of fish population dynamics (Ricker 1975; Hilborn and Walters 1992; Quinn and Deriso 1999), and understanding the relationship between stock size and recruitment is one of the most critical aspects of fisheries management (Hilborn and Walters 1992). Depending on the context, fish recruitment can be defined as the number of individuals surviving to enter the reproductive population (spawning recruitment), the harvestable population (fisheries recruitment), or a specific stage characterized by ages or sizes (Ricker 1975). Spawning recruitment is critical to the maintenance of fish populations and guarantees fish populations remain as renewable natural resources. The quantity and quality of recruits to a spawning population affects fisheries recruitment and thus sustainability of harvest. For some species, spawning recruitment and fishery recruitment converge when fish enter the reproductive population at the same age or size. When fish enter the fishery before reaching maturity, as is frequently the case in Walleye Sander vitreus fisheries, there is greater risk

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Received September 21, 2012; accepted July 2, 2013
Published online September 23, 2013
of recruitment overfishing (Hilborn and Walters 1992; Quinn and Deriso 1999). Therefore, fish recruitment has been a major concern of fisheries scientists and managers alike.

Understanding the stock–recruitment relationship continues to be a core issue for fisheries research and management. Optimal harvest and sustainable development of fisheries have been the two most important goals for fisheries managers (Hilborn and Walters 1992; Quinn and Deriso 1999). In order to achieve these goals, fisheries management needs to create fishing strategies and tactics for both short-term and long-term fisheries plans. One approach that fisheries researchers use to evaluate these strategies and tactics is to simulate fish population dynamics and fishing events. Such evaluations cannot be done without recruitment information. For semelparous species, biological reference points used for management policies, such as fishing mortality and spawner-stock biomass, can be directly derived from a defined stock–recruitment relationship (Hilborn and Walters 1992). The stock–recruitment relationship is also essential for understanding the population productivity and setting harvest rules for iteroparous species.

Many factors influencing egg production and the early survival of fish species potentially influence recruitment, and stock–recruitment relationships are typically quite variable (Hilborn and Walters 1992; Myers 2001). It has long been debated whether fish recruitment is related to spawning stock size, environmental factors, or both (Hilborn and Walters 1992; Myers 2001). Number and quality of spawners determine the quantity and quality of eggs they produce. However, a large amount of uncertainty exists in the survival of eggs and larval stages, as well as in the survival of juvenile stages. Environmental fluctuations are mainly responsible for this uncertainty, but biotic factors, such as cannibalism (Forney 1976) and competition among larvae, may also affect larval and juvenile mortality. Fish eggs and larvae are especially vulnerable to their environmental conditions due to their fragile nature, and year-class strength of many fish species can be established during these early life stages. Some of these environmental conditions include temperature (O’Gorman et al. 2004), water movement (Beletsky et al. 2007; Zhao et al. 2009), prey abundance (Madenjian et al. 1996), and predation (Madenjian et al. 2005). Unfortunately, in many cases these environmental variables are not routinely or accurately monitored, or some of the key variables are not measured at all. As a result, development of predictive stock–recruitment relationships for most fish species are frequently hindered by lack of reliable environmental information or incomplete understanding of environmental influences on recruitment.

The Lake Erie Walleye population has been extensively exploited by commercial and recreational fisheries for centuries (Regier et al. 1969; Hatch et al. 1987), and this species is one of the two most economically valuable species harvested from Lake Erie. Species-specific estimates of value of harvest are not available, but the total value of Great Lakes fisheries has been estimated at over US$7 billion (Southwick Associates 2008). Lake Erie is believed to account for about half that value, and Walleye is one of the largest fisheries in Lake Erie. During the past several decades, the Lake Erie Walleye population recovered from historically low levels in the early 1960s to a level that has supported harvests averaging about 5 million adult Walleyes annually. A formal assessment and quota management of the Walleye population in Lake Erie was only established in the late 1970s (Hatch et al. 1987).

Stock–recruitment relationships are important tools for evaluating harvest policies. Following Busch et al. (1975), who reported that a more rapid spring warming rate resulted in faster development of eggs and earlier hatch dates, which further resulted in eggs having a shorter period of susceptibility to storm damage, Shuter and Koonce (1977) described Walleye recruitment as a power function of spawning-stock size and an exponential function of daily increase in water temperature during spring (i.e., spawning season). Using data for the 1979 through 1993 year-classes, Madenjian et al. (1996) developed a Ricker stock–recruitment relationship using the spring water warming rate and abundance of age-0 Gizzard Shad Dorosoma cepedianum as two environmental variables. Gizzard Shad abundance in fall was thought to influence the proportion of mature females in the Walleye population that spawn the following spring because age-0 Gizzard Shad represent a high lipid source to adult females during the fall and early winter months (Henderson and Nepfzy 1994). Both Shuter and Koonce (1977) and Madenjian et al. (1996) provided useful information that can be used to better understand Walleye population dynamics and help evaluate the management policies. However, changes in the Lake Erie food web since the Madenjian et al. (1996) study, such as the invasion of dreissenid mussels and the decline in age-0 Gizzard Shad abundance during the 1990s (FTG 2010), suggest that a re-evaluation of the existing stock–recruitment model is warranted.

Our primary objective was to develop an updated Walleye stock–recruitment model building on the efforts of Shuter and Koonce (1977) and Madenjian et al. (1996) and using data for the 1978 through 2006 year-classes. The secondary objective was to apply a deterministic simulation driven by this new stock–recruitment model to characterize the population dynamics and some biological reference points under the average environmental condition, assuming that the derived stock–recruitment relationship holds for the simulation period.

METHODS

Data.—The Madenjian et al. (1996) model used spring warming rate and an index of abundance of age-0 Gizzard Shad as exponent modifiers to a base Ricker stock–recruitment model. We investigated these and other environmental and biotic variables in our modeling effort. Other environmental variables were mean springtime wind velocity, prevailing wind vector, three different measures of winter thermal conditions (December–March, January–March, and February–March cumulative degree-days), and winter duration (number of days
mean daily temperature was \(<6^\circ\)C). Wind velocity variables addressed mechanisms presented by Busch et al. (1975), that high winds subject eggs to potential mechanical damage from storms, and by Zhao et al. (2009), that wind currents affect whether drifting larvae are carried toward suitable or unsuitable nursery areas. Winter duration variables addressed hypotheses forwarded by Hokanson (1977) regarding minimum latency time for gonad maturation (see Discussion). Other biotic variables were total forage biomass, which addressed the fat storage hypothesis (Henderson and Nepszy 1994), and biomass of potential egg predators (White Perch *Morone americana* and Round Goby *Neogobius melanostomus*). Wind data were taken from the National Oceanic and Atmospheric Administration data from Toledo, Ohio. Recruitment and spawner biomass data were taken from reports of the Walleye Task Group (WTG 2009). The WTG is a standing committee of the Lake Erie Committee of the Great Lakes Fishery Commission, composed of management and research biologists from the several provincial and state governments with management authority of the Walleye population in Lake Erie. The task group is charged with estimating the recommended allowable harvest of Walleyes, which is the primary biological criterion used to establish annual total allowable catch of Walleyes in Lake Erie. The WTG (2009) estimated annual abundances of Walleyes ages 2 to 7 and older from 1978 to 2008 using a statistical catch-at-age (SCAA) model implemented using Auto Differentiation Model Builder (ADMB; Otter Research 2000). We estimated spawning-stock biomass of Walleyes at age 4 and older using the observed annual mean weight at age and the estimated Walleye abundances (WTG 2009), and this estimated spawning-stock biomass was the index of spawning-stock size (independent variable). The calculation of spawning-stock biomass by this method implicitly accounted for population age structure and weight–fecundity relationship suggested by Venturelli et al. (2010). We assume a linear weight–fecundity relationship as demonstrated for Walleyes in Lake Erie (Wolfert 1969). The estimated abundance of age-2 Walleyes from the SCAA model analysis was the index of recruitment (dependent variable).

We used daily mean temperature observations collected from the water intake location for the Union Municipal Water Intake at Leamington, Ontario, to calculate all thermal variables. The intake for the water plant is approximately 9 m offshore. Water temperatures throughout the water column in western Lake Erie are nearly homothermal for most of the year. A complete time series of water temperature measurement at Walleye spawning grounds was not available. However, temperatures recorded at Put-in-Bay, Ohio, from 1961 to 1992, which were used by Madenjian et al. (1996), were positively and linearly related to temperatures from the Union Municipal Water Intake, where a complete time series of measurements was available. The warming rate was calculated as the slope of the linear regression model of water temperature versus days of the year from 1 April to 15 May (Busch et al. 1975; Shuter and Koonce 1977; Madenjian et al. 1996). We used the annual abundance estimate of age-0 Gizzard Shad and several other known forage species of adult Walleyes (e.g., Rainbow Smelt *Osmerus mordax*, Emerald Shiner *Notropis atherinoides*, Yellow Perch *Perca flavescens*, White Perch) from bottom-trawl surveys conducted during autumn throughout the western basin (FTG 2009) to represent the abundance of age-0 Gizzard Shad, other forage species, and potential egg predators.

**Model development and model selection.**—First, we identified the external variables that were significantly related to Walleye recruitment by determining whether the external variable was statistically significant or close to statistically significant (*P < 0.10*) when the variable was included in a Walleye stock–recruitment model. Of all of the environmental and biotic variables considered, only spring warming rate and age-0 Gizzard Shad abundance were significantly related to Walleye recruitment. Therefore, the only external variables included in our best model selection process were spring warming rate and age-0 Gizzard Shad abundance. From previous studies (Busch et al. 1975; Shuter and Koonce 1977; Madenjian et al. 1996), we expected that spring warming rate and abundance of age-0 Gizzard Shad are both positively related to number of recruits of the Lake Erie Walleye.

We standardized each external variable by subtracting the mean from each individual observation. By doing so, the estimated stock–recruitment model essentially represents the relationship under average environmental conditions. Two commonly used stock–recruitment relationships, the Beverton–Holt (Beverton and Holt 1957) and Ricker (1975) models, were applied to the indices of spawning-stock size and recruitment, as well as to the standardized data for the environmental variables.

The Beverton–Holt model was

\[
R = \left( \frac{\alpha_1 \times S}{1 + \beta_1 \times S} \right) \times \exp(\gamma_{11} \times X_1 + \gamma_{12} \times X_2),
\]

and the Ricker model was

\[
R = \alpha_2 \times S \times \exp(-\beta_2 \times S) \exp(\gamma_{21} \times X_1 + \gamma_{22} \times X_2),
\]

where *R* is recruitment (number of age-2 fish), *S* is spawning-stock biomass (biomass of age-4 and older fish) producing the recruitment, *X_1* is standardized spring warming rate, for which zero represents an average warming rate, and *X_2* is standardized Gizzard Shad abundance, for which zero represents average abundance. Nonlinear least-squares regression implemented by Matlab 6.0 was used to fit the above models. A least-squares version of the corrected Akaike information criterion (AIC_c; Akaike 1981) was used to select between the two models and variables and was calculated by:

\[
\text{AIC}_c = N \times \ln \left( \frac{\text{SSE}}{N} \right) + 2 \times K + \frac{2 \times K \times (K + 1)}{N - K - 1},
\]
where $N$ is sample size, SSE is the sum of squares of the residuals, and $K$ is the number of parameters.

Simulating biological reference points for Lake Erie Walleye fisheries using the derived stock–recruitment relationship.—For a semelparous fish species, biological reference points can be directly derived from its stock–recruitment relationship (Ricker 1975; Hilborn and Walters 1992; Quinn and Deriso 1999). However, a simulation is needed to find these parameters for an iteroparous fish population with a multiple age structure. We set up an age-structured matrix model to simulate the population dynamics of Lake Erie Walleye. Consistent with the current management practice, the model included six age-classes from age 2 to age 7 and older. The number of age-2 fish was treated as annual recruitment and calculated from the derived stock–recruitment relationship under mean environmental conditions (see the above section for details). Annual spawning-stock biomass (SSB) was calculated by:

$$\text{SSB}_t = \sum_{i=4}^{7+} N_{t,i} \times W_i,$$

where $SSB_t$ is the spawning-stock biomass in year $t$, $N_{t,i}$ is number of fish of age $i$ in year $t$, and $W_i$ is mean weight at age $i$ and calculated from observations made from 1978 to 2009 (WTG 2009). Natural mortality rate ($M_i$) was assumed to be 0.32/year, which is currently used in the stock assessment model (WTG 2011). For simplicity, we only simulate Walleye gillnet fisheries, and age-specific fishing selectivity estimated by the WTG to determine the recommended allowable harvest for 2009 (WTG 2009) was selected to model age-specific fishing mortality rates ($F_i$), as follows:

$$F_i = S_i \times F,$$

where $S_i$ is the age-specific fishing selectivity for fish of age $i$, and $F$ is the fishing mortality rate for fully selected (ages 4, 5 and 6) fish. The following equations were used to simulate abundance ($N$), catch ($C$), and yield($Y$) of the population from ages $i = 2–7+$ at year $t$:

$$N_{t,i} = N_{t-1,i-1} \times \exp[-(F_{t-1,i-1} + M)], \text{ for ages 2 to 6},$$

$$N_{t,7+} = N_{t-1,7+} \times \exp[-(F_{t-1,7+} + M)] + N_{t-1,6} \times \exp[-(F_{t-1,6} + M)], \text{ for age 7+},$$

$$C_i = \sum_{i=2}^{7+} \frac{F_{t,i}}{F_{t,i} + M} \times N_{t,i} \times \{1 - \exp[-(F_{t,i} + M)]\},$$

and

$$Y_i = \sum_{i=2}^{7+} C_{t,i} \times W_i.$$

Each simulation was run long enough to reach population equilibrium, at which point population abundance and recruitment remained constant and population age structure reached a stable age structure. We first ran the simulation under no fishing to derive population carrying capacity (equilibrium abundance under no fishing), stable age structure, spawning biomass, and recruitment at equilibrium. A replacement line is the line connecting the origin $(0, 0)$ to the point with coordinates of equilibrium spawning biomass and corresponding recruitment in the derived stock–recruitment space. The inverse of the slope of the replacement line is the spawner biomass produced by a recruit (SPR$_F = 0$) through its lifetime. We compared replacement lines under the following different harvest policies (Quinn and Deriso 1999):

1. $F_{\text{MSY}}$: fishing mortality at maximum sustainable yield (MSY);
2. $F_{10%}$: fishing mortality at which the slope of the curve of yield versus fishing mortality is 10% of the slope at the origin of the curve;
3. $F_{\text{max}}$: fishing mortality at maximum yield per recruit;
4. $F_{0.1}$: fishing mortality at which the slope of the curve of yield per recruit versus fishing mortality is 10% of the slope at the origin of the curve;
5. $F_{\text{max}}$: fishing mortality that produces the maximum recruitment;
6. $F_{20%}$: fishing mortality that reduces spawning biomass to 20% of the equilibrium level at no fishing pressure.

We also compared the above policies with the abundance-dependent harvest policy currently used by Lake Erie fisheries management agencies (WTG 2011), which adjusts $F$ based on estimated abundance (Figure 1) as follows:

1. $F = 0.1$ when estimated Walleye abundance is below 15 million fish;

![FIGURE 1](image-url) Variable fishing rate harvest policy currently used for managing harvest of Walleyes in Lake Erie.
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**TABLE 1.** Model selection and parameter estimates for Lake Erie Walleye stock–recruitment analysis using nonlinear least-squares regression. Stock–recruit (SR) models: Ricker (equation 1 in the text); B-H: Beverton–Holt (equation 2 in the text). SSB: spawning stock biomass; WR: spring warming rate; GS: age-0 Gizzard Shad index; ER: evidence ratio. Parameters in right-hand columns refer to those in equations (1) and (2) in the text for the respective models.

<table>
<thead>
<tr>
<th>SR models</th>
<th>Variables</th>
<th>AICc</th>
<th>Weight</th>
<th>ER</th>
<th>α</th>
<th>β × 10^-8</th>
<th>γ₁</th>
<th>γ₂ × 10^-5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ricker</td>
<td>SSB, WR</td>
<td>405.938</td>
<td>0.2492</td>
<td>1.00</td>
<td>(0.45, 2.24)</td>
<td>(0.9, 6.0)</td>
<td>(6.1, 15.0)</td>
<td>NA</td>
</tr>
<tr>
<td>B-H</td>
<td>SSB, WR</td>
<td>405.943</td>
<td>0.2485</td>
<td>1.01</td>
<td>(-0.55, 4.4)</td>
<td>(-9, 28.9)</td>
<td>(6.2, 14.8)</td>
<td>NA</td>
</tr>
<tr>
<td>B-H</td>
<td>SSB, WR, GS</td>
<td>405.973</td>
<td>0.2448</td>
<td>1.02</td>
<td>(-0.31, 3.24)</td>
<td>(-7.5, 17.7)</td>
<td>(2.0, 13.4)</td>
<td>(-4.0, 14.5)</td>
</tr>
<tr>
<td>Ricker</td>
<td>SSB, WR, GS</td>
<td>405.992</td>
<td>0.2424</td>
<td>10.28</td>
<td>(0.30, 2.17)</td>
<td>(-0.9, 6.0)</td>
<td>(2.1, 13.7)</td>
<td>(-4.2, 14.7)</td>
</tr>
<tr>
<td>Ricker</td>
<td>SSB</td>
<td>412.676</td>
<td>0.0086</td>
<td>29.05</td>
<td>(0.07, 3.30)</td>
<td>(-0.9, 8.6)</td>
<td>(-4.2, 14.7)</td>
<td>(–4.0, 14.5)</td>
</tr>
<tr>
<td>B-H</td>
<td>SSB</td>
<td>413.218</td>
<td>0.0065</td>
<td>38.106</td>
<td>(-15.73, 27.56)</td>
<td>(-130, 199)</td>
<td>(2.0, 13.4)</td>
<td>(–4.0, 14.5)</td>
</tr>
</tbody>
</table>

(2) \( F = 0.02 \times \text{(abundance in millions)} - 0.2 \) when Walleye abundance is between 15 and 20 million fish;

(3) \( F = 0.0075 \times \text{(abundance in millions)} + 0.05 \) when Walleye abundance is between 20 and 40 million fish;

(4) \( F = 0.35 \) when Walleye abundance is greater than 40 million fish.

Based on \( F \) for each harvest policy, we used population structures from 2007 to 2009 estimated through the stock assessment program as the initial population to compare the following indices among the simulated policies: (1) time period (years) to reach population equilibrium, (2) mean harvest for the time period, (3) variance of yield for the time period, and (4) CV (SD/mean) of yield for the time period. We assumed that the derived stock–recruitment relationship holds for the simulation period.

**RESULTS**

Three recruitment models were ranked by AICc to be equally supported by the data (Table 1). All included spring warming rate and one included fall abundance of age-0 Gizzard Shad as factors. However, because the 95% CI for the density-dependent parameter, \( \beta \), for the highest-ranking Beverton–Holt model included zero, the model was not supported given these data. Therefore, the Ricker model with spring warming rate as an independent variable was selected as the best stock–recruitment model representing the relationship under average environmental conditions (Figure 2). Although this model was selected as the best stock–recruitment model, it explained only 39% of the variation in Walleye recruitment. Moreover, this model tended to overestimate Walleye recruitment during the late 1990s and 2000s (Figure 3). Coincidentally, on average, Walleye recruitment during the late 1990s and 2000s was lower than that during the 1980s (Figure 3).

Using the Ricker model, we estimated carrying capacity under average environmental conditions and no harvest as 45 million kg for age-2 and older Walleyes and 46 million kg for the spawning-stock biomass (i.e., age 4 and older). The modeled equilibrium age distribution had a smaller proportion of younger fish and a higher proportion of older fish than the observed average age distribution from 1978 to 2008 estimated by the WTG (2009) (Figure 4). Under no harvest, the equilibrium percentage of age-2 Walleyes was 27%, which is 10 percentage points lower than the observed 37%. Observed and modeled proportions were similar for fish ages 4 and 5, but then diverged again for older fish. For Walleyes age 7 and older, the modeled stable age distribution was 20% compared with the currently observed 5%.

Equilibrium fishing mortality under current harvest policy for the simulated population was \( F_{eq} = 0.29 \) (Table 2; Figure 5). The population reached equilibrium in 76 years, averaging a yield of 6.4 million kg. Fishing mortality at MSY was marginally lower (\( F_{MSY} = 0.28 \)), producing less than 1% gain in yield. At \( F_{MSY} \) the population took 46 more years to reach equilibrium than at \( F_{eq} \), but variance in average annual yield was reduced by

![Figure 2](image-url)
FIGURE 3. Observed (solid circles) and predicted year-class strength (number at age 2) by the selected Ricker stock–recruitment model with spring warming rate as covariate for Walleye in Lake Erie.

64%. Mean yield at $F_{eq} = 0.25$ was marginally lower than that at $F_{eq}$, time to equilibrium was 27 years higher, and variance in yield was 42% lower. At $F_{0.1} = 0.36$, variance in yield was minimized, but yield decreased by 13% and time to equilibrium nearly tripled compared with that at $F_{eq}$. The two highest $F$ scenarios, $F_{max} = 0.38$ and $F_{stp} = 0.39$, resulted in greatly reduced variance but also reduced average annual yields (by 28% at $F_{max}$ and by 19% at $F_{stp}$) and took 3.6–4.5 times as many years to reach equilibrium compared with $F_{eq}$. Under the most conservative harvest policy of $F_{maxr} = 0.17$, variance was maximized, years to reach equilibrium was minimized, and mean annual yield was 17% below equilibrium yield.

DISCUSSION

Our best regression model of the stock–recruitment relationship for Lake Erie Walleyes, based on data for the 1978 through 2006 year-classes, included just spawning-stock size and spring warming rate as the independent variables, and explained 39% of the variation in Walleye recruitment. Therefore, Walleye recruitment in Lake Erie appeared to be primarily dependent on factors other than spawning-stock size and spring warming rate. Using data for the 1979 through 1993 year-classes, Madenjian et al. (1996) also found that spawning-stock size and spring warming rate explained only about 40% of the variability in Walleye recruitment, but the addition of age-0 Gizzard Shad abundance to the regression model increased the amount of Walleye recruitment variability explained by the model to 92%.

There are several potential explanations for the loss of the Gizzard Shad term in the Walleye stock recruitment model for Lake Erie. One possibility is that age-0 Gizzard Shad abundance in the fall had lost its influence on Walleye recruitment sometime during the late 1990s or 2000s. However, age-0 Gizzard Shad has remained the majority, in terms of numbers and mass, of the fall diet of Lake Erie Walleyes through the 1990s and 2000s (ODNR 2011). A second possibility is that Gizzard Shad density needs to be at some minimum threshold to have an influence on Walleye energy reserves and that Gizzard Shad density has dropped below that threshold. A third possibility for the lack of inclusion of the Gizzard Shad term in our best regression model was that the ability of fishery management agencies to accurately track the year-to-year variability in the abundance of age-0 Gizzard Shad

<table>
<thead>
<tr>
<th>Variable</th>
<th>$F_{eq}$</th>
<th>$F_{MSY}$</th>
<th>$F_{ey}$</th>
<th>$F_{max}$</th>
<th>$F_{0.1}$</th>
<th>$F_{maxr}$</th>
<th>$F_{stp}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average annual fishing mortality</td>
<td>0.29</td>
<td>0.28</td>
<td>0.25</td>
<td>0.38</td>
<td>0.36</td>
<td>0.17</td>
<td>0.39</td>
</tr>
<tr>
<td>Years to reach equilibrium</td>
<td>76</td>
<td>122</td>
<td>103</td>
<td>344</td>
<td>231</td>
<td>56</td>
<td>276</td>
</tr>
<tr>
<td>Mean yield $\times 10^5$ kg</td>
<td>6.40</td>
<td>6.45</td>
<td>6.33</td>
<td>4.63</td>
<td>5.58</td>
<td>5.30</td>
<td>5.18</td>
</tr>
<tr>
<td>Variance of yield $\times 10^{10}$</td>
<td>26.5</td>
<td>9.58</td>
<td>15.5</td>
<td>12.0</td>
<td>3.19</td>
<td>32.0</td>
<td>6.42</td>
</tr>
<tr>
<td>CV</td>
<td>0.081</td>
<td>0.048</td>
<td>0.062</td>
<td>0.075</td>
<td>0.032</td>
<td>0.107</td>
<td>0.049</td>
</tr>
</tbody>
</table>
has decreased during the 1990s and 2000s. This explanation was supported by two lines of evidence. First, the abundance of age-0 Gizzard Shad in Lake Erie peaked during the 1980s but then declined during the early 1990s in a long-term survey conducted in shallower waters ($\leq 6.1$ m) independent of the one we used for our estimate of Gizzard Shad abundance (Stapanian et al. 2007). Similarly, Walleye recruitment was higher during the 1980s than during the late 1990s and 2000s. Thus, although age-0 Gizzard Shad abundance and Walleye recruitment has weakened during the 1990s and 2000s. Furthermore, bottom-trawl survey effort in shallower waters, where age-0 Gizzard Shad density tends to be higher, has declined during the late 1990s and 2000s (Ontario Ministry of Natural Resources and Ohio Department of Natural Resources, unpublished data). Taken together, these results suggested a diminishment in the ability to accurately track the year-to-year changes in age-0 Gizzard Shad abundance.

Another possibility for the loss of the Gizzard Shad term in the stock–recruitment model is that thermal influences on Walleye metabolism adversely affects fat reserves generated from consuming large amounts of Gizzard Shad. Hokanson (1977) reported that 185 d of temperatures $< 6^\circ C$ after 31 October were the optimal thermal conditions for maturation of Walleye gonads. A period of 185 d after 31 October ends on 4 May. Temperatures typically reach $8^\circ C$ in early April; hence, the maximum period for temperatures of $< 6^\circ C$ in Lake Erie is shorter than 185 d. For the period 1979–1993 modeled by Madenjian et al. (1996) temperatures at the Union Municipal Water Intake, Leamington, cooled down to and remained below $6^\circ C$ on 22 November on average; for the period 1994–present, temperatures cooled to $6^\circ C$ on 5 December on average, 13 d later. Between 1 November and 31 March there were, on average, 125 d of temperature $< 6^\circ C$ from 1979 through 1993 but only 112 d from 1994 to the present. Between 1 November and 31 March there were 387 mean accumulated degree-days from 1979 to 1993 compared with 572 from 1994 to the present. Jones et al. (2006) also observed that the duration of winter in Lake Erie has decreased since the 1960s. According to Hokanson’s (1977) thermal criterion, conditions for maturation of Walleye gonads in Lake Erie have been deteriorating as temperatures have been rising over the past couple of decades. Under the mechanism proposed by Henderson and Nepszy (1994) in which fat reserves developed from consuming Gizzard Shad in autumn are carried over to spring, metabolic costs from warmer temperatures in late autumn and throughout winter may be offsetting energetic gains. Thus, fish are presently in poorer condition at the onset of spawning than they were in the past. Poorer overall condition and poorer gonad condition may account for poorer recruitment in recent years.
Coupling Walleye recruitment models with population simulations facilitates evaluation of the trade-offs inherent to management of harvest. Changes in yield and variation in yield can be evaluated in the context of the particular stock–recruitment relationship for the population being studied. Outcomes of any such exercise will necessarily be dependent on the particular stock–recruitment model used. For example, the value of the initial slope parameter $\alpha$ of the Ricker stock–recruitment relationship had a substantial influence on the population simulation results. For the stock–recruitment model that we used in the simulation modeling, the fishing rate that produced equilibrium maximum sustainable harvest is 0.28, and rates above that level are less efficient and may result in recruitment overfishing. However, under different stock–recruitment parameters, the relative positions of the fishing rates presented in Figure 5 may change greatly. Thus, conclusions will vary from one model (one set of parameters) to another. This result and because our new model differed in its parameter values from those presented by Madenjian et al. (1996) demonstrated that there is value in periodically updating stock–recruitment models and assessing uncertainty in model parameters.

Three limitations of our simulation model preclude firm conclusions from the model outcomes. First, the Lake Erie Walleye population is composed of more than one stock (Stepien and Faber 1998; Strange and Stepien 2007), yet estimates of spawning-stock size and recruitment are not presently available for individual stocks. Second, our simulation study was carried out deterministically and did not consider model uncertainties. However, complete evaluation of management strategies needs to incorporate the uncertainties from various sources, including the stock–recruitment relationship, stock assessment model, and fisheries-dependent and independent surveys (Berger 2011). Because we lack stock–specific stock–recruitment models, a thorough evaluation that includes stochastic sources of variation is not presently possible. Third, the loss of the Gizzard Shad term reduces the predictive power of the stock–recruitment model compared with previous models. We suspect that age-0 Gizzard Shad abundance has continued to have an important effect on Lake Erie Walleye recruitment, but the ability to track year-to-year variability in age-0 Gizzard Shad abundance has diminished during the late 1990s and 2000s. We recommend research be directed at better quantifying age-0 Gizzard Shad abundance in Lake Erie, developing stock–specific stock–recruitment models, and assessing uncertainty in model parameters.

ACKNOWLEDGMENTS

We thank the Lake Erie Committee’s Walleye Task Group and Forage Task Group for providing data and for supporting this research. Water temperature data were provided by G. Dunmore of the Ontario Clean Water Agency, C. Vandergoot, A. Cook, and three anonymous reviewers provided constructive reviews. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government or Canadian Government. This article is contribution 1778 of the U.S. Geological Survey, Great Lakes Science Center.

REFERENCES


ODNR (Ohio Department of Natural Resources). 2011. Ohio’s Lake Erie fisheries, 2010. ODNR, Division of Wildlife, Columbus.


North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

Effects of Catfish Angler Catch-Related Attitudes on Fishing Trip Preferences

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Published online: 08 Oct 2013.

To cite this article: Clifford P. Hutt, Kevin M. Hunt, J. Warren Schlechte & David L. Buckmeier (2013) Effects of Catfish Angler Catch-Related Attitudes on Fishing Trip Preferences, North American Journal of Fisheries Management, 33:5, 965-976, DOI: 10.1080/02755947.2013.822443

To link to this article: http://dx.doi.org/10.1080/02755947.2013.822443

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ARTICLE

Effects of Catfish Angler Catch-Related Attitudes on Fishing Trip Preferences

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Abstract
To assist the Texas Parks and Wildlife Department in developing a statewide catfish management plan, we surveyed 1,078 freshwater catfish anglers to examine their catch-related attitudes and trip preferences by using a stated choice experiment. Respondents were presented with a series of paired hypothetical fishing trip scenarios for catfish and were asked to choose the trips that they most preferred. Trip scenarios varied by the relative number of catfish that were caught and harvested, relative size of catfish that were caught, water body type, level of site development, and distance traveled (i.e., representing travel costs). A conditional logit model was fitted to analyze angler preferences by determining the influence of trip attributes on angler choice. Model results indicated that anglers' choice of fishing trips was most influenced by distance traveled, followed by the catch-related aspects of the trip, with catfish size having a greater influence than the numbers of catfish caught or harvested. We then conducted a latent class analysis of catfish anglers, which involved the use of cluster analysis to assign anglers to five groups based on their catch-related attitude scores, and we reran the stated choice model for each cluster. Clusters ranged from harvest-oriented anglers to size-oriented anglers that were focused on catching large trophy fish. Results from these models can assist fisheries managers in setting management goals and objectives that best meet the needs of their clientele.

Freshwater catfish species (Channel Catfish Ictalurus punctatus, Blue Catfish I. furcatus, and Flathead Catfish Pylodictis olivaris) have not traditionally been the focus of most inland fisheries agencies (Michaletz and Dillard 1999). However, this is changing in many of the states where catfish are frequently targeted by anglers. The U.S. Fish and Wildlife Service reported that in 2006, 1.035 million (56%) Texas anglers spent 11.6 million days pursuing catfish—more than any other species of fish. This interest in fishing for catfish has prompted the Texas Parks and Wildlife Department (TPWD) to initiate a plan to guide catfish management and research activities. One important element needed for the successful management of catfish is to understand the desires and motivations of Texas’ catfish anglers (Kellert and Brown 1985; Connelly et al. 1990; Fisher 1997). Previous studies of catfish anglers have examined preferred fishing locations (Wilde and Riechers 1994; Schramm et al. 1999; Reitz and Travnichek 2008), consumption and regulations (Wilde and Riechers 1994), and angler motivations (Fedler and Ditton 1994; Wilde and Ditton 1999). Although these previous studies were useful, there were concerns that the studies were oversimplified. Typically, respondents were asked single-item questions to rate the importance of individual characteristics of the angling experience. Anglers were rarely asked to make explicit trade-offs, and there was no good way to quantify such trade-offs. The TPWD decided that a new approach was needed to address these shortcomings.

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Received December 17, 2012; accepted June 27, 2013
Published online September 23, 2013
We chose to employ a discrete stated choice model (SCM) approach in an effort to obtain a more comprehensive picture of the trip preferences of catfish anglers (Aas et al. 2000; Gillis and Ditton 2002; Oh et al. 2005; Dorow et al. 2010; Carlin et al. 2012). Specifically, we used an SCM approach to examine how catch-related trip attributes (number of catfish caught, number of catfish harvested, and size of catfish caught) and non-catch-related trip attributes (site development, type of water body, and distance traveled) influenced the selection of hypothetical fishing trip scenarios among Texas-resident catfish anglers. Additionally, we incorporated data on anglers’ catch-related attitudes into a latent class analysis (LCA) to gain a better understanding of catch-related preference heterogeneity among Texas catfish anglers. Unlike previous methods of examining angler preferences, the SCM requires anglers to make choices between hypothetical trip or management scenarios, thus giving this method the added benefit of requiring anglers to make trade-offs between alternatives. In doing so, SCM experiments give researchers and managers better insights into which aspects of a fishing experience are truly important to anglers (Louvière and Timmermans 1990; Hunt 2005).

Stated choice models derive individual preferences and utility by asking individuals to make choices between hypothetical commodities, or scenarios, which vary over several attributes (Louvière and Timmermans 1990; Hunt 2005; Oh et al. 2005). In studies designed to derive angler preferences, the hypothetical scenario in question is often a fishing trip or fishing site (Gillis and Ditton 2002; Oh et al. 2005; Dorow et al. 2010). Each scenario used to fit the choice model consists of multiple attributes that make up the primary characteristics of the fishing trip, and these attributes are varied along several levels from one scenario to the next. Respondents may be asked to rate their level of preference for each scenario, to rank a series of scenarios from most to least preferred, or to choose their most preferred scenario from a series of paired scenarios (Louvière and Timmermans 1990; Boxall and Adamowicz 2002). With individual choice, ranks, or ratings serving as the dependent variable and scenario attributes serving as the independent variables, the researcher is able to (1) determine the extent to which each attribute influences trip preferences and (2) estimate the part-worth utilities derived from individual attribute levels (Louvière and Timmermans 1990; Gillis and Ditton 2002). Finally, coefficients generated by the model can be used to estimate the probability that an angler will choose a given hypothetical scenario (Blamey et al. 1999).

Several studies have used SCMs to examine the effect of fishing regulations (e.g., length limits, creel limits, and equipment restrictions), angler expectations (i.e., size and number of fish caught), and travel costs (i.e., distance traveled) on trip choice and preferences. Aas et al. (2000) used an SCM to examine the effect of three regulations and expectations of average fish size and number of fish caught on the trip choices made by anglers targeting Brown Trout Salmo trutta in Norway. Aas et al. (2000) found that an angler’s probability of choosing a given trip decreased as regulations became stricter and that the probability increased as angler expectations of the size and number of fish caught increased. Gillis and Ditton (2002) used an SCM to examine the preferences of Atlantic billfish (Istiophoridae) anglers, and they found strong support for the establishment of no-kill tournaments and hook restrictions. Oh et al. (2005) used an SCM to study the effect of four regulations, average fish size, catch probability, and trip cost on the fishing trip choices and willingness to pay (WTP) of Texas anglers targeting Red Drum Sciaenops ocellatus. Dorow et al. (2010) used an SCM to study the management preferences of European Eel Anguilla anguilla anglers in Germany and found that while the anglers supported moderate increases in minimum size and bag limits, they were opposed to large changes that would result in significant harvest reductions. Carlin et al. (2012) used an SCM to examine the marginal effects of fishing regulations and catch expectations on the site choice preferences of Walleye Sander vitreus anglers. These studies all concluded that the SCM approach offered substantial benefits to fisheries managers by illustrating the degree to which different management alternatives affected angler preferences.

Despite the apparent usefulness of SCMs for examining the intricacies of angler preferences, most angler preference studies have instead relied upon revealed preference models (Hunt 2005; Carlin et al. 2012). Revealed preference methods utilize data on actual behavioral choices (e.g., selection of fishing sites) and related attribute data to assess individual preferences (Kaoru et al. 1995; Dorr et al. 2002). Many economists favor revealed preference methods because of the methods’ reliance on actual behavior, as opposed to the use of hypothetical scenarios in stated preference methods, which rely on the imperfect relationship between behavioral intentions and actual behavior (Ajzen 1991; Ajzen et al. 1996; Diamond and Hausman 1994). However, other researchers have pointed out that the hypothetical nature of stated preference studies can also be a strength, as it allows for the examination of novel scenarios and the influence of attributes from which data may not be readily available for use in revealed preference studies (Louvière and Timmermans 1990; Boxall and Adamowicz 2002; Hunt 2005; Carlin et al. 2012).

Several researchers have also argued that another failing of many SCM studies is their use of conditional or multinomial logit models that assume homogeneity of preferences across the surveyed population (Train 1998; Provencher et al. 2002; Morey et al. 2006). In reality, preferences are rarely homogeneous whether the population in question is composed of anglers or any other group. Researchers have proposed several methods of addressing preference heterogeneity in SCM studies. One method involves interacting the scenario attributes with relevant descriptive variables within the choice model (Dellaert and Lindberg 2003; Carlin et al. 2012). These descriptive variables could be sociodemographic, behavioral, or attitudinal in nature and would indicate how preferences for given attributes may differ across the range of the descriptive variable. Another method uses an LCA approach to divide individuals into groups based
on similar characteristics or attitudes, and then separate SCMs are run for each group (Boxall and Adamowicz 2002; Morey et al. 2006; Oh and Ditton 2006). Studies utilizing LCAs have concluded that running separate SCMs on different subgroups provided greater insight into the heterogeneity of preferences within the study populations and, more importantly, into the causes of that heterogeneity.

We chose to incorporate data on catfish anglers’ catch-related attitudes (also called consumptive orientation or catch orientation) into our SCM by using the two approaches described above to provide insight into how catch-related attitudes influence angler preferences and explain preference heterogeneity among Texas catfish anglers. Catch orientation of recreational anglers has been defined as an individual’s “disposition to catch fish, attitudes toward keeping or releasing fish caught, and the importance of the number and size of fish caught” (Anderson et al. 2007: 181). Many studies of angler motivations have found that motives unrelated to catch are generally ranked higher than catch-related motives (Driver and Cooksey 1977; Fedler and Ditton 1994; Fisher 1997), whereas other studies have found that catch-related aspects of fishing trips are better predictors of fishing satisfaction (Arlinghaus 2006; Hutt and Neal 2010). Anglers’ attitudes toward these catch-related aspects of fishing will greatly influence their opinions regarding management goals and regulations and their choice of fishing trips. It is therefore reasonable to assume that incorporating catch-related attitude data into the SCM would help to explain additional variation in individual choice and preference heterogeneity.

Our goal was to use an SCM approach to develop a better understanding of Texas catfish anglers’ trip preferences and how these preferences might be influenced by angler catch-related attitudes. Thus, we used an LCA (i.e., cluster analysis) that divided anglers into groups (i.e., market segments) based upon their catch-related attitudes. Using this methodology, we estimated catfish anglers’ part-worth utilities for catch-related and non-catch-related trip attributes, both overall and across subgroups of anglers with similar attitudinal profiles.

METHODS

Questionnaire Design and Implementation

Survey implementation.—The sample for the mail survey consisted of 1,078 resident anglers who had responded to the 2009 Survey of Texas Anglers conducted by TPWD. Respondents were selected for the catfish angler study if they (1) indicated that they had fished for catfish in the previous year or (2) listed “catfish” or a particular catfish species as one of their three most preferred freshwater fish to catch in Texas. We developed and implemented a second 11-page, self-administered mail questionnaire to collect the necessary study data. The first five pages collected data on general angling behavior and catch-related attitudes. Results from that portion of the survey are reported by Hunt et al. (2013). The next four pages were composed of the questions needed for the SCM and their associated instructions. The final page consisted of several sociodemographic questions. The survey was implemented via Dillman’s (2007) tailored design method to increase the angler response rate. All procedures were approved by the Mississippi State Institutional Review Board (IRB) for the Protection of Human Subjects (IRB Docket 10-102).

Catch-related attitudes scale.—Participants were asked to respond to a 12-item scale (Anderson et al. 2007) pertaining to their catch-related attitudes toward catfish. The scale was designed to measure four constructs associated with catch orientation (catching something [CATSOM], catching numbers of fish [CATNUM], catching large/trophy fish [CATLAR], and keeping fish [KEEPFISH]). Respondents were instructed to indicate whether they agreed or disagreed with each item on a five-point, Likert-type scale (response format: 1 = strongly disagree; 2 = disagree; 3 = neutral; 4 = agree; 5 = strongly agree). Three items were reverse coded for analysis purposes because they were written to solicit a response inverse to that of other items within their construct, thereby avoiding response set bias (Maranell 1974).

Stated choice scenarios.—The catfish angler questionnaire included a series of choice sets that were designed to collect data for estimation of an SCM (Figure 1). Attributes and levels used in the choice sets were selected based on discussions with fisheries biologists and researchers from TPWD (Table 1). Attributes were related to the number of catfish caught during the fishing trip, the number of catfish harvested, the average size of catfish caught, the type of water body on which the trip took place, the level of site development at the fishing site, and the distance traveled to the site. Number of levels per attribute was limited to three to (1) reduce the number of choice sets that would have to be generated to fit the models, (2) limit respondent burden, and (3) minimize costs (Oh et al. 2005).

A fractional factorial design was used to develop a tractable number of choice sets while still maximizing the orthogonality needed to fit the necessary SCMs (Louvière 1988; Bennett and Adamowicz 2001). To further minimize respondent burden, we also blocked choice sets into uncorrelated groups to reduce the number of choice sets presented to each individual (Bennett and Adamowicz 2001). The Statistical Analysis Systems (SAS) macros %mktex and %mktblock were used to generate a fractional factorial design of 54 choice sets that were divided into nine blocks of six paired trip comparisons (Kuhfeld 2005). Separate questionnaire versions were then designed for each of the nine blocks of paired trip comparisons, and 119–120 individuals were randomly assigned to receive each version.

Data Analysis

Nonresponse analysis.—To determine whether we needed to adjust the population estimates for nonresponse bias (Fisher 1996), logistic regression was used to assess whether age, gender, or residence location had a significant effect on individual response probabilities for both the 2009 Texas Statewide Angler Survey and the 2010 Survey of Texas Freshwater Catfish Anglers. Data used in the nonresponse analyses were taken from TPWD’s electronic database of licensed anglers. A detailed
FIGURE 1. An example of the choice sets presented in a 2010 Texas catfish angler survey that was used to collect data for the purpose of fitting a stated choice model. The survey respondent was presented with choice sets that each included two hypothetical fishing trip scenarios and a “neither” option. Choice set scenarios were varied over six trip attributes (see Table 1 for attribute levels). Respondents were asked to indicate which hypothetical fishing trip they would prefer to take or whether they were interested in neither trip.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Trip A</th>
<th>Trip B</th>
</tr>
</thead>
<tbody>
<tr>
<td>CATCH</td>
<td>Same as usual</td>
<td>Half as many caught as usual</td>
</tr>
<tr>
<td>HARVEST</td>
<td>Twice as many harvested as usual</td>
<td>None harvested</td>
</tr>
<tr>
<td>SIZE</td>
<td>Smaller than usual, many sub-legal</td>
<td>Smaller than usual, many sub-legal</td>
</tr>
<tr>
<td>TYPE OF WATER</td>
<td>Small pond or reservoir (under 100 acres)</td>
<td>Large reservoir (over 100 acres)</td>
</tr>
<tr>
<td>LEVEL OF SITE DEVELOPMENT</td>
<td>Undeveloped site</td>
<td>Basic site development</td>
</tr>
<tr>
<td>DISTANCE</td>
<td>Located 11-100 miles from home</td>
<td>Located over 100 miles from home</td>
</tr>
</tbody>
</table>

Which trip do you MOST prefer?  
(Circle only one)  
| TRIP A | TRIP B | NEITHER |

Downloaded by [Department Of Fisheries] at 21:10 27 October 2013
TABLE 1. Attribute levels used in the stated choice experiment conducted in the follow-up survey of Texas catfish anglers (April–June 2010). Level 2 represents a “status quo” scenario, which is needed as a reference point for variations. Effects coding (−1, 0, 1) used in the stated choice analysis is presented in parentheses for all attributes except distance traveled, for which travel cost values (2011 US$) are reported.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Level 1</th>
<th>Level 2</th>
<th>Level 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catch</td>
<td>Half as many fish caught as usual (−1)</td>
<td>Same as usual (0)</td>
<td>Three times as many fish caught as usual (1)</td>
</tr>
<tr>
<td>Harvest</td>
<td>No fish harvested (−1)</td>
<td>Same as usual (0)</td>
<td>Twice as many fish harvested as usual (1)</td>
</tr>
<tr>
<td>Size</td>
<td>Fish smaller than usual, many sublegal (−1)</td>
<td>Same as usual (0)</td>
<td>Fish larger than usual, some of trophy size (1)</td>
</tr>
<tr>
<td>Water body type</td>
<td>Large (&gt;100 acres) reservoir (−1)</td>
<td>River or stream (0)</td>
<td>Small pond or small (&lt;100 acres) reservoir (1)</td>
</tr>
<tr>
<td>Level of site development</td>
<td>Undeveloped site: rustic shoreline access, with no boat ramps, restrooms, or picnic tables (−1)</td>
<td>Basic site development: gravel shoreline trails with a boat launch, portable restroom facilities, and picnic tables (0)</td>
<td>Well-developed site: well-maintained trails, some paved, with fishing piers, marinas, permanent restroom facilities, and sheltered picnic areas (1)</td>
</tr>
<tr>
<td>Distance traveled and associated costs&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Located within 10 mi of home ($11.30)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Located 11–100 mi from home ($56.50)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Located over 100 mi from home ($169.50)&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Travel costs were calculated based on round-trip mileage costs (derived by AAA 2010).

<sup>b</sup>Travel cost values were used in the overall models and the models for angler clusters 1–5.

description of the methods and results from our nonresponse analysis is provided by Hunt et al. (2013). Respondent sampling weights were used to adjust all frequencies, sample means, proportions, and univariate statistical analyses to correct for nonresponse bias. However, response weights were not used to adjust responses to the SCM due to its experimental nature.

**Confirmatory factor analysis.**—Confirmatory factor analysis in LISREL (Kelloway 1998) was used to validate the four-construct model of catch-related attitudes. We evaluated model fit using the Satorra and Bentler (1988) chi-square (S-B \( \chi^2 \)), the goodness-of-fit index (GFI), the comparative fit index (CFI), and the root mean square error of approximation (RMSEA; Kelloway 1998). The S-B \( \chi^2 \) was used to assess model fit due to our use of ordinal data, which are neither continuous nor multivariate normal by definition and thus required the use of both a standardized model and an asymptotic covariance matrix (Jöreskog 2002). Validly measured constructs should exhibit item factor loadings (\( \lambda \)) of 0.7 or greater, composite reliability (CR) scores of 0.7 or greater, and average variance extracted (AVE) estimates of 0.5 or greater (Kelloway 1998; Garver and Mentzer 1999). Acceptable models should have nonsignificant \( \chi^2 \) statistics, GFI and CFI values greater than 0.90, and RMSEA values less than 0.05 (Kelloway 1998; Garver and Mentzer 1999). We used the GFI, CFI, and RMSEA as fit statistics because \( \chi^2 \) statistics are highly sensitive to sample sizes larger than 250 and may lead to the rejection of acceptable models when used in isolation to judge model fit (Garver and Mentzer 1999).

**Latent class analysis and stated choice models.**—We used an LCA approach to address the effects of catch-related attitudes on preference heterogeneity. Hierarchical cluster analysis (Ward’s method) and squared Euclidean distance (Hair et al. 2010) in SPSS software were used to divide catfish anglers into groups based on their catch-related attitude construct scores. The final number of clusters was determined by comparing the degree of change in the clustering coefficient by number of clusters per iteration of the analysis (Aldenderfer and Blashfield 1984). The clustering coefficient serves as a measure of the between-cluster variation given the number of clusters in the selected solution, with a sharp increase indicating that two highly dissimilar clusters have been combined. Stated choice models were then fitted for each group and the overall sample by using the TRANSREG and PHREG procedures in SAS (Kuhfeld 2005; SAS 2008). The TRANSREG procedure was used to code attribute data via effects coding (Bech and Gyrd-Hansen 2005). In effects coding, the attribute level that was expected to be least preferred was assigned a code of −1, the level hypothesized to be the most preferred was given a code of 1, and the status quo scenario was given a code of 0 (Table 1). A travel cost value was calculated for each level of the distance traveled attribute and was used as a continuous variable in the SCM so that implicit values, or WTP, could be calculated by dividing each attribute level’s coefficient by the travel cost coefficient. The three levels of distance traveled presented in the choice scenarios were recoded to 10, 50, and 150 mi, respectively. Travel cost was calculated for each distance level as the round-trip driving costs for that distance (Table 1) assuming a composite average operating cost of US$0.565 per mile (AAA 2010). This operating cost estimate included fuel, maintenance, tire, insurance, license, depreciation, and finance costs associated with operation of a vehicle.
driving 15,000 mi/year (AAA 2010). However, all WTP estimates presented should be considered conservative estimates because we did not include an opportunity cost of time estimate in our calculations of travel costs (Parson 2003).

After the final coding of attribute levels, the choice models were fitted using the PHREG procedure, which fits a conditional logit model (Kuhfeld 2005). In a conditional logit model, the dependent variable (in this case, choice) is binary coded depending on whether the given scenario was chosen or not; independent variables were the coded scenario attributes. Coefficients were calculated for categorical attribute levels coded as either –1 or 1 and for trip cost. Calculated coefficients represented the part-worth utilities of individual attribute levels (Louvière 1988; Blamey et al. 1999; Gillis and Ditton 2002; Oh and Ditton 2005). Finally, the results of the individual LCA models were used to calculate choice probabilities and WTP estimates for five hypothetical trip scenarios across the identified latent groups by using the equations described by Blamey et al. (1999).

RESULTS

Catch-Related Attitudes

Confirmatory factor analysis indicated that a four-construct, 12-item measurement model of catch-related attitudes provided a good fit to the data (S-B \( \chi^2 = 92.30, df = 48 \); GFI = 0.94; CFI = 0.93; RMSEA = 0.045; Table 2). Factor loadings, CR scores, and AVE scores are reported in Table 2. Most (10 of 12) of the items used in the measurement model exhibited fair (\( \lambda > 0.6 \)) to good (\( \lambda > 0.7 \)) factor loadings, indicating acceptable convergent validity. Three of the four constructs exhibited good CR (\( > 0.7 \)) and AVE (\( > 0.5 \)) scores, indicating strong content and discriminant validity (CATSOM: CR = 0.75, AVE = 0.51; CATNUM: CR = 0.77, AVE = 0.53; KEEPFFISH: CR = 0.81, AVE = 0.60). Conversely, the fourth construct (CATLAR: CR = 0.68, AVE = 0.42) exhibited fair scores for content and discriminant validity.

Overall Stated Choice Model

Respondents chose one of two hypothetical fishing trips over the “neither” option in 86% of the choice scenarios for which data were collected. This is reflected in the positive sign for the alternative-specific constant coefficient in all models (Table 3). Among trip-related attributes, distance traveled (representing angler costs) was a significant determinant of choice for all models (Table 3). In the overall model, the catch-related coefficients were all significant (\( P < 0.001 \)) with signs in the expected directions, indicating that decreases in catch, harvest, and size of catfish caught had a significantly negative effect on angler utility, while increases in catch-related attributes had a positive

<table>
<thead>
<tr>
<th>Construct and factor item</th>
<th>Mean</th>
<th>SD</th>
<th>( \lambda )</th>
<th>CR</th>
<th>AVE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catching something (CATSOM)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A fishing trip can be successful even if no fish are caught</td>
<td>3.85</td>
<td>1.07</td>
<td>0.61</td>
<td>0.75</td>
<td>0.51</td>
</tr>
<tr>
<td>If I thought I wouldn’t catch any fish, I wouldn’t go fishing</td>
<td>2.64</td>
<td>1.23</td>
<td>0.66</td>
<td>0.51</td>
<td>0.66</td>
</tr>
<tr>
<td>When I go fishing, I’m not satisfied unless I catch something</td>
<td>2.68</td>
<td>1.12</td>
<td>0.85</td>
<td>0.51</td>
<td>0.66</td>
</tr>
<tr>
<td>Catching numbers of fish (CATNUM)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.77 0.53</td>
</tr>
<tr>
<td>The more fish I catch, the happier I am</td>
<td>3.85</td>
<td>1.06</td>
<td>0.68</td>
<td>0.77</td>
<td>0.53</td>
</tr>
<tr>
<td>A successful fishing trip is one in which many fish are caught</td>
<td>3.27</td>
<td>1.11</td>
<td>0.87</td>
<td>0.77</td>
<td>0.53</td>
</tr>
<tr>
<td>I’m happiest with a fishing trip if I at least catch the daily bag limit of fish</td>
<td>2.82</td>
<td>1.12</td>
<td>0.60</td>
<td>0.77</td>
<td>0.53</td>
</tr>
<tr>
<td>Catching large/trophy fish (CATLAR)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I would rather catch one or two big fish than 10 smaller fish</td>
<td>2.99</td>
<td>1.04</td>
<td>0.52</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>I’m happiest with a fishing trip if I catch a challenging game fish</td>
<td>3.55</td>
<td>0.98</td>
<td>0.68</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>I like to fish where I know I have a chance to catch a “trophy” fish</td>
<td>3.14</td>
<td>0.98</td>
<td>0.72</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>Keeping fish (KEEPFFISH)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I usually eat the fish I catch</td>
<td>3.92</td>
<td>1.16</td>
<td>0.54</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>I’m just as happy if I don’t keep the fish I catch</td>
<td>3.51</td>
<td>1.07</td>
<td>0.83</td>
<td>0.81</td>
<td>0.60</td>
</tr>
<tr>
<td>I’m just as happy if I release the fish I catch</td>
<td>3.54</td>
<td>1.07</td>
<td>0.91</td>
<td>0.81</td>
<td>0.60</td>
</tr>
</tbody>
</table>

\(^{a}\text{Item was reverse coded for CFA, and summated scores were used for cluster analysis. Means and SDs were calculated with raw data.}\)

\(^{b}\text{Satorra–Bentler } \chi^2 = 92.30 (df = 48), \text{ goodness-of-fit index (GFI) } = 0.94, \text{ comparative fit index (CFI) } = 0.93, \text{ and root mean square error of approximation (RMSEA) } = 0.045. \text{ Acceptable fit is indicated by a nonsignificant } \chi^2 \text{ statistic, GFI and CFI values greater than 0.90, and an RMSEA less than 0.05 (Kelloway 1998; Garver and Mentzer 1999).} \)
effect (Table 3). Size of catfish caught was the second-best predictor of respondent choice after distance traveled (Table 3); the no-harvest level had the next-greatest negative impact on trip choice after reduced size (Table 3). The reduced harvest level had a greater effect on choice than the reduced catch level, whereas the opposite was true for the increased catch and harvest levels (Table 3).

The final two attributes included in the SCMs were water body type and the level of site development. These attributes had the least impact on respondent choice in the overall model. The status quo scenario for these attributes involved a trip on a river or stream with basic access site development (i.e., a boat launch and minimal amenities; Table 1). There was no significant difference in angler utility between trips on rivers or streams and trips taken on large reservoirs, indicating that anglers were indifferent toward fishing on one or the other (Table 3). However, there was a significant negative relationship between trip choice and fishing on a small reservoir (Table 3). The SCMs also indicated that angler utility did not significantly differ between fishing at a site with a basic level of development and fishing at a well-developed site, but angler utility was significantly reduced for trips to undeveloped sites that did not provide a boat ramp (Table 3).

**Latent Class Analysis**

We identified five clusters of anglers based on four constructs of catch-related attitudes using hierarchical cluster analysis with Ward’s method in SPSS. A sharp increase in the clustering coefficient after the five-cluster solution indicated that further combinations of clusters would only serve to group individuals with dissimilar construct scores. Groups ranged in size from 37 to 146 individuals (8–32% of the sample; Table 3). Significant differences were found across groups for the most preferred catfish species ($P < 0.001$), typical size of catfish caught ($P < 0.001$), and typical number of catfish harvested ($P = 0.009$; Table 4). However, the typical number of catfish caught did not differ significantly across groups ($P = 0.148$), suggesting that there was a significant difference in harvest rate among groups (Table 4).

Cluster 1 ($n = 146; 32\%$ of the sample) was labeled “casual anglers” because these anglers exhibited relatively low summed scores on all four catch-related attitude constructs (Table 4). Compared with the overall sample, trip choice by casual anglers was similarly affected by changes in catfish size and reductions in harvest (Table 3). However, casual anglers’ choice of trip scenarios was much less affected by changes in catch, and they were indifferent to increases in harvest, water body type, or level of site development (Table 3).

Cluster 2 ($n = 121; 26\%$ of the sample) was labeled “number anglers” because their summed scores were highest on the CATNUM construct (Table 4). The effect of attribute levels on number anglers’ trip choice was similar to that observed for the overall sample, with the exception that number anglers were indifferent ($P > 0.05$) to reductions in harvest, water body type, and level of site development (Table 3).

Cluster 3 ($n = 81; 18\%$ of the sample) was labeled “harvest anglers” because this cluster had a significantly higher summed score on the KEEPFISH construct than any of the other clusters (Table 4). Harvest anglers also had the lowest summed score on the CATLAR construct. Aside from distance traveled, harvest anglers’ trip choice was most strongly influenced by changes in harvest levels, with the negative effect of reducing harvest to zero (model coefficient [$\beta = -0.682, P < 0.001$; WTP $= -$71.81] being twice as great as the effect of doubling the harvest ($\beta = 0.331, P < 0.01$, WTP $= $34.85; Table 3). The only other attribute level to have a significant effect on trip
choice for harvest anglers was a reduction in catfish size ($\beta = -0.276, P < 0.05, WTP = -$19.11; Table 3). However, harvest anglers were indifferent toward increases in catfish size.

Cluster 4 ($n = 77$; 17% of the sample) was labeled “number and size anglers” because this group had high average summated scores on the CATNUM and CATLAR constructs and also had the highest score on the CATSOM construct (Table 3). Trip choice by number and size anglers was most affected by changes in catch (half: $\beta = -0.552, P < 0.001, WTP = -$53.33; triple: $\beta = 0.551, P < 0.001, WTP = $56.30) and increases in harvest ($\beta = 0.395, P < 0.01, WTP = $40.35; Table 3) compared with the other clusters. Cluster 4 was also the only cluster for which the choice of trips was negatively affected by small reservoirs ($\beta = -0.310, P < 0.01, WTP = -$31.65) and undeveloped sites ($\beta = -0.337, P < 0.01, WTP = -$34.39; Table 3).

Cluster 5 ($n = 37$; 8% of the sample) was labeled “size anglers” because this cluster had the highest summed score on the CATSOM construct (Table 4). Compared with the other clusters, size anglers’ trip choice was by far the most affected by changes in catfish size (smaller: $\beta = -0.934, P < 0.001, WTP = -$79.54; larger: $\beta = 1.071, P < 0.001, WTP = $93.83; Table 3). Unlike the other clusters, size anglers were completely indifferent toward harvest, with neither a decrease ($\beta = -0.037, P > 0.05, WTP = -$3.81) nor an increase ($\beta = -0.006, P > 0.05, WTP = -$2.48) in harvest having any influence on their choice of fishing trips (Table 3).

Finally, we used the results of the SCMs to calculate each cluster’s choice probabilities and WTP for five hypothetical management scenarios (Table 5). These scenarios ranged from a large reservoir or river catfish population with poor fishing quality (scenario 1) to an intensely managed small reservoir with high-quality catfish fishing (scenario 5); the latter scenario would be typical of a private fee fishing enterprise or an intensely managed urban fishery. All five angler clusters had negative WTP for scenario 1; for all clusters, the highest choice probability and highest WTP were observed for scenario 5 (Table 5). However, the pattern of choice probabilities and WTP across groups varied considerably for the other choice scenarios (Table 5). While scenario 2 (increased catch and harvest) provided the second-highest choice probability and WTP for four of the five clusters, scenarios 3 and 4 provided negative WTP for some groups and positive WTP for others. Scenario 3 (larger catfish but no harvest) provided the most disparate results across groups; the harvest anglers’ WTP ($WTP = -$74.49) and the number and size anglers’ WTP ($WTP = -$35.87) gave this scenario their lowest WTP, whereas the size anglers gave it their second-highest WTP ($WTP = $93.49; Table 5).

**DISCUSSION**

Aggregation of results to the statewide level can obscure preference heterogeneity across distinct subpopulations of anglers (Fedler and Ditton 1994). We found this to be true for some
attributes, but we also found some strong commonalities across anglers. For example, we found that travel cost (i.e., distance traveled) was a significant determinant of choice overall and for all latent groups, as would be predicted by economic theory (Lancaster 1966). Next, the catch-related aspects of a fishing trip consistently influenced catfish anglers’ choices of hypothetical fishing trips. Although the importance of harvesting fish appeared to vary across angler clusters, all five groups were concerned with the number and size of catfish caught. All groups had strong negative utility for smaller catfish. Even those angler groups that scored low on the CATNUM and CATLAR attitude constructs were unwilling to exchange other trip attributes for reductions in the number and size of catfish they typically caught. However, more consistent with anglers’ attitudes, the LCAs did suggest that anglers with weaker attitudes toward catching numbers of catfish and catching larger catfish received less utility from increases in the number and size of catfish caught than did angler groups that scored higher on CATNUM and CATLAR.

Whereas catch and release is popular among some catfish anglers (Wilde and Ditton 1999; Arterburn et al. 2002), 70% of the anglers in this study harvested their fish (Hunt and Hutt 2010). Thus, it appears that Texas anglers are quite similar to Missouri anglers (Reitz and Travnicek 2008) in exhibiting a focus on Amenities, overall satisfaction is still often related to site attributes. Texas anglers preferred to fish in locations that were not crowded, that gave them a feeling of solitude, and that provided recreational opportunities aside from fishing (Hunt et al. 2013). Anglers in both Texas (Hunt et al. 2013) and Mississippi (Schramm et al. 1999) also liked to fish in areas that were free of litter, but Mississippians seemed much less concerned about crowding. Similarly, Mahasuweerachai et al. (2010) found that...
the greatest utility for anglers in an urban fishery came from the 
addition of flush toilets. Thus, while fisheries managers looking 
to promote a quality catfish fishery have a significant amount of 
leeway in choosing the setting of the fishery, they should also 
obtain a good understanding of anglers’ desires for non-catch-
related attributes.

While catfish anglers indicated a preference for large reser-
voirs and rivers over small reservoirs, they also indicated that 
the distance they needed to travel and the quality of the fishing 
were of far greater importance to their selection of a fishing trip. 
This observation is of particular relevance for fisheries managers 
and fee fishing providers, as the provision of the most preferred 
catfish angling scenario examined (scenario 5, Table 5) would 
require intense fishery management, including the stocking of 
catchable-sized catfish, pond fertilization, and potentially even 
the installation of fish feeding devices. Such measures may 
be economically practical on small, contained waters, but they 
would be far too costly for use on the large, open waters for 
which catfish anglers reported a minor preference. As the fish-

ing venue is changed, managers may wish to re-evaluate the 
importance of site attributes.

Fedler and Ditton (1994) showed that anglers have heteroge-
nous motivations at both the population level (i.e., all anglers) 
and the subpopulation level (e.g., catfish anglers). We found 
that catch-related attitudes were useful as criteria in accounting 
for preference heterogeneity because of their direct relationship 
to the catch-related aspects of fishing trips. The nature of the 
five angler subgroups identified by the LCA was not surprising, 
but quantifying the utility each angler subgroup receives from 
different fishing trip attributes will be needed to enable fisheries 
managers to devise management plans that are best suited for 
meeting the subgroups’ specific needs. Management strategies 
should focus on providing a variety of experiences. Reitz and 
Travnichek (2008) proposed an approach that involved provid-
ing both harvest-oriented fisheries (i.e., with Channel Catfish) 
and trophy opportunities (i.e., with Blue Catfish or Flathead 
Catfish). At the same time, determining the relative size of each 
cluster will also help managers determine the number of fish-
eries resources that will be required to meet each angler sub-
group’s needs. For example, 58% of the catfish anglers surveyed 
belonged to either the casual angler subgroup or the number 
angler subgroup, and these two groups had relatively similar 
preference profiles based on their SCM results. Neither group 
showed interest in incurring large travel costs for anything but 
the highest quality catfish fishing trips (scenario 5, Table 5). 
Given the preference profiles of the casual angler and number 
angler subgroups, their needs could best be met by providing cat-
fish fishing opportunities around major population centers and 
by managing for slightly larger catfish than are typically caught 
by these subgroups. The plurality (42–46%) of anglers in both 
groups indicated that the typical size of catfish they caught was 
only 10–15 in (Table 4); therefore, managers would only need 
to provide marginally larger catfish to increase the utility gained 
by these anglers. Managers overseeing urban fisheries that are 
stocked with catchable-size catfish may simply consider replac-
ing a portion of those stocked catfish with slightly larger fish 
while also stocking the occasional trophy-size fish (e.g., retired 
broodfish, catfish collected from local reservoirs, etc.). We en-
vision three possibilities; they are not inexpensive and they will 
have detractors, but these options should be considered within 
the context of maintaining the interest of urban anglers. The 
first possibility is to have hatcheries to hold and grow out larger 
catfish. Mahasuweerachai et al. (2010) found that urban catfish 
anglers in Oklahoma were willing to pay more for city license 
fees if larger catfish were stocked. Given Texas anglers’ greater 
WTP for larger catfish, they would likely be willing to do the 
same. The second possibility is to have managers harvest larger 
catfish from other locations on occasion and transport them to 
urban fisheries. If this option is followed, we recommend lim-
iting transport to areas within the same watershed. The final 
option would be to combine the use of automated feeders and 
restrictive creel limits to speed the on-site growth of catfish. 
This final option would likely work best on larger ponds that are 
located in smaller communities and therefore do not receive as 
much effort as a typical urban fishery (Schramm 2008).

Some previous studies have shown low interest in trophy 
catfish fishing (Wilde and Ditton 1999). However, our results 
more closely resemble those of Schramm (2008), who showed that 
there is a significant interest in trophy catfish. Our study 
estimated that size anglers made up 8% of the catfish anglers 
surveyed, making this group more of a niche market among 
catfish anglers. Given that the size angler group is relatively 
small, fewer fisheries are required to meet these anglers’ needs; 
furthermore, because size anglers have a much greater WTP 
(i.e., distance they are willing to travel), managers will have far 
greater flexibility to target fisheries that are capable of meeting 
needs related to high-quality trophy fisheries. Because changes 
in harvest levels either way had no significant influence on size 
anglers’ selection of fishing trips, this group will be much more 
amenable to the types of restrictive regulations that are required 
to manage for trophy fisheries.

We recognize that there are limitations to the methods used 
in this study. We employed relative measures of catch, harvest, 
and size in order to identify general differences in preferences 
across groups rather than presenting them with specific 
measurements of catfish numbers or size. This decision was 
made because at the time of our study, TPWD was in the early 
stages of developing its catfish management plan and was more 
interested in identifying general patterns of angler preferences 
as opposed to assessing the effects of specific management 
measures. Future studies with an eye toward identifying the 
specific effects of changes in fishery regulations should select 
more specific attributes and levels accordingly, such as those 
used by Carlin et al. (2012). Such studies should also consider 
using a combined approach (i.e., stated preference and revealed 
preference) that incorporates actual behavioral data to calibrate 
the results of the preference model and to generate more specific 
predictions of how changes in site characteristics will influence
angler behavior (Haener et al. 2001). However, fisheries managers that are developing regional management plans with limited agency resources would do well to adopt the present approach to evaluate angler preferences and identify management goals that would best meet the needs of their clientele. We found that an LCA using catch-related attitude scores allowed us to identify distinct market segments of the Texas catfish angler population, each with slightly different preference profiles. The identification of preference heterogeneity across groups will allow fisheries agencies to develop a variety of fisheries management strategies that can be applied across water bodies and that are capable of meeting the needs of different angler groups rather than approaching management with a “one size fits all” mentality.

REFERENCES

Creel Survey Sampling Designs for Estimating Effort in Short-Duration Chinook Salmon Fisheries

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Abstract
Chinook Salmon Oncorhynchus tshawytscha sport fisheries in the Columbia River basin are commonly monitored using roving creel survey designs and require precise, unbiased catch estimates. The objective of this study was to examine the relative bias and precision of total catch estimates using various sampling designs to estimate angling effort under the assumption that mean catch rate was known. We obtained information on angling populations based on direct visual observations of portions of Chinook Salmon fisheries in three Idaho river systems over a 23-d period. Based on the angling population, Monte Carlo simulations were used to evaluate the properties of effort and catch estimates for each sampling design. All sampling designs evaluated were relatively unbiased. Systematic random sampling (SYS) resulted in the most precise estimates. The SYS and simple random sampling designs had mean square error (MSE) estimates that were generally half of those observed with cluster sampling designs. The SYS design was more efficient (i.e., higher accuracy per unit cost) than a two-cluster design. Increasing the number of clusters available for sampling within a day decreased the MSE of estimates of daily angling effort, but the MSE of total catch estimates was variable depending on the fishery. The results of our simulations provide guidelines on the relative influence of sample sizes and sampling designs on parameters of interest in short-duration Chinook Salmon fisheries.
the fishery; Apperson and Wilson 1998). Because fisheries are based on quotas or harvest shares, in-season estimates of total catch and harvest are needed.

Although quotas or harvest shares are common in commercial fisheries, they are relatively uncommon in sport fisheries. Various forms of mandatory reporting are regularly used to estimate total catch in commercial fisheries. The highly dispersed angling effort and catch in Chinook Salmon sport fisheries in the Columbia River basin preclude the use of mandatory reporting. Additionally, these fisheries are often of relatively short duration, commonly lasting from days to a maximum of a few months (e.g., Janssen and Kiefer 1999; Apperson 2003; Keniry et al. 2004), which can further complicate creel survey design and total catch estimation.

In general, Chinook Salmon sport fisheries in the Columbia River basin occur on long sections of large rivers with dispersed shore access and multiple fixed access points (i.e., boat launches and public shore access). As such, estimates of effort and catch are typically derived from on-site creel surveys, such as access–access, aerial–access, roving–access, aerial–roving, or roving–roving surveys (Malvestuto 1983; Pollock et al. 1994, 1997). When designing creel surveys, there are multiple considerations, including survey type, number of days to survey, number of angler interviews, and number of angler counts. Survey type is typically determined by access to the fishery. For instance, access-based surveys are generally conducted in fisheries that have relatively few, well-defined access areas, whereas roving-based surveys are conducted in fisheries that have diffuse access (Pollock et al. 1994). Previous research has been conducted on the number of days to survey and the number of counts to conduct (Lester et al. 1991; Malvestuto and Knight 1991). However, because of the relatively short seasons in Chinook Salmon fisheries and the high variability in temporal and spatial trends in effort and catch due to the migratory nature of salmon, the number of days to survey and the number of counts can vary greatly depending on the length of the fishery (Martinson and Shelby 1992; Bernard and Clark 1996; Keefer et al. 2004).

Another consideration when designing a creel survey is the method used to select sampling units (Knight and Malvestuto 1991; Malvestuto and Knight 1991; Deroba et al. 2007). For instance, a three-stage cluster sample is common in creel surveys, where (1) days are randomly selected, (2) a portion of the day to be surveyed is randomly selected, and then (3) count times are randomly selected (Malvestuto 1983; Pollock et al. 1994). For creel surveys such as those used in Chinook Salmon sport fisheries, days are frequently identified as the primary sampling units (Malvestuto 1983; Pollock et al. 1994). In most probabilistic surveys, as the number of primary sampling units (i.e., days) sampled increases the distribution of the variable of interest (i.e., total effort, catch, or harvest in creel surveys) approaches a normal distribution (Thompson 2012). This serves as the statistical basis for expected parameter estimates of interest in probabilistic creel surveys. However, because the number of primary sampling units available for selection in many Chinook Salmon fisheries is limited and because in-season estimates are needed, the statistical properties of estimates are unknown.

In addition to selecting days to sample, scheduling the times to conduct counts also must be considered when instantaneous counts are used (Hoening et al. 1993; Pollock et al. 1994). Counts can be scheduled by using various designs, including simple random, systematic, stratified, cluster, or nonuniform probability sampling (Malvestuto et al. 1978; Hoening et al. 1993; Kozfkay and Dillon 2010). Bias and precision of effort and catch estimates in creel surveys can vary depending on the method used to select sampling units (Bernard et al. 1998). The relative efficiency of more complex survey designs in comparison with simple random sampling (SRS) is known as design effect and has not been extensively evaluated in short-duration fisheries (Cochran 1977).

Although research on creel survey sampling design is extensive, most research has focused on total catch over a month, season, or year (Malvestuto et al. 1978; Rasmussen et al. 1998). Daily or weekly catch and associated variability are rarely of interest to managers. As a result, very little previous research is applicable to sampling designs associated with estimating daily or weekly effort and catch. However, due to the quotas imposed and in-season management of Chinook Salmon fisheries in the Columbia River basin, estimates for short time periods are necessary. Therefore, the objectives of this research were to evaluate various sampling designs and sample sizes used to estimate effort and total catch in Chinook Salmon fisheries. The relative accuracy per unit cost was also evaluated.

METHODS

Thompson (2012) suggested that simulation of sampling distributions is one of the most effective tools to evaluate sampling strategies and estimators. As such, censuses of angling activity were conducted on reaches of three short-duration Chinook Salmon fisheries in Idaho, which served as theoretical angling populations. Monte Carlo simulations were then conducted based on these populations, and the resulting sampling distributions were evaluated to determine the performance of sampling designs and sample sizes.

Censuses of angling activity (i.e., fishing time and catch) were conducted on 200–700–m reaches of Chinook Salmon fisheries on the Clearwater, Little Salmon, and South Fork Salmon rivers, Idaho, by using direct visual observation. Observation reaches were selected nonrandomly to increase sample sizes (i.e., angling effort and total catch) and to facilitate discreet observations of anglers. It was assumed that the nonrandomly selected observation reaches were representative of the target population. Survey days were also selected nonrandomly and were conducted near the peak of angling activity in each fishery. Roving–roving or roving–access creel surveys throughout the entire fishery were conducted by Idaho Department of Fish and Game (IDFG) creel clerks while our observations of anglers were taking place concurrently in localized census reaches.
Based on the instantaneous counts of anglers in the census reach compared with IDFG creel clerks’ counts of the entire fishery, census reaches accounted for approximately 28% of angling effort in the entire fishery on the Clearwater River, 19% of effort on the Little Salmon River, and 6% of effort on the South Fork Salmon River.

Distributions of angling effort and catch observed in the census reaches served as the theoretical angling population that was resampled by using Monte Carlo simulations. Observations were conducted for 7 d at each reach on the Clearwater, Little Salmon, and South Fork Salmon rivers, for a total of 21 observation days. An additional 2 d of observations were conducted on the Little Salmon River (i.e., days 8 and 9) to evaluate a nonuniform probability sampling (NUP) design. Observers arrived before the legal fishing time started and remained present until the end of legal fishing time; by regulation, fishing was limited to daylight hours only. Discreet observations were conducted so as not to influence angler decisions on fishing locations, fishing times, fish harvest, or reporting to IDFG creel clerks. For instance, in the Clearwater and Little Salmon rivers, angling activity was observed from afar by using spotting scopes. Two observers were used on the South Fork Salmon River: one observer fished and relayed information to the other observer, who discreetly recorded data. Data were recorded on the time each angler entered and exited 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 identification number at the start of their fishing episode, which was defined as the angler’s first cast. The end of the fishing event was defined as the time the angler exited the fishing area and was no longer available for counting in a roving creel survey. If an angler exited the fishery for 5 min or more, that angler was assumed to be unavailable for counting in a roving effort count and was recorded as not fishing. When such anglers re-entered the fishery, they were re-assigned their initial identification numbers. All data were recorded on a per-angler basis to avoid bias or variance that may arise from interviewing anglers to estimate mean catch rate or from selecting sampling units for instantaneous counts.

**Simple random sampling.**—To estimate daily angling effort using SRS, sampling units (i.e., minutes to conduct counts) were selected with equal probability without replacement. Instantaneous counts were conducted at the selected count times. Total angling effort (\( \hat{E} \)) in hours for each day in all fisheries was estimated as

\[
\hat{E}_{\text{SRS}} = T \bar{I},
\]

where \( T \) is the total number of hours in the fishing day and \( \bar{I} \) is the mean of \( I \) angler counts. Sample variance \( (s^2_{\text{SRS}}) \) was estimated as

\[
s^2_{\text{SRS}} = \frac{1}{n-1} \sum_{i=1}^{n} (\bar{I} - I_i)^2,
\]

where \( n \) is the number of counts. Variance of the total angling hours \( (\hat{V}(\hat{E}_{\text{SRS}})) \) was estimated using methods described by Pollock et al. (1994):

\[
\hat{V}(\hat{E}_{\text{SRS}}) = T^2 \left( \frac{s^2_{\text{SRS}}}{n} \right).
\]

The finite population correction is ignored in equation (3) because the sampling fraction does not exceed 5% (Cochran 1977). We estimated 95% CIs for estimates of effort as

\[
\hat{E}_{\text{SRS}} \pm 1.96 \times \sqrt{\hat{V}(\hat{E}_{\text{SRS}})}.
\]

Total daily catch \( \hat{C_j} \) for the \( j \)th day was estimated as

\[
\hat{C_j} = \hat{E}_{\text{SRS}} \times R,
\]

where \( R \) is the true mean daily catch rate for all anglers (i.e., ratio of means; Jones et al. 1995; McCormick et al. 2012).
**Systematic sampling.**—Systematic sampling was simulated in a manner similar to SRS, but angler counts were conducted systematically. The first instantaneous angler count time was randomly selected within the first k minutes of the day, where k equals the length of time in the day divided by the number of total counts (Cochran 1977). Additional counts were conducted at each kth time thereafter. The mean of angler counts ($\bar{I}_{SYS}$) and total daily effort was estimated using equation (1). It was assumed that the population was ordered randomly; sample variance, population variance, and 95% CIs were estimated using equations (2), (3), and (4), respectively (Scheaffer et al. 2006). Total daily catch was estimated using equation (5).

**Cluster sampling.**—Morning and afternoon cluster sampling is a design with two clusters available to be sampled, one of which is selected for sampling. This is one of the most common creel survey sampling designs (Malvestuto 1983; Pollock et al. 1997; Rasmussen et al. 1998). However, days may be divided into more than two clusters, and the number of clusters selected for sampling can vary. We evaluated the effect of using two, four, and eight clusters (CL2, CL4, and CL8, respectively) on estimates of effort and catch. With each design, the number of clusters sampled was half the total number of clusters available for sampling. Such a design would require creel clerks to work the same number of hours regardless of the number of clusters available for sampling. Total effort was estimated using the methods described by Scheaffer et al. (2006):

$$E_{CL} = \frac{N}{n} \sum_{i=1}^{n} M_i \bar{I}_i,$$

(6)

where $N$ is the number of clusters in the population, $n$ is the number of clusters selected in the sample, $M_i$ is the number of elements (i.e., minutes) in the $i$th cluster, and $\bar{I}_i$ is the mean count of anglers in the $i$th cluster. Total daily catch was estimated using equation (5), with $R$ in this case representing the catch rate within the clusters that were sampled. Nonparametric bootstrap 95% CIs were calculated for each estimate of total daily effort by using the percentile method (Efron and Tibshirani 1993).

**Nonuniform probability sampling.**—To simulate an NUP design, selection probabilities of sampling units (i.e., minutes to conduct counts) were calculated based on the mean number of anglers fishing during each minute of the fishing day from the initial 7-d observation period on the Little Salmon River. An additional 2 d of observation (i.e., days 8 and 9) were conducted on the Little Salmon River and served as the population that was resampled to evaluate the NUP design. A sample of count times was selected without replacement. Total daily effort was estimated using the Horvitz–Thompson estimator (Cochran 1977; Pollock et al. 1994):

$$\hat{E}_{HT} = \sum_{i=1}^{n} (I_i / \pi_i),$$

(7)

where $\pi_i$ is the inclusion probability of the $i$th unit (i.e., minute). The inclusion probability was estimated using methods described by Thompson (2012):

$$\pi_i = 1 - (1 - p_i)^n,$$

(8)

where $p_i$ is the probability of unit $i$ being selected. Total daily catch was estimated with equation (5). The additional 2 d were also sampled using the SRS and SYS designs to compare results with those from the NUP design.

**Simulations and evaluation.**—Sampling designs were evaluated using Monte Carlo simulations. For each design, 5,000 samples of effort and total daily catch were simulated. We conducted simulations in which the number of counts varied from two to eight to determine the effect of sample size on bias and precision. Because weekly estimates of harvest are needed in many Chinook salmon fisheries, 5,000 estimates of total weekly catch were simulated for each daily sampling design. Total weekly catch was estimated using an SRS design in which days were selected with equal probability without replacement. Scenarios were examined where the number of days sampled varied from four to seven. Total weekly catch ($\hat{C}$) was estimated as

$$\hat{C} = \sum_{i=1}^{L} D_i \hat{C}_i,$$

(9)

where $D_i$ is the number of days in the $i$th stratum (i.e., week) and $\hat{C}_i$ is the mean catch per day in the $i$th stratum.

Bias was estimated as the difference between the mean of the empirical sampling distribution and the true population parameter (i.e., effort, total daily catch, or total weekly catch). Relative bias was estimated as bias divided by the true population parameter. To assess the accuracy and precision of each estimator, the mean square error (MSE) was estimated as the mean squared difference between the estimate and the true value for each population parameter $\theta$:

$$\text{MSE}(\hat{\theta}) = \frac{\sum_{i=1}^{n} (\hat{\theta}_i - \theta)^2}{n} / 5,000.$$  

(10)

Coverage of 95% CIs of daily effort estimates was also evaluated. In theory, 95% of all CIs should encompass the true population parameter; for iterations with CIs that did not encompass the true parameter values, 50% should be below the true value and 50% should be above the true value. The percentage of CIs that encompassed the true population parameter was calculated along with the direction of CIs that did not encompass the known population value. In an actual creel survey, catch rate would likely be estimated and would add variability to the sampling distribution of total daily and weekly catch estimates; therefore, CI coverage was only evaluated for estimates of daily effort. Simulations and statistical analysis were conducted...
using the R statistical computing language (R Development Core Team 2009).

Cost analysis.—Because not all survey designs are equal in cost, the accuracy per unit cost was evaluated. We did not evaluate all six designs because costs are likely to be highly variable among fisheries and may not be informative. Specifically, only the SYS and CL2 designs were evaluated because an SYS design surveys the entire day and a CL2 design will always survey half the day, thereby providing a more direct comparison of efficiency. Accuracy was defined as the reciprocal of MSE. The cost of a creel survey typically includes equipment, personnel, and travel costs. For the cost analysis, equipment and travel costs were assumed to be equal between survey designs. The relative cost of surveying one full day was set to 1 unit, and cost was increased by 1 unit for each additional day (e.g., 4 d cost 4 units, 5 d cost 5 units, and so forth). This was assumed to be the relative cost for an SYS design. Because a CL2 design only requires a creel surveyor for half of a day, the relative cost for 1 d with this design was set to 0.5 units. The accuracy per relative unit cost was evaluated with the number of days surveyed varying from four to seven. The cost associated with conducting a count can vary by fishery depending on the length of time and amount of travel required to conduct a count; therefore, the accuracy per unit cost was evaluated for a design in which the number of counts was held constant at four. An increase in the accuracy per unit cost would indicate a more efficient design.

RESULTS
Over the 21-d observation period, anglers caught a total of 242 Chinook Salmon: 39 fish were caught on the Clearwater River, 130 were caught on the Little Salmon River, and 73 were caught on the South Fork Salmon River (Table 1). In total, 580 angler trips were observed, encompassing 2,620 h of angling effort. Overall, angler catch rates were relatively low and varied from 0.008 to 0.068 fish/h on the Clearwater River, from 0.092 to 0.229 fish/h on the Little Salmon River, and from 0.033 to 0.169 fish/h on the South Fork Salmon River.

Simulated estimates of daily angling effort for all sampling designs and all sample sizes were relatively unbiased (Figure 1).

| TABLE 1. Summary of angling activity in Chinook Salmon fisheries observed for 7 d on the Clearwater River, 9 d on the Little Salmon River, and 7 d on the South Fork Salmon River, Idaho, during the 2011 season. |
|---------------------|---------------------|---------------------|---------------------|---------------------|
| Day | Total anglers | Total hours fished | Mean hours fished per angler | Number of fish caught | Daily catch rate (fish/h) |
| Clearwater River |
| 1 | 49 | 254.63 | 5.2 | 8 | 0.031 |
| 2 | 47 | 264.23 | 5.62 | 8 | 0.030 |
| 3 | 31 | 251.18 | 8.10 | 9 | 0.036 |
| 4 | 14 | 44.28 | 3.16 | 3 | 0.068 |
| 5 | 37 | 122.93 | 3.32 | 6 | 0.049 |
| 6 | 42 | 123.57 | 2.94 | 4 | 0.052 |
| 7 | 24 | 128.68 | 5.36 | 1 | 0.008 |
| Little Salmon River |
| 1 | 46 | 195.93 | 4.26 | 29 | 0.148 |
| 2 | 20 | 71.07 | 3.55 | 15 | 0.211 |
| 3 | 25 | 96.25 | 3.85 | 22 | 0.229 |
| 4 | 27 | 136.68 | 5.06 | 18 | 0.132 |
| 5 | 40 | 183.85 | 4.60 | 17 | 0.092 |
| 6 | 37 | 116.72 | 3.15 | 19 | 0.163 |
| 7 | 23 | 93.83 | 4.08 | 13 | 0.139 |
| 8 | 26 | 70.93 | 2.72 | 7 | 0.099 |
| 9 | 24 | 97.03 | 4.04 | 8 | 0.082 |
| South Fork Salmon River |
| 1 | 6 | 30.45 | 5.08 | 1 | 0.033 |
| 2 | 5 | 43.05 | 8.61 | 2 | 0.046 |
| 3 | 9 | 59.88 | 6.65 | 5 | 0.083 |
| 4 | 8 | 71.13 | 8.89 | 6 | 0.084 |
| 5 | 29 | 124.42 | 4.29 | 21 | 0.169 |
| 6 | 29 | 105.9 | 3.65 | 17 | 0.161 |
| 7 | 32 | 101.23 | 3.16 | 8 | 0.079 |
FIGURE 1. Average among-day bias in estimated angling effort from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panels), Little Salmon River (middle panels), and South Fork Salmon River (bottom panels), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and five different sampling designs were evaluated: simple random sampling (SRS), systematic random sampling (SYS), a two-cluster design (CL2), a four-cluster design (CL4), and an eight-cluster design (CL8). Left panels represent sampling designs in which the full day is available for sampling (SRS and SYS); right panels represent designs in which the day is subsampled. Box plots represent quartiles of among-day estimates of bias.

The largest estimated absolute bias for any survey day was calculated for the Clearwater River using a CL4 sampling design with six counts, where effort was overestimated by 2.66 h and the relative bias was 2.1%. The largest relative bias was 5.62%, which was observed for the Clearwater River using a CL2 sampling design and two counts. All other simulated estimates of relative bias were less than 1.6%. The SYS design resulted in the lowest variance in estimates of bias among days, whereas the CL2 design resulted in the highest among-day variance (Figure 1). Increasing the number of angler counts generally failed to decrease bias in effort estimates for all designs. Among-day variance in bias tended to decrease with increasing counts for the SRS and SYS designs, whereas this trend was not generally observed with the cluster designs. Among-day variance in bias generally decreased with increasing numbers of clusters (Figure 1).

Because bias of all effort estimates was relatively small, variance of the sampling distribution accounted for most of the...
observed MSE. As such, the MSE reduces to the approximate variance of the sampling distribution. Taking the square root of the variance equals the SD, which represents the expected SE of the estimate (Särndal et al. 1992). Therefore, trends in reported MSE between designs and sample sizes can be interpreted as the relative change in expected precision of the estimates. With the exception of a two-count SRS design on the Little Salmon River, the SYS design resulted in the lowest average MSE of all designs for each respective number of counts (Figure 2). The SYS design also resulted in the lowest among-day variance in MSE. Increasing the number of counts for all designs resulted in decreased MSE values. For both of the full-day sampling designs (i.e., SRS and SYS), large decreases in MSE were not observed beyond four counts. Relative decreases in MSE with increasing numbers of angler counts for the cluster designs were not as great as those observed for the full-day sampling designs.

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**FIGURE 2.** Average among-day mean square error (MSE) of estimated angling effort from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panels), Little Salmon River (middle panels), and South Fork Salmon River (bottom panels), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and five sampling designs (defined in Figure 1) were evaluated. Left panels represent sampling designs in which the full day is available for sampling (SRS and SYS); right panels represent designs in which the day is subsampled. Error bars represent one SD of among-day MSE in each fishery.
Increasing the number of clusters consistently decreased the MSE of simulated estimates of effort. Average MSE from the CL\(_2\) sampling design was consistently larger than that from the CL\(_4\) design and more than twice as large as the MSE from the CL\(_8\) design. Among-day variance of estimated MSE was, on average, more than double that observed for the full-day sampling designs and decreased at a much lower rate with increasing numbers of angler counts.

Use of an SRS design to estimate effort resulted in 95% CIs that were too small, regardless of the fishery and number of angler counts conducted (Figure 3). Overall, 95% CI coverage was most accurate when the SYS design was used. Confidence intervals were closest to 95% when four counts were conducted with the SYS design; beyond four counts, mean CIs were generally too large. For the cluster designs, four counts were necessary to produce CIs that were within 10% of true 95% CIs. Conducting more than five counts with all three cluster designs resulted in CIs that had greater coverage than 95%. For all designs, numbers of counts, and fisheries, the CI coverage was relatively unbiased (i.e., CIs that did not encompass true effort were not consistently overestimates or underestimates).

Similar to estimates of effort, bias in simulated estimates of total daily catch was relatively low. Total bias for all sampling designs and numbers of angler counts was less than 0.2 fish (Figure 4). The trends observed with estimates of effort were also observed with the MSE of total daily catch estimates in that the full-day sampling designs resulted in lower MSE and lower among-day variance than did the cluster designs (Figure 5). Unlike estimates of MSE for effort, increasing the number of clusters resulted in a larger MSE for total daily catch on the Little Salmon River. The CL\(_4\) design also resulted in a larger average MSE than the CL\(_2\) design for the Clearwater and South Fork Salmon rivers. The CL\(_8\) design provided the lowest average MSE for the Clearwater and South Fork Salmon rivers.

Bias in estimated total weekly catch was also relatively small and did not exceed 1.2 fish for any sampling design, combination of days sampled, or number of counts (Figure 6). However, variability in bias among sampling designs and numbers of counts decreased as the number of days sampled increased. For the Little Salmon and South Fork Salmon rivers, bias tended to be negative (i.e., to underestimate actual total weekly catch) when SRS and SYS designs were used but was still relatively small. Bias for all other designs and sample sizes was evenly distributed about zero.

The SRS and SYS designs resulted in MSEs of total catch estimates that were consistently smaller than those from cluster designs (Figures 7, 8). For the Clearwater River, MSEs of total weekly catch estimates from the full-day sampling designs were less than half of the MSEs from the cluster designs. With all sampling designs, decreases in MSE were observed by increasing the number of sampling days from four to seven. This decrease was relatively consistent regardless of the sampling design or number of counts. On average, the CL\(_2\) sampling design resulted in MSE estimates that were smaller than those of the CL\(_4\) and CL\(_8\) cluster designs, regardless of the number of days sampled (Figure 8). Similar to daily estimates of total catch, increasing the number of counts beyond four did little to decrease MSE estimates for the full-day sampling designs (Figure 7). Small decreases in MSE of total weekly catch estimates were observed with the cluster designs by increasing the number of counts (Figure 8). Smaller decreases in MSE were observed by increasing the number of counts as the number of clusters increased (i.e., cluster size was reduced).

When sampling on the Little Salmon River was simulated for two additional days, estimates of total daily angling effort and total catch were unbiased when using the NUP, SRS, and SYS designs. All estimates of bias in total angling hours were less than 0.12 fish. On day 8 and day 9, the NUP design resulted in estimates of MSE for effort that were consistently smaller than those obtained from the SRS design (Figure 9). Except when one count or four counts were conducted on day 8, the SYS design consistently resulted in smaller MSEs of effort estimates. Conducting four counts on day 8 using the SYS design resulted in a larger MSE than when three counts were conducted. Conducting three counts with the SYS design on day 9 resulted in a larger MSE than when only two counts were conducted. Similar to the results for most other designs from previous days, large decreases in MSE were not observed beyond four counts with the NUP design. Because the same catch rate was used to compare effort and total catch, relative trends in MSE of total daily catch between sampling designs were identical to those observed in effort estimates. Trends in CI coverage of the SYS design for days 8 and 9 were similar to those observed with the SYS design during the primary simulation (i.e., days 1–7 in the Clearwater, Little Salmon, and South Fork Salmon River fisheries). However, CIs were biased when three counts were conducted on day 8 and when two or four counts were conducted on day 9. For day 8, 100% of the CIs that did not encompass the true effort were biased high; for day 9, 100% of the CIs that did not encompass the true effort were biased low when two or four counts were conducted.

Although the SYS design may cost up to twice as much as the CL\(_2\) design, it generally resulted in greater efficiency (i.e., increasing accuracy per unit cost) than the CL\(_2\) design when four counts were conducted (Figure 10). With both designs, efficiency increased as the number of days surveyed increased. For the Clearwater and South Fork Salmon rivers, accuracy per unit cost was always greater from the SYS design than from the CL\(_2\) design; the disparity increased with an increasing number of days surveyed. For the Little Salmon River, the CL\(_2\) design was more efficient when 4 or 5 d were surveyed, whereas the SYS design was more efficient when 6 or 7 d were surveyed.

**DISCUSSION**

All of the sampling designs evaluated in this study produced estimates of effort, total daily catch, and total weekly catch that
were relatively unbiased. The characteristics of angler effort and catch for each day and river where census data were collected were highly variable, suggesting that over time, all of the sampling designs are likely unbiased (i.e., a wide range of fishing activity was observed, with similar trends in bias and precision among days and fisheries in the simulation). Actual catch rates were used to estimate total catch in this study, thereby allowing for evaluation of sampling designs used to estimate effort. However, estimation of mean catch rate may introduce bias into estimates of total catch (McCormick et al. 2012). The results of our simulation show that estimates of effort and total catch are likely unbiased when a well-designed probabilistic survey is used; therefore, emphasis can be placed on evaluating variance when planning surveys.

FIGURE 3. Average among-day 95% CI coverage of estimated angling effort from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panels), Little Salmon River (middle panels), and South Fork Salmon River (bottom panels), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and five sampling designs (defined in Figure 1) were evaluated. Left panels represent sampling designs in which the full day is available for sampling (SRS and SYS); right panels represent designs in which the day is subsampled. Error bars represent one SD of among-day 95% CI coverage in each fishery. Dashed horizontal line denotes 95%.
FIGURE 4. Average among-day bias of estimated daily catch from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panels), Little Salmon River (middle panels), and South Fork Salmon River (bottom panels), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and five sampling designs (defined in Figure 1) were evaluated. Left panels represent sampling designs in which the full day is available for sampling (SRS and SYS); right panels represent designs in which the day is subsampled. Box plots represent quartiles of among-day estimates of bias.

Except when two counts were conducted, the SYS design consistently resulted in the lowest average MSE, followed by the SRS, CL₈, CL₄, and CL₂ designs. The SYS and SRS surveys also resulted in the lowest among-day variance in MSE. Cluster designs can result in multimodal estimates of effort and catch if angling activity has a multimodal distribution. For instance, if angling effort and catch rates are higher in the morning than in the afternoon and a CL₂ design is used, effort and catch will be overestimated when a morning shift is surveyed. Conversely, effort and catch will be underestimated when an afternoon shift is selected. Although this results in unbiased estimates over time, the bimodal distribution of effort and catch estimates will inflate the MSE.

In addition to having the lowest MSE, SYS samples are often easier to draw and execute (i.e., instantaneous counts; Cochran 1977; Pollock et al. 1994). Because instantaneous counts may
FIGURE 5. Average among-day mean square error (MSE) of estimated daily catch from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panels), Little Salmon River (middle panels), and South Fork Salmon River (bottom panels), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and five sampling designs (defined in Figure 1) were evaluated. Left panels represent sampling designs in which the full day is available for sampling (SRS and SYS); right panels represent designs in which the day is subsampled. Error bars represent one SD of among-day MSE for total daily catch in each fishery.

take up to an hour to conduct, an SYS design allows for time between counts that may not be present with an SRS design (Pollock et al. 1994); this time may allow creel clerks to con-
duct angler interviews and ensures that sampling effort is spread evenly throughout the sampling period (Cochran 1977). Al-
though the SYS design provided the lowest MSE for estimates of effort and catch, if the population is not randomly ordered then the MSE can be highly variable, as was observed for sam-
pling days 8 and 9 on the Little Salmon River. On those days, angling effort on the Little Salmon River was apparently peri-
odic and caused variable MSE depending on the \( k \)-value (i.e., number of counts) that was used (Cochran 1977). When \( k \) was
equal to the period, all observations were similar and resulted in low MSE estimates. Although the SYS design resulted in the lowest MSE, the use of an SYS design to select sampling units within clusters could have reduced the MSEs obtained with the cluster designs.

With few exceptions, trends that were observed for daily effort estimates between sampling designs were also observed for daily catch estimates. The SYS and SRS designs consistently resulted in lower average MSE values than the cluster designs, with SYS surveys providing the lowest average MSE. Although increasing the number of clusters available for sampling decreased the MSE of effort estimates, the MSE of total daily catch estimates was variable between fisheries. Because actual catch rates were used to estimate total catch, the relationship between catch rate and effort within the clusters that were sampled was responsible for the variation. While the
cluster designs were unbiased in our simulations, care should be taken when conducting interviews to estimate mean catch rate by using cluster designs. Rasmussen et al. (1998) and Su and Clapp (2013) found that bias was introduced into daily estimates of harvest when using a CL$_2$ sampling design. This resulted from conducting afternoon interviews of anglers who had fished in the morning, whereas effort was only estimated for the evening shift. In a roving–roving or roving–access survey, effort and catch rate should be estimated on the same sample of anglers. The authors (Rasmussen et al. 1998; Su and Clapp 2013) suggested using an estimate of harvest rate over the entire stratum (i.e., week in our simulations) instead of calculating daily estimates or asking anglers to split their harvest between shifts to alleviate this potential bias. Bernard et al. (1998) recognized that if the day is subsampled (i.e., cluster sample) via a roving–access design, bias can be introduced into estimates of catch rate, particularly for anadromous fisheries that have short-term trends in abundance and catch. Bernard et al. (1998) also suggested that fisheries with low bag limits (e.g., most of the short-duration Chinook Salmon fisheries in the Columbia River basin) increase the potential for bias. Bias can be reduced and the precision of estimates can be increased if the sampling periods are the same length as the fishing day (Bernard et al. 1998).

Even though our results constitute a direct comparison of bias and precision among various sampling designs with the same amount of sampling effort (i.e., angler counts), the results did not necessarily provide a direct comparison of cost. Despite the benefits of SYS and SRS designs relative to cluster designs,
FIGURE 8. Mean square error (MSE) of estimated weekly catch from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panel), Little Salmon River (middle panel), and South Fork Salmon River (bottom panel), Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and three different sampling designs were evaluated: two-cluster (CL2), four-cluster (CL4), and eight-cluster (CL8) designs. The number of days sampled varied from four to seven.

the cost of executing full-day samples will likely be higher than the cost of obtaining cluster samples (Cochran 1977). The SYS and SRS designs require that counts have the potential to occur throughout the entire fishing day. As a result, creel clerks either must be available for the entire day or must work periodically throughout the day. A CL2 design would require creel personnel to only work half of the survey day, a likely reason for the design’s popularity in creel surveys. However, the SYS design was generally more efficient (i.e., accuracy per cost) than the CL2 design. Increasing the number of clusters available for sampling beyond two creates a potential need for creel clerks to work periodically throughout the day, and costs will likely be highly variable among fisheries. The cost for each fishery will also vary with differing numbers of counts. In this study, cost comparisons were only made for the SYS and CL2 designs, where the number of counts was held constant because of the potential variability in costs among fisheries. However, the MSEs reported in this study can be used to assess relative efficiencies of designs for situations in which costs are known. Additionally, accuracy was similar or greater when the number of clusters was increased, suggesting that efficiency would also decrease. Increasing the number of clusters will always increase the cost relative to that of the CL2 design. When planning a survey, cost and personnel availability should be weighed against the relative bias and precision of estimates (McCormick et al. 2012).

Previous research has been conducted on sample sizes that are necessary to achieve desired levels of precision in roving creel surveys. In a study of fisheries in Ontario lakes, Lester et al. (1991) evaluated the relationship between within- and
among-day variability to provide guidelines on the number of sample days and number of counts that would achieve a coefficient of variation of 0.2. However, Lester et al. (1991) did not evaluate the effect of various sampling designs on sample size requirements. Results of our simulations suggest that the choice of survey design can have a large effect on the precision of estimates. Exact estimates of precision were not presented in our simulations because census data were only collected on a portion of a larger fishery. Since simulated estimates of effort and daily and weekly catch were unbiased, the reported MSEs can provide guidelines on expected relative precision based on the sampling design, number of counts, and number of days sampled. For instance, increases in precision of daily effort estimates from increasing the number of counts are expected to be greater with SRS and SYS designs than with cluster designs. The trend was exacerbated as the number of clusters increased, and this was a result of increasing the between-cluster variance and decreasing the within-cluster variance by reducing the size of the cluster. In most simulated sampling designs, increases in precision were not observed beyond four counts; however, conducting four counts with \( n \) number of sampling days frequently resulted in MSEs that were similar to those obtained from conducting eight counts in \( n - 1 \) sampling days. In this scenario, the cost of both options can be assessed and surveys

FIGURE 9. Mean square error (MSE) of estimated angling effort from roving creel surveys in a simulated Chinook Salmon fishery on day 8 (top panel) and day 9 (bottom panel) for the Little Salmon River, Idaho, during the 2011 season. The number of instantaneous angler counts varied from two to eight, and three different sampling designs were evaluated: nonuniform probability sampling (NUP), simple random sampling (SRS), and systematic random sampling (SYS).

FIGURE 10. Relative accuracy of total weekly catch estimates per unit cost from roving creel surveys in three simulated Chinook Salmon fisheries on the Clearwater River (top panel), Little Salmon River (middle panel), and South Fork Salmon River (bottom panel), Idaho, during the 2011 season. The number of instantaneous angler counts was four, and two different sampling designs were evaluated: systematic random sampling (SYS) and a two-cluster design (CL2). The number of days sampled varied from four to seven.
can be planned to maximize precision per unit cost (Cochran 1977; Lester et al. 1991; Scheaffer et al. 2006). Additionally, allocating time to counts can potentially reduce the number of interviews that can be conducted, thus reducing the precision of mean catch rate estimates (Pollock et al. 1994).

The SYS design consistently produced the most accurate 95% CIs on estimates of daily effort in our primary simulation (i.e., days 1–7 in the Clearwater, Little Salmon, and South Fork Salmon River fisheries). However, CIs were biased for estimates from days 8 and 9. The difference in accuracy of CIs likely occurred because the population was ordered randomly on days 1–7, whereas it was periodic on days 8 and 9. The bias in CIs was only present when the length of time between counts was equal to the period of the population. Variance was calculated under the assumption that the population was ordered randomly (Scheaffer et al. 2006). Repeated systematic sampling can be conducted to determine the structure of the population being sampled (i.e., random, ordered, or periodic) and to provide more accurate estimates of variance and CIs (Cochran 1977; Pollock et al. 1994; Scheaffer et al. 2006). Pollock et al. (1994) recommended taking several independent samples and estimating variance directly from the replicate samples. Results of our simulations, particularly for the Little Salmon River on days 8 and 9, confirm that angling effort can be periodic and that repeated sampling increases the accuracy of variance estimates.

Most probabilistic creel survey designs have the potential to be unbiased over time if they are planned and executed properly, but not all designs will result in similar precision (Pollock et al. 1994). Additionally, methods used to conduct angler interviews can influence bias in total catch estimates from creel surveys (Bernard et al. 1998; Rasmussen et al. 1998; McCormick et al. 2012). Because our simulations did not incorporate estimates of bias and precision from estimation of mean catch rate, which can be highly variable depending on the survey design (McCormick et al. 2012), our estimated MSEs of daily and weekly catch were conservative. However, the results of the simulations provide guidelines on the relative influence of sample size and designs on fishery parameters. Such information is useful in preventing inefficient use of resources (i.e., oversampling) or ineffective management based on unreliable data (i.e., from too little sampling).

ACKNOWLEDGMENTS

We thank Nick Porter for assistance with data collection and IDFG management biologists for providing their expertise on sampling locations and current survey designs. We thank M. R. Falcy, F. M. Wilhelm, C. J. Williams, Z. Su, and two anonymous reviewers for their comments on an earlier version of this manuscript. Funding for this project was provided by IDFG through Federal Aid in Sport Fish Restoration. The Idaho Cooperative Fish and Wildlife Research Unit is jointly sponsored by the University of Idaho, U.S. Geological Survey, IDFG, and Wildlife Management Institute. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES


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Published online: 08 Oct 2013.

To cite this article: Pang-hua Gu, Jian-guo Xiang, Yi-fang Chen, Yan-liang Li, Jun Tang, Song-guang Xie & Yushun Chen (2013) A Comparison of Different Age Estimation Methods for the Northern Snakehead, North American Journal of Fisheries Management, 33:5, 994-999, DOI: 10.1080/02755947.2013.822445

To link to this article: http://dx.doi.org/10.1080/02755947.2013.822445

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ARTICLE

A Comparison of Different Age Estimation Methods for the Northern Snakehead

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Abstract
We used otoliths, scales, pectoral fins, dorsal fins, basioccipital bones, opercular bones, interopercular bones, vertebrae, teeth, and cleithra sampled from 221 known-age Northern Snakeheads Channa argus argus representing five age-groups to determine and compare age estimation methods for this species. Results showed that accuracy of age estimation methods varied among structures: 85.68% of otoliths, 68.91% of scales, 49.25% of pectoral fin rays, and 27.67% of opercular bones yielded age estimates that were consistent with the actual fish ages. Ages determined from other structures, such as interopercular bones, dorsal fins, basioccipital bones, and vertebrae, had lower rates of agreement (<20%) with actual ages. The current results suggest that age estimation with otoliths, especially sagittal otoliths, is the most accurate method for use with Northern Snakeheads. Furthermore, analysis of scales can be used as a supplementary approach, especially for younger (age < 3) Northern Snakeheads.

The Northern Snakehead Channa argus argus is one of the most widespread benthic carnivorous fishes (Meng 1989). The life span of this fish is relatively short; Northern Snakeheads naturally reach the period of senescence after 5 years' growth, so it is usually difficult to catch fish older than age 5 in the wild (Zhang et al. 1999). In China, the Northern Snakehead has been a favorite seafood fish because of its tasty meat, and it has been used as a top predator in ecosystem biomanipulation. In the USA, the Northern Snakehead became known as “Frankenfish” when it was discovered in a Maryland pond in 2002, having

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Received March 14, 2013; accepted June 27, 2013
Published online September 25, 2013
already destroyed the native aquatic ecosystem and biological diversity (Cunningham 2005).

It is necessary to develop an accurate age estimation method for managing Northern Snakeheads in natural water bodies since different age estimation methods may vary in precision (Campana 2001; Zymonas and McMahon 2009; Kowalewski et al. 2012). Some methods require ages from several structures to be compared for more accurate estimation (Boxrucker 1986; Welch et al. 1993; Isermann et al. 2010), and the availability of known-age reference fish is usually very helpful for these comparisons (Buckmeier 2002; Maceina et al. 2007). Moreover, the timing of first annulus formation in Northern Snakeheads has not been reported in recent years.

Scales have long been considered one of the most reliable structures for use in fish age estimation, and the precision of age estimates from scales can be similar to the precision from otoliths for some species (e.g., Kruse et al. 1993). To our knowledge, most previous studies have only used the scale method for aging Northern Snakeheads (e.g., Zhu and Liang 1999; Yu et al. 2008). However, we have found no study evaluating whether the scale method is the most accurate approach relative to other methods such as otolith analysis, which is widely used in age determination for other fishes.

Because otoliths are within the fish’s body, the information contained in otoliths is resistant to disturbance by external environmental factors. This is in contrast to scales, which have direct exposure to the environment, making the rings on scales too complex to identify in some situations. Otoliths possess some advantageous characteristics, such as sustained growth and a low probability of being absorbed. For example, Hoxmeier et al. (2001) found that for Bluegills Lepomis macrochirus in Illinois reservoirs, ages estimated from otoliths were more precise than those estimated from scales. In the present study, we hypothesized that for Northern Snakeheads, the otolith method would provide more reliable and more accurate age estimates than scales.

Other calcified structures can also be used to estimate fish age. For example, vertebral bones were used to estimate ages of Shortfin Mako Isurus oxyrinchus (Ribot-Carballal et al. 2005). Polat et al. (2001) found that in comparison with otoliths and scales, vertebrae were the most reliable structure for determining the age of European Flounder Pleuronectes flesus luscus. Furthermore, Wang and Dai (2006) used scales, opercular bones, dorsal fin spines, vertebrae, and cleithra to estimate age in the cyprinid fish Tor (Folifer) brevifilis brevifilis and found that among all pairs of structures, the combination of scales and opercular bones had the highest tally rate and yielded the most reliable predictions of fish age. In addition, pectoral fins, basioccipital bones, teeth, and other hard structures can also be used for age estimation. To our knowledge, no previous study has compared different age estimation methods for use with Northern Snakeheads. Thus, in the current study, we examined otoliths, scales, pectoral fin rays, dorsal fin rays, opercular bones, interopercular bones, basioccipital bones, vertebrae, teeth, and cleithra from known-age Northern Snakeheads to compare the various age estimation methods for this species.

**METHODS**

**Experimental fish.**—Samples of known-age Northern Snakeheads were collected from farming ponds at a field research station near Yuanjiang City, Hunan Province, China (101°39′E, 28°46′N). The samples (n = 221 fish) were collected in March, April, May, June, and December 2009 (Northern Hemisphere Time; Table 1) and included five different age-groups: age 0, age 1, age 2, age 3, and age 4 and older (age 4 +; including five age-4 fish, two age-5 fish, and one age-6 fish). We removed every age structure from each fish to observe and compare the annual rings in the laboratory. Two trained readers, who did not have any age information for each specimen, examined the aging structures twice within a 20-d interval. Unreadable structures or the results of a sample that showed an irreconcilable difference between the two readers were considered as disagreeing with the actual fish age.

**Otoliths.**—We followed standard methods to handle the various structures (DeVries and Frie 1996; Campana 2001). Otoliths were removed, cleaned, immersed in xylene for approximately 5 min, and examined with a dissecting microscope. Otoliths with unclear annual rings were ground with sandpaper to make the annuli more distinct for age reading (Tandon and Johal 1996). The first one or two increments deposited on the otolith were often broader and less distinct than subsequent increments (Gunn et al. 2008). An annulus is the translucent margin at the end of 1 year’s growth (Xie and Watanabe 2005).

**Scales.**—Scales were removed from three locations on the fish’s body: at the base of the pectoral fin (front area), above the lateral line but below the first dorsal fin (middle area), and above the lateral line but below the last dorsal fin (back area). Over 10 scales from each site on each fish were cleaned and dried in the laboratory. Of these, 8–10 scales were pressed on glass slides and examined under a microscope (DeVries and Frie 1996).

**Other structures.**—The leading pectoral or dorsal fin rays were excised as close to the body as possible by using

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dissecting scissors. Whole or proximal portions of fin rays were set in epoxy and sectioned (0.5–0.7 mm) on the transverse plane by using a slow-speed saw. If necessary, fin ray sections were ground wet or dry with 600-grit sandpaper (Sylvester and Berry 2006). Sections for each fin ray were pressed on microscope slides and aged under a dissecting microscope (Buckmeier et al. 2002). The opercular bones, interopercular bones, vertebrae, basioccipital bones, teeth, and cleithra were removed from fish that had been boiled in water for 2–3 min. These structures were boiled in 1% NaOH solution for 5–10 min, washed clean, dried in air, and then observed under a microscope (Hua et al. 2005).

Data processing.—We used percent agreement and the coefficient of variation (CV = [SD/mean] × 100) to evaluate the accuracy and precision of estimated ages within and between the two trained readers (Chang 1982; Campaña et al. 1995; Hoxmeier et al. 2001; Blackwell and Kaufman 2012). Percent agreement was calculated as (A/n) × 100, where A is the number of fish with an estimated age (i.e., from a given structure) that agreed with the actual age, and n is the total number of fish in the sample.

The agreement rate obtained for each age-group represented the efficiency and accuracy of a given method for estimating the age of fish at a particular life stage, whereas the mean agreement rate for each method was used to compare accuracy among the aging methods. A paired t-test was also used to compare results between the two readers.

RESULTS

Timing of Annulus Formation

Samples collected during four consecutive months (March–June 2009) showed the following pattern: in March, the edges of otoliths were in the white layer, but 40.91% of scales began to form annular rings (Figure 1). In April, the narrow dark layer emerged on the otolith edge, but the annual ring did not form on it, whereas 63.64% of scales showed the beginning of annular deposition at the edge. In May, 37.50% of otoliths and 66.67% of scales had a newly formed annular zone. In June, 97.73% of otoliths and 76.69% of scales had clear annuli. Thus, the annual ring in Northern Snakeheads began to form in April and became fully formed in June.

Characteristics of Annual Rings on Hard Structures

Although there were rings on the pectoral fins, dorsal fins, vertebrae, basioccipital bones, opercular bones, and interopercular bones, most of the annuli were ambiguous and it was difficult to estimate age. In addition, no rings were found on the teeth or cleithra, so those structures were excluded from further analysis.

On otoliths, there were some periodic growth zones, with alternately deposited wide white layers and narrow dark layers, the latter of which were regarded as the growth rings. Although annular rings could be observed in all the three types of otolith, the ring structures on most of the asteriscus and lapillus otoliths were not continuous. Therefore, these otolith types were not considered as aging structures for Northern Snakeheads. Annuli were more pronounced on sagittal otoliths, and in young-age Northern Snakehead samples there were complete rings around the cross section of the sagittal otolith (Figure 2). All age-groups exhibited high clarity of annual rings in the depression of the lateral sagittae. The annuli on scales were also clear, appearing dispersed in the front area of the scale and transitional characteristics in the lateral areas (Figure 3), but the crumbliness was not obvious on scales from younger-age fish.

Evaluation of Results from Different Age Determination Methods

The mean agreement rates between the two readers were 92.17% for otoliths, 85.38% for scales, 63.91% for pectoral fins, and 58.61% for opercular bones (Figure 4). Paired t-tests showed that ages estimated with otoliths, scales, and pectoral fins did not significantly differ between the two readers (P = 0.20, 0.31, 0.21, respectively), whereas the ages determined...
with opercular bones were significantly different between the readers \((P = 0.00061)\). Agreement rates between the readers on ages estimated from basioccipital bones, vertebrae, interopercular bones, and dorsal fins were all below 30%, and there were also many subjective errors between readers when annual rings were counted from these structures. The mean CV in age estimates between readers was 2.83% for otoliths, 6.92% for scales, 27.04% for pectoral fin rays, and 23.83% for opercular bones.

Among all of the structures used for age determination, otoliths from age-1 Northern Snakeheads had the highest occurrence rate (100%) of annual rings (i.e., percentage of structures that had rings to count), and the average percent agreement for otoliths was 85.68% (Figure 5). The mean percent agreement for scales was 68.91%. Other structures had relatively clear annual rings along with too many false rings, hindering the estimation of age. The values of percent agreement from these structures were also low: only 49.25% for pectoral fins, 27.67% for opercular bones, and less than 20% for dorsal fins, interopercular bones, vertebrae, and basioccipital bones.

The percent agreement of annual rings on scales in the five age-groups of Northern Snakeheads was variable: 99.66% for age-0 fish, 58.40% for age-1 fish, 69.82% for age-2 fish, 54.23% for age-3 fish, and 62.44% for age-4+ fish (Figure 6). We also found that scales removed from the base of the pectoral fin had the highest percent agreement and the highest occurrence rate of annual rings (average agreement rate = 74.06%) in all age-groups; the average agreement rates were 68.47% for scales from the middle area and 64.20% for scales from the back area. In addition, the agreement rates between pairs of structures were 94.72% for otoliths and scales, 63.35% for otoliths and pectoral fins, and 60.84% for scales and pectoral fins.
DISCUSSION

We found that annulus formation was generally earlier on scales than on otoliths. The annuli on scales were formed from March to June, similar to the results of a previous study of Northern Snakeheads in Poyang Lake, central Yangtze River basin (Yu et al. 2008). We therefore conclude that the annulus formation period in scales is longer than that of otoliths but is relatively scattered. The rings on the otoliths were formed between April and June. The period of annulus formation on otoliths was shorter and centralized. The first annual ring on calcified structures did not form in age-1 Northern Snakeheads until June, so the two readers may have underestimated the age of the specimens that were collected from March to June. We suggest that when using hard structures to estimate the age of Northern Snakeheads, the sampling date must be considered, as it may be better to sample the fish sometime after June to avoid underestimation of fish age to some extent.

Results from the present study showed that the sagittal otolith was the best structure for use in Northern Snakehead age estimation. Buckmeier et al. (2002) also validated the otolith and pectoral spine methods and recommended the use of otoliths for estimating the age of Channel Catfish Ictalurus punctatus. Use of sagittal otoliths as aging structures for Northern Snakeheads is preferable not only because of the clear rings, high accuracy, and repeatability but also because the annuli could be distinguished easily (even on the otolith edge) in Northern Snakeheads older than 4 years. Although this method involves killing the fish, the use of sagittal otoliths seems to be the most reliable approach for determination of age in Northern Snakeheads.

Generally, scales can be obtained easily without sacrificing the fish and also can be observed directly, but the use of scales as aging structures has some drawbacks, including the presence of false annuli, difficulties in locating the first annulus, and crowding of annuli along the outer scale margin in older specimens. Since the 1970s, researchers have noted that the use of scales to estimate fish age has limitations (e.g., Jessop 1972; Beamish 1981), and some studies have shown that the scale aging method is not appropriate for certain species (e.g., Schill et al. 2010). In the present study, especially for Northern Snakehead specimens over age 3, the number of annual rings on the scales was less than the actual fish age, as further evidenced by the lower agreement rate for these age-classes. There are several possible reasons for the inaccuracy of scale-based age estimates. First, some of the scales we collected might have been regenerated ones; the potential for obtaining regenerated scales is higher when fish of greater ages are sampled, and the number of rings on such scales would always be limited. Second, as the fish grow, the rings on their scales may become increasingly crowded, possibly causing two rings to be read as one ring or causing a ring to be considered discontinuous by the reader. Our results did suggest that there were many regenerated and secondary scales on Northern Snakeheads, as 23.53% of the scale samples had no rings. Therefore, we should consider these problems when using the scale approach for aging older fish. Our results are similar to those from previous studies emphasizing that the scale aging method is appropriate for younger, but not older, fish (Borkholder and Edwards 2001; Maceina and Sammons 2006; Sylvester and Berry 2006; Gunn et al. 2008).

Previous studies have demonstrated the effectiveness of using other structures in fish age determination (e.g., Logsdon 2007; Quist et al. 2007; Colombo et al. 2010). Very early in the current study, we found that teeth and cleithra did not have any useful rings with which to estimate fish age, so these structures were excluded from further analysis. Although for pectoral fins the total agreement rate between the two readers was 63.91% ($P > 0.05$), the agreement with actual age was only 49.25%, which is relatively low. The use of opercular bones is not recommended, as this method involves killing the fish and has lower accuracy and repeatability than the pectoral fin method. Other structures, such as dorsal fin rays, interopercular bones, basioccipital bones, and vertebrae, had similar defects: too many incomplete or false rings on these structures, a low accuracy rate, poor repeatability, and the need to sacrifice fish to collect the structures. Therefore, we suggest that these other structures should only serve to supplement the use of otoliths and scales in estimating the age of Northern Snakeheads.

ACKNOWLEDGMENTS

The current study was financially supported by grants from the State Key Laboratory of Freshwater Ecology and Technology (2010FB19), the Hunan Department of Education (09A032), and the Research Program of Hunan Province, China (2009NK3095). We appreciate the two journal reviewers who helped us to improve the manuscript.

REFERENCES


North American Journal of Fisheries Management

Sluiceway Operations to Pass Juvenile Salmonids at The Dalles Dam, Columbia River, USA

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Published online: 08 Oct 2013.

To cite this article: Gary E. Johnson, Fenton Khan, John R. Skalski & Bernard A. Klatte (2013) Sluiceway Operations to Pass Juvenile Salmonids at The Dalles Dam, Columbia River, USA, North American Journal of Fisheries Management, 33:5, 1000-1012, DOI: 10.1080/02755947.2013.822441

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ARTICLE

Sluiceway Operations to Pass Juvenile Salmonids at The Dalles Dam, Columbia River, USA

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Abstract

Existing ice and trash sluiceways are commonly used as benign, nonturbine routes for downstream passage of juvenile salmonids at hydropower dams. At The Dalles Dam on the Columbia River, we studied various operational configurations of sluiceway weirs to maximize sluiceway passage of juvenile Pacific salmon Oncorhynchus spp. and steelhead O. mykiss. We applied hydroacoustic methods to compare fish passage rates and sluiceway efficiencies for two weir configurations in each year: three weirs (SL 1; i.e., collectively referring to the three weirs above main turbine unit [MU] 1) versus six weirs (SL 1+18) during 2004; and middle (SL 2+5) versus east (SL 2+19) powerhouse weir locations during 2005. Horizontal distributions at the sluiceway and turbines and the effects of operating turbines beneath open sluiceway gates were also analyzed. Sluiceway passage efficiency relative to the powerhouse (SLYphs) varied between study years, between spring and summer, and between day and night. In 2004, sluiceway passage rates were significantly higher (P = 0.0003) for SL 1+18 than for SL 1 during summer–night but were not significantly different between the two configurations during the other three season–day/night periods. The SLYphs was significantly higher for SL 1+18 than for SL 1. The location comparison during 2005 revealed no significant differences between the SL 2+5 and SL 2+19 configurations, except for summer–day. The experimental findings led to recommendations for long-term operations of The Dalles Dam sluiceway: open six rather than three sluiceway weirs to take advantage of the maximum hydraulic capacity of the sluiceway; open the three weirs above the westernmost operating MU and the three weirs at SL 8, where turbine passage rates are relatively high; operate the MUs below open sluiceway weirs as a standard procedure; operate the sluiceway 24 h/d year-round to maximize its benefits to juvenile salmonids; and use the same weir configuration year-round. These operational concepts are transferable to dams where sluiceway surface flow outlets are used to protect downstream-migrating fishes.

Use of existing sluiceways is a common practice for facilitating downstream passage of juvenile salmonids at hydropower dams (Čada and Sale 1993; Johnson and Dauble 2006). Originally installed as a component of many dams to transfer ice and debris downstream, sluiceways also serve as a form of surface flow outlet for juvenile salmonids (Johnson and Dauble 2006), providing a nonturbine route for these surface-oriented fishes (Bentley and Raymond 1969; Liscom 1971; Smith et al. 2010). Over a century ago, Mather (1875) provided design requirements for a sluiceway to pass fish downstream. Sluiceway operation at many dams simply involves lifting a gate off a weir during a prescribed time period (Hanson 1999). At other dams, however, managers must decide how many weirs to open, where and when to open them, and whether to operate nearby turbine
units (Johnson et al. 2005b). Because sluiced water is lost to hydropower production, managers must balance the needs of fisheries resources and power production in the context of limited water supplies (Čada 1998; Larinier 1998; Larinier and Travade 1999, 2002; Coutant and Whitney 2000).

At The Dalles Dam (TDA; Figure 1) on the Columbia River, the U.S. Army Corps of Engineers (USACE) and fisheries managers are developing long-term measures for optimizing sluiceway operations to protect downstream-migrating juvenile Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss*. This work is a high priority in the endeavor to increase juvenile salmonid survival through the Federal Columbia River Power System (NMFS 2000, 2004, 2008). Juvenile salmonids pass TDA through one of three routes: turbines, the spillway, or the sluiceway. At TDA, turbine-passed juvenile salmonids generally have the lowest survival rate, whereas spillway- and sluiceway-passed juveniles have the highest (e.g., Johnson et al. 2011; turbine: mean = 0.86–0.89, SE = 0.02–0.04; spillway: mean = 0.96–0.97, SE = 0.01; sluiceway: mean = 0.94–0.99, SE = 0.01–0.02). In addition to passing water during high flow events, the spillway is opened during spring and summer to provide a nonturbine passage route for juvenile salmonids. Overall, about 10, 75, and 15% of the total project passage of juvenile salmonids occur through the turbines, spillway, and sluiceway, respectively, depending on species, flows, and other factors. One advantage of the TDA sluiceway, like many other sluiceways, is its proximal location relative to turbine intakes. When sluiceway weirs are open, there is surface flow to pass fish that might otherwise pass downward into the turbine intakes. Most importantly for water management, sluiceways pass three to nine times more fish per unit volume of water than do spillways (Johnson and Dauble 2006). At the TDA sluiceway, optimizing the operation of weirs was one approach undertaken by managers to maximize the survival of juvenile salmonids at TDA powerhouse.

Original TDA sluiceway operations for juvenile salmonid passage were established based on the results of mark–recapture studies using sluiceway fyke nets in the late 1970s and early 1980s. Nichols (1979) found that the sluiceway weirs at the west end of the powerhouse above main turbine units (MUs) 1 and 2 (three sluiceway weirs are associated with each MU and

![FIGURE 1. Map of the Pacific Northwest, showing locations of The Dalles Dam and other dams on the main-stem Columbia and Snake rivers.](image-url)
are numbered accordingly: e.g., SL 1 [weirs SL 1-1, 1-2, and 1-3] is located above MU 1; SL 2 [weirs SL 2-1, 2-2, and 2-3] is located above MU 2; etc.) had higher passage rates (number of fish per unit time) for yearling Chinook Salmon *O. tshawytscha* than did weirs at the middle region of the powerhouse (SL 10). Nichols (1980) found higher passage rates for marked subyearling Chinook Salmon at the east-end sluiceway weirs (SLs 17 and 18) than at the west-end sluiceway weirs (SLs 1 and 2), although in a repeat study Nichols and Ransom (1981) reported no significant difference between east and west sluiceway passage rates for Chinook Salmon. Nichols (1980) recommended that the sluiceway be operated 24 h/d because noticeable numbers of juvenile Chinook Salmon used the sluiceway at night, although the highest passage rates were during daylight hours. Based on these data, fisheries managers recommended that the sluiceway weirs at the west end of the dam’s powerhouse (SL 1) be kept open 24 h/d to pass juvenile salmonids during spring and summer. The TDA sluiceway was operated like this for 23 years from 1981 through 2003.

The efficacy of the west-end sluiceway operation for both spring and summer emigrants was brought into question by more recent fish approach and passage rate data and hydraulic calculations. In 1997, researchers using radiotelemetry determined that out of the total number of steelhead and yearling Chinook Salmon detected at TDA, about 60% of the steelhead and 56% of the Chinook Salmon were first detected while entering the forebay off the eastern end of the powerhouse (Hensleigh et al. 1999). This pattern was consistent with the results of other radiotelemetry studies at TDA (Holmberg et al. 1997; Sheer et al. 1997; Hansel et al. 2005, 2007). Hydroacoustic studies showed that the distribution of fish passing at the powerhouse was uniform or skewed toward the west end during spring but was skewed toward the east end during summer (Moursund et al. 2001, 2002; Ploskey et al. 2001a, 2001b). In addition, managers asked whether operating the turbines beneath open sluiceway weirs would be preferred for purposes of enhancing fish passage rates at the sluiceway. Finally, engineers determined in 2003 that TDA sluiceway was being operated at less than maximum hydraulic capacity when only the three gates for SL 1 were open; up to three additional gates could be opened before the maximum hydraulic capacity of the sluiceway channel (∼126 m³/s) was reached. Collectively, these biological and engineering studies provided the impetus for renewed sluiceway operations research during 2004 and 2005.

This study focused on passage at TDA for the juvenile salmonid run at large (i.e., the collective population of fish passing downstream through the dam). Overall, the run at large during spring is dominated by yearling Chinook Salmon, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, and steelhead (hereafter, yearling salmonids, > 1 year old), whereas subyearling Chinook Salmon dominate the out-migration during summer (hereafter, subyearling salmonids, < 1 year old; FPC 2005, 2006). We provided data that could be used by managers to optimize sluiceway operations for the run at large by statistically comparing fish passage rates and sluiceway efficiencies for two weir configurations during 2004 and two additional weir configurations during 2005. The sluiceway weir comparisons and the configurations used to test them were as follows (turbines and weirs used in 2004 and 2005 differed because of dam maintenance schedules):

1. Three weirs versus six weirs: SL 1 (three weirs) versus SLs 1 and 18 (SL 1+18; six weirs) from 19 April through 11 July 2004. The SL 1 weirs were chosen because they were at the west end of the powerhouse, and SLs 1 and 18 represented weir locations at both ends of the powerhouse.
2. Locations at the middle versus east regions of the powerhouse: SLs 2 and 5 (SL 2+5; six weirs, middle) versus SLs 2 and 19 (SL 2+19; six weirs, east) from 18 April through 16 July 2005. These weirs were chosen to represent locations in the west (SL 2), middle (SL 5), and east (SL 19) areas of the powerhouse.

We also analyzed horizontal distributions of fish passage rates at the sluiceway and turbines and the effects of operating turbines beneath the open sluiceway weirs to provide supporting data that were relevant to optimizing sluiceway operations. The findings were applied to generate recommendations for powerhouse operations that enhance sluiceway passage rates and reduce turbine passage rates, thereby increasing smolt survival at TDA.

**STUDY SITE**

Located at river kilometer 309 on the Columbia River, TDA is owned and operated by USACE. Full-pool elevation is rated at 48.8 m above mean sea level (msl), and minimum operating pool elevation is 47.2 m above msl. The thalweg intersects the dam at the eastern end of the powerhouse, and there are deep areas in front of the powerhouse, although much of the forebay is relatively shallow (<19.8 m deep). The powerhouse at TDA is 637 m long and contains 22 MUs, providing a total generating capacity of 1,800 MW and a total hydraulic capacity of 10,619 m³/s. Two small “station service” turbine units that supply power to the dam are located between MUs 8 and 9. The powerhouse also has two fish units at the west end that provide attraction flow to the east fish ladder for upstream-migrating adult salmonids. The turbine intake ceiling intersects the trash racks at an elevation of 43 m above msl. The spillway is 420.6 m long and comprises 23 bays with 15.2-m-wide radial gates.

The sluiceway at TDA is a channel that extends the entire length of the forebay side of the powerhouse. The sluiceway has three 6.1-m-wide weirs positioned over each of the 22 MUs. Water enters the sluiceway channel from the forebay when weir gates are moved off the weir sills at an elevation of 46 m above msl. A maximum of six sluiceway weirs can be opened at any time before reaching the hydraulic capacity of the sluiceway channel (∼126 m³/s). Flow into the sluiceway is dependent on water surface elevation in the forebay and on the number and location of open weirs. Sluiceway discharge is a relatively small proportion of total project discharge (about 2%) and total...
TABLE 1. Hydraulic calculations for the sluiceway at The Dalles Dam on the Columbia River (reservoir level = 48.28 m; open weir elevation = 46.03 m above mean sea level; Manning’s roughness = 0.014). The three sluiceway weirs at SL 1 (i.e., above main turbine unit 1) are nearest to the sluiceway channel outlet, and the three weirs at SL 19 are furthest from the outlet. These data (provided by the U.S. Army Corps of Engineers, Portland District) are calculated and have not been verified by field measurements.

<table>
<thead>
<tr>
<th>Configuration</th>
<th>Sluiceway weir</th>
<th>Weir number</th>
<th>Flow over weir (m³/s)</th>
<th>Average velocity over weir (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2004</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SL 1</td>
<td>1</td>
<td>1</td>
<td>29.99</td>
<td>2.19</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>29.76</td>
<td>2.16</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3</td>
<td>29.14</td>
<td>2.13</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>88.89</strong></td>
<td></td>
</tr>
<tr>
<td>SL 1+18</td>
<td>1</td>
<td>1</td>
<td>28.71</td>
<td>2.07</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>24.81</td>
<td>1.80</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3</td>
<td>21.66</td>
<td>1.58</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>126.04</strong></td>
<td></td>
</tr>
<tr>
<td><strong>2005</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SL 2+5</td>
<td>2</td>
<td>1</td>
<td>28.46</td>
<td>2.07</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2</td>
<td>24.44</td>
<td>1.77</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>3</td>
<td>21.21</td>
<td>1.55</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>4</td>
<td>18.66</td>
<td>1.37</td>
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<tr>
<td></td>
<td>5</td>
<td>5</td>
<td>17.05</td>
<td>1.25</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>6</td>
<td>16.25</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>126.04</strong></td>
<td></td>
</tr>
<tr>
<td>SL 2+19</td>
<td>2</td>
<td>1</td>
<td>28.54</td>
<td>2.07</td>
</tr>
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<td></td>
<td>2</td>
<td>2</td>
<td>24.61</td>
<td>1.80</td>
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<td>19</td>
<td>4</td>
<td>18.12</td>
<td>1.31</td>
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<td>5</td>
<td>16.54</td>
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<td></td>
<td>19</td>
<td>6</td>
<td>15.72</td>
<td>1.16</td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>125.02</strong></td>
<td></td>
</tr>
</tbody>
</table>

powerhouse discharge (about 4%). Total sluiceway discharge at a forebay water surface elevation of 48.3 m above msl for the four weir configurations we studied ranged from 94 to 126 m³/s; flows over individual weirs increase as distance to the sluiceway channel outlet decreases (Table 1).

Flow approaches a sluiceway entrance at an oblique angle relative to the powerhouse, becoming more perpendicular to the dam within 1.5–4.5 m of the outlet. In cross section, flow is horizontal (parallel to the surface) until it is near the dam, where it goes up to the sluiceway or down to the turbine intake. Flow into the sluiceway has a gradual acceleration until it is over the weir; water then accelerates rapidly into the sluiceway channel. Computational fluid dynamics modeling revealed that near-field forebay velocities at TDA were generally less than 0.6 m/s except very near the sluiceway weirs (Rakowski et al. 2006).

METHODS

Fixed-aspect hydroacoustics.—We used the fixed-aspect hydroacoustic technique (Thorne and Johnson 1993) to estimate passage rates of yearling and subyearling salmonids at TDA during the spring and summer of 2004 and 2005. These fish dominate the fish community passing downstream through TDA during these seasons, as inferred from direct capture sampling at John Day Dam, located 40 km upstream (FPC 2005, 2006; see species composition results). This means that the passage rate estimates likely were not biased by the detection of nontarget species. Statistically significant associations between estimates of fish passage rates from concurrent hydroacoustic and net catch data have been used to validate the fixed-aspect technique at Columbia River dams and other dams (Ransom et al. 1996; Ploskey and Carlson 1999).

The acoustic screen model (Johnson 2001) is the basis for the fixed-aspect hydroacoustic technique. It is essentially an echo-counting technique (Simmonds and MacLennan 2005) that relies on single echoes from individual fish passing through the volume ensonified by successive transmissions of sound energy from an underwater transducer (i.e., acoustic sampling volume; Foote 1991). The beginning and end ranges of the sampling volume are prescribed by the user. The nominal beam angle of the sampling volume is the angle off-axis at which the sound intensity has dropped by half, while the effective beam angle is defined by the echo-detection threshold and the echo level, which depend on fish target strength, target position in the beam, beam pattern, and other factors. Effective beam width is determined by detectability modeling during the data analysis process. Echoes from fish in the sampling volume are combined into fish tracks by using spatial correlation algorithms, taking advantage of the fact that the sampling volume is ensonified successively in fixed-aspect hydroacoustics (Kieser and Mulligan 1984). The conversion from echoes to tracks basically changes the sampling volume into a sampling plane or an “acoustic screen.”

The assumptions of the acoustic screen model may be categorized as detection, identification, and weighting. Detection is the ability of the hydroacoustic system to accurately acquire fish echo data. The detection assumptions are that (1) sound energy does not affect fish behavior; (2) all targets of interest in the acoustic beam return receivable echoes; (3) detectability for each transducer is known accurately; and (4) hydroacoustic system performance is stable during the study. Identification involves converting fish echoes into fish tracks, as described above. This process assumes that (1) targets do not overlap; (2) there are no false targets; (3) fish tracked at a particular passage route in the dam actually pass there; (4) a given fish is counted only once; and (5) the identification process is consistent across transducers. Weighting is the analysis step in which individual fish tracks are extrapolated spatially to the full width...
Figure 2. Plan view of The Dalles Dam, showing numbers for main turbine units (MUs) and sluiceway weirs (three sluiceway weirs are associated with each MU: e.g., SL 1 represents the three weirs [SL 1-1, 1-2, and 1-3] above MU 1) and the hydroacoustic transducer locations used for estimating downstream passage of juvenile salmonids in 2004 and 2005. Numbers at the powerhouse designate MUs.

(transducer aiming vertically) or height (transducer aiming horizontally) of the passage location being sampled (this step is explained in detail below). The assumptions for weighting are that (1) the effective beam angle for each sampling location is accurately known; (2) target strength characteristics are the same among sample locations or can be accurately estimated for fish tracks; and (3) the horizontal distribution of fish within the sampling location is uniform.

Sampling locations.—Single- and split-beam transducers were deployed to sample fish passage at the sluiceway and turbines (Figure 2). Transducer sampling volumes were positioned to minimize ambiguity in ultimate fish passage routes and the potential for multiple detections of the same fish. Single-beam transducers (6°) were installed at all MU sampling locations except MU 2, which had a 6° split-beam transducer. Six-degree transducers were used to minimize reverberation from intake walls. At all operating MUs, one of three intakes was sampled. The station service units were not sampled because the small spacing of the trash racks there precluded fish passage. The intake that was sampled at a given MU and the horizontal placement of the transducer within that intake were randomly chosen. At the sluiceway, 6° split-beam transducers were installed at all open sluiceway weirs (SLs 1 and 18 during 2004; SLs 2, 5, and 19 during 2005). Passage at each sluiceway weir was monitored by using a pair of transducers (one on each side wall of the entrance to a given weir) that were installed at an elevation of 46.6 m above msl and aimed horizontally and back at a 60° angle to the plane of the sill just upstream of the weir. The acoustic beams for the transducer pairs formed an “X” to optimize the sampling volume horizontally across the sill just upstream of
the weir. Systematic samples (i.e., same order among sampling locations each hour) were collected at 1-min intervals, 24 h/d. Each location was sampled 6–10 times/h depending on the number of transducers that were connected to the echo sounder for the hydroacoustic system at that location.

Data collection, processing, and analysis.—Data collection involved the use of five single-beam hydroacoustic systems, four split-beam hydroacoustic systems (Precision Acoustic Systems [PAS], Seattle, Washington), and either Harp-1B (single-beam) or Harp-SB (split-beam) Data Acquisition/Signal Processing Software (Hydroacoustic Assessments, Inc., Seattle). Each system consisted of a PAS Model 103 echo sounder, cables, transducers, and a computer. All systems operated at a transmission frequency of 420 kHz. Echo sounder transmission rates were 15 pings/s at the turbine intakes and 20 pings/s at the sluiceway. Broadband systems (100 kHz) were used at the sluiceway to decrease pulse widths (80 μs) and to increase target resolution (~0.1-cm separation distance). At the turbines, narrow-band systems (20 kHz) with 200-μs pulse widths were used because target resolution was not an issue. All systems used a voltage output threshold of −56 dB referenced to 1 μPa at 1 m and were calibrated before and after the studies to measure three system characteristics: source levels, receiving sensitivities, and transducer beam pattern factors (Simmonds and MacLennan 2005). The raw output from the fixed-aspect hydroacoustic systems was composed of digitized echoes (records), including data fields for range from the transducer, time, pulse width, and other measurements of echo characteristics.

The digitized echo files were processed (or “tracked”) to extract fish detections. Custom computer programs were developed by the Pacific Northwest National Laboratory (PNNL) to track fish from the echo files. Tracking parameters were specific to each route (sluiceway or turbine) and included the range from the transducer, minimum number of echoes within a specific number of transmissions from a transducer, mean range, maximum ping gap, threshold, mean target strength (split beam) or echo strength (single beam), echo count, slope, linearity, and azimuth direction of travel (split beam; Johnson et al. 2005b, 2006). Tracking parameters were set to include all fish at the expense of including spurious noise tracks because the noise tracks could be removed by filtering. The tracked data were filtered by using parameters such as mean target strength (−55 to −39 dB) and pulse width (150–300 ms) to separate acceptable tracks (fish) from unacceptable tracks (noise). The percentage of unacceptable tracks varied depending on transducer location and wind conditions. Iterative adjustments to filter parameters and examination of resulting echograms were performed by staff experienced in the analysis of hydroacoustic data to finalize the filter parameter values.

Under the assumption of simple random sampling, we applied finite sampling theory (Cochran 1977) to estimate hourly fish passage rates and associated sampling error (Skalski et al. 1993). Even though sampling was necessarily systematic through time among the transducers, random sampling is a reasonable assumption because sampling locations (one of three turbine intakes) and transducer positions at a given sampling location were chosen at random. The only exception was for side-looking transducers at the sluiceway weirs, where the water column was too small for vertical randomization. Each accepted fish track was expanded spatially by the ratio of the route width (vertical acoustic beams) or height (horizontal beams) to the diameter of the beam at the range of detection as follows:

\[
SEC_{fhi} = \frac{W}{2 \cdot R \cdot \tan \left(\frac{\theta}{2}\right)},
\]

where \(SEC_{fhi}\) is the spatially expanded count for fish \(f\) detected during hour \(h\) at the \(i\)th location, \(W\) is the width (m; or height) of the passage route, \(R\) is the range (m) from the transducer, \(tan\) is the tangent function, and \(\theta\) is the effective transducer beam angle (degrees). Transducer beam diameter at the range of detection can be visualized as the length of the opposite side of an isosceles triangle with an apex angle \(\theta\).

The sum of \(SEC_{fhi}\) was then extrapolated temporally to an entire hour by multiplying the inverse of the hourly sampling fraction as follows:

\[
H_{hi} = \sum_{f} SEC_{fhi} \cdot \left(\frac{60}{m_{hi}}\right),
\]

where \(H_{hi}\) is the hourly passage rate for hour \(h\) at the \(i\)th location summed over all fish detected, and \(m_{hi}\) is the number of minutes sampled during hour \(h\) at the \(i\)th sampling location.

Missing hourly data were estimated by using extrapolation from data collected before or after the missing hour(s) for a given location, interpolation from data collected before and after the missing hour(s) for a given location, or regression relationships with data from adjacent locations. This was necessary for less than 1% of the hourly data across all transducers.

Hourly passage rates by location were used to estimate various performance metrics, including the total sluiceway passage (\(SL_{passage}\)) and sluiceway efficiency relative to the powerhouse (\(SLY_{phas}\)):

\[
SL_{passage} = \sum_{h} \sum_{i} H_{hi},
\]

where hourly passage rates were summed across the hours sampled and across the sluiceway weir sampling location; and

\[
T = \sum_{h} \sum_{i} (H_{hi} \cdot x),
\]

where \(T\) is total turbine passage and \(x\) is the number of intakes per unit (two intakes per fish unit; three intakes per MU). The
SLY \_phs \text{ was then calculated as } 

\[
\text{SLY} \_\text{phs} = \frac{\text{SL}_{\text{passage}}}{\text{SL}_{\text{passage}} + T}.
\]

Skalski et al. (1993) described the statistical characteristics of various sampling approaches for fixed-aspect hydroacoustic data, including variance estimation for the hourly passage rate estimators. We calculated 95% asymptotic CIs for passage rate estimates as the product of 1.96 and the square root of total variance.

**Experimental design and statistical analysis.**—Separate spring and summer study periods were established from the 20-year record of juvenile salmonid passage indices at John Day Dam (www.cbr.washington.edu/dart/), which is the closest upstream dam where juvenile salmonid monitoring routinely occurs. The two weir configurations (i.e., treatments) in each study year were sampled according to a randomized block design (Cochran and Cox 1957). During 2004, each treatment lasted 1 d, producing 2-d blocks; thus, there were 24 blocks during spring and 18 blocks during summer. During 2005, each treatment lasted 3 d to accommodate a concurrent radiotelemetry study; there were eight 6-d blocks during spring and seven 6-d blocks during summer. A treatment day began at 0800 hours, and 15–45 min were required to change sluiceway weir operations from one treatment to the other.

Sluiceway passage rates and SLY \_phs \text{ were used as response variables in a two-way (block and treatment) ANOVA to statistically compare the two sluiceway configurations used in each year. Separate analyses for day and night periods were performed for each metric to isolate day–night effects; day was defined as 0600–2000 hours in spring and 0600–2100 hours in summer. The sluiceway passage rate and efficiency data were transformed using the natural logarithm and arcsine functions, respectively, to stabilize variances. A logarithm is appropriate for rate data, and the arcsine is appropriate for proportions. Two-tailed statistical tests were used because the direction of the treatment response was not certain.}

**RESULTS**

**Run Timing and Species Composition**

In both 2004 and 2005, passage of yearling salmonids peaked in mid- to late May and passage of subyearlings peaked in late June, as monitored at John Day Dam (FPC 2005, 2006). The monitoring data on passage timing and species composition at John Day Dam are representative of those at TDA because of the short travel times (~1 d) for downstream migrants between the two dams (Johnson et al. 2007). During spring 2004, species composition of the total salmonid out-migration (the run at large) was as follows: 60% of out-migrants were yearling Chinook Salmon, 16% were steelhead, 11% were Sockeye Salmon, 9% were Coho Salmon, and 4% were subyearling Chinook Salmon. During summer 2004, 89% of the salmonid out-migrants were subyearling Chinook Salmon, and yearling salmonids composed the remainder. During spring 2005, species composition was as follows: 61% of out-migrants were yearling Chinook Salmon, 24% were steelhead, 8% were Coho Salmon, 4% were Sockeye Salmon, and 3% were subyearling Chinook Salmon. During summer 2005, subyearling Chinook Salmon constituted 96% of the total out-migration. Overall, during both 2004 and 2005, juvenile salmonids represented 98% of the total smolt monitoring catch at John Day Dam, with the remaining 2% being other salmonids and incidentals. In addition, as part of another study using an acoustic imaging instrument (Johnson et al. 2009), yearling and subyearling salmonids were observed at TDA sluiceway during 2005. Salmonid yearlings and subyearlings were the predominant fish passing TDA, as detected by the hydroacoustic systems during our sluiceway research in 2004 and 2005.

**Project Discharge and Dam Operations**

During the 2004 and 2005 investigations, daily project discharge at TDA averaged about 5,663 m\(^3\)/s, which was 23–29% below the 10-year average project discharge (Table 2). Spillway discharge constituted 34–39% of total project discharge. Sluiceway discharge was 3.3–4.0% of total powerhouse discharge, with an average forebay elevation of 48.1–48.4 m above msl. Power peaking occurred during the morning (0400–1000 hours)

**Table 2. Discharge (Q) characteristics at The Dalles Dam during four study periods: spring 2004 (19 April–5 June), summer 2004 (6 June–11 July), spring 2005 (18 April–4 June), and summer 2005 (5 June–16 July).**

<table>
<thead>
<tr>
<th>Study period</th>
<th>Mean total Q (m(^3)/s)</th>
<th>Percent of 10-year average</th>
<th>Percent of total Q</th>
<th>Spill of total Q</th>
<th>Sluiceway of total Q</th>
<th>Average forebay elevation (m above mean sea level)</th>
<th>Temperature range (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004 Spring</td>
<td>5,918</td>
<td>76</td>
<td>59</td>
<td>39</td>
<td>2</td>
<td>48.37</td>
<td>11.2–15.6</td>
</tr>
<tr>
<td>Summer</td>
<td>5,550</td>
<td>77</td>
<td>59</td>
<td>39</td>
<td>2</td>
<td>48.31</td>
<td>15.6–20.1</td>
</tr>
<tr>
<td>2005 Spring</td>
<td>5,805</td>
<td>76</td>
<td>64</td>
<td>34</td>
<td>2</td>
<td>48.28</td>
<td>9.4–15.3</td>
</tr>
<tr>
<td>Summer</td>
<td>5,125</td>
<td>71</td>
<td>61</td>
<td>37</td>
<td>2</td>
<td>48.16</td>
<td>15.3–20.2</td>
</tr>
</tbody>
</table>
TABLE 3. Summary of sluiceway passage efficiency relative to the powerhouse (SLYphs; total sluiceway passage divided by the sum of sluiceway passage and turbine passage; presented with 95% CI) at The Dalles Dam.

<table>
<thead>
<tr>
<th>Season</th>
<th>Period</th>
<th>SLYphs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2004</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>0.486 ± 0.028</td>
</tr>
<tr>
<td></td>
<td>Night</td>
<td>0.392 ± 0.025</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0.442 ± 0.019</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2005</td>
</tr>
<tr>
<td></td>
<td>Day</td>
<td>0.321 ± 0.017</td>
</tr>
<tr>
<td></td>
<td>Night</td>
<td>0.352 ± 0.024</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>0.333 ± 0.014</td>
</tr>
</tbody>
</table>

and evening (1800–2200 hours). Turbine operations varied from hour to hour and from day to day. During 2004, MUs 3, 4, 6, and 7 were off-line during the entire study; MUs 1 and 2 went off-line unexpectedly in early June 2004. During 2005, MUs 1, 3, and 4 were off-line during the entire study, and MUs 15 and 16 were off-line during most of the study. Water temperatures ranged from 9.4°C to 20.2°C.

Sluiceway Passage Efficiency

The SLYphs varied between study years, between spring and summer, and between day and night (Table 3). The SLYphs was highest during 2004 spring–day (0.486) and lowest during 2004 summer–night (0.155). The sluiceway was 11–26% (absolute) more efficient during spring than during summer. The SLYphs was higher during day than during night in 2004, but the opposite was found in 2005. The ratio of the fractions of sluiceway passage (Table 3) and discharge (Table 2), also known as sluiceway effectiveness (Johnson and Dauble 2006), ranged from 5.5 to 12.3 for the four year × season combinations.

Comparison of Sluiceway Configurations

For the three-weir versus six-weir comparison in 2004, sluiceway passage rates (number of juvenile salmonids/d) were significantly higher ($P = 0.0003$) for SL 1+18 than for SL 1 during summer–night (Table 4). Sluiceway passage rates, however, were not significantly different between the two configurations for the other three season–day/night periods. The SLYphs was significantly higher for the six-weir configuration (SL 1+18) than for the three-weir configuration (SL 1; Table 4). This finding was consistent across all four of the season–day/night periods that were studied during 2004.

The location comparison in 2005 revealed no significant differences (two-tailed test, $\alpha = 0.05$) between the SL 2+5 and SL 2+19 configurations, except for SLYphs during summer–day (Table 4). Point estimates for both of the response variables—sluiceway passage rate and SLYphs—were higher for SL 2+5 than for SL 2+19.

Horizontal Distributions

For configurations in which six gates were open (SL 1+18, SL 2+5, and SL 2+19), the western or downstream three gates (weirs 1–3; defined in Table 1) typically had a higher fraction of SLpassage than the eastern or upstream gates (weirs 4–6; Figure 3). One exception was summer 2004, when 55% of SLpassage occurred at weirs 4–6 (SL 18). The pattern of highest passage into the sluiceway at the western portion of the powerhouse was more pronounced during spring than during summer.

The horizontal distribution of turbine passage normalized for turbine operations (passage rate per unit discharge) was highest
FIGURE 3. Horizontal distribution of juvenile salmonid passage at The Dalles Dam during each year × season period and for each sluiceway configuration (SL 1, SL 1+18, SL 2+5, and SL 2+19). Data are passage proportions for each set of weirs (weirs 1–3, 4–6; see Table 1) in a given configuration out of the total passage for that configuration (Comb. = combined data for both configurations used within a given year × season period). See Table 1 for weir flow characteristics.

toward the eastern portion of the powerhouse during each of the four year × season periods (Figure 4). Horizontal distribution of turbine passage was reasonably consistent among the periods studied and was especially consistent from spring to summer within a given study year.

Operations of Turbines beneath Open Sluiceway Gates

Sluiceway passage rates were significantly higher ($P < 0.001$) when turbines beneath the open gates were on than when they were off (Table 5). Sluiceway efficiency relative to the western region of the powerhouse (Fish Unit 1 through MU...
5) was also significantly higher ($P < 0.001$) when the turbines beneath the open sluiceway entrance were on than when those turbines were off. The results for sluiceway efficiency relative to the eastern portion of the powerhouse were not significant ($P = 0.071$).

### DISCUSSION

In this study, the fixed-aspect hydroacoustic technique (Thorne and Johnson 1993) was applied to estimate fish passage rates for statistical comparisons of sluiceway weir configurations, allowing us to determine optimum sluiceway operations for TDA. The fixed-aspect hydroacoustic technique is well established at the nine lowermost dams on the Columbia River and the four lowermost dams on the Snake River (Johnson et al. 1992, 2005a; Thorne and Johnson 1993; Skalski et al. 1996; Ploskey and Carlson 1999; Ploskey et al. 2008). The present study addressed the run at large of juvenile salmonids passing TDA during the study periods; species-specific data were not obtained. Studying the run at large was appropriate because the data represented the downstream-migrating salmonid population in composite—the scale at which sluiceway operations are necessarily conducted. It would be impractical, if not impossible, to conduct species-specific sluiceway operations because migration periods overlap, especially during spring, when multiple salmonid species emigrate (FPC 2005, 2006).

Our overall findings regarding the passage rates of juvenile salmonids at TDA were consistent with results from some previous studies but not others. A concurrent radiotelemetry study during 2004 identified SLY values of 55% and 32% for tagged yearling and subyearling Chinook Salmon, respectively (Hansel et al. 2005), whereas our SLY estimates were 44% and 18%, respectively (Table 3). In our study and the Hansel et al. (2005) study, sluiceway passage rates were highest in the westernmost open sluiceway weirs during both spring and summer, a finding that is consistent with a recent acoustic telemetry study (Johnson et al. 2011). During 2010, SLY values calculated from passage efficiencies provided by Johnson et al. (2011: their Table ES.2) were 39% for yearling Chinook Salmon, 58% for steelhead, and 63% for subyearling Chinook Salmon. These acoustic telemetry results compare well with our findings during spring, but for unknown reasons they are not similar to the results we obtained during summer.

Our results from relatively low flow years with total project discharge at about 75% of the 10-year mean are applicable to average or higher flow years because sluiceway discharges would not be affected by higher total discharge. Sluiceway discharge at TDA is dependent on forebay elevation, which fluctuates daily only by approximately 0.5 m, because TDA is a run-of-the-river hydropower project. Generally, more water is spilled, turbine flows are maximized, and sluiceway flows remain fairly constant when total discharge is high. The number of open sluiceway weirs at TDA was our focus in 2004. Although most of the fish passage into the sluiceway occurred through the west weirs (SL 1), opening the weirs in the eastern portion of the dam provided an incremental benefit of about 11% to SL passage in spring and about 65% to SL passage in summer. The passage data did not indicate any negative effects of opening six weirs as opposed to three weirs. Furthermore, the amount of total flow into the sluiceway increased when three additional weirs were opened (e.g., 89 m$^3$/s for three weirs versus 126 m$^3$/s for six weirs, with forebay elevation at 48.3 m above msl; Table 1). This additional flow—especially because it comes from the forebay surface waters—likely contains juvenile salmonids during the spring and summer emigration seasons because these fish exhibit a surface-oriented vertical distribution (Andrew and Geen 1960; ISG 2000; Smith et al. 2010). In conclusion, the data indicate that for juvenile fish protection at TDA, it is better to open six sluiceway weirs rather than three sluiceway weirs, because the use of six weirs takes advantage of the maximum hydraulic capacity of the sluiceway.

The best location for the six open weirs was emphasized in the 2005 study (Johnson et al. 2006) that compared the SL 2+5 and SL 2+19 configurations. Although the sluiceway passage rate or SLY results were not significantly different between the two configurations ($P > 0.025$; two-tailed test, $\alpha = 0.05$), opening the three weirs associated with the westernmost operating turbine is certainly justified by the horizontal distribution of sluiceway passage observed in this study (Figure 3) and other studies (Nichols 1980; Hansel et al. 2005, 2007; Johnson et al. 2011). The westernmost set of three weirs consistently passed the highest proportion of total sluiceway-passed fish, SL passage. Operating three adjacent weirs in tandem is preferred because the combined forebay flow field (the region in the forebay where water accelerates toward the weir of a surface flow outlet; Johnson and Dauble 2006) will be larger and presumably more effective than flow fields for one or two open weirs. Placement of three additional weirs is less straightforward than placement of the three westernmost weirs but may be informed by the horizontal distribution of fish passage rates. A higher proportion of fish passed at the three additional weirs for the SL 2+5 configuration than for the SL 2+19 configuration during both spring and summer (Figure 3), indicating that placement of three additional weirs at the western half of the powerhouse may be advisable because fish would be less concentrated at the westernmost weirs.

### Table 5

<table>
<thead>
<tr>
<th>Location</th>
<th>Response variable</th>
<th>MU on</th>
<th>MU off</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>MU 1, MU 2</td>
<td>SL 1 passage</td>
<td>99</td>
<td>36</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>SLY$_{phs, west}$</td>
<td>0.682</td>
<td>0.340</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>MU 18, MU 19</td>
<td>SL 18 passage</td>
<td>37</td>
<td>21</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>SLY$_{phs, east}$</td>
<td>0.363</td>
<td>0.442</td>
<td>0.071</td>
</tr>
</tbody>
</table>

The table provides statistical comparisons of sluiceway weir configurations at the Dalles Dam. The results indicate that passage efficiency is significantly higher when turbines are on compared to when they are off.
Locating the three additional weirs where the highest turbine passage consistently occurs is another potential strategy. Application of this strategy at TDA would require locating these weirs at MU 8 and MU 22, based on the horizontal distribution of fish passage rate per unit flow during 2004 and 2005 (Figure 4). No single location, however, stands out as being best for the three additional weirs. The decision may ultimately be based on non-fish priorities for turbine operations at TDA because of our findings regarding whether to open sluiceway weirs above operating turbines or above nonoperating turbines (described below).

Another concern for fish operations at TDA is whether to operate turbine units beneath open sluiceway weirs as a standard procedure. Data from 2004 provided an opportunity to evaluate this question because at times, the turbines beneath open sluiceway weirs were inadvertently off. Our finding of higher sluiceway passage rates with turbine units operating below and adjacent to the open sluiceway weirs (Table 5) is consistent with sluiceway evaluations conducted at Ice Harbor Dam in 1982 and 1983 (Johnson et al. 1984). Turbine discharge provides bulk flow toward the surface-skimming weirs (Johnson et al. 1992; Johnson and Dauble 2006). Therefore, turbine units below open sluiceway weirs should be operated continuously as a standard fish operations procedure.

When to open sluiceway weirs for purposes of juvenile salmonid passage is another topic of concern to operations managers. On a daily basis, fish pass into the sluiceway at TDA during all hours: no single day–night, crepuscular, or other period shows consistently high or low passage rates (Johnson et al. 2006). Therefore, we recommend operating the sluiceway 24 h/d to maximize the opportunity for fish passage via a nonturbine route at the TDA powerhouse. On a seasonal basis, sluiceway operations to cover the main spring emigrations of yearling salmon and steelhead and the summer emigration of subyearling Chinook Salmon are obviously warranted. In fact, the findings support use of the same operations for spring and summer emigrants. Currently, the sluiceway is operated to enable passage of juvenile salmonids and adult steelhead from 1 March through 15 December of each year. We suggest that the sluiceway at TDA be operated year-round to maximize survival of salmonids moving downstream.

Year-round sluiceway operations would help protect the relatively few but valuable fish migrating downstream during winter, with no net cost in discharge if the sluiceway operation is offset by a very slight reduction in the spill rate during spring and summer. Emigrations occurring outside the usual spring and summer periods reflect an atypical life history strategy for Columbia River salmonid populations above Bonneville Dam. Such life history strategies should be protected because they contribute to increased life history diversity and, hence, population resiliency (Waples et al. 2009; Beechie et al. 2010). The additional 75 d of sluiceway discharge (127 m3/s) for year-round operations could be provided by reducing the spill rate from 40% to 39% for the typical 144-d spill period (assuming a total project discharge average of 7,079 m3/s during 10 April–31 August).

Two strategies could be pursued to enhance sluiceway passage rates: (1) improve weir entrance conditions for the existing maximum discharge and (2) increase sluiceway hydraulic capacity. The potential for improved entrance conditions is indicated by observations of fish approaching the sluiceway weirs but rejecting the entrance (Johnson et al. 2004, 2009). Design considerations for sluiceway entrance conditions are provided by Haro et al. (1998), Johnson et al. (2005a), and Johnson and Dauble (2006). In addition, attraction lighting on the deck above open sluiceway gates should be investigated as a means of enhancing sluiceway passage rates at night (e.g., Ploskey et al. 2011) because juvenile salmonids orient to the water’s surface (Andrew and Geen 1960; ISG 2000; Smith et al. 2010). Another strategy could be to construct and evaluate a “portable sluiceway weir” with specially designed entrance shaping at the sluiceway. Use of a portable sluiceway weir at TDA would allow for removal of confounding location effects, thus permitting a statistically valid comparison between the fish response to hydraulic conditions created by newly designed entrance conditions and the response to conditions at an existing sluiceway entrance. The hydraulic capacity of the sluiceway could be increased by opening a sluiceway conduit through the dam at the eastern end of the powerhouse. Higher sluiceway discharge would increase the size of the sluiceway flow nets in the forebay, thereby increasing the opportunity for fish attraction to the flow (Johnson and Dauble 2006).

In conclusion, we recommend the following long-term operations for the sluiceway at TDA: open six sluiceway weirs to take advantage of the maximum hydraulic capacity of the sluiceway; open the three weirs above the westernmost operating MU and the three weirs at MU 8, where turbine passage rates are relatively high; operate the turbine units below open sluiceway weirs as a standard procedure; operate the sluiceway 24 h/d year-round to maximize its benefits to juvenile salmonids; and use the same operations for spring and summer emigrants. These operational concepts are transferable to dams where sluiceway surface flow outlets are used to protect downstream-migrating fishes. Sluiceways provide a readily available, inexpensive method for the passage of surface-oriented fish moving downstream at hydropower dams.

ACKNOWLEDGMENTS

This research was funded by USACE through the Anadromous Fish Evaluation Program, Columbia River Fish Mitigation Project. We sincerely appreciate contributions by Bob Cordie, Mike Langesly, Steve Schlenker, and Miro Zyndol (USACE); Alan Wirtz (PAS); Susan Ennor, Eric Fischer, David Geist, James Hughes, Megan Peters, Gene Ploskey, Cindy Rakowski, Marshall Richmond, Ida Royer, John Serkowski, and Chris Vernon (PNNL); and three peer reviewers. Pacific Northwest National Laboratory is operated by Battelle for the U.S. Department of Energy under Contract Number DE-AC05-76RL01830.
Reference to trade names does not imply endorsement by the U.S. Government.

REFERENCES


FPC (Fish Passage Center). 2006. 2005 annual report. FPC, Columbia Basin Fish and Wildlife Authority, Portland, Oregon.


North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 08 Oct 2013.

To cite this article: Fenton Khan, Ida M. Royer, Gary E. Johnson & Sean C. Tackley (2013) Sluiceway Operations for Adult Steelhead Downstream Passage at The Dalles Dam, Columbia River, USA, North American Journal of Fisheries Management, 33:5, 1013-1023, DOI: 10.1080/02755947.2013.793629
To link to this article: http://dx.doi.org/10.1080/02755947.2013.793629

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ARTICLE

Sluiceway Operations for Adult Steelhead Downstream Passage at The Dalles Dam, Columbia River, USA

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Abstract
Sluiceways at hydroelectric dams are designed to enable floating ice and debris to pass through the dams and may be used as an effective, nonturbine, surface route for out-migrating fishes to pass through dams. Each year, the sluiceway at The Dalles Dam on the Columbia River, USA, is normally operated between 1 April and 30 November and the spillway between 10 April and 31 August to enable downstream-migrating juvenile Pacific salmonids to pass. The only route available for fishes to pass the dam between 1 December and 31 March is through the turbines. This study evaluated downstream passage of adult steelhead Oncorhynchus mykiss at The Dalles Dam during various periods between 1 November and 10 April for years 2008 through 2010. The purpose of the study was to determine the efficacy of operating the sluiceway between 1 December and 31 March to provide a relatively safe, nonturbine, surface outlet for downstream passage of adult steelhead that overwinter in the lower Columbia River (i.e., fallbacks) or for adult steelhead attempting to emigrate back to the marine environment after spawning (i.e., kelts). We applied a fixed-location hydroacoustic technique to estimate downstream passage rates at the sluiceway and turbines. The sluiceway was used by 91–99% of the adult steelhead during all sampling periods; the remaining 1–9% passed through the turbines. This implies that adult steelhead preferred the sluiceway for downstream passage at the dam. Our results indicate that keeping the sluiceway open between 1 December and 31 March may provide an optimal, nonturbine surface route for downstream passage of overwintering or postspawned adult steelhead at The Dalles Dam. Similar operations are relevant at hydroelectric dams with surface-flow outlets, such as sluiceways, for safe downstream passage of fish species of management concern.

Hydroelectric dams present barriers for fish migrating both upstream and downstream in a river system (Coutant and Whitney 2000; Wertheimer and Evans 2005; Arnekleiv et al. 2007). Many of these dams were designed and constructed with fishways (fish ladders) to provide passage routes for upstream migrants (Coutant and Whitney 2000; Williams et al. 2001; Arnekleiv et al. 2007); in general, fish migrating downstream must pass through dams by way of turbines, spillways, and sluiceways (Raymond 1988; Coutant and Whitney 2000; Johnson et al. 2000; Williams et al. 2001; Johnson and Dauble 2006; Arnekleiv et al. 2007). Turbine passage, however, can be detrimental to fishes because they may be killed or injured as they pass through the turbines (Coutant and Whitney 2000; Williams et al. 2001; Johnson and Dauble 2006). Therefore, spillways and sluiceways are considered safer routes for downstream fish passage (Schoeneman et al. 1961; Scruton et al. 2007; Wertheimer and Evans 2005; Johnson and Dauble 2006). Johnson and Dauble (2006) describe sluiceways as optimal surface-flow outlets for downstream-migrating juvenile anadromous fishes to pass through hydroelectric dams.

Federal Columbia River Power System (FCRPS) hydroelectric dams in the lower Columbia River basin, USA, were

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Received July 19, 2012; accepted March 27, 2013
Published online September 25, 2013
constructed with fish ladders to provide routes for upstream-migrating anadromous fishes, such as adult Pacific salmon and steelhead *Oncorhynchus mykiss*, to pass through the dams. These dams have been retrofitted with passage structures (e.g., bypass and collection systems), and changes to spillway and sluiceway operations have been implemented to increase the survival of juvenile salmonids migrating downstream to the ocean (Raymond 1988; Coutant and Whitney 2000; Johnson et al. 2000; Williams et al. 2001; Ploskey et al. 2008). Passage considerations for downstream-moving adult steelhead have generally lagged in relation to upstream passage, but are now gaining attention from fishery managers concerned with the low numbers of steelhead populations in the Columbia and Snake River systems (NMFS 2003; Wertheimer 2007), which are listed under the Endangered Species Act (NMFS 1997; McClure et al. 2003). Post-spawn downstream-migrating steelhead, commonly called kelts, may play an important role in strengthening these stocks because these fish are iteroparous (repeat spawners). Iteroparity is thought to be a life history strategy that spreads genetics over multiple years, providing a hedge against stochastic events (Taborsky 2001; Keefer et al. 2008b; Narum et al. 2008).

Steelhead kelts from the Columbia River basin may navigate through as many as eight hydroelectric dams on the lower Snake and Columbia rivers before reaching the ocean (Hatch et al. 2003). Due to their compromised physiological state because of energy loss from upstream migration and spawning (Booth et al. 1997), kelts may be especially vulnerable to the adverse effects of dams as they pass through them (Evans et al. 2004; Wertheimer 2007; Keefer et al. 2008b). Wertheimer and Evans (2005) estimated mortality rates of 84–96% for radio-tagged kelts that were released at Lower Granite Dam (the uppermost passable dam on the Snake River) by the time they reached the study site below Bonneville Dam (the last dam on the Columbia River); these fish had to pass seven dams. Mortality rates for fish released at dams on the lower Columbia River ranged from 20–40%; these fish had to pass two or three dams. This mortality rate probably selects against repeat spawning in steelhead populations and contributes to the low incidence of iteroparity among steelhead populations in the Snake River system (0.4–1.2% at Lower Granite Dam; Keefer et al. 2008b). Carlson et al. (2012) suggest survival estimates for tagged fish passing through turbines may be low because of the effects of tag burden on these fish.

Strategies such as kelt reconditioning, transport, and dam operations are being investigated as potential means to increase adult steelhead survival and populations. Attempts, with some success, have been made to recondition kelts in an artificial environment until the fish are deemed healthy enough to be returned to the river (Evans et al. 2001; Ruzycki et al. 2003; Branstetter et al. 2006). Fish-collection facilities have also collected kelts for transport around the FCRPS dams (Hatch et al. 2003; Evans et al. 2008). This has been shown to improve kelt survival in the Snake River system, but Evans et al. (2008) found this option to be only somewhat effective at improving their survival through the lower Columbia River dams. Finally, and the option investigated here, dam operations can be changed for the safe downstream passage of in-river adult steelhead.

In addition to kelts, upstream-migrating adult salmonids may move back downstream through hydroelectric dams (Keefer et al. 2008a; Holbrook et al. 2009). These fish are commonly termed “fallbacks.” Fallback behavior at dams may occur when adult salmonids deviate from their normal upstream migration to spawning grounds, traveling beyond their natal streams (“overflowing”), then moving back downstream through the dams to return to said streams (Reischel and Bjornn 2003; Boggs et al. 2004). Furthermore, summer steelhead that are destined for upriver spawning areas may overwinter in the main-stem Columbia River, fall back at dams, and re-ascent, sometimes more than once, during the essentially nonmigratory winter period (Keefer et al. 2008a). Fallback behavior may sometimes be caused by the particular configurations and operations of available routes for fishes to pass through dams (e.g., fish ladders, navigation locks, turbines, spillway, and bypass systems; Reischel and Bjornn 2003). Adult steelhead fallback at The Dalles Dam (TDA) can be attributed to several phenomena, including dam configuration and operations, overshoots that missed their natal tributary, and overwintering behavior.

Roughly 12% of adult summer steelhead are estimated to overwinter in the main-stem Columbia River and active upstream migration tapers off as river temperatures decline (Keefer et al. 2008a). Fallbacks have been documented at all lower Columbia and Snake River dams (e.g., Boggs et al. 2004; Keefer et al. 2008a), but Keefer et al. (2008a) found that from November until spawning occurred in spring, the highest proportion of fallbacks occurred at TDA (28%) compared with other Columbia and Snake River dams. Mortality rates are not well known; however, simply because these fish must pass through some dams more than once, overwintering steelhead are less likely than other migrating fishes to make it to their upriver natal tributaries (Keefer et al. 2005; Keefer et al. 2008a), and the numbers of fish arriving at spawning grounds have been estimated to be very low (Keefer et al. 2005).

The sluiceway at TDA was normally operated from 1 April through 30 November, and the spillway was operated from 10 April through 31 August for juvenile salmon out-migration as mandated by National Marine Fisheries Service (NMFS) Biological Opinions on the operation of the FCRPS (NMFS 2003, 2008). For the remainder of the year (1 December through 31 March), the only available downstream fish passage route was through turbines. Turbine passage may have detrimental consequences for adult steelhead fallbacks (occur year-round, with a nadir in January; Keefer et al. 2008a) and for steelhead kelts (start out-migration to the ocean in March or sooner; Wertheimer and Evans 2005; Wertheimer 2007). Therefore, the NMFS stipulated that an evaluation of TDA sluiceway operations be conducted between 1 December and 31 March as a nonturbine, surface outlet for safe passage of adult steelhead fallbacks and kelts (NMFS 2008). In March 2011, as a result of this study,
TABLE 1. Sampling periods and configurations of the turbines and sluiceway at The Dalles Dam for estimating adult steelhead downstream passage using fixed-aspect hydroacoustics during five periods in 2008–2010. Transducers were installed at all main turbine units and open sluice weirs for each sampling period (A–E).

<table>
<thead>
<tr>
<th>Sampling period A–E</th>
<th>Configuration</th>
<th>Sluice weir</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) 1 Nov–15 Dec 2008</td>
<td>All 22 main turbine units + 6 open sluice weirs</td>
<td>1-1, 1-2, 1-3, 5-2, 18-1, 18-2</td>
</tr>
<tr>
<td>(B) 1 Mar–10 Apr 2009</td>
<td>All 22 main turbine units + 6 open sluice weirs</td>
<td>1-1, 1-2, 1-3, 5-2, 18-1, 18-2</td>
</tr>
<tr>
<td>(C) 1 Nov–15 Dec 2009</td>
<td>All 22 main turbine units + 4 open sluice weirs</td>
<td>1-2, 1-3, 18-1, 18-2</td>
</tr>
<tr>
<td>(D) 16 Dec 2009–7 Mar 2010</td>
<td>All 22 main turbine units only</td>
<td>sluiceway closed</td>
</tr>
<tr>
<td>(E) 8 Mar–10 Apr 2010</td>
<td>All 22 main turbine units + 4 open sluice weirs</td>
<td>1–2, 1–3, 18–1, 18–2</td>
</tr>
</tbody>
</table>

Sluiceway operations for fish passage were changed to start on 1 March and end on 15 December.

In this study, we tested various sluiceway and turbine operations at TDA during five periods between 1 November and 10 April of years 2008 through 2010 (Table 1), a period when the sluiceway is normally closed and adult steelhead fallbacks and kelts are expected to be passing through the dam. We expected the sluiceway to be the preferred passage route, when open, because salmonids are generally surface oriented (Schoeneman et al. 1961; Coutant and Whitney 2000; Johnson et al. 2000; Scruton et al. 2003; Wertheimer and Evans 2005; Johnson and Dauble 2006; Arnekleiv et al. 2007; Scruton et al. 2007; Wertheimer 2007). It was unknown whether adult steelhead would sound and pass through the turbines when the sluiceway was closed, or hold in the forebay until the sluiceway was reopened before passing the dam. While high mortality is associated with turbine passage, the possibility of steelhead kelts holding in the forebay is also of concern, considering the importance of returning these kelts quickly to saltwater to commence ocean feeding and improve survival and repeat spawning rates (Evans and Beaty 2001; Wertheimer and Evans 2005; Wertheimer 2007). Our objectives were to (1) estimate total fish passage by route for adult steelhead, (2) determine if and when the sluiceway was used by adult steelhead to pass the dam, and (3) determine whether adult steelhead passed through the turbines when the sluiceway was unavailable.

These data are important to fisheries and hydropower managers for deciding when to operate the sluiceway as a surface route for adult steelhead to safely pass because water passing through the sluiceway cannot be used for power production.

STUDY SITE

The Dalles Dam, operated by the U.S. Army Corps of Engineers, is located on the Columbia River, at river kilometer 309, and is the second closest dam in the FCRPS to the Pacific Ocean (Figure 1). It has a 637-m-long powerhouse with 22 main turbine units (MUs), each with 3 intakes, a total generating capacity of 1,800 megawatts, and a total powerhouse hydraulic capacity of 10,619 m³/s. The main turbine units are numbered from west to east (Figure 2). Two small “station service” turbine units that supply power to the dam are located between main units 8 and 9. Two turbine units that pass fish, located on the west end of the powerhouse, supply water to the east fish ladder as attraction flow for upstream-migrating adult salmonids. The 420.6-m-long spillway comprises 23 bays with 15.2-m-wide radial gates.

The sluiceway, which was designed to let ice and debris pass, is a rectangular channel that extends the entire length of the forebay side of powerhouse at the water surface. Three 6.1-m-wide sluiceway entrances (weirs) are located above each main turbine unit intake, and two are located above each fish turbine unit intake. A gate at each weir may be raised off the weir sill (elevation
46 m above mean sea level [msl]), to open the weir and allow water to flow into the sluiceway. Full-pool elevation is rated at 48.8 m above msl, and the minimum operating pool elevation is 47.2 m above msl. When any of the sluiceway weirs (SLs) are opened, water and migrating fishes near the water surface may be skimmed from the forebay into the sluiceway, passing the fishes through an outlet to the sluiceway outfall at the tailrace of the dam. Overall, sluiceway discharge is a relatively small proportion (about 2–4%) of total river flow passing through the dam (total project discharge), which includes turbine operations and spillway operations, when the spillway is operated.

Flow into the sluiceway is dependent on forebay elevation and the number and location of open weirs. For example, given a forebay surface elevation (water level) of 48.2 m and six open weirs, flows over the individual weirs range from 16 m$^3$/s at the east end of the powerhouse to 27 m$^3$/s at the west end, for a total flow of approximately 127 m$^3$/s (data provided by U.S. Army Corps of Engineers, Portland District). During our five study periods (Table 1), the mean daily project discharge at TDA for 1 November to 15 December (2008 and 2009) was 2,634–3,823 m$^3$/s, for 1 March to 10 April (2009 and 2010) was 2,832–4,474 m$^3$/s, and for 16 December 2009 to 7 March 2010 was 2,576.8–4,785.5 m$^3$/s (Columbia Basin Research Data Access in Real Time internet site [DART; http://www.cbr.washington.edu/dart/dart.html]; Figure 3).

To provide context for the downstream passage results of our study, we obtained counts of returning adult steelhead as they passed upstream through TDA using the fish ladders during migration in 2008 and 2009. Enumeration of adult steelhead was accomplished by fish-counting personnel and video recordings at the ladders from approximately mid-February to the end of November of any year. Most adult steelhead passed over the ladders between June and November (Figure 4). In 2008, the total number of returning adult steelhead was approximately 277,000 and in 2009, more than 515,000 were counted passing via the ladders.

METHODS

Fixed-aspect hydroacoustics.—Passage data were collected using fixed-aspect hydroacoustics. This technique has been used successfully to evaluate downstream fish passage at all 13 dams on the main-stem Snake and Columbia rivers (Johnson et al. 1992; Thorne and Johnson 1993; Skalski et al. 1996; Ploskey and Carlson 1999; Ploskey et al. 2001:B1–B32; Johnson et al. 2000, 2005, 2006; Ploskey et al. 2008). Use of fixed-aspect hydroacoustics has been validated with net catches in other studies (e.g., Ransom et al. 1996; Ploskey and Carlson 1999). Single-beam and split-beam hydroacoustic techniques and the acoustic screen model are described by G. E. Johnson in Ploskey...
SLICEWAY FOR STEELHEAD DOWNSTREAM PASSAGE

FIGURE 2. Plan view of The Dalles Dam showing hydroacoustic transducer and DIDSON acoustic camera locations for estimating adult steelhead downstream passage through the sluiceway and turbines in 2008–2010. Numbers at the powerhouse designate main turbine units. The fish units and the station service units (between MU 8 and MU 9) were not sampled. In the inset, the bold number designates MU 1 and small numbers designate the three sluiceway weirs at MU 1 (SL 1-1, 1-2, 1-3). Transducers deployed at the sluiceway weirs (open circles) were not used in all years. Sampling locations are listed in Table 1.

FIGURE 3. Daily discharge at The Dalles Dam from October 2008 through April 2010. Shaded regions, with letters in parentheses, correspond to the five sampling periods listed in Table 1. Data were obtained from Columbia Basin Research Data Access in Real Time (DART; http://www.cbr.washington.edu/dart/dart.html).

et al. 2001: B1–B32, Thorne and Johnson (1993), and Simmonds and MacLennan (2005).

The data-collection systems consisted of three single-beam and five split-beam hydroacoustic systems (Precision Acoustic Systems [PAS], Seattle, Washington). The PAS-103 Multi-Mode Scientific Echo Sounders were controlled by Harp-1B (single-beam) or Harp-SB (split-beam) Data Acquisition/Signal Processing Software (Hydroacoustic Assessments, Inc., Seattle, Washington). Each system operated at 420 kHz. Echo sounder transmission rates were 15 pings/s (pps) at the turbine intakes and 33 pps at the sluiceway. All systems used a voltage output threshold of −26 to −56 dB (1 µPa at 1 m) and were calibrated before and after the studies to measure three system characteristics: source levels, receiving sensitivities, and transducer beam pattern factors (Simmonds and MacLennan 2005). Systematic sampling (same order among sampling locations each hour) was conducted at 1-min intervals. Each location was sampled 10, 15, 20, or 30 times per hour, depending on the number of transducers connected to the echo sounder. Sampling was conducted 24 h/d
FIGURE 4.  (A) Upstream daily passage of adult steelhead counted at The Dalles Dam fish ladders in 2008 and 2009. Visual counting generally begins on 1 April and ends on 31 October of any year. Video observations are generally used from February 20 through December 7. (B) Total number of adult steelhead counted at The Dalles Dam fish ladders in 2008 and 2009. Data were obtained from the Fish Passage Center (http://www.fpc.org).

for 7 d/week during each of the five sampling periods between 2008 and 2010 (Table 1).

Single-beam transducers (6° beam) were installed at all main turbine-unit sampling locations, except for main turbine-units 2, 5, 16, and 18, each of which had a split-beam transducer (6° beam; Figure 2). The fish turbine and station service units were not sampled because the spacing of the grates of the trash racks in front of the intakes is small, preventing large, adult-size fish from passing into the turbines. One of the three intakes at each main turbine unit was randomly selected for sampling. Only the sluiceway weirs that were generally operated for fish passage (two on the east end of the powerhouse and four on the west end), as prescribed by fishery and hydrosystem managers and based on previous research of fish passage at the sluiceway (e.g., Johnson et al. 2003; Hansel et al. 2005; Johnson et al. 2005, 2006), were open during the study periods. Split-beam transducers (6° beam) were installed at each of the three sluiceway weirs above main unit 1 (SLs 1-1, 1-2, 1-3), one weir above main unit 5 (SL 5-2), and two weirs above main unit 18 (SLs 18-1, 18-2; Figure 2).

Hydroacoustic fish targets of interest were verified as being adult salmonids, assumed to be adult steelhead, by imaging them with a Dual Frequency Identification sonar (DIDSON) acoustic camera from 1 November through 15 December 2008 and 1 March through 10 April 2009. The DIDSON camera was aimed across the front of SLs 1-1 and 1-2 and used only to verify the fish targets of interest were adult salmonids (Figure 2). The instrument was used in the low-frequency mode, and the frame rate was 6–7 frames/s.

Data analysis.—The adult fish we detected were assumed to be prespawn (fallbacks) and postspawn (kelts) steelhead because of their acoustically detected size, as revealed by the fixed-aspect hydroacoustic systems. The acoustic images from the DIDSON camera verified that the targets were adult salmonids; the images showed the typical morphology of large adult salmonids and that these fish passed into the sluiceway tail-first, which is common salmonid behavior (Johnson et al. 2000; Scruton et al. 2003). The DIDSON samples did not show other types of large fishes entering the sluiceway during the sampling periods when it was used. Furthermore, the seasonal timing of adult steelhead appearing at the dam was consistent with life history patterns for adult steelhead observed in other studies (Bjorn et al. 2000; Keefer et al. 2008a).

The echo data were processed (“tracked”) with custom computer programs that were developed by the Pacific Northwest National Laboratory software engineers. Mean target strength was used as an indicator of fish size to distinguish relatively large adult steelhead from smaller targets such as juvenile American Shad *Alosa sapidissima* and juvenile salmon, which were present during our study periods. Based on information obtained for adult steelhead in the Columbia River (Robert Wertheimer, U.S. Army Corps of Engineers, personal communication) and from measurements obtained from the DIDSON video files, we assumed, for data processing, a minimum size for fish of interest to be about 30 cm. The relationship between fish length and target strength for adult salmon, as described by Burwen and Fleischman (1998), was used to obtain mean target strength
for adult steelhead. We used filters for target strength, slope, speed, pulse width, and azimuth (direction of travel) during data processing to eliminate any small size fishes and unacceptable tracks (noise) before further analysis. Subsamples of the data were manually checked to confirm that valid fish tracks remained after filtering.

Assuming simple random sampling, we applied finite sampling theory (Cochran 1977) to estimate the hourly fish passage rates and associated sampling error. Even though sampling was necessarily systematic through time among the transducers, random sampling is a reasonable assumption because sampling locations (one of three turbine intakes) and transducer positions at a given sampling location were chosen at random. The only exception is for side-looking transducers at the sluiceway weirs where the water column is too small for vertical randomization. Each accepted fish track was expanded spatially by the ratio of the route width (vertical acoustic beams) or height (horizontal beams) to the diameter of the beam at the range of detection as follows:

\[
SEC = \frac{W}{2 \cdot R \cdot \tan \left(\frac{\theta}{2}\right)},
\]

where \(SEC\) = spatially expanded count, \(W\) = width or height (m) of the passage route, \(R\) = range from the transducer (m), \(\tan\) = tangent function, and \(\theta\) = effective beam angle (degrees).

The sum of spatially expanded counts of fish for a given hour and sampling location was then extrapolated temporally to an entire hour by multiplying by the inverse of the hourly sampling fraction as follows:

\[
H_{hi} = \sum_j SEC_{jhi} \left(\frac{60}{m_{hi}}\right),
\]

where \(H_{hi}\) = the hourly passage rate for the \(h\)th hour at the \(i\)th location summed over all fish detected, and \(m_{hi}\) = the number of minutes sampled during the \(h\)th hour at the \(i\)th sampling location.

Hourly passage rates by location were used to estimate various performance metrics, including total sluiceway passage \((SL)\) and total turbine passage \((T)\) as follows:

\[
SL = \sum_h \sum_i H_{hi},
\]

\[
T = \sum_h \sum_i (H_{hi} \cdot x),
\]

where \(h\) represents the elapsed time of sampling (h) and \(i\) represents the sluiceway weir sampling locations; and

\[
T = \sum_h \sum_i (H_{hi} \cdot x),
\]

where \(T\) is total turbine passage, \(h\) represents the hours sampled, \(i\) represents the turbine intake sampling locations, and \(x\) is the number of intakes per unit (two intakes per fish unit and three intakes per main unit).

Skalski et al. (1993) describe the statistical characteristics of fixed-aspect hydroacoustic data, including variance estimation for the hourly passage rate estimators. Ninety-five percent asymptotic CIs for passage estimates were calculated as the product of 1.96 and the square root of total variance.

**RESULTS**

**Total Passage Estimates**

From 1 November through 15 December (fall) 2008, we estimated \(1,790 \pm 250\) (total passage \(\pm 95\%\) CI) adult steelhead passed the dam through the turbines and sluiceway combined, averaging 40 fish/d (Table 2; Figure 5). During this same period in 2009, we estimated total passage to be \(879 \pm 165\), averaging 20 fish/d. For these two fall study periods, 91–95% of the total number of adult steelhead that passed went through the sluiceway. Turbine passage only occurred on four separate days in 2008 when an estimated 86 fish passed, and five separate days in 2009 when an estimated 75 fish passed. Only main turbine units 7, 8, and 18 were used by adult steelhead for passage in 2008 and units 8, 16, and 18 were used in 2009.

Between 1 March and 10 April (spring) 2009, we estimated a total of \(1,766 \pm 277\) adult steelhead passed through the turbines and sluiceway combined, averaging 43 fish/d (Table 2; Figure 5). During this same period in 2010, an estimated \(1,985 \pm 234\) adult steelhead passed the dam, averaging 58 fish/d (note, the

<table>
<thead>
<tr>
<th>Sampling period A–E</th>
<th>Total steelhead passage ± 95% CI</th>
<th>Sluiceway ± 95% CI</th>
<th>Turbines ± 95% CI</th>
<th>Turbine passage (% of total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) 1 Nov–15 Dec 2008</td>
<td>1,790 ± 250</td>
<td>1,704 ± 237</td>
<td>86 ± 78</td>
<td>4.8</td>
</tr>
<tr>
<td>(B) 1 Mar–10 Apr 2009</td>
<td>1,766 ± 277</td>
<td>1,673 ± 264</td>
<td>93 ± 84</td>
<td>5.3</td>
</tr>
<tr>
<td>(C) 1 Nov–15 Dec 2009</td>
<td>879 ± 165</td>
<td>804 ± 156</td>
<td>75 ± 55</td>
<td>8.5</td>
</tr>
<tr>
<td>(D) 16 Dec 2009–7 Mar 2010</td>
<td>62 ± 40</td>
<td>Closed</td>
<td>62 ± 40</td>
<td>100</td>
</tr>
<tr>
<td>(E) 8 Mar–10 Apr 2010</td>
<td>1,985 ± 234</td>
<td>1,958 ± 229</td>
<td>27 ± 48</td>
<td>1.4</td>
</tr>
</tbody>
</table>
FIGURE 5. (A) Daily estimates of adult steelhead downstream passage at The Dalles Dam sluiceway and (B) turbines during four study periods when the sluiceway and turbines were sampled concurrently (i.e., November–December 2008 and 2009, March–April 2009 and 2010). (C) Daily estimates of adult steelhead downstream passage at the turbines during a period when the sluiceway was closed from 16 December 2009 through 7 March 2010.}

start of sluiceway operation was delayed from 1 March to 8 March due to maintenance at the dam; Table 2; Figure 5). The majority of adult steelhead (95–99%) passed through the sluiceway during both of these spring study periods. We estimated a total of 93 adult steelhead passed through the turbines (main units 8, 21, 22) in the 2009 study and 27 passed through one main turbine unit (unit 8) in 2010.

**Turbine Passage Estimates**

The only sampling period that examined turbine passage when the sluiceway was closed was from 16 December 2009 through 7 March 2010 (winter). During this period, we estimated 62 ± 40 (total ± 95% CI) adult steelhead passed through the turbines (Table 2; Figure 5). This estimate equates to an average of less than one (0.8) adult steelhead passing through the turbines each day during the sampling period.

**DISCUSSION**

It is well documented that adult steelhead pass downstream at hydroelectric dams on the lower Snake and Columbia rivers (e.g., Hatch et al. 2003; Boggs et al. 2004; Wertheimer and Evans 2005; Wertheimer 2007; Keefer et al. 2008a, 2008b). Therefore, these fish are vulnerable to the adverse effects of the dams as they pass through them (Evans et al. 2004; Wertheimer 2007; Keefer et al. 2008a). Our study applied the fixed-aspect hydroacoustic technique to evaluate adult steelhead passage at The Dalles Dam. Estimates of total passage of adult steelhead at the sluiceway and turbines, when they were operated concurrently for four of our study periods, show between 879 (1 November to 15 December, 2009) and 1,790 (1 November to 15 December, 2008) passed the dam in the fall and between 1,766 (1 March to 10 April, 2009) and 1,985 (7 March to 10 April, 2010) passed in the spring (Table 2). We found the sluiceway was readily used by a majority (91–99%) of adult steelhead of total fish estimated passing through the dam during each of the four study periods. For our turbine-only study (16 December 2009 to 8 March 2010), when the sluiceway was closed, we estimated a total of 62 adult steelhead passed through the turbines during the 82-d period.

Wertheimer and Evans (2005), who conducted a radio-telemetry study of steelhead kelts at multiple dams on the Columbia and Snake rivers in spring months (April–June), found that during periods of nonspill operations, as experienced during our study, passage efficiency of the sluiceway at TDA was 64.3% ($N = 28$ in 2001). Although our estimated sluiceway passage efficiency of 91–99% is higher than theirs, this difference may be attributed to their small sample size, our longer sampling periods, or a difference in passage rates between postspawn (kelts) and prespawn (fallback) steelhead. The latter likely compose the majority of the adult steelhead in our study because prespawn steelhead may overwinter in the reservoir, and some may fall back through the dam in early spring to get to natal streams (NMFS 2003; Keefer et al. 2008a). Regardless, the two studies show a high percentage of adult steelhead use the sluiceway as a surface route for downstream passage through the dam compared with the low numbers that passed through the turbines. Similarly, Arnekleiv et al. (2007) found downstream-migrating Brown Trout *Salmo trutta* smolts and kelts preferred to use a surface flow outlet to pass through a hydroelectric dam, when given the opportunity, and few of these fish sounded to 0.5 m to pass through a fishway entrance; no fish sounded to 2.0 m to pass through submerged turbine shafts.

Our results indicate adult steelhead passed the dam through the sluiceway during the last days before it was closed on 15 December 2008 and 2009 and again on the day it was opened in March (2009 and 2010), suggesting these fish are probably available to pass through the dam during winter months (December–March) when the sluiceway and spillway are normally closed, but they are choosing not to sound and travel through the turbines. Very few steelhead passed through the turbines between 16 December 2009 and 7 March 2010, when
the sluiceway was closed. Kemp et al. (2005) found large-size Pacific salmon smolts were reluctant to enter confined, dark spaces with increasing water velocities. Brown Trout kelts (an example of a larger-size salmonid) may exhibit similar behavior at the turbines of a dam because of body size (Arnekleiv et al. 2007). In addition, in their study of different spill operations, Arnekleiv et al. (2007) found Brown Trout kelts would traverse the dam during bottom spill and turbine operations and would only pass downstream during surface spill operations. The results of our study suggest adult steelhead may display similar behavior by holding in the forebay above TDA, during the periods when the sluiceway and spillway are normally closed, and waiting for the surface outlets to be available to pass through the dam. Holding time for adult steelhead kelts in a forebay of a dam could be greatly reduced by providing a surface outlet for these fish to pass through the dam (Wertheimer and Evans 2005).

The large numbers of returning adult steelhead counted at TDA fish ladders in 2008 and 2009 (approximately 277,000–515,000; Figure 4) may be an indication of the annual return rates of these fish, and therefore suggest that reasonably large numbers of adult steelhead may fall back through the dam in fall and winter months (November–February), some as overshoots to get back to natal streams below the dam. Others may fall back through the dam while overwintering in the forebay of the dam before migrating to upriver spawning grounds. Furthermore, in early spring (before April) many of these fish may migrate back downstream to return to the ocean as postspawned kelts (Wertheimer 2007; Keefer et al. 2008b). Prior to a change in operations in March 2011, as a result of this study, the sluiceway was typically opened on 1 April to facilitate downstream passage of juvenile salmon, adult salmonid fallbacks, and steelhead kelts. Steelhead kelt out-migration may begin as early as March or sooner; therefore, the former operation (1 April) may have negative consequences for earlier outmigrating individuals.

This study shows that adult steelhead were present and passed through the sluiceway, in relatively large numbers compared with turbine passage, during the fall of 2008 and 2009 and in the early spring of 2009 and 2010 when the sluiceway and turbines were operated concurrently (Table 2). Relatively few adult steelhead passed through the turbines during all five periods of our study (Table 2). Wertheimer and Evans (2005), Johnson et al. (2005, 2006, 2009), and Johnson and Dauble (2006) all found the sluiceway at TDA to be an efficient and effective surface outlet route for juvenile salmonids and steelhead kelts to pass through the dam as they migrate downstream in spring and summer months (April–July). Similarly, our results indicate adult steelhead prefer this route, over turbines, to pass through the dam in fall, winter, and early spring months (November–March).

The life history and migration behaviors of steelhead present challenges for fisheries and hydrosystem managers tasked with identifying and implementing actions to aid recovery efforts for these fish populations in the Columbia River basin. Mainstem overwintering behavior makes summer steelhead migrants vulnerable to the effects of falling back through dams. In addition, the iteroparity of some steelhead exposes out-migrating kelts to both the direct effects of fallback and problems associated with migration delay, if a route to pass through a dam is not available. Although success in terms of ultimate fate and fitness is difficult to measure, providing safe passage routes for steelhead fallbacks and kelts probably results in incremental improvements in survival through the hydrosystem. All 13 dams on the main-stem Columbia and Snake rivers with upstream passage facilities for adult salmonids have installed surface-flow outlets, modified operations of surface flow outlets (e.g., spillways and sluiceways), or are developing surface-flow outlets to enable passage of juvenile salmonids. Fishery managers are considering the use of these structures as downstream routes for adult steelhead to improve passage and protect them from hydroelectric turbines (NMFS 2008). Our results support the notion that adult steelhead, in lieu of turbines, will readily use relatively safe surface outlets at hydroelectric dams, such as the sluiceway at TDA, for downstream passage to pass through a dam. As a result of our study, fishery managers decided in March 2011 to extend operation of the sluiceway at TDA for adult steelhead downstream passage in early spring and late fall; that is, open it on 1 March (instead of 1 April) and keep it open until 15 December (instead of closing it on 30 November).

ACKNOWLEDGMENTS

This research was funded by the U.S. Army Corps of Engineers, Portland District through the Anadromous Fish Evaluation Program. We sincerely appreciate support and contributions by David Clugston, Robert Cordie, Mike Langeslay, Natalie Richards, Steve Schlenker, Robert Wertheimer, and Miro Zydol (U.S. Army Corps of Engineers); Alan Wirtz (Precision Acoustic Systems); Susan Ennor, Eric Fischer, David Geist, James Hughes, Megan Peters, Gene Ploskey, Chris Vernon, and Mark Weiland (Pacific Northwest National Laboratory), and three anonymous reviewers. Pacific Northwest National Laboratory is operated by Battelle for the U.S. Department of Energy under Contract DE-AC05-76RL01830. Reference to trade names does not imply endorsement by the U.S. Government.

REFERENCES

Booth, R. K., E. B. Bombardier, R. S. McKinley, D. A. Scruton, and R. F. Goossen. 1997. Swimming performance of post spawning adult (kelts) and


NMFS (National Marine Fisheries Service). 2003. Preliminary conclusions regarding the updated status of listed ESUs of West Coast salmon and steelhead. NMFS, Northwest Fisheries Science Center, West Coast Salmon Biological Review Team, Seattle.


A Bioenergetics Approach to Assessing Potential Impacts of Avian Predation on Juvenile Steelhead during Freshwater Rearing

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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.816395
A Bioenergetics Approach to Assessing Potential Impacts of Avian Predation on Juvenile Steelhead during Freshwater Rearing

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Received February 13, 2013; accepted June 4, 2013
Published online September 25, 2013
Avian predation on juvenile fish in freshwater and estuarine habitats has been the focus of considerable research in European and North American watersheds (reviewed in Hoenig-hauser and Peicic 2010). Because of the commercial and recreational value of salmonid species of the genera *Oncorhynchus* and *Salmo*, a number of studies have focused on estimating the consumption of juvenile salmonids by piscivorous birds (Elson 1962; Feltham 1995; Wiese et al. 2008). These studies typically used estimates of the daily consumption of salmonids by specific avian predators and extrapolated to the proportion of the population or cohort that was consumed. For example, Wood (1987a) estimated that in a British Columbia watershed the mortality attributed to mergansers removed 6.9–8.4% of hatchery-raised Chum Salmon *Oncorhynchus keta* smolts and 3.3–6.0% of wild Chum and Coho Salmon *O. kisutch* fry, whereas Feltham (1995) estimated that mergansers ate 3–16% of the Atlantic Salmon *Salmo salar* smolts out-migrating from the North Esk River in Scotland.

Many studies have applied bioenergetics models to estimate the consumption of salmonids by avian predators (Forsell 1983; Feltham 1995; Roby et al. 2003; Wiese et al. 2008). Such models, however, require accurate measurement or estimation of predator diet (species composition and prey size), energetic requirements, and population size (Wood 1987b; Feltham 1995; Roby et al. 2003; Wiese et al. 2008). A variety of methods have been employed to estimate these variables for different avian predators. Bird diets have been estimated by examination of the stomach contents of lethally captured birds, forced regurgitations, and regurgitated pellets (reviewed in Cairns 1998 and Gagliardi et al. 2007) or via observation of birds foraging (e.g., Forsell 1983). Energy consumption by predators commonly has been calculated from measurements of “daily energy expenditure” (DEE, also referred to as the field metabolic rate), which may be estimated using allometric relationships between metabolism and body mass (Wiese et al. 2008) or directly using doubly labeled water (Feltham 1995; Roby et al. 2003). In other studies (e.g., Wood and Hand 1985), energy consumption has been estimated via observations of prey handling time.

Consumption estimates are sensitive to the values used for calculation; ideally, data specific to a given system should be used when estimating predation rates on salmonids (Feltham 1995). However, it may not always be possible to directly measure the diet or energetic requirements of predators in a system of interest. For example, protective measures may prevent the collection of stomach contents. Alternatively, habitat characteristics or bird behavior may preclude capture of foraging birds or observations of foraging. For imperiled prey populations, however, establishing boundaries on the plausible range of predation-caused mortality in the absence of rigorous local diet data may be essential for focusing future research or informing management strategies.

Pacific salmonids (genus *Oncorhynchus*) have undergone population declines across much of their range, and currently many populations are listed as threatened or endangered under the U.S. Endangered Species Act (ESA; Gustafson et al. 2007). The Central California Coast steelhead *Oncorhynchus mykiss* Distinct Population Segment (CCC–steelhead DPS) is listed as threatened under the ESA (Good et al. 2005). Water diversions, habitat degradation, and reduced ocean productivity are cited as the main reasons for continued population decreases (Good et al. 2005), with little consideration of the potential role of predation by piscivorous birds. Although the mortality associated with avian predators has been quantified in larger systems in

**Abstract**

Avian predation on juvenile salmonids is an important source of mortality in freshwater and estuarine habitats when birds and salmonids overlap spatially and temporally. We assessed the potential impact of avian predation upon juvenile steelhead *Oncorhynchus mykiss* in a coastal watershed in central California. We conducted stream surveys between 2008 and 2010 to determine the composition, distribution, and density of piscivorous birds in areas that provide rearing habitat for juvenile steelhead. The most commonly sighted bird species were common mergansers *Mergus merganser* and belted kingfishers *Megaceryle alcyon*. The density of avian predators varied spatially and temporally but was greatest in the estuary regardless of season and decreased with increasing distance from the estuary. In the absence of local predator diet data, we applied a bioenergetics model to estimate the potential predation on juvenile steelhead by mergansers and kingfishers in the Scott Creek estuary. Model parameters included (1) published values of bird energetic requirements and steelhead energy density, (2) the number of birds present in the estuary during the closure period (from stream surveys), and (3) the size frequency and abundance of steelhead present in the estuary during closure. We predicted the extent of predation for different values of steelhead in bird diets, accounting for uncertainty in the estimates using a Monte Carlo simulation approach. With the assumed contribution of steelhead to the diet ranging from 20% to 100%, the population of kingfishers foraging in the Scott Creek estuary had the potential to remove 3–17% of annual production, whereas mergansers had the potential to remove 5–54% of annual steelhead production. Our results suggest that predation by avian species, particularly mergansers, is an important source of mortality for threatened steelhead populations in central California and should be addressed in future salmonid research and recovery planning.
California (Evans et al. 2011; Adrean et al. 2012; Collis et al. 2012), relatively little attention has been focused on the effects of avian predation on Pacific salmonids in smaller coastal watersheds. Recent observations, however, suggest that predation is an important source of mortality that may slow the recovery of steelhead in central California (Frechette et al. 2012). For example, passive integrated transponder (PIT) tags originally deployed in juvenile steelhead were found on a seabird breeding colony, indicating that western gulls *Larus occidentalis* eat a minimum of 1–4% of out-migrating salmonids from central California watersheds (Frechette et al. 2012). However, the extent of predation on juvenile steelhead by other species of piscivorous birds, particularly predation occurring during the period of freshwater rearing, remains largely unknown. There is also a lack of the data necessary to estimate the extent of avian predation on steelhead in the small coastal watersheds of central California, including predator identity, numbers, distribution, diet, and energetic requirements. For some watersheds within the range of the CCC–steelhead DPS, however, steelhead populations have been well characterized.

Scott Creek, located 80 km south of San Francisco, is one such watershed. Although predation on steelhead by western gulls at the mouth of Scott Creek was the focus of previous research (Frechette 2010; Frechette et al. 2012), little is known regarding predation on steelhead by other species of avian predators. Our study had two main objectives. The first was to identify the common avian predators in Scott Creek and determine where they were concentrated spatially and temporally. The second was to create a simple bioenergetics model for estimating predation on steelhead by piscivorous birds in the absence of local avian diet and energetic requirements given (1) local fish abundance and size frequency and (2) predator identity and abundance. This model allowed assessment of the extent of predation on a threatened steelhead population and will help identify future research needs.

**METHODS**

**Study Site**

Scott Creek is a small, coastal watershed in Santa Cruz County (Figure 1) that empties into the Pacific Ocean 80 km south of San Francisco (37°02′28″N, 122°13′50″W). Located near the southern extent of the CCC–steelhead DPS, steelhead life history has been well characterized for Scott Creek, and annual estimates are available for out-migrating steelhead smolts, returning adults, and estuary-reared juveniles (e.g., Smith 1990; Bond et al. 2008; Hayes et al. 2008, 2011; Satterthwaite et al. 2012). Coho Salmon also occur in Scott Creek, although during the course of this study Coho Salmon were considered functionally absent from the system because of a recent population decrease (Spence and Williams 2011).

Scott Creek is typical of the watersheds in central California, terminating in a small estuary that is seasonally closed by a sandbar to form a lagoon. The physical characteristics of the watershed have previously been well described (Bond et al. 2008; Hayes et al. 2008, 2011). Briefly, Scott Creek experiences highly variable flows, with winter flows reaching 28 m³/s whereas summer flows may be as low as 0.08 m³/s. Sandbar formation generally occurs during low-flow periods in late summer and autumn (Shapovalov and Taft 1954). Water clarity and depth in the estuary vary throughout the year, ranging from very clear during periods when the estuary is connected to the ocean and water depth is low to very turbid during estuary closure (D. Frechette, personal observation). Shelter from predators may exist in the form of woody debris, freshwater algae, and parts of the surrounding bulrush marsh. Water clarity is generally good in the upper and middle watershed (sections 2–5; Figure 1), except during winter storms; shelter from predators is in the form of woody debris, vegetation, boulders, and overhanging banks (Hayes, unpublished data).

Although juvenile steelhead may rear exclusively in the upper watershed, many juveniles migrate downstream to the estuary (lagoon), where they take advantage of enhanced growth opportunities (Bond et al. 2008; Hayes et al. 2008). After spending time in the estuary, steelhead may either migrate to sea in the same year before sandbar formation or remain in the lagoon after...
sandbar closure (Shapovalov and Taft 1954; Bond et al. 2008; Hayes et al. 2008, 2011). Steelhead that remain in the lagoon throughout the summer and autumn migrate back upstream in late autumn as decreasing dissolved oxygen, increasing temperature, and an influx of saltwater cause environmental conditions in the closed lagoon to become unfavorable (Hayes et al. 2011). These lagoon-reared juveniles then perform a second downstream migration the following spring in which they enter the ocean (Shapovalov and Taft 1954; Hayes et al. 2011).

**Bird Surveys**

We assessed the species composition and distribution of piscivorous water birds by walking transects that were randomly selected using a general randomized tessellation stratified (GRTS) sampling program (Larsen et al. 2008), giving all habitat units within the watershed an equal, nonzero probability of being selected. For logistical reasons, the transects were then grouped into five survey units, hereafter referred to as stream sections. Stream section length ranged from 0.59 km to 2.2 km (mean length = 1.2 km). The stream sections were representative of all habitat types within Scott Creek and encompassed 40% of the 23 km of habitat available to steelhead.

We conducted surveys between December 2008 and December 2010, with a mean intersurvey interval of 13 d. During winter and spring (December through early June), the surveys were conducted in conjunction with surveys for spawning steelhead. During the remainder of the year the surveys were solely for the purposes of counting birds. The survey methods were consistent throughout the study, namely, a modification of the double-observer approach described by Nichols et al. (2000). Two observers walked stream sections from downstream to upstream and recorded visual sightings of birds. For each sighting, the observers recorded the species, number present, location, behavior, time of observation, and GPS location when possible. The second observer followed the primary observer, so as to not influence the sightings made by the primary observer (Nichols et al. 2000). Unlike the methods described by Nichols et al. (2000), the second observer alerted the primary observer of missed birds, which were subsequently recorded after the sighting occurred. We used this approach to enable the second observer to carry the equipment necessary to record steelhead spawning data during the winter and spring surveys. All stream sections were surveyed in 1 d. The order in which sections were surveyed was randomly selected, and all surveys began within 2 h of sunrise to minimize the effects that daily patterns of bird activity may have had on observations.

To identify the most common avian predators in Scott Creek, we calculated the percent of total sightings represented by each species observed during each year. We used a generalized linear model to test the hypothesis that the density of birds in the Scott Creek watershed varied spatially and temporally, using a quasi-Poisson error distribution with log link to account for overdispersion in the bird density data; the residual deviance greatly exceeded the residual degrees of freedom for the corresponding Poisson errors model. The terms included in the model were the month, distance from the creek mouth, and the interaction between month and distance. The response variable was bird density. The midpoint of each stream section was used to define the distance from the creek mouth.

**Bioenergetics Modeling**

We estimated the consumption of salmonids by avian species in the Scott Creek estuary by means of a bioenergetics model that incorporated bird abundance data from the stream surveys and steelhead abundance and size frequency data from long-term monitoring programs in Scott Creek (Figure 2). We lacked sufficient predator diet composition and energy requirement data for this system, so we used published values for the daily energy requirements of predators and conditioned the model using a range of values for the percentage of steelhead in bird diets (hereafter referred to as the “target contribution” of steelhead to the diet). Specifically, we used five different values for the target contribution: 20, 40, 50, 70, and 100% steelhead, which approximately encompassed the range of values presented in the literature for kingfishers and mergansers (Forsell 1983; Shearer et al. 1987; Kålås et al. 1993; Feltham 1995; Cairns 1998; Wiese et al. 2008). We applied the bioenergetics model to the estuary during the period of bar closure because we lacked the data on total fish abundance and year-round size distributions necessary to apply the model to the upper watershed. We conducted bioenergetic modeling using custom-written R code (R Development Core Team 2011; available in the online supplement).

To estimate the consumption of fish by avian predators, we first estimated the energy content per fish based on the size distribution of the fish captured via seine net in the Scott Creek lagoon during 2009 and 2010. We pooled all fish captured in the lagoon each year between July and November, for which mass were recorded, and calculated the energy content of each fish by multiplying its mass by 4.6 kJ/g (Roby et al. 2003; Adrean et al. 2012). We then followed one of two pathways to estimate the number of fish eaten during the period of lagoon closure; we used the first pathway (Monte Carlo simulation 1; Figure 2) when the target contributions resulted in a bird’s eating more than one fish per bird-day on average. We used the second pathway (Monte Carlo simulation 1a) when the target contributions resulted in a bird’s eating less than one fish per bird-day. Although the second pathway is the only one that can be applied in situations when birds have low energetic requirements compared with average fish energy content, Monte Carlo simulation 1 was preferred when possible due to its ability to incorporate the variability introduced into the estimates by explicitly considering individuals.

**Monte Carlo simulations 1 and 2.**—To estimate the number of fish eaten by an individual bird on a single day (hereafter referred to as a bird-day), we simulated an individual bird’s consumption by randomly sampling individual fish with replacement from the distribution of fish sizes until the estimated amount of energy “consumed” was equal to the target contribution, within the
FIGURE 2. Flow chart for the bioenergetics model used to estimate steelhead consumption by avian predators in Scott Creek.
average energy content of a single fish. We generated a distribution of the expected number of fish eaten per bird-day and 95% CIs for the number of fish eaten by a single bird during 1 d using a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 1).

To estimate the number of fish eaten during the lagoon closure period, we determined the total number of bird-days during the lagoon closure period from counts made during stream surveys. To estimate the number of birds present in the estuary for each day between counts (inferred counts), we used linear interpolation. We then summed the total observed or inferred daily counts between July and November of each year to calculate the total number of bird-days during the lagoon period for each species (Figure A.1 in the appendix). To estimate total steelhead consumption during this period, we made a number of draws equal to the estimated number of bird-days from the distribution of total fish eaten per bird-day. We extracted the median and 95% CIs by repeating this process in a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 2).

Monte Carlo simulation 1a.—When target contributions resulted in a bird’s eating less than one fish per bird-day on average, we dropped the focus on individual consumption. Instead, we multiplied the daily energy requirement of an individual bird by the total number of bird-days during the lagoon period to obtain the total energy requirement for a given species for the duration of the lagoon closure period. We then simulated the consumption of steelhead by that species by randomly sampling individual fish (with replacement) from the distribution of fish sizes until the estimated amount of energy “consumed” was equal to the target contribution, within the average energy content of a single fish. We generated a distribution of the expected number of fish eaten by a single species during the lagoon period (with 95% CIs) using a Monte Carlo simulation (20,000 replicates; Figure 2; Monte Carlo simulation 1a).

Monte Carlo simulation 3.—We applied an additional Monte Carlo simulation to estimate the percentage of the initial lagoon production in Scott Creek eaten by birds each year (Figure 2; Monte Carlo simulation 3). We defined the initial lagoon population as the abundance estimated during the first month after sandbar closure in each year (July in 2009 and August in 2010), which approximates lagoon recruitment prior to predation during the lagoon closure period in a given year. We estimated the monthly lagoon population using the 2-d mark–recapture sampling design described in Satterthwaite et al. (2012). Briefly, we conducted beach seining in the lagoon using a 30-m × 20-m nylon seine net and the methods described by Bond et al. (2008). We estimated lagoon abundance using the Ricker modification of the Peterson method (Ricker 1975), quantifying the uncertainty in the lagoon abundance using a Bayesian posterior distribution corresponding to a uniform prior. We estimated the proportion of the initial lagoon production consumed by birds by iteratively drawing from the posterior distribution of the lagoon abundance estimate and comparing this with the previously described distribution of bird predation.

Merganser Diet Analysis

We opportunistically collected mergansers that were found dead during field efforts for diet analysis (n = 5 adults). Although we recognize that these birds may not be representative of the population of mergansers foraging in Scott Creek, we thought it useful to analyze their stomach contents to determine whether the mergansers in Scott Creek consumed steelhead in the size range available in the estuary. We identified fish otoliths, scales, and bones; invertebrate parts, intact fish and invertebrates; and PIT tags from previously tagged salmonids. We used scales, otoliths, and PIT tags to determine the presence of salmonids in diet samples. We determined the minimum number of individual fish in each diet sample using intact otoliths (all species) and PIT tags (salmonids only).

We determined the minimum number of individuals eaten by each bird using otoliths by first counting the number of right and left otolith pairs and then adding the number of unpaired otoliths (left or right) depending on which were most numerous (e.g., Lance et al. 2001). We also calculated the percent frequency of occurrence for each prey taxon, defined as the percent of stomachs examined that contained a given prey taxon (described by Cairns 1998). We then determined the FLs of putative steelhead eaten by mergansers based on back-calculation of fish length using a fish length–otolith width relationship (see below). Otoliths recovered from the diet samples were photographed with a microscope-mounted Nikon digital camera (DXM1200; 3,840 × 3,072 pixels) and identified to genus. We measured otolith width along the transverse axis from the dorsal to the ventral margin at the widest point of the otolith using OPTIMAS software (Media Cybernetics, Silver Spring, Maryland).

To calculate a relationship between FL and otolith size, we extracted otoliths from 24 steelhead from Scott Creek of known length. The fish included in this analysis represented the size range of steelhead captured in juvenile traps in Scott Creek and individuals captured in both the upper watershed and estuary habitat (Figure A.2). The relationship between FL and otolith width was approximately linear and is described by the equation

\[
FL (\text{mm}) = 115.11\cdot\text{otolith width (mm)} - 56.656
\]

\[(R^2 = 0.847, \ P < 0.0001).\] This regression was then applied to either the right or left otoliths recovered from merganser diet samples to determine the size of the salmonids eaten by each bird. We used only otoliths that were at most moderately eroded for back-calculation of fish length (Tollit et al. 1997).

Functioning PIT tags were scanned using a portable PIT tag reader (Allflex USA, Dallas-Fort Worth Airport, Texas). Tag identity was matched to individual statistics for each fish from a database held by the NOAA Fisheries Southwest Fisheries Science Center in Santa Cruz, California. We determined whether tagged steelhead were of hatchery or wild origin and the length and mass from the most recent date on which each fish was...
captured. Further (anecdotal) information on the size of steelhead preyed upon came from common mergansers (n = 3) and belted kingfishers (n = 1) that were scanned for PIT tags when they were captured alive in the watershed. These birds were captured as part of an associated study (Frechette, unpublished data) using mist nets, a method that has been commonly employed for bird capture (e.g., Remsen and Good 1996). We also obtained anecdotal information on the sizes of salmonids preyed upon by mergansers from dead steelhead that were visually observed being regurgitated by foraging mergansers. Visual observation of regurgitation occurred when observers disturbed a flock of six foraging mergansers during a bird survey.

RESULTS

Bird Surveys

We conducted 25 surveys in Scott Creek during the first year (December 2008–November 2009) and 30 surveys during the second year (December 2009–November 2010). At least one predatory bird was seen during each survey (Table 1). The most commonly observed birds were belted kingfishers and common mergansers, which were the only species observed in sections 4 and 5 of the upper watershed. Kingfishers were observed during 18 of the 25 surveys during 2008–2009 and 24 of the 30 surveys during 2009–2010 and were more commonly observed in the upper watershed than in the estuary. We observed mergansers during 15 of the 25 surveys in 2008–2009 and 18 of the 30 surveys in 2009–2010. Mergansers and kingfishers accounted for 61% (2009) and 77% (2010) of all sightings of piscivorous birds in Scott Creek.

The generalized linear model demonstrated that stream section, month, and the interaction of stream section and month were important explanatory covariates of total bird density. Specifically, these terms led to significant reductions in model deviance (Table 2). The mean density of birds (birds/river kilometer) was greatest in the estuary and decreased with increasing distance from the estuary. Mean bird density varied considerably with time (Figure 3).

Bioenergetics Modeling

We applied the bioenergetics model to common mergansers and belted kingfishers because sightings of these two species were far greater than sightings of all other species combined (Table 1). We used the daily food intake for female common mergansers estimated by Feltham (2,243 kJ/d, which accounts for 80% of the assimilation efficiency of fish) in our model because we could not distinguish between female and immature male mergansers (Gregory et al. 1997) and most sightings during surveys were of female or immature mergansers. Feltham (1995) estimated daily food intake from predictions of the field metabolic rate (FMR) from the body mass of 16 mergansers using the relationship between body mass and FMR of 9 mergansers (from the same system) obtained with the doubly labeled water technique. We used 300 kJ for the daily energetic requirement of belted kingfishers, which is intermediate between the daily food intake estimated from visual observations of kingfisher foraging (294 kJ) and estimates made using a bioenergetics model (303 kJ) for kingfishers on the Mad River, California (Forsell 1983). All estimates of kingfisher daily energy intake accounted for an assimilation efficiency of 82.1% (after Vessel

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<tbody>
<tr>
<td></td>
<td>No. of surveys</td>
<td>% of surveys</td>
</tr>
<tr>
<td>Black-crowned night heron</td>
<td>6</td>
<td>24</td>
</tr>
<tr>
<td>Nycticorax nycticorax</td>
<td></td>
<td></td>
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<tr>
<td>Belted kingfisher <em>Megaceryle alcyon</em></td>
<td>18</td>
<td>72</td>
</tr>
<tr>
<td>Common merganser</td>
<td>15</td>
<td>60</td>
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<tr>
<td><em>Mergus merganser</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Double-crested cormorant</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Phalacrocorax auritus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great blue heron <em>Ardea herodias</em></td>
<td>14</td>
<td>56</td>
</tr>
<tr>
<td>Great egret <em>Ardea alba</em></td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>Green heron <em>Butorides virescens</em></td>
<td>8</td>
<td>32</td>
</tr>
<tr>
<td>Hooded merganser</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td><em>Lophodytes cuchullatus</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pied-billed grebe <em>Podilymbus podiceps</em></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Snowy egret <em>Egretta thula</em></td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>
TABLE 2. Analysis of deviance for the generalized linear model of avian predator density in Scott Creek. Model terms were added sequentially from first to last.

<table>
<thead>
<tr>
<th>Model</th>
<th>Deviance reduction</th>
<th>Residual df</th>
<th>Residual deviance</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td></td>
<td>274</td>
<td>502.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>47.85</td>
<td>251</td>
<td>454.44</td>
<td>1.69</td>
<td>0.03</td>
</tr>
<tr>
<td>Distance from estuary</td>
<td>180.62</td>
<td>250</td>
<td>273.82</td>
<td>147.52</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Month × distance</td>
<td>67.44</td>
<td>227</td>
<td>206.38</td>
<td>2.39</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

The bioenergetics model that Forsell (1983) used incorporated mean air temperature, time and energy budgets, and bird body mass (Koplin 1972; Koplin et al. 1980).

We could not directly infer the size selection of steelhead by predators in the Scott Creek estuary, so we assumed equal probabilities of predation on all size-classes of steelhead captured during lagoon seining (56–280 mm FL). We assumed that the steelhead eaten by common mergansers included all lengths because Kålås et al. (1993) observed that mergansers ate Atlantic Salmon as great as 364 mm TL, with no observed difference in length between hatchery Atlantic Salmon taken by mergansers and those available. We restricted the length of fish eaten by belted kingfishers to 180 mm based on the observations of Forsell (1983).

We estimated that common mergansers would eat a median of two steelhead per day when the target contribution

FIGURE 3. Generalized linear model–predicted monthly densities of avian predators in the Scott Creek estuary (section 1), the upstream section contiguous with the estuary (section 2), and the uppermost portion of the watershed that was surveyed (section 4) from January 2009 to December 2010. The squares represent means and the whiskers represent standard errors.
TABLE 3. Results of bioenergetics modeling. Estimates for each target contribution of steelhead to the diet (20, 40, 50, 70, and 100% steelhead) of common mergansers and belted kingfishers are presented with 95% CIs for each metric. It was not possible to calculate the consumption of steelhead by an individual kingfisher for a target contribution less than 70%, so the energy consumed over total kingfisher-days was used to estimate the steelhead eaten by kingfishers for each target contribution during the lagoon period.

<table>
<thead>
<tr>
<th>Year and predation category</th>
<th>Target contribution (%)</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
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<tr>
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<tr>
<td></td>
<td>Common mergansers</td>
<td>95% confidence limits</td>
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<td></td>
</tr>
<tr>
<td>2009</td>
<td>Steelhead eaten per bird-day</td>
<td>20</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>40</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50</td>
<td>5</td>
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<td></td>
<td></td>
<td>70</td>
<td>7</td>
<td>3</td>
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<td></td>
<td></td>
<td>100</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Steelhead eaten in lagoon (61 bird-days)</td>
<td>20</td>
<td>102</td>
<td>92</td>
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<tr>
<td></td>
<td></td>
<td>40</td>
<td>223</td>
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<td></td>
<td></td>
<td>100</td>
<td>578</td>
<td>544</td>
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<tr>
<td>2010</td>
<td>Steelhead eaten per bird-day</td>
<td>20</td>
<td>2</td>
<td>1</td>
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<tr>
<td></td>
<td></td>
<td>40</td>
<td>5</td>
<td>3</td>
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<td>70</td>
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<td></td>
<td></td>
<td>100</td>
<td>13</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Steelhead eaten in lagoon (108 bird-days)</td>
<td>20</td>
<td>250</td>
<td>234</td>
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<tr>
<td></td>
<td></td>
<td>40</td>
<td>537</td>
<td>513</td>
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<td></td>
<td>Belted kingfishers</td>
<td>95% confidence limits</td>
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<td>2009</td>
<td>Steelhead eaten per bird-day</td>
<td>70</td>
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<td></td>
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<td>100</td>
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<tr>
<td></td>
<td>Steelhead eaten in lagoon (107 bird-days)</td>
<td>20</td>
<td>39</td>
<td>33</td>
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<td></td>
<td>40</td>
<td>79</td>
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<td>89</td>
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<td>70</td>
<td>139</td>
<td>127</td>
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<td>100</td>
<td>199</td>
<td>185</td>
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<tr>
<td>2010</td>
<td>Steelhead eaten per bird-day</td>
<td>70</td>
<td>1</td>
<td>1</td>
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<td></td>
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<td>100</td>
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<td>Steelhead eaten in lagoon (147 bird-days)</td>
<td>20</td>
<td>59</td>
<td>52</td>
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<td>40</td>
<td>118</td>
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<td>100</td>
<td>295</td>
<td>279</td>
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was set at 20% (95% CI: 2009 = 1–3 steelhead [FL, 56–280 mm]; 2010 = 1–4 steelhead [FL, 59–270 mm]). When the target contribution was set at 100%, we estimated that mergansers would eat 9 steelhead per day (95% CI = 5–14) during 2009 and 13 steelhead per day (95% CI = 9–17) during 2010 (Table 3). We estimated that there were 61 merganser-days during 2009 and 108 merganser-days during 2010 in the Scott Creek lagoon; the greater number of merganser days during
2010 translated into greater consumption of steelhead in 2010. We obtained Monte Carlo estimates of the median total consumption of 102 (95% CI = 92–114) steelhead eaten during 2009 and 250 (95% CI = 234–266) during 2010 with a target contribution of 20%. A target contribution of 100% resulted in estimates of 578 (95% CI = 544–612) steelhead eaten during 2009 and 1,398 (95% CI = 1,357–1,439) eaten during 2010.

The steelhead in the lagoon that we assumed were of sizes accessible to belted kingfishers (≤180 mm FL) had a mean energy content that was approximately half of the 300 kJ per day required by kingfishers (161 kJ/fish in 2009 and 149 kJ/fish in 2010). Therefore, it was unlikely that a kingfisher would eat more than one steelhead per day at a target contribution of 70%, and it was not possible to estimate the daily consumption of individual kingfishers for target contributions less than 70%. When the target contribution was set at 100%, the median requirement was 1 steelhead per day (95% CI = 1–3 [56–180 mm FL]) during 2009 and 2 steelhead per day (95% CI = 1–3 [59–180 mm FL]) during 2010. We used the total energy required over 107 kingfisher-days (2009) and 147 kingfisher-days (2010) to obtain Monte Carlo estimates of the median total consumption of steelhead during the lagoon closure period in each year. A target contribution of 20% resulted in an estimate of 39 (95% CI = 33–47) steelhead being eaten during 2009 and 59 (95% CI = 52–66) being eaten during 2010, whereas a target contribution of 100% resulted in estimates of 199 (95% CI = 185–215) during 2009 and 295 (95% CI = 279–311) during 2010.

The estimated initial lagoon population was 1,474 steelhead (95% CI = 1,184–1,967) in July 2009 and 2,727 steelhead (95% CI = 2,242–3,480) during August 2010. We estimated that at a target contribution of 20%, the consumption of steelhead in the Scott Creek lagoon by common mergansers would be 5–6% of the initial lagoon population during 2009 and between 10% and 11% during 2010. If mergansers ate only steelhead (target contribution = 100%), we estimated that they would consume 32–37% of the initial lagoon population during 2009 and between 15% and 52% during 2010. We estimated that at a target contribution of 20% the consumption of steelhead by belted kingfishers would be between 3% and 4% of the initial lagoon population during 2009 and 2010. At a target contribution of 100%, kingfishers would consume 15–17% of the initial lagoon population during 2009 and between 13% and 15% during 2010.

Common Merganser Diet Analysis

We examined the stomach contents of five adult mergansers that were collected dead in Scott Creek between March 12, 2008, and March 8, 2010. Because these birds were collected upstream of the estuary and were dead at the time of collection, we do not expect their stomach contents to be representative of the typical merganser diet in Scott Creek. We identified salmonids, sculpins Cottus spp., Three-Spined Sticklebacks Gasterosteus aculeatus, and several taxa of invertebrates, including Trichoptera (caddisflies), Coleoptera (beetles), Orthoptera (crickets), and Decapoda (crayfish). Sculpins were the most frequently occurring prey item eaten by these adult mergansers, having a frequency of occurrence (FO) of 100% and a minimum number of individuals (MNI) of 1–2 sculpins per stomach. Three-Spined Sticklebacks were present in four of the five mergansers (FO, 80%). The only remains recovered from the sticklebacks were bony plates, which did not allow for the enumeration of individuals. We identified salmonids in the stomachs of four of the five merganser carcasses (FO, 80%; MNI: 1–9 individuals per stomach) from the presence of PIT tags and otoliths. We also detected PIT tags in the stomachs of two of the four mergansers captured alive between January and September 2008. Although we could not differentiate between Coho Salmon and steelhead based on otoliths because of similarities in otolith structure, all of the PIT tags recovered were from steelhead of natural origin.

We estimated the lengths of 10 steelhead recovered from the stomachs of two common mergansers using the otolith width–FL regression (equation 1; mean = 132 mm, range = 67–176, SD = 30). We obtained additional steelhead lengths from fish freshly regurgitated by mergansers while foraging (n = 3; FL = 111–118 mm). The PIT tags detected in mergansers captured alive were from fish handled more than 50 d before capture. Thus, the FL at last handling (71 and 112 mm) likely underestimate the size of the fish when eaten. We found a PIT tag from one steelhead in the stomach of a belted kingfisher that was captured via a mist net at the head of the estuary. The fish had been measured 4 d prior to the bird’s capture and had a FL of 131 mm. The diet data that we present here cannot be considered a complete representation of the diets of mergansers in Scott Creek or of those foraging in the estuary because all but one merganser was collected/captured upstream of the estuary. However, all of the lengths of steelhead eaten by mergansers inferred from stomach contents and regurgitated fish (67–201 mm FL) fell within the range of steelhead captured during lagoon seining (56–280 mm FL).

DISCUSSION

We developed a bioenergetics model to estimate the proportion of juvenile steelhead that would be consumed by avian predators under varying assumptions as to the contribution of steelhead to predator diets. The model enabled estimation of the consumption of steelhead in the absence of local predator diet and energy requirement data, relying on the known abundances of predators and prey and the size distribution of prey. We assessed our model with data from Scott Creek, a small coastal watershed in central California that has been the site of much contemporary research on steelhead (e.g., Bond et al. 2008; Hayes et al. 2008, 2011). Although steelhead life history is well documented in this system, relatively little is known regarding survival and the sources of mortality during freshwater rearing. Permitting restrictions prevented the lethal capture of birds for diet analysis. Furthermore, the lethal removal of large numbers...
of birds could change the predator–prey dynamics of a small system such as Scott Creek. The use of forced regurgitations to obtain stomach contents was also unlikely to be useful because we found that birds quickly learned to evade capture in mist nets in Scott Creek (Frechette, unpublished data). Our model is well suited for systems in which an indirect approach to assessing avian predation on fish is necessary because the collection of rigorous bird diet data is not feasible.

To apply our model in Scott Creek, we first conducted stream surveys to determine the identity and density of potential avian predators. Bird presence in the watershed varied spatially and temporally, with the estuary supporting the greatest number of predators (Figure 3). Although we observed several species of piscivorous birds in Scott Creek, common mergansers and belted kingfishers accounted for 62% of total sightings during the first year of the study and 70% during the second year (Table 1). Some of the less abundant species, such as great blue herons, may be effective predators (Wood 1987a), but due to their rarity likely contributed little to the total predation of steelhead in Scott Creek. For this reason, we only included mergansers and kingfishers in the bioenergetics model. We applied the model to steelhead in the lagoon habitat, where we had sufficient steelhead abundance and size frequency data. Given adequate abundance and size frequency data, this model could also be applied to the upper watershed.

Our avian predator density estimates were based on bird counts conducted within the stream corridor. Thompson (2002) discussed two main sources of bias associated with the estimation of bird populations from count data: bias that originates from the selection of sampling units and bias that originates from the counting process. The counting process may introduce bias because of the misreporting or misidentification of individuals or the failure to adjust counts when the detection probability is less than 1.0 (Thompson 2002). Our survey units (stream sections) were selected randomly using a GRTS sampling program, so that all habitat units had equal, nonzero probabilities of being selected, thus eliminating the bias resulting from nonrandom selection of sampling units. Because one of three highly trained observers identified the birds during all surveys, we believe that the bias from misreporting and or misidentification was negligible. Given our survey methods, it was not feasible for us to determine the detection probability because the calculation of that probability using a double-observer approach requires independent observations by the primary and secondary observers (Nichols et al. 2000; Thompson 2002). As noted above, in this study the secondary observer relayed all of the sightings missed by the primary observer. However, it was rare for the secondary observer to sight a bird missed by the primary observer. This could be because some birds were easy to see and both observers saw them or the birds were difficult to see and both observers missed them. Because of the narrow width of the strip and the open nature of the habitat, we believe that nearly all of the birds within the strip were observed and recorded. If many birds were not counted (detection probability was <1; Thompson 2002), we would have underestimated predator density and thus the predation pressure on juvenile salmonids.

Prey availability and habitat features may limit the foraging of avian species, which would account for the differences in predator distribution between the estuary and the upper watershed. Common mergansers tend to be most concentrated in estuarine habitat and the lower-gradient, wider sections of rivers (Wood 1987a; Gregory et al. 1997). Such habitat is characteristic of the estuary and middle watershed in Scott Creek, where the greatest number of sightings of mergansers occurred. Belted kingfishers (the most commonly observed species in Scott Creek) typically establish territories, the size of which is limited by the availability of suitable pool habitat for foraging (Salyer and Lagler 1949). Kingfishers were more commonly observed upstream of the estuary, where pool habitat is common. Given a greater number of kingfisher-days in the upper watershed and typically smaller fish sizes (requiring more fish to meet daily energetic requirements), kingfishers are likely having an even greater impact upstream than in the estuary. More data are necessary, however, to compare steelhead predation in the upper watershed with predation in the estuary.

The prevalence of common mergansers and belted kingfishers in the lagoon was likely tied to changes in prey availability between the two years. During 2010 we recorded a greater number of bird-days in the lagoon for both species, which may have been in response to the greater initial abundance of steelhead estimated for that year. Despite the greater prevalence of kingfishers than mergansers in the lagoon during both years, mergansers had a greater effect on steelhead (Figure 4a, b) because of their greater energetic requirements.

Our finding that the annual predation on steelhead by common mergansers is much greater than that by belted kingfishers is comparable to the results of a study of predation on juvenile Atlantic Salmon in New Brunswick. Elson (1962) found that mergansers contributed significantly to Atlantic Salmon mortality while predation by kingfishers was negligible by comparison. We estimated that merganser predation in the estuary habitat removed between 6% and 54% of annual steelhead production while kingfisher predation removed 3–17% (using the range of percent contributions that we employed). Comparison with previous studies is difficult because bioenergetics approaches to estimating predation rely on parameters that must either be directly measured or borrowed from the published literature. Bird diet composition, daily food requirements, and the number of predators in the system of interest are not easy to measure, however, and different methods often are used to estimate them (Shearer et al. 1987; Wiese et al. 2008).

The use of different measures to estimate diet may change the relative importance of salmonids in predator diets. For example, in the Mad River belted kingfishers ate a variety of fish, including salmonids, sculpins, and sticklebacks. Salmonids comprised 68.9% of the kingfisher diet by live weight consumed but only 33.9% of the diet by percent frequency of occurrence (Forsell 1983). The contribution of salmonids to predator diets may also
FIGURE 4. Estimated percentages of annual steelhead production (natural and hatchery combined) eaten by (A) common mergansers and (B) belted kingfishers in the Scott Creek estuary during 2008 and 2009. The whiskers represent 95% CIs. Note the difference in the scales of the y-axes.
vary substantially among watersheds, possibly because of watershed characteristics or prey availability. Cairns (1998) reviewed studies of avian predation on salmonids in Canada’s Maritime Provinces and reported that in major salmon rivers Atlantic Salmon comprised 9.2–90.3% of common merganser diets and 5.2–56.4% of belted kingfisher diets. Additionally, estimates from within the same system may vary considerably among years. In the mid-Columbia River, for example, salmonids comprised 12.7% of common merganser diets (mean aggregate percentage fish mass) in 2002 (n = 7) but 40.9% (n = 31) in 2004 (Wiese et al. 2008).

Estimates of predator energetic requirements introduce additional uncertainty into bioenergetics estimates of avian predation, with various methods producing estimates of daily energy intake that range from 0.21 to 0.48 kg of food per day (Elson 1962; Latta and Sharkey 1966; Wood and Hand 1985; Shearer et al. 1987; Wood 1987a). Given such variability in the estimates of diet composition and energetic requirements, we believe that our approach provides a useful solution by estimating a range of values for predator diet composition when local diet data are lacking. Models of fish consumption by birds were more sensitive to changes in the size of fish eaten and the proportion of fish in the diet than to changes in the energy requirements of birds or the energy density of fish (Feltham 1995; Madenjian and Gabrey 1995). Therefore, we believe that fixing the energy requirements of birds and the energy density of steelhead was unlikely to introduce appreciable bias into our model, relative to the unavoidable uncertainty in other parameters with higher sensitivities. We fixed the energetic requirements for common mergansers at the value published by Feltham (1995) for female mergansers. Because females have lower energy requirements than males (Feltham 1995), our model was more likely to underestimate predation than to overestimate it. For belted kingfishers, we used the daily energetic requirements estimated by Forsell (1983) for the Mad River during winter. If kingfishers have greater energetic requirements in the winter, our model may have overestimated their predation on steelhead during the summer lagoon period.

Because we had insufficient diet data with which to infer the size selectivity of avian predators, we used the most parsimonious approach: a single size-frequency distribution for the lagoon closure period from which we assumed equal probabilities of predation on all size-classes of steelhead captured during lagoon seining, given predator specific-size constraints. The size frequency of the steelhead present in the lagoon changes during the closure period, with fish increasing in size from July (mean size: 21.7 g in 2009 and 23.7 g in 2010) to November (mean size, 66.1 g in 2009 and 54.9 g in 2010). Use of a single size-frequency distribution, therefore, will overestimate the sizes of fish eaten early in the lagoon period but underestimate the sizes of those eaten in October and November. Thus, the model will underestimate the number of fish eaten early in the year and overestimate the number of fish eaten late in the year. From a population perspective, however, predation late in the year may have a greater impact on future adult returns because some of the fish eaten early in the year might have died of other causes before attaining the lifecycle stage of those eaten later in the year. With more frequent bird surveys, we could apply the bioenergetics model to estimate predation during specific months in order to account for the change in steelhead size frequency over time.

Our model was also conditional on bird-days. Our survey approach prevented the estimation of error for bird counts. As previously discussed, we believe that there was little error in counting birds because of the open nature of the canopy in the lagoon and the narrow width of the survey transect. Because we could not estimate the error associated with bird counts, we chose not to estimate the variability in the calculation of bird-days (via linear interpolation) for inclusion in the model. Our final estimates of the consumption of steelhead by common mergansers and belted kingfishers during the lagoon period do not include any variability from either error in bird counts or error in estimating bird-days. Application of a true double-observer approach (Nichols et al. 2000; Thompson 2002) would enable estimation of the error in bird counts. The variability associated with bird counts could then be used to estimate the variability in the estimation of bird-days for incorporation into the model.

The range of values that we chose for the contribution of steelhead to bird diets (20–100%) nearly encompasses the range of values in the literature for belted kingfishers and common mergansers (Forsell 1983; Shearer et al. 1987; Kålås et al. 1993; Feltham 1995; Cairns 1998; Wiese et al. 2008). A diet of 100% steelhead was unrealistically high and was included to represent a worst-case scenario. Although we could not characterize the diet of mergansers in the Scott Creek estuary using stomach contents because the birds were collected dead and in the upper watershed, most stomachs contained the remains of sculpins, Three-Spined Sticklebacks, and steelhead. A diet of ≤20% salmonids is likely too low. Although the presence of other prey species can ameliorate the predation pressure on steelhead, mergansers and kingfishers have targeted salmonids over other species in systems where salmonids were productive (Elson 1962; Wood 1987b). There are few other prey species in the Scott Creek lagoon, and the biomass is dominated by juvenile steelhead (Beck et al. 2006); therefore, we assumed that avian predators target steelhead over Three-Spine Sticklebacks and Tidewater Gobies Eucyclogobius newberryi (the next most common species in the lagoon in terms of biomass). With the contribution of steelhead to merganser diets as low as 40%, mergansers would eat 15–20% of the annual production in the lagoon. Lagoon-reared fish comprise 95% of the returning adult population (Bond et al. 2008). Avian predation rates of 15–20% therefore, may have a significant effect on this imperiled steelhead population because of their disproportionate contribution to the breeding population.

Our study represents progress toward quantifying the mortality of ESA-listed steelhead from predation during freshwater rearing. A combination of stream surveys and bioenergetics modeling allowed us to identify the predators that likely
have the greatest effect on steelhead in this small coastal watershed. Rarely observed predators, such as great blue herons and pied-billed grebes, were not likely to exert significant predation pressure relative to the more common belted kingfishers and common mergansers. Furthermore, due to their smaller size and lower energy requirements, kingfishers likely affect steelhead populations to a lesser degree than mergansers. Directing resources toward understanding merganser foraging habits and better quantifying the diet of mergansers may be the most effective way to improve estimates of freshwater rearing mortality for steelhead along the central California coast.

ACKNOWLEDGMENTS

This project was funded by the California Sea Grant College Program (R/FGH-205), the California Department of Fish and Game Fisheries Restoration Grant Program, the University of California–Santa Cruz (NSF DEB-1009018), and the International Women’s Fishing Association Scholarship. Site access and project support were provided by the U.S. Fish and Wildlife Service, California State Parks, the Briggs Family, CalPoly Swanton Pacific Ranch, and Big Creek Lumber. S. Auten, B. Dietterick, M. Pavelka, J. Webb, and C. Winchell were especially helpful. This work would not have been possible without the help of the technicians, interns, and volunteers that assisted with bird surveys, especially T. Brown, I. Cole, E. Donnelly, J. Harding, B. Kohli, M. Pavelka, J. Perez, B. Perlman, A. Soberij, and J. Toone. All protocols were approved by the Institutional Animal Care and Use Committee at San Jose State University and the University of California–Santa Cruz. All birds were banded and carcasses collected under USGS master banding permit 23411 issued to Shaffer.

REFERENCES


Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead Rainbow Trout (Salmo gairdneri gairdneri) and Silver Salmon (Oncorhynchus kisutch). California Department of Fish and Game, Fish Bulletin 98.


Appendix: Daily Bird Counts and Length–Otolith Width Relationship

![Common Merganser and Belted Kingfisher Counts](image)

**FIGURE A.1.** Counts of common mergansers and belted kingfishers from stream surveys conducted in 2009 and 2010 versus day of the year. The dashed lines illustrate the linear interpolations used to estimate the number of bird-days in the Scott Creek lagoon.

![Length–Otolith Width Relationship](image)

**FIGURE A.2.** Relationship between steelhead FL and otolith width, described by the equation $FL = 115.11 - 0.847$ (R² = 0.847, P < 0.0001).
Detecting Noncompliance in the Summer Flounder Recreational Fishery Using a Mark–Recapture Growth Model

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Published online: 08 Oct 2013.

To cite this article: Mark J. Henderson & Mary C. Fabrizio (2013) Detecting Noncompliance in the Summer Flounder Recreational Fishery Using a Mark–Recapture Growth Model, North American Journal of Fisheries Management, 33:5, 1039-1048, DOI: 10.1080/02755947.2013.820244

To link to this article: http://dx.doi.org/10.1080/02755947.2013.820244

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ARTICLE

Detecting Noncompliance in the Summer Flounder Recreational Fishery Using a Mark–Recapture Growth Model

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Abstract

We used a mark–recapture growth model to investigate recreational angler compliance with minimum length regulations in a popular Chesapeake Bay fishery. Angler noncompliance can severely degrade the ability of fishery managers to avoid overexploitation and to achieve objectives of rebuilding plans. To discern noncompliance in the recreational fishery for Summer Flounder Paralichthys dentatus, we fitted a growth model to 3,474 recapture records from a tagging study conducted by volunteer anglers in Virginia from 2000 to 2011. Most of the tagged fish were small (i.e., sublegal size), and the average time at liberty was 86 d. Based on the growth model, Summer Flounder growth patterns changed at 34.7 cm, possibly representing the length at which the majority of fish reach maturity. The mean size of harvested fish increased in response to increases in the minimum size limit, although harvest of sublegal fish continued. Throughout the 12 years of the study, 33–79% of the tagged fish that were recaptured and harvested were predicted to be sublegal based on the growth model. The percentage of sublegal fish that were harvested increased dramatically when large (>5 cm) increases in minimum size limits were implemented. We conclude that Virginia recreational anglers responded to management regulations by adjusting the minimum size of harvested fish but that some anglers continued to harvest sublegal fish.

Noncompliance with management regulations can severely degrade the ability of fishery managers to avoid overexploitation of fish populations (Gigliotti and Taylor 1990; Sullivan 2002) and to achieve objectives of rebuilding plans. In recent decades, recreational fishing effort has increased considerably and was implicated in the decline of some fish stocks (Post et al. 2002; Coleman et al. 2004; Cooke and Cowx 2004). Typically, recreational fisheries are managed through regulations (e.g., seasons, bag limits, and size limits) that minimize the impacts of individual anglers on the population. Unfortunately, angler noncompliance with management regulations may be common in some fisheries and can be as high as 90% (Glass and Maughan 1984; Paragamian 1984; Schill and Kline 1995; Pierce and Tomcko 1998; Sullivan 2002). A simulation study indicated that even moderate levels of noncompliance could cause declines in the number of legal-sized fish that are harvested (Gigliotti and Taylor 1990).

Quantifying the extent of angler noncompliance is a challenging task because noncompliance is difficult to measure accurately (Schill and Kline 1995; Sullivan 2002). Previous studies of angler noncompliance have primarily used creel surveys, citation records, or angler interviews. Each of these methods has inherent weaknesses and biases associated with angler behavior. For example, Pierce and Tomcko (1998) found that estimated levels of angler noncompliance (i.e., percentage of harvest that was sublegal) based on creel surveys and citation records were biased low, and they concluded that anglers concealed their sublegal catches from creel clerks and enforcement officers. The

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Received April 9, 2013; accepted June 18, 2013
Published online October 3, 2013
results of Pierce and Tomcko (1998) indicated that estimates of noncompliance based on voluntary tag returns were more accurate than those based on other methods. In this study, we use data collected from a recreational angler tagging program in the Chesapeake Bay region to quantify angler noncompliance with minimum size regulations.

The Virginia Game Fish Tagging Program (VGFTP) is a cooperative project between the Virginia Marine Resources Commission (VMRC) and the Virginia Institute of Marine Science (VIMS); the program trains recreational anglers to tag and release popular game fishes throughout the coastal waters of Virginia. Benefits of this program include a relatively low cost and a collaborative relationship between scientists and the angling community (Lucy and Davy 2000). Since the program was initiated in 1995, up to 200 recreational anglers per year volunteer to tag fish during their normal fishing activities. The large numbers of participants in the program released thousands of tagged fish annually throughout coastal waters of Virginia. These releases and the subsequent recaptures provided sufficient data for modeling of fish growth and for examining compliance with established management regulations. We chose to analyze the mark-recapture data collected for Summer Flounder *Paralichthys dentatus*, one of the most targeted commercial and recreational fish species along the U.S. Atlantic coast (Terceiro 2002).

Due to the extensive recreational and commercial fishing pressure on Summer Flounder, effective management is critical to ensure the sustainability of this population. Since 2000, the population along the east coast has been the subject of a rebuilding plan. The Mid-Atlantic Fisheries Management Council and the Atlantic States Marine Fisheries Commission jointly manage Summer Flounder through regulations on both the commercial and recreational fisheries (Terceiro 2002). Currently, 40% of the quota is allocated to the recreational fishery and 60% is allocated to the commercial fishery. The recreational fisheries sector has exceeded its allotted quota in multiple years, most likely due to the difficulties inherent in monitoring the activities of recreational anglers (Terceiro 2002). To reduce the recreational fishery harvest, managers throughout the Atlantic states have implemented bag and size limits that have changed annually. To gain insight into the rate of noncompliance by recreational anglers, we fitted growth models to the mark-recapture data collected by the VGFTP and compared the reported sizes of recaptured fish with predicted sizes.

Individual growth models are a valuable tool in fisheries science because growth trajectories are critical to many aspects of fish stock dynamics. Growth models are most commonly applied to size-at-age data, but they can also be fitted to mark-recapture data consisting of fish sizes and the dates when fish were released and recaptured (Haddon 2011). Growth models are typically used to estimate parameters for stock assessments, but they have also been used to observe ontogenetic changes (Ross et al. 1995; Hearn and Polacheck 2003). For example, Hearn and Polacheck (2003) found that a two-phase growth model better represented the growth of Southern Bluefin Tuna *Thunnus maccoyii* than the standard single-phase von Bertalanffy growth model. Those authors concluded that the two phases might be the result of fish behavioral changes related to ontogeny. We suspect that similar ontogenetic changes in growth may occur in Summer Flounder because they undertake long-distance spawning migrations from coastal bays and estuaries to spawning grounds on the continental shelf (Kraus and Music 2001).

We used mark-recapture growth models to describe the growth of Summer Flounder and to observe changes in recreational angler noncompliance with changes in minimum length limits in Virginia. Although previous studies have used recapture data to assess angler noncompliance (Pierce and Tomcko 1998), the incorporation of a growth model into this analysis allowed us to better quantify the extent of noncompliance relative to changes in minimum size regulations. In addition, the growth model provided a means to investigate changes in growth related to ontogeny (i.e., length at maturity) and to examine measurement error associated with trained taggers and untrained anglers.

**METHODS**

Tagging program.—The VGFTP trains volunteer anglers to tag and release game fishes as part of their routine fishing activities. All volunteer taggers were provided with tagging equipment and were trained to properly measure, handle, and tag multiple species (Lucy et al. 2002). Based on this training, we assumed that the length measurements reported by VGFTP taggers were accurate within rounding error. Taggers were also given data sheets to record information pertinent to their releases, such as the tag number, species, date, TL, release location, and release condition (i.e., excellent, good, fair, and poor). These data sheets were submitted to the VGFTP and were compiled into a database that was queried when recreational and commercial fishers reported recaptures.

During 2000–2011, VGFTP participants released 47,513 tagged Summer Flounder throughout the Virginia portion of Chesapeake Bay. All of the Summer Flounder were tagged with a Halprint t-bar anchor tag inserted in the dorsal musculature near the tail. Each tag was labeled with a unique identifying number, a phone number for reporting recaptures, and a reward notice. Tagged fish had a truncated length range (21–57 cm) compared with that observed in fishery-independent surveys (5–76 cm; Bonzek et al. 2008) because most of the fish that were larger than the recreational size limit were harvested by the taggers. During this study, the minimum size limit varied between 39 and 48 cm TL.

Of the 47,513 tagged Summer Flounder that were released within Chesapeake Bay, 5,494 recaptures were reported to the VGFTP, but some of these data were excluded from the growth analysis because they were outliers, were tagged as exceptionally small fish (<25 cm), or were not at liberty for a sufficient
duration to allow observation or measurement of growth. We used only those recapture records that included a recapture date and a measurement of fish length. Through personal discussion with anglers, we learned that some of the reported length “measurements” were actually approximations that were visually estimated by the angler. Unfortunately, the type of length measurement (measured or estimated) was not recorded, so we were unable to quantify the accuracy and bias associated with length estimation. We removed eight obvious outliers from the data set based on the following criteria: (1) if the fish was recaptured within 1 year of release and the difference between release and recapture lengths was more than 25 cm; or (2) if the fish was recaptured after more than 1 year at liberty and the length at tagging exceeded the length at recapture by more than 5 cm. We also excluded data from fish that were smaller than 25 cm when tagged (n = 860) because we wanted to restrict our analysis to fish that were approximately age 1 or older (Brust 2008). In addition, fish that were at liberty for less than 10 d (n = 1,145) were excluded from the growth analysis because they were unlikely to exhibit observable growth; however, because those fish should have had nearly identical lengths upon release and recapture, we used their data to determine the bias in reported lengths of recaptured fish. To do this, we calculated the mean difference between the lengths at release and recapture, and used their data to model growth; data from an additional 1,145 recaptures were used to examine bias in reported lengths.

**Growth model.**—We selected a two-phase mark–recapture growth model that included a parameter to account for individual variability in growth. For all recaptured individuals (i), this model has the form:

$$E[ΔL_{i(i)}] =$$

$$\begin{cases}
L_{∞(i)} - l_{i(i)} & \text{if } t_{2(i)} \leq t^*_{i(i)} \\
1 - e^{-k_1(t_{2(i)} - t_{i(i)})} & \text{if } t_{2(i)} > t^*_{i(i)}
\end{cases} + \varepsilon$$

where $ΔL_{i(i)}$ is the growth increment, $L_{∞(i)}$ is the asymptotic maximum length, $L^*$ is the length at which growth patterns change, $l_{i(i)}$ is the length at tagging, $k_1$ is the growth coefficient during the first growth phase, $k_2$ is the growth coefficient during the second growth phase, $t_{1(i)}$ is the release date, $t_{2(i)}$ is the recapture date, $t^*_{i(i)}$ is the date when an individual reaches $L^*$, and $\varepsilon$ is the unexplained error, which includes model error and measurement error. Note that $t^*_{i(i)}$ is not an estimated parameter but is calculated as

$$t^*_{i(i)} = t_{1(i)} - \left\lfloor \frac{\log(1 - \frac{L_{∞(i)} - l_{i(i)}}{x_{\text{meas}} - l_{i(i)}})}{k_1} \right\rfloor.$$ (2)

To estimate a value for $L_{∞(i)}$, we follow the method of Wang (1998), who used the first-order approximation,

$$E[L_{∞(i)}|t_{1(i)}] = L_{∞} + \beta [t_{1(i)} - \bar{t}_i],$$ (3)

where $L_{∞}$ is the mean asymptotic maximum length for the population and $\beta$ is an estimated parameter, the magnitude of which indicates the amount of individual variability in maximum length.

This growth model combines the models of Wang (1998) and Hearn and Polacheck (2003), which were both based on Fabens’ (1965) modification of the von Bertalanffy growth equation for mark–recapture data. Fabens’ (1965) model has been used extensively but has been criticized because it does not account for individual variability in the von Bertalanffy growth parameters (Francis 1988; Hampton 1991; James 1991; Wang 1998; Laslett 2002). To account for individual variability, Wang (1998) incorporated an extra parameter ($\beta$) into the Fabens (1965) equation to allow $L_{∞}$ to vary among individuals. Hearn and Polacheck (2003) also modified Fabens’ (1965) equation to estimate a length at which growth patterns change, possibly due to fish reaching maturity. The original Hearn and Polacheck (2003) model estimated $L_{∞}$ values for each of the two growth phases (larger than $L^*$ and smaller than $L^*$), but their results showed limited support for estimating two $L_{∞}$ parameters. Due to this limited support and because a single mean maximum length is more plausible biologically, we chose to use a more parsimonious model and therefore estimated a single $L_{∞}$. A combination of the Wang (1998) and Hearn and Polacheck (2003) equations resulted in a model of increased complexity, but model selection using Akaike’s information criterion (AIC; Akaike 1973) indicated overwhelming support (AIC weight = 0.997) for the combined model over the Fabens (1965), Wang (1998), or Hearn and Polacheck (2003) models (Henderson 2012).

Model parameters were estimated by using maximum likelihood, with an error structure that was designed to account for biases due to measurement error and process error. It is well documented that growth models based on mark–recapture data can suffer from biases when individual variability exists in growth parameters, particularly if the $L_{∞}$ parameter varies among individual fish (Francis 1988; Hampton 1991; James 1991; Wang 1998; Laslett 2002). As a result of this individual variability, the variance in the expected growth increment increases with increasing time at liberty (Hampton 1991; James 1991; Hearn and Polacheck 2003). To partially compensate for this bias, we
expressed the variance of the expected growth increment ($V[\Delta l_{ij}]$) using a conditional error term that separately estimates terms for tagger measurement error ($\sigma^2_m$), angler measurement error ($\sigma^2_a$), and process error ($\sigma^2_p$) that is linearly dependent on the time at liberty:

$$V[\Delta l_{ij}] = \begin{cases} 
\sigma^2_m + \sigma^2_p [t_{2(i)} - t_{1(i)}] & \text{if recaptured by a VGFTP tagger} \\
\sigma^2_m + \sigma^2_a + \sigma^2_p [t_{2(i)} - t_{1(i)}] & \text{if recaptured by an untrained angler.}
\end{cases}$$

(4)

Although we refer to “measurement” and “process” errors, these two error terms are confounded and are not separately estimable because we do not have independent estimates of measurement error. Therefore, the error term $\sigma^2_m$ should be considered a composite of measurement error and components of the process error that are not related to time at liberty (Hearn and Polacheck 2003). Once again, based on AIC model selection, this three-term error structure was overwhelmingly supported over simpler error structures (Henderson 2012).

Under the assumption that the growth increment was normally distributed (which was empirically supported by the data based on a comparison between the fit of the normal and the lognormal distributions to the growth increment response using the fitdistr function in R), the parameters for the various models and error terms were estimated by minimizing the following negative log-likelihood:

$$-\log(L) = \frac{1}{2} \sum_{i=1}^{n} \left[ \log(2\pi[V[\Delta l_{ij}]]) + \frac{[\Delta l_{ij} - E[\Delta l_{ij}]]^2}{V[\Delta l_{ij}]} \right].$$

(5)

This was accomplished using the bounded Broydon–Fletcher–Goldfarb–Shanno (BFGS) minimization method (Byrd et al. 1995) implemented with the optim function in R. To improve the efficiency of the minimization procedure, we constrained the $L_\infty$, $k_1$, $k_2$, and $L^*$ parameters to be greater than zero. We note that because the bounded BFGS method uses derivatives to determine the optimal combination of parameters, this approach may be problematic if the derivative of the likelihood is not continuous. However, we used this method because it is efficient and because parameter estimates were less sensitive to starting values than non-derivative-based methods (e.g., the Nelder–Mead method).

**Angler noncompliance.**—We used the residuals from the growth model to examine the bias in the length measurements reported by recreational anglers. The residual growth was calculated as the difference between the observed and predicted growth. We first plotted the residuals against the release length and time at liberty to verify that the residuals were centered at zero throughout the range of observations. We next partitioned the residuals into two sets: fish that were released after recapture and fish that were harvested. Finally, we partitioned the residuals for harvested fish into two groups: (1) fish with a model-estimated size indicating that they were sublegal upon recapture; and (2) fish with a model-estimated size indicating that they were legal upon recapture. For this analysis, we used recaptures from recreational anglers because commercial fishers did not report a sufficient number of recaptures to reliably estimate rates of noncompliance by that sector. In analyzing the residuals from recreational angler recaptures, our null hypothesis was that there was no length measurement bias and that the mean residual was therefore equal to zero. We tested this hypothesis for each group of residuals (i.e., released fish, harvested fish, harvested fish that were expected to be of sublegal size, and harvested fish that were expected to be of legal size) by using $t$-tests at an $\alpha$-value of 0.05.

We used the model estimates of fish length to investigate changes in lengths of harvested fish through time, and we compared these changes with changes in minimum size limits for Summer Flounder in Virginia. We calculated the annual mean estimated length of all harvested fish ($\hat{L_H}$), the annual mean estimated length of harvested fish that were predicted to be sublegal ($\hat{L_S}$), and the annual percentage of harvested fish that were predicted to be sublegal. The 95% confidence intervals (CIs) for all means and percentages were calculated using the methods described by Zar (1999).

**RESULTS**

Recaptures were more likely to occur shortly after release, and the differences between the reported tagging and recapture lengths were highly variable (Figure 1). Throughout the 12 years of the study, most (91.23%) of the tagged Summer Flounder were recaptured within 6 months of release, and the mean
time at liberty was 86 d (95% CI = 80.9–90.1 d). The length measurements of Summer Flounder recaptured within 6 months of release ranged from 18 cm smaller to 24 cm larger (quartile range = 0.0–3.2 cm) than their lengths at the time of tagging. This implies that large inaccuracies occasionally occurred in the measurements (or length estimates) reported by the taggers, the anglers that recaptured and reported the fish, or both. Some of these inaccuracies may have been the result of rounding error. Nearly half of the recapture lengths were reported to the nearest 1 in (i.e., 2.54 cm), and an additional 30% were reported to the nearest 0.5 in (i.e., 1.27 cm; Table 1). A similar pattern was also apparent in the lengths reported by the trained taggers. Despite the lack of precision, the reported length measurements were not biased. The mean observed growth for fish that were at large for less than 10 d was 0.11 cm (95% CI = 0.09 to 0.22 cm) and was not significantly different from zero (t = 0.84, df = 1,144, P = 0.40).

The growth model that was fitted to these mark–recapture data provided estimates of the tagged population’s \( L_\infty, \beta, L^*, k_1, \) and \( k_2 \) and the difference in measurement error between trained taggers and untrained anglers (\( \sigma_m \) and \( \sigma_u \), respectively; Table 2). The estimated \( L_\infty \) from the mark–recapture growth model (50 cm) was considerably smaller than estimates reported in previous studies based on Summer Flounder length-at-age data (56–116 cm; Table 3). The model-estimated value for the \( \beta \)-parameter, which represents the degree of individual variability in \( L_\infty \), was quite large relative to the \( \beta \)-estimates reported by Wang (1998) for tiger prawns \( P. esculentus \) and rock lobsters \( P. ornatus \). This result implies that Summer Flounder exhibit high amounts of individual variation in growth (specifically \( L_\infty \)), but it may also reflect the considerable measurement error observed with these data. The estimated \( L^* \) was 34.7 cm; however, the likelihood profile plot for this parameter shows that likelihood values did not differ greatly when the \( L^* \) value ranged between 32 and 35 cm (Figure 2), suggesting variability in the length at which an individual’s growth pattern changes. The estimated growth coefficient \( k_1 \) (0.81) was greater than the estimated \( k_2 \) (0.52); both of these estimates were larger than the values previously reported for von Bertalanffy models fitted to length-at-age data (Table 3). Finally, the estimate of \( \sigma_m \) was nearly 1.5 cm larger than the estimated \( \sigma_u \), suggesting that the VGFTP training improved taggers’ measurement accuracy relative to untrained anglers.

No pattern was evident in the residuals from the growth model relative to fish size or time at large, but a pattern emerged when residuals were examined relative to the status of recaptured fish (i.e., either harvested or released). Regardless of the fish size at tagging, model residuals were centered at zero, with no evident trend (Figure 3a). As the size at tagging increased, the variance appeared to decrease; however, this was primarily due to the lower sample sizes for fish that were 40 cm or larger at the time of tagging. A similar pattern was observed for growth relative to time at liberty (Figure 3b). A positive bias in residuals was

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>( L_\infty ) (cm)</td>
<td>50.17</td>
<td>2.42</td>
</tr>
<tr>
<td>( L^* ) (cm)</td>
<td>34.69</td>
<td>0.56</td>
</tr>
<tr>
<td>( k_1 ) (year(^{-1}))</td>
<td>0.81</td>
<td>0.14</td>
</tr>
<tr>
<td>( k_2 ) (year(^{-1}))</td>
<td>0.52</td>
<td>0.12</td>
</tr>
<tr>
<td>( \beta )</td>
<td>0.65</td>
<td>0.10</td>
</tr>
<tr>
<td>( \sigma_m )</td>
<td>1.94</td>
<td>0.06</td>
</tr>
<tr>
<td>( \sigma_u )</td>
<td>1.47</td>
<td>0.07</td>
</tr>
<tr>
<td>( \sigma_p )</td>
<td>2.13</td>
<td>0.23</td>
</tr>
</tbody>
</table>

FIGURE 2. Likelihood profile plot for the length (\( L^* \); cm TL) at which the von Bertalanffy growth coefficient changed based on the mark–recapture growth model for Summer Flounder that were tagged by participants in the Virginia Game Fish Tagging Program (2000–2011). The negative log-likelihood values are those calculated when the \( L^* \) parameter was held constant and all other parameters were estimated.
TABLE 3. Von Bertalanffy growth model parameters (\(L_\infty\) = asymptotic maximum length; \(k\) = growth coefficient; \(t_0\) = theoretical age at length of zero) estimated from individual length-at-age data for Summer Flounder (the Brust [2008] study parameters were estimated from mean length-at-age data).

<table>
<thead>
<tr>
<th>Source</th>
<th>Years of study</th>
<th>Calcified structure</th>
<th>Sex</th>
<th>(L_\infty) (cm)</th>
<th>(k) (year(^{-1}))</th>
<th>(t_0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shepherd</td>
<td>1977–1978</td>
<td>Otoliths</td>
<td>Both</td>
<td>96.88</td>
<td>0.16</td>
<td>−0.01</td>
</tr>
<tr>
<td></td>
<td>1977–1978</td>
<td>Scales</td>
<td>Both</td>
<td>116.32</td>
<td>0.13</td>
<td>−0.16</td>
</tr>
<tr>
<td>Fogarty</td>
<td>1976–1979</td>
<td>Scales</td>
<td>Male</td>
<td>72.72</td>
<td>0.18</td>
<td>−0.26</td>
</tr>
<tr>
<td></td>
<td>1976–1979</td>
<td>Scales</td>
<td>Female</td>
<td>90.61</td>
<td>0.16</td>
<td>0.05</td>
</tr>
<tr>
<td>Desfosse</td>
<td>1987–1990</td>
<td>Scales</td>
<td>Male</td>
<td>55.87</td>
<td>0.33</td>
<td>−0.79</td>
</tr>
<tr>
<td></td>
<td>1987–1990</td>
<td>Scales</td>
<td>Female</td>
<td>75.78</td>
<td>0.29</td>
<td>−0.53</td>
</tr>
<tr>
<td>Brust</td>
<td>1999–2006</td>
<td>Unknown</td>
<td>Male</td>
<td>65.25</td>
<td>0.23</td>
<td>−1.50</td>
</tr>
<tr>
<td></td>
<td>1999–2006</td>
<td>Unknown</td>
<td>Female</td>
<td>78.49</td>
<td>0.22</td>
<td>−1.12</td>
</tr>
</tbody>
</table>

evident for fish that were harvested upon recapture (Figure 4). Of the 398 fish harvested by recreational anglers in this study, over half (54.0%) were of sublegal size based on lengths estimated from the growth model. The residuals from the growth model were centered at zero for harvested fish that were estimated to be of legal size (Figure 5a); the mean residual for these fish was 0.62 cm (95% CI = 0.20–1.05 cm). This was significantly different from zero (\(t = 2.89, df = 182, P = 0.004\)), indicating a slight positive bias that could be the result of rounding error. A majority (85.05%) of the harvested fish that were estimated to be sublegal had positive residuals (Figure 5b), and the mean residual for these fish was 2.87 cm (95% CI = 2.33–3.41 cm), which was also significantly different from zero (\(t = 10.51, df = 214, P < 0.001\)). Based on the large percentage of residuals that were positively biased and the magnitude of the mean residual, it is unlikely that the observed measurement bias for fish that were estimated to be sublegal was due solely to rounding error.

Recreational anglers responded to changes in minimum size regulations in Virginia, but they continued to harvest sublegal Summer Flounder. From 2000 to 2006 (with the exception of 2002), the mean \(\hat{L}_H\) was nearly equal to or greater than the minimum size limit. Interestingly, in 2002 the minimum size limit was increased by 5 cm from the previous year (Figure 6a). Between 2007 and 2010, when the minimum size limit was greater than 45 cm, the \(\hat{L}_H\) was consistently lower than the minimum size limit. The mean \(\hat{L}_S\) also varied with minimum size limit regulations (Figure 6b). The difference between \(\hat{L}_S\) and the minimum size limit ranged from 1.14 to 4.46 cm and was largest during years when the minimum size limit was greater than 45 cm (Figure 7). The proportion of harvested fish that were sublegal was also related to the minimum size limit. Throughout this study, 33–79% of harvested fish reported to the VGFTP were estimated to be sublegal based on the growth model, but due to small sample sizes, the 95% CIs for these percentages were quite large (Figure 6c). The percentage of sublegal harvest had local maxima during 2002 and 2007, years in which the minimum size limit regulation increased considerably (5 cm) from that of the previous year. The percentage of sublegal harvest was also relatively high in 2009 and 2010, when the minimum size limit was over 45 cm.

DISCUSSION

Growth models fitted to recreational angler mark–recapture data can provide insight into recreational anglers’ noncompliance with minimum size limit regulations. The growth models allowed us to observe biases in the reported length measurements for sublegal Summer Flounder that were harvested by recreational anglers in Virginia. Based on model predictions, recreational anglers appeared to respond to changes in size regulations by adjusting the minimum length of the fish they harvested; however, anglers that chose to harvest sublegal Summer Flounder kept fish that were approximately 1–4 cm smaller than the minimum size limit. The largest differences between the minimum size limit regulation and the mean size of harvested sublegal fish were observed during years when the minimum size limit was greater than 45 cm. Furthermore, the highest proportions of sublegal fish were harvested during years when minimum size limits changed substantially relative to previous years (e.g., in 2002 and 2007) or when large size limits were maintained for consecutive years (2009–2010). These increases in noncompliance most likely occurred because the larger minimum size limits reduced the catch rate of legal-sized fish (Sullivan 2002), thus motivating some anglers to harvest sublegal fish.

Although we believe that our results describing noncompliance provide insight into the behavior of recreational anglers that captured Summer Flounder in Virginia, there are limitations to using data that are collected by an angler tagging program. First, the VGFTP relies on anglers to voluntarily report recaptures, but the overall reporting rate in this program remains unknown. Anglers that harvest sublegal fish may be less likely to report recaptures under the assumption that they could be fined. If reporting rates were lower for harvested sublegal Summer Flounder, then our
estimate for the percentage of the VGFTP recreational harvest that was smaller than the minimum size limit is conservative. A second limitation of using angler tagging data is that the Summer Flounder that were tagged and released by the VGFTP were disproportionally sublegal. As a result, the observed proportions of harvested fish that were sublegal cannot be used to make inferences regarding the recreational fishery as a whole. Because very few larger fish were tagged and released as part of the VGFTP, we suspect that the sublegal proportion of fish harvested in the recreational fishery was lower than indicated in Figure 6c. However, even low levels of noncompliance can degrade the benefits derived from instituting minimum size regulations (Gigliotti and Taylor 1990). Finally, Summer Flounder are known to exhibit sexually dimorphic growth (Poole 1961; Fogarty 1981), but we were unable to separately model the growth of males and females because sex could not be determined without sacrificing the animal. Observations from fishery-independent surveys of the Summer Flounder population in Chesapeake Bay indicate that very few males larger than 45 cm are captured and that females comprise over 90% of the age-2 and older individuals in the Summer Flounder population (Bonzek et al. 2008). Therefore, if sexually dimorphic growth patterns were responsible for the observed measurement bias, we would expect that nearly all individuals over 45 cm would also have a positive measurement bias. However, a measurement bias among larger fish was not discernible from our data (Figures 3a, 5a), implying that our conclusions regarding noncompliance were not influenced by sexually dimorphic growth. Despite the limitations of the data, we believe our results (1) provide useful observations on the habits of recreational anglers in response to changes in harvest regulations and (2) confirm the belief among managers that increasing minimum size regulations may increase angler noncompliance.

Another contribution of this study was that we quantified the bias and precision of length measurements reported by recreational anglers. For Summer Flounder that were recaptured by recreational anglers within 10 d of release, the reported length at recapture differed by up to 24 cm from the length reported at the time of tagging. These recapture measurements were neither positively nor negatively biased. This lack of precision in angler measurements is large compared with that observed in other
FIGURE 5. Residuals from the mark–recapture growth model for Summer Flounder that were harvested by recreational anglers between 2000 and 2011: (a) fish with model-estimated lengths suggesting that they were of legal size at the time of recapture (n = 184) and (b) fish with model-estimated lengths suggesting that they were of sublegal size at the time of recapture (n = 214). The zero line, around which all residuals should be centered, is displayed as a dashed gray line in both plots.

FIGURE 6. Minimum size limit for Summer Flounder in the Virginia recreational fishery between 2000 and 2011 (gray line) presented in comparison with mean attributes (± 95% confidence interval [CI]) of angler-harvested fish that were reported to the Virginia Game Fish Tagging Program (black line): (a) mean model-estimated length of harvested fish; (b) mean model-estimated length of harvested fish that were of sublegal size (based on the growth model) at the time of recapture; and (c) mean percentage of harvested fish that were of sublegal size (based on the growth model) at the time of recapture.

studies (Ferguson et al. 1984; Page et al. 2004), which may be the result of some recreational anglers estimating—instead of measuring—the lengths of recaptured fish that were obviously sublegal. The lack of precision was also due to rounding error. Nearly 50% of the reported length measurements were rounded to the nearest 1 in, and an additional 30% were rounded to the nearest 0.5 in. This pattern was not surprising, as rounding error from recreational anglers has previously been noted in other studies (Ferguson et al. 1984; Page et al. 2004). Rounding error was prevalent for both trained taggers and untrained anglers, but results from the growth model imply that the length measurements provided by trained taggers were more accurate than those reported by untrained anglers.

Despite the biases and lack of precision in the length measurements reported by recreational anglers, we were able to fit a relatively complex growth model to these data. Summer Flounder growth appears to be related to ontogeny, with the growth coefficient $k$ decreasing when the fish reach approximately 35 cm, and this may be the approximate length at which Summer Flounder reach maturity. We hypothesize that growth rates decline after maturity because fish begin to expend more energy on gonad production and seasonal spawning migrations (Lester et al. 2004; Rijnsdorp and Witthames 2005). The likelihood profile plot for the change point in the growth model indicated that individuals might reach this change point (maturity) when they attain a TL between 32 and 35 cm. We have two hypotheses regarding this relatively large range:
the angler tagging program most likely affected our estimates of
Bay (Bonzek et al. 2008), and exclusion of the larger fish from
Flounder can reach and exceed 70 cm TL within Chesapeake
only 3% of the recaptured fish were larger than 50 cm. Summer
population; one reason is that less than 1% of the tagged fish and
data indicating that female Summer Flounder reached maturity
This conclusion is supported by Terceiro (2002), who presented
increased relative to that observed during the 1970s and 1980s.
Summer Flounder reproductive maturity studies conducted during the 1970s and 1980s indicated that the length
at which 50% of Summer Flounder had matured was approxi-
amately 30 cm (summarized by Packer 1999). It is possible that as
the Summer Flounder population’s abundance has increased and
as the age structure has become less truncated (Terceiro 2011),
the length at which Summer Flounder become mature has in-
creased relative to that observed during the 1970s and 1980s.
This conclusion is supported by Terceiro (2002), who presented
data indicating that female Summer Flounder reached maturity
at a larger length in the 1990s (high stock abundance) than in
the 1980s (low stock abundance).

We caution that the growth parameters reported here are
not representative of the entire mid-Atlantic Summer Flounder
population; one reason is that less than 1% of the tagged fish and
only 3% of the recaptured fish were larger than 50 cm. Summer
Flounder can reach and exceed 70 cm TL within Chesapeake
Bay (Bonzek et al. 2008), and exclusion of the larger fish from
the angler tagging program most likely affected our estimates of
\( L_{\infty} \) and \( k \). Due to the well-known correlation between \( L_{\infty} \) and \( k \), reliable estimates of growth beyond the length range of the
data cannot be obtained (Hearn and Polacheck 2003). This may
partially explain our low estimates of \( L_{\infty} \) and high estimates of \( k \) in comparison with previously published growth models
based on length-at-age data (Table 3). Another reason that our
model does not represent the mid-Atlantic population is that the
observed bias in the reported lengths of harvested sublegal
fish could have resulted in incorrect estimates of the growth
model parameters. However, we suspect that any influence of
the observed measurement bias on the growth model parameter
estimates would be minor because the harvested number of
sublegal fish constituted a small percentage (6%) of the total
observations.

The results from this study have management implications
for the Summer Flounder fishery in Virginia and for recreational
fisheries in general. The upper range of the estimated Summer
Flounder length at maturity (35 cm) is nearly identical to the
current minimum size limit for Summer Flounder commercial
fisheries along the coast (35.6 cm). Thus, more research is war-
ranted to determine whether the minimum size limit for the
commercial fishery should be increased to improve the proba-
bility that Summer Flounder will have the opportunity to spawn
prior to becoming vulnerable to the commercial fishery. Our
results also indicate that angler behavior should be incorporated
into management decisions to improve the efficacy of regula-
tions, as was previously suggested (Hilborn and Walters 1992;
Ludwig et al. 1993; Radomski et al. 2001; Beard et al. 2003). In a
large body of water like Chesapeake Bay, it is infeasible to have
a significant enforcement presence for preventing the sublegal
harvest of regulated species. Results from our study indicate
that angler compliance may be maximized by implementing (1)
gradual changes in minimum size limits or (2) minimum size
limits that result in sufficiently high catch rates of legal-sized
fish to satisfy anglers. If population levels are depleted such that
drastic management actions are required to rebuild the biomass
of the stock, we suggest conducting a survey to determine angler
preferences for fishing constraints (Dawson and Wilkins 1981;
Renyard and Hilborn 1986) and incorporating the results into
new management measures.

ACKNOWLEDGMENTS

We thank the many people who developed, maintained, and
participated in the VGFTP. In particular, we thank Jon Lucy
(VIMS), Claude Bain III (VMRC), Susanna Musick (VIMS),
Lewis Gillingham (VMRC), Todd Sperling (VMRC), and Ann
Burnet (VMRC). This manuscript benefited from comments
by Rob Latour (VIMS), Tracey Sutton (VIMS), Harry Wang
(VIMS), Steve Cadri (University of Massachusetts Amherst),
and Susanna Musick (VIMS). This work was completed with
funding from VIMS and the National Oceanic and Atmospheric
Administration Sea Grant Population Dynamics Fellowship to
M.J.H. This paper is Contribution Number 3309 of the Virginia
Institute of Marine Science, The College of William and Mary.

REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum like-
Proceedings of the 2nd international symposium on information the-
ory, Tsahkadsor, Armenia, USSR, Sept 2–8, 1971. Akadémiai Kiadó,
Budapest.


Rudolf, C. 1996. Life history and


North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
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Prescribed-Fire Effects on an Aquatic Community of a Southwest Montane Grassland System
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Published online: 08 Oct 2013.


To link to this article: http://dx.doi.org/10.1080/02755947.2013.824934

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Prescribed-Fire Effects on an Aquatic Community of a Southwest Montane Grassland System

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Abstract
The use of prescription fire has long been recognized as a reliable management tool to suppress vegetative succession processes and to reduce fuel loading to prevent catastrophic wildfires, but very little attention has been paid to the effects on aquatic systems. A late-fall prescribed burn was implemented to characterize effects on an aquatic community within a montane grassland system in north-central New Mexico. The fire treatment was consistent with protocols of a managed burn except that the fire was allowed to burn through the riparian area to the treatment stream to replicate natural fire behavior. In addition to summer and fall preburn assessment of the treatment and reference stream, we characterized immediate postfire effects (within a week for macroinvertebrates and within 6 months for fish) and seasonal effects over a 2-year period. Responses within the treatment stream were compared with an unburned reference stream adjacent to the prescription burn. During the burn, the diel range in air temperature...
increased by 5°C while diel range in water temperature did not change. Carbon–nitrogen ratios did not differ between treatment and reference streams, indicating the contribution of ash from the surrounding grassland was negligible. Although total taxa and species richness of aquatic macroinvertebrates were not altered, qualitative indices revealed departure from preburn condition due to loss of sensitive taxa (mayflies [order Ephemeroptera] and stoneflies [order Plecoptera]) and an increase in tolerant taxa (midges [order Chironomidae]) following the burn. Within 1 year of the burn, these attributes returned to preburn conditions. The density and recruitment of adult Brown Trout *Salmo trutta* did not differ between pre- and postburn collections, nor did fish condition differ. Fire is rarely truly replicated within a given study. Although our study represents one replication, the results will inform managers about the importance in timing (seasonality) of prescription burn and anticipated effects on aquatic communities.

Forested ecosystems in western North America have evolved with fire and rely on its influence to increase ecological productivity through mobilization of nutrients to increase energy flow. The timing and severity of fire remain causes of concern. Heavy fuel loads and low fuel moisture attributable to periods of drought or seasonal ebbs in precipitation exacerbate fire conditions. The impacts of fire on aquatic systems are complex and not entirely dependent on fire severity but on the fundamental characteristics of the watershed (Bèche et al. 2005), stream channel morphology (Benda et al. 2003), riparian vegetation (Rieman et al. 2003; Pettit and Naiman 2007), and the frequency of postfire disturbances such as flooding (Vieira et al. 2004). The persistence of aquatic communities is closely related to periodic disturbances that shape habitat quantity (Rieman and McIntyre 1995), quality (Minshall et al. 2001), and heterogeneity (Resh et al. 1988). The direct effects of wildfire include increases in stream temperature (Hitt 2003) and changes in aquatic chemistry, which can approach lethal toxicity thresholds for fishes (Spencer and Hauer 1991). Indirect effects include the loss of streamside vegetation, resultant increases in stream temperature from increased solar radiation, and increased sedimentation (Gresswell 1999).

Fire effects can vary in severity from acute (between the onset of fire and the initial runoff postfire) to chronic (extending for years) and influence both biotic communities and abiotic components of aquatic systems (Minshall 2003). Acute effects result in localized changes to the structure and composition of the riparian area, including accumulation of downed woody debris, shifts in composition of aquatic macroinvertebrates and fish densities due to mortality or emigration (Minshall et al. 1997; Hitt 2003; Bèche et al. 2005; Burton 2005; Howell 2006), decreases in stream channel stability with variable discharge (Rieman and Clayton 1997; Dunham et al. 2007), elevated sediment transport (Benda et al. 2003), and elevated water temperatures (Dunham et al. 2007). In sharp contrast, chronic effects from a severe burn due to vegetative regrowth and in-stream woody debris are not often realized for decades. Long-term effects also will occur if stream channels undergo geomorphic reorganization, if the variability in timing and amount of runoff exceeds normal annual and interannual patterns that disrupt hydrologic patterns, and if riparian areas are unable to stabilize soil erosion and ameliorate heat insolation (Dunham et al. 2003).

Land managers have employed controlled burning or prescription fire to proactively manage potential hazardous fuel loading while maintaining ecological integrity of forested and grassland systems. If carefully planned, prescriptions for woodland fire should protect against erosion and sedimentation to aquatic systems and have little to no effect on water quality (USEPA 2005). Fires that burn down through the litter to the mineral soil will adversely affect water quality through erosion. The amount of erosion will depend on the fire severity, amount of ground cover remaining on the soil, grade of the slope (the steeper, the more likely soils will move), erodibility of the soil, removal of riparian vegetation, time and amount of rainfall postburn, and time it takes for the site to revegetate. While the effects of prescription fire on water quality have received some attention (Richter et al. 1982; Stephens et al. 2004; Bèche et al. 2005; Elliott and Vose 2005), less attention has been paid to short- and long-term effects on fish and macroinvertebrate communities. Bèche et al. (2005) related low to moderate burn severity from a prescription burn to only minor effects in the benthic macroinvertebrate community despite altered periphyton levels. Populations of fishes to prescription burns have been less documented and would presumably be related to severity, size, and patchiness of the burn. Arkle and Pilliod (2010) found no immediate or delayed effects to fish populations in Idaho streams within watersheds subjected to prescribed burns of low to moderate severity. While the authors did not observe deleterious effects, this is not sufficient evidence to assume prescribed burns, if conducted according to protocol, would not affect fish populations and the invertebrate communities they rely upon.

Our goal was to assess the impacts of a prescribed burn during the cool autumn season on an aquatic community within a grassland system on the Valles Caldera National Preserve, New Mexico. An important management goal of the Valles Caldera National Preserve, hereafter referred to as the Preserve, is to utilize prescription burn throughout its grasslands and Ponderosa pine *Pinus ponderosa* forests as a reliable management tool to return pre-settlement fire regimes and reduce fuel loading to prevent uncharacteristic wildfires. Extensive logging operations and wildfire suppression during the 20th century throughout the Preserve resulted in increased secondary succession and encroachment of shrubs and trees on grasslands that provide recreational hunting and fishing opportunities. To evaluate the
ecological impacts of managed low-intensity fire on the Preserve, we designed and implemented an experimental prescribed burn in one of the Preserve’s upland watersheds (Valle Toledo). A prescribed-burn treatment consistent with protocols for a managed burn in the fall season (November) was applied to low-gradient, open-meadow grassland and adjacent Ponderosa pine forest, except that the fire was allowed to burn through the riparian area to the stream bank to replicate natural fire behavior. Our objectives were to characterize immediate (within a week), seasonal, and long-term (2 years) effects of this prescription burn on water quality, benthic macroinvertebrate communities, and fish populations. Thus, our null hypothesis was that no detectable effects of selected variables would be observed between burned and unburned treatments.

METHODS

Study site description.—The Valles Caldera National Preserve encompasses approximately 36,000 ha of the Jemez Mountains in north-central New Mexico (Sandoval County). Approximately 9,000 ha of the Preserve are grassland valles (Spanish term for treeless valleys), surrounded by upland montane coniferous forests. Within the watershed are a series of first- and second-order streams with riparian areas composed of sedges Carex spp., bunchgrasses Danthonia spp., Festuca spp., Phleum spp., sod-forming grasses Poa spp., and rushes Juncus spp. Average pre-1900 fire return intervals in forested areas throughout the Preserve varied from 5 to 20 years, while grassland fires in the open meadows of the valles occurred on average every 1.6 years (Touchan et al. 1996; Allen 2002; Allen et al. 2008; Dewar 2011).

Prescribed-fire treatment.—The prescribed burn was undertaken in Valle Toledo 1–2 November 2005. A late-season burn was selected because of higher fuel moisture reducing chances of a burn escaping the targeted area. Valle Toledo is a 1,040-ha grassland containing a second-order stream (Rio San Antonio) bordered by a first-order stream (Rito de los Indios; Figure 1). The burn covered 728 ha or approximately 70% of the target area. Areas that did not burn either had insufficient fuel loads or were too moist and replete with green vegetation. The majority of riparian areas within the study reaches of the stream were burned to the stream edge resulting in successful attainment of the targeted goal, which was to replicate natural fire behavior. Grassland fuel loads (dry mass) averaged 1,740 kg/ha. Flame lengths in the grassland ranged from 0.3 m to 3.0 m high, with the rate of spread averaging 0.4 m/s. In the forest, the fire...
burned less intensively; subcanopy herbaceous fuel loads averaged 1,205 kg/ha, with flame lengths between 0.1 and 0.3 m and a spread rate of 0.04 m/s.

Study stream.—Rio San Antonio is a second-order stream draining approximately 120 km². The portion of the stream flowing through the Valle Toledo is slightly entrenched and gravel dominated, with a well-developed flood plain (Rosgen 1994). Rito de los Indios is a spring-fed, first-order stream that drains approximately 19 km². The portion of the Rito de los Indios that flows through the Valle Toledo is characterized as slightly entrenched, gravel and cobble dominated, with a well-developed flood plain (Rosgen 1994). Although Rito de los Indios exhibited lower width-to-depth ratios, the stream was selected to represent reference conditions due to its close proximity to the burn area and comparable physical features, such as entrenchment, substrata, and area of flood plain. Hereafter, the Rio San Antonio and Rito de los Indios will be referred to as the treatment and reference streams, respectively.

Water quality and C:N ratios in sediment.—Water quality was assessed by placing two data sondes (Model 6920, Yellow Springs Instruments, Yellow Springs, Ohio) within the reference and treatment streams upstream from the confluence (Figure 1). Water temperature (°C), dissolved oxygen (mg/L), pH, and conductivity (µS/cm) were monitored at 15 min intervals from June to November 2005 and from April to November 2006 and 2007. Air temperature (°C) was obtained from a weather station within the Valle Toledo. Monthly cumulative precipitation (mm) throughout the study (June 2005–September 2007) was obtained from the Quemazon snow telemetry station located near the eastern boundary of the Rio San Antonio watershed (Los Alamos County, New Mexico).

In each of the treatment and reference streams, three study reaches were arbitrarily selected to collect sediments (n = 3) preburn (fall 2005), immediately postburn (late-fall 2005), following snowmelt but before monsoonal summer rains (6 months postburn, spring 2006), and 1 year postburn (fall 2006). To assess the contribution of carbon from ash, sediments were collected to assess carbon and nitrogen ratios (C:N) using a Hess-style plastic sediment sampler (500 mm [height] by 200 mm [diameter]). Sediments were processed through a series of U.S. Standard stainless steel sieves that ranged from 0.25 mm to 16 mm and then oven dried (60°C). From smallest-sized fractions (0.25–0.5 mm), a subsample was analyzed for carbon and nitrogen by high-temperature combustion on a ThermoQuest Elemental Analyzer (Model NC2100, CE Instruments, Wigan, UK). Percentages of carbon and nitrogen gases were eluted on a gas chromatography column, detected by thermal conductivity, and integrated to yield carbon and nitrogen content (Pella 1990a, 1990b). Carbon and nitrogen were confirmed by mass percent loss on ignition by combustion at 500°C for 2 h. Pre- and postcombustion weights of each sample were determined as mass percent loss of organic matter (Ben-Dor and Banin 1989; Nelson and Sommers 1996).

Macroinvertebrates.—Three study reaches in each stream (treatment and reference) were selected to collect benthic macroinvertebrates preburn (spring and fall 2005), immediately after the burn (late-fall 2005), and four times postburn (spring and fall 2006, spring and fall 2007; Figure 1). These study reaches spanned the study areas adjacent to the burned area in the reference stream (Rito de los Indios) and were 5–10 m upstream of where sediments were collected. Two habitats were sampled each season for benthic macroinvertebrates: riffles of comparable substrates (i.e., pebble and cobble ranging from 50 to 150 mm) and pools (<0.5 m depth). Macroinvertebrates were sampled within a few weeks of the preburn sample date to minimize seasonal variation and to avoid peak flows. Within each reach, benthic aquatic macroinvertebrates were collected from three pools and three riffles using a modified Hess-type circular sampler (0.06 m²; Jacobi 1978). This was repeated across all three reaches within treatment and reference streams. Collections were usually completed within two consecutive days to minimize spurious effects of weather. Samples were preserved in 99% ethanol in the field and later identified to lowest taxonomic level possible.

The ecological metrics of Plafkin et al. (1989) and Barbour et al. (1992, 1999) were used to assess the effects of the burn on community structure, community balance, and functional feeding components of the aquatic macroinvertebrate community and were compared with preburn conditions through time and across habitat (pools and riffles). The Hilsenhoff Biotic Index (Hilsenhoff 1987) assessed the sensitivity of the aquatic macroinvertebrate community to sediment and nutrient perturbation. Additional indices included mayflies (order Ephemeroptera), stoneflies (order Plecoptera), and caddisflies (order Trichoptera), collectively referred to as the EPT index. Additionally, when midges (order Chironomidae) (i.e., tolerant organisms) are included with the EPT assemblage [EPT/EPT + Chironomidae], an even distribution among all four taxonomic groups indicates optimal biotic conditions, whereas a shift to a lower ratio indicates a disproportionately greater number of tolerant chironomids.

Fish surveys.—Preliminary surveys in both treatment and reference streams revealed a fish community dominated by Brown Trout _Salmo trutta_. Longnose Dace _Rhinichthys cataractae_ were incidental throughout the study and not considered in the analysis. Three transects (50 m each) were established in close proximity to the macroinvertebrate sample sites within treatment and reference streams to obtain a representative selection of runs, riffles, and pools (Figure 1). Baseline data for the Brown Trout population within both streams was collected spring and fall 2005 to assess adult (≥170 mm) and juvenile (<170 mm) densities (number of fish/100 m of stream) and relative weight (Wr) prior to the prescribed burn. Treatment and reference streams were surveyed spring and fall of 2006 and 2007 to evaluate delayed effects from the prescribed burn as well as annual recruitment to the Brown Trout population. Within
each sample reach, Brown Trout were sampled using three-pass depletion with a backpack electrofishing unit and direct current (Model LR-24, Smith-Root, Vancouver, Washington). Block nets (6-mm mesh) were set above and below the sample reach to prevent emigration and immigration of fish during electrofishing. Upon capture, total length (TL; mm) and weight (g) were recorded for all captured fish. These fish were subsequently placed in a live box within the stream until completion of the final electrofishing pass and then returned to the sample reach.

Abundance estimates for each sampled reach were calculated based on maximum likelihood removal methods (Zippin 1958) and corrected to relative density (number of fish/100 m²) by measuring stream wetted width every 10 m throughout the 50-m electrofishing reach. Adult and juvenile population estimates were calculated separately to minimize potential bias associated with differences in capture efficiency using electrofishing among size-classes. Juvenile fish were not captured during spring electrofishing occasions. Thus, the density of juvenile fish was estimated for only fall surveys and used to evaluate recruitment. Adult fish were assigned to age-classes from length frequencies and assigned to age-classes and Wr indices for ages 2–5; age estimates from length-frequency histograms were verified from a subsample of scales from the population. Fish body condition was evaluated prior to and following the prescribed fire using Wr for lotic Brown Trout (Milewski and Brown 1994).

Data analyses.—As this study was based on only one prescription burn in one watershed, the “treatment” was not replicated; however, fire studies are often opportunistic and lack replication (van Mantgem et al. 2001). Our replications were spatial units within burned and reference areas. Therefore, we restricted our conclusions to differences between pre- and post-burn collections at our treatment (burned) and reference (unburned) sites.

Models with equal and unequal variances were fit as well as different covariance structures over time using PROC MIXED in SAS (SAS 2009). The model with the lowest Akaike information criterion value corrected for small samples (AICc; Akaike 1973) was selected to make inferences. Residual analysis was conducted to identify outliers to visually assess variance structures incrementally. Unless otherwise noted, model assumptions of equal variance and normality were met. Differences were statistically different when \( P \leq 0.05 \).

Differences in C:N ratios were assessed using a repeated measures analysis of variance (ANOVA) comparing sites (treatment and reference) during 2005 (preburn spring and postburn fall) and postburn spring and fall 2006. Site \( \times \) time comparisons were conducted within seasons (e.g., spring versus spring and fall versus fall). To identify differences between the treatment and reference areas, the treatment \( \times \) time interaction was examined because a main effect for treatment without an interaction would reflect differences between treatment and reference areas prior to the burn that were maintained throughout the study period regardless of the burn.

Summary statistics were calculated for the treatment and reference areas using raw abundance for each habitat (pool, riffle) across seasons (spring, fall) to obtain total standing crop (total number of organisms/m²) and taxa richness (total number of detected taxa). Differences in total standing crop and species richness of benthic macroinvertebrates were assessed using repeated measures ANOVA with a \( 2 \times 2 \) factorial treatment structure using sites (treatment and reference) by habitat (pools and riffles). To identify differences in total standing crop and species richness between treatment and reference areas, treatment \( \times \) time interactions were examined for each habitat using preplanned contrasts to identify an immediate burn effect (preburn fall 2005 versus late-fall 2005) and longer-term effects (preburn spring 2005 versus postburn spring 2006 and 2007, preburn fall 2005 versus postburn fall 2006 and 2007).

Differences in fish density and Wr by age-classes (ages 2 and 3) were assessed using repeated measures ANOVA comparing sites (treatment and reference) over time (preburn, postburn 2005, postburn 2006, postburn 2007). Site \( \times \) time comparisons were conducted within seasons (e.g., spring versus spring and fall versus fall). To identify differences between the treatment and reference areas, the treatment \( \times \) time interaction was examined because a main effect for treatment without an interaction would reflect differences between treatment and reference areas prior to the burn that were maintained throughout the study period regardless of the burn. Few age-4 and age-5 fish were captured throughout the study and thus were not analyzed, but summary statistics are reported.

RESULTS

Water Quality and C:N Ratios in Sediment

Prior to the burn, the diel range in air temperature was 21°C (−8.0°C to +13.0°C) while the diel range in stream temperature was 6°C (7.4–13.4°C). During the burn (1–2 November), the diel range in air temperature increased to 26°C (−8.0°C to +18°C) in contrast to the diel range for stream temperature which remained 6°C (7.1–13.1°C). Despite the rise in air temperature, stream temperatures were within the diel range prior to the burn. Between preburn and immediate postburn, daily maximum temperatures did not exceed the criteria for impaired coolwater streams in New Mexico (20°C; New Mexico Environment Department 2006). Water temperature, dissolved oxygen concentrations, conductivity, and pH varied little prior to, during, and immediately after the burn within the treatment stream and were deemed acceptable when compared with water quality criteria of coldwater fishes (New Mexico Environment Department 2006). Mean daily water temperature before the burn in 2005 was 15.1°C and did not vary after the burn in 2006 (15.1°C) or 2007 (15.0°C; Table 1). Conductivity and pH in the treatment stream throughout summer months (1 June–31 August) did not vary pre- and postburn (Table 1).

An increase in C:N was observed over time (\( F_{2,18} = 5.76, P = 0.012 \)) for both treatment and reference sites, but there
was no detectable treatment × time interaction (\(F_{4,18} = 1.49, P = 0.247\)), indicating changes were not attributable to the burn (Figure 2). Average C:N varied between preburn spring (11.5 ± 0.42 [mean ± standard error]) and after-snowmelt postburn spring 2006 (13.2 ± 0.39) similarly to the reference site (preburn spring = 13.4 ± 0.47 versus postburn spring = 16.2 ± 0.37) indicating the contribution of a source unrelated to the fire from within the watershed. Preplanned contrasts of C:N changes between the two time frames (preburn spring 2005 and postburn spring 2006) revealed no significant difference (\(T_{18} = -0.78; P = 0.448\)) between treatment and reference sites, further indicating no fire effect.

### Macroinvertebrates

A diverse assemblage of aquatic benthic macroinvertebrates totaling 110 taxa was collected throughout the study (Table A.1 in the Appendix). Of this total, 88% were insects and included stoneflies (Plecoptera: 5 taxa), mayflies (Ephemeroptera: 7 taxa), caddisflies (Trichoptera: 18 taxa), true flies (Diptera: 52 taxa), damselflies and dragonflies (Odonata: 2 taxa), true bugs (Hemiptera: 3 taxa), beetles (Coleoptera: 8 taxa), and an aquatic moth (Lepidoptera: 1 taxon; see Appendix). The most dominant group belonged to the true fly family Chironomidae (nonbiting midges), which consisted of 34 genera or 31% of the total taxa collected throughout the study. All dominant taxa collected preburn were collected postburn throughout sites in the treatment stream, while one dominant taxi (caddisfly Limnephilus sp.) appeared for the first time in the reference stream 1 year and 2 years postburn.

The top-ranked model allowing for unequal variances over time for total standing crop in fall collections revealed no detectable treatment × time interaction prior to the burn (2005) and immediately following the burn (2005; \(F_{3,11} = 2.01, P = 0.171\)). Thus, no immediate burn effects on total standing crop of benthic macroinvertebrates in either pools or riffles were observed between treatment and reference sites (Figure 3). This conclusion was reaffirmed in the preplanned contrasts that indicated little change for total standing crop in pools (\(T_{11} = 0.31, P = 0.760\)) and riffles (\(T_{11} = -1.95, P = 0.078\)). When we compared total standing crop in the fall prior to the burn (2005) with fall collections 1 year (2006) and 2 years (2007) postburn, the top-ranked model allowing for unequal variances over time also revealed no differences in the treatment × time interaction (\(F_{6,14,4} = 1.73, P = 0.183\)). Preplanned contrasts of changes in total standing crop revealed no detectable differences in pools (\(T_{11} = -0.20, P = 0.843\)) or riffles (\(T_{11} = -2.0, P = 0.066\)). In spring collections, the top-ranked model allowing for unequal variances among treatments revealed no treatment × time interaction prior to the burn (2005), 1 year postburn (2006), and 2 years (2007) postburn (\(F_{6,12,3} = 2.10, P = 0.127\)). Preplanned contrasts of changes in total standing crop revealed no detectable differences in either habitat (\(P > 0.30\)).
Changes in species richness in the treatment stream prior to the burn (2005) and immediately following the burn (2005) were not affected by fire as indicated by no detectable treatment × time interaction ($F_{3, 16} = 0.96, P = 0.436$). There were no immediate effects of the burn on species richness in either pools or riffles between treatment and reference sites (Figure 4). Preplanned contrasts of changes in species richness indicated differences were negligible in pools ($T_{16} = 0.00, P = 1.0$) and riffles ($T_{16} = -1.67, P = 0.115$). When we compared species richness in the fall prior to the burn (2005) with fall collections 1 year (2006) and 2 years (2007) postburn, the top-ranked model revealed no treatment × time interaction ($F_{6, 24} = 2.10, P = 0.090$). The preplanned contrasts of changes in species richness throughout the fall collections revealed no detectable differences in pools ($T_{24} = -0.17, P = 0.869$), but differences were observed in riffles ($T_{24} = -3.34, P = 0.003$). These differences were due to a decrease in species richness in riffles throughout the treatment site, while species richness increased in riffles throughout the reference site (Figure 4). The top-ranked model for species richness revealed no treatment × time interaction prior to the burn in spring (2005) and in the following springs postburn ($F_{6, 24} = 1.03, P = 0.428$). Preplanned contrasts of changes in species richness revealed no significant differences in pools ($T_{24} = -1.55, P = 0.135$) or riffles ($T_{24} = -1.08, P = 0.289$).

Small sample size ($n = 3$), considerable variation within pools and riffles, and seasonal response of taxa obscured detectable differences between pre- and postburn sample collections. However, changes in sensitive and tolerant taxa across time and microhabitat in the treatment stream are worth noting. A decline in the EPT index in both riffles and pools immediately postburn were due to a decline in mayfly *Tricorythodes* sp.
and the predacious stonefly *Isoperla* sp. (Figure 5). *Tricorythodes* sp. decreased from 128.0/m² (SE, 26.82) prior to the burn to 74.0/m² (18.66) by the first spring. By the second spring, mayfly had rebounded throughout the pools (219.0/m² ± 72.20). *Isoperla* sp. decreased in riffles from 81.3/m² (13.58) prior to the burn to 3.0/m² (3.00) in spring 2006 and began to return to preburn levels by spring 2007 (49.0/m² ± 13.58).

Changes of the EPT/(EPT + Chironomidae) index in pools (Figure 5) occurred immediately postburn as a result of an increase in the tolerant chironomid *Microtendepes* sp. throughout the treatment sites. Prior to the burn, *Microtendepes* sp. increased throughout the treatment pools from 4.3/m² (1.33) to 56.0/m² (18.21) immediately following the burn returning to preburn levels (2.0/m² ± 1.15) by fall of 2007. Two years postburn, departure from preburn conditions was negligible throughout pools in the treatment stream as reflected by the suite of ecological indices.

**Fish**

Regardless of season, we did not detect an effect of the burn treatment on adult salmonid density (Figure 6). Changes in population densities of adult Brown Trout in the fall prior to the burn and 1 year postburn (fall 2006) in treatment and reference streams did not differ as revealed by no detectable treatment × time interaction ($F_{2,12} = 0.15, P = 0.861$). Changes in population densities between preburn spring (2005) and postburn spring (2006) in treatment and reference streams did not differ ($F_{2,5,26} = 1.74, P = 0.262$) according to the top-ranked model that allowed for heterogeneous variances over time. Densities of adult Brown Trout decreased from 79.6 fish/100 m² (SE, 14.48) prior to the burn (fall 2005) to 56.3 fish/100 m² (1.03) 1 year postburn (fall 2006). A similar response was also observed during the same time frame in the reference sites, where densities decreased from 105.0 fish/100 m² (29.3) to 67 fish/100 m² (15.5) (Figure 6). The top-ranked model allowing for unequal variances
over time for recruitment revealed no detectable treatment \( \times \) time interaction \((F_{2,7,2} = 0.05, P = 0.952)\). Recruitment in juvenile fish was greater in the treatment stream (range 20.3–20.7 fish/100 m\(^2\)) than in the reference stream (3.3–6.7 fish/100 m\(^2\)) throughout the study (Figure 6).

The top-ranked model allowing for unequal variances by treatment for \( W_r \) in age-2 fish revealed no detectable treatment \( \times \) time interaction for fall \((F_{2,7,93} = 0.51, P = 0.616)\). Spring collections did not demonstrate any treatment \( \times \) time interaction either \((F_{2,12} = 0.61, P = 0.558)\), but the top-ranked model assumed equal variances over time and treatments. There was, however, a detectable difference in \( W_r \) of age-3 fish as seen in the treatment \( \times \) time interaction for fall collections \((F_{2,12} = 9.84, P = 0.003; \) Table 2\). Preplanned contrasts revealed significant differences \((T_{12} = -4.41, P = 0.001)\) in changes of \( W_r \) between treatment and reference sites for age-3 Brown Trout between preburn (2005) and postburn (2006). Age-3 Brown Trout in the treatment site exhibited a decrease in \( W_r \), while the same age-group experienced an increase in \( W_r \) at the reference site (Table 2). Differences in \( W_r \) changes for age-3 fish between the two streams were no longer evident by 2007 \((T_{12} = -1.79, P = 0.098)\). Although spring collections exhibited a similar pattern of decreasing condition at the treatment site and increasing fish condition at the reference site, these differences were not statistically different \((F_{2,12} = 1.71, P = 0.222; \) Table 2\).

**DISCUSSION**

As global temperatures increase over the next century (IPCC 2007), projected aridity throughout the Southwest will be intensified by La Niña events beyond recent human record (Seager et al. 2007). Grasslands, as well as low-elevation to mid-elevation forests, comprise the largest land cover in the southwestern USA and are prone to frequent fires (Litschert et al. 2012). Severity and wildfire intervals throughout these systems are expected to increase due to precipitation patterns that increase fuel loads during wet El Niño conditions followed by drier La Niña cycles. As such, prescribed burns by land managers during cool
seasons should become more commonplace as a safe, effective approach to returning fire to the landscape.

The detrimental effects of fire often occur when a burn is followed by precipitation events resulting in increased stream flow and elevated sediment transport (Benda et al. 2003; Wondzell and King 2003). While the timing of the burn in late fall was planned to maximize soil moisture, the Southwest was also experiencing drought conditions that minimized chances for heavy rainfall and effects that an inflow of ash would have had on the aquatic community (USDM 2011). During the first 8 months of the study (November 2005 – June 2006), the Preserve experienced lower than normal precipitation, reducing spring snowmelt runoff and the contribution of ash from surrounding grasslands and riparian area. By the time precipitation returned to the Preserve with the onset of summer monsoon rains July 2006, regrowth of vegetation was returning to the grasslands and riparian areas, minimizing erosion processes and ash input. Within a southwestern grassland, Gori and Backer (2005) demonstrated prescription fire increased ground cover of perennial grasses throughout burned plots compared with unburned plots, thereby increasing the watershed’s capacity to capture runoff and reduce soil erosion. Others have noted the importance of riparian vegetation as a sediment trap for postfire sediment deposition to pools (Spina and Tormey 2000).

Fire mobilizes organic matter increasing the C:N signature within the top soil layer (Ojima et al. 1994; Monleon et al. 1997; Rhoades et al. 2004), where precipitation and snowmelt eventually carry these to stream sediments. The hydrology throughout the Preserve is snowmelt dominated and the grasslands had not experienced an extensive burn since Federal acquisition in 2000. Thus, we anticipated an increase in C:N within the treatment stream (Rio San Antonio) following the first spring snowmelt. However, the low to moderate burn severity, combined with lower-than-average precipitation within the first year of the burn, resulted in reduced ash and particle deposition to Rio San Antonio. Of note, C:N ratios were slightly higher (15–20%) throughout Rito de los Indios than in Rio San Antonio, reflecting the contribution of organic matter from the close proximity of the forested watershed. Conifers are the dominant vegetation

| Year | Season | Age 2 | | Age 3 | | Age 4 and Age 5 |
|------|--------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|      |        | Treatment | Reference | Treatment | Reference | Treatment | Reference |
| 2005 | Spring  | 128 (10.6) | 89 (5.0) | 108 (1.4) | 84 (2.5) | 78 (4.8) | 71 (4.5) |
|      | Fall    | 130 (4.9) | 91 (0.7) | 105 (1.2) | 85 (2.3) | 87 (7.5) | 76 (4.5) |
| 2006 | Spring  | 128 (3.8) | 94 (3.6) | 100 (3.7) | 87 (3.7) | 84 (8.0) | 78 (3.0) |
|      | Fall    | 129 (2.9) | 98 (0.02) | 99 (1.8) | 94 (0.1) | 83 (2.4) | |
| 2007 | Spring  | 122 (6.2) | 96 (1.1) | 99 (3.1) | 80 (2.1) | 90 (4.2) | 70 (0.6) |
|      | Fall    | 136 (8.6) | 96 (0.3) | 109 (1.0) | 95 (2.3) | 98 (5.6) | 88 (4.4) |
within the watershed of the Rito de los Indios and may have contributed to a higher seasonal pulse of particulate C relative to N (McGroddy et al. 2004; Starry et al. 2005). While this may have affected the C:N ratio of the reference stream, C:N ratio in the treatment stream varied only slightly throughout the study, indicating negligible ash and particle deposition from the burn.

Macroinvertebrate communities are relatively sensitive and tend to respond rapidly to changes in temperature and dissolved oxygen and to shifts of instream substrate (Vannote and Sweeney 1980; Ward and Stanford 1982) resulting in insect drift (Earl and Blinn 2003). Taxonomic richness and community composition were related to hydrological disturbances that affected habitat stability postfire (Vieira et al. 2004) and varied according to time between disturbances rather than total number of disturbances (Death and Winterbourn 1995). While the prescribed burn had no immediate or longer-term effects on the benthic macroinvertebrate community, we noted shifts in ecological indices reflected in the reduction of a sensitive stonefly *Isoperla* sp. in riffle habitat, reduction of a mayfly *Tricorythodes* sp. in pool habitats, and an increase in moderately tolerant chironomid midges in both habitats. Pippin and Pippin (1981) and Vieira (2003) reported that while densities of benthic macroinvertebrates in wildfire-affected streams recovered within 1 year, taxa richness was less resilient with the loss of several species of stoneflies for up to 3 years postfire.

The absence of fire effects on Brown Trout is clearly related to the prescribed burn’s minimal impact on water quality, stream habitat, and food resources (macroinvertebrates). In addition, the fish population’s lack of response may be due in part to the presence of small springs within both streams upstream of the burn area, which may have ameliorated changes in water quality from the fire. Dunham et al. (2007) noted groundwater inflow in streams having less pronounced changes in water temperature after severe wildfires in an Idaho watershed. The authors point out that despite the loss of vegetation throughout the riparian areas and the potential for long-term effects on the hydrology, groundwater inflow would ameliorate water temperature fluctuations and fish would be less likely to suffer exposure to daily peak temperatures from solar insolation of suspended sediments. The overall health and condition of the Brown Trout population in this study revealed a population skewed toward younger, healthier fish with overall decreases in Wc as fish age. While there appeared to be a treatment effect on older fish, as seen in diminished Wc of age-3 fish in the Rio San Antonio, we were unable to tease apart the combined effects of fire with overwintering and lower-than-normal rain patterns.

Fire has long been recognized as one of the most influential of the natural disturbances affecting aquatic systems in the western United States (see review by Gresswell 1999). Factors related to a changing climate (e.g., earlier snowmelt, higher summer temperatures) have been positively associated with increased wildfire activity in recent decades (Westerling et al. 2006; Littell et al. 2009). In the Southwest, average annual air temperatures have increased 0.29°C per decade with a reduction in summer flows (2% per decade; Zeigler et al. 2012). No doubt aquatic communities throughout the region will be at greater risk to wildfire. We demonstrated, however, that a cool season prescription burn through the riparian area within a Southwest montane grassland system can be successfully conducted when fire risk conditions are low and with minimal impact on the aquatic community. Within montane landscapes, prescription burns offer a reliable tool to reduce the severity of fire effects while enhancing resiliency of aquatic communities. Fire behavior is complex, and because each fire will be different, we encourage monitoring prior to and after a prescribed burn to assess the effects that the timing (seasonality) and the magnitude of the fire have on aquatic communities relative to management goals.

ACKNOWLEDGMENTS

Financial support for this study was provided by a grant from the U.S. Department of Agriculture Forest Service, Rocky Mountain Experimental Research Station, Albuquerque, New Mexico, and the Valles Caldera National Preserve. Additional support was provided by New Mexico State University, Agriculture Experiment Station, Department of Fish, Wildlife and Conservation Ecology; and U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit. D. McGuire (McGuire Consulting, Española, New Mexico) was consulted on identification of Chironomidae (nonbiting midges) and M. Myers (U.S. Fish and Wildlife Service, Albuquerque, New Mexico) was consulted on identification of Trichoptera (caddisflies). D. Klemm (U.S. Environmental Protection Agency, Cincinnati, Ohio) identified the Hirudinea (leeches). K. Montgomery and J. Gulbransen of the Valles Caldera National Preserve assisted with collection, some sample processing, and sample site verifications. The project was conducted under New Mexico State University Animal Care and Use Committee procedures under Project 2007-014. Mention of trade names or commercial products does not constitute endorsement or recommendations for use by the U.S. Government.

REFERENCES


### APPENDIX: MACROINVERTEBRATES

**TABLE A.1. Taxa list of aquatic macroinvertebrates collected prior to the prescribed burn in 2005 and after the burn through 2007 among riffles and pools of the treatment (Rio San Antonio) and reference (Rito de los Indios) streams on the Valles Caldera National Preserve, New Mexico.**

<table>
<thead>
<tr>
<th>Taxon Family or genus and species</th>
<th>Family or genus and species</th>
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<tr>
<td><strong>Plecoptera (stoneflies)</strong></td>
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<tr>
<td>Amphinemura sp.</td>
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<tr>
<td>Pteronarcella badia</td>
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<td>Isoperla sp.</td>
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<td>Swelta sp.</td>
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<td>Hesperoperla pacifica</td>
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<td>Baetis tricaudatus</td>
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<td>Acentrella insignificans</td>
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<td>Ecdyonurus sp.</td>
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<td>Cinygmula sp.</td>
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<td>Paraleptophlebia sp.</td>
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<td>Tricorythodes sp.</td>
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<td>Drunella grandis</td>
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<tr>
<td><strong>Ephemeroptera (mayflies)</strong></td>
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<tr>
<td>Baetis tricaudatus</td>
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<tr>
<td>Acentrella insignificans</td>
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<td>Ecdyonurus sp.</td>
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<td>Paraleptophlebia sp.</td>
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<td>Tricorythodes sp.</td>
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<td>Drunella grandis</td>
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<tr>
<td><strong>Trichoptera (caddisflies)</strong></td>
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<tr>
<td>Rhyacophila brunea cpx.</td>
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<td>Glossosoma sp.</td>
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<td>Prototilia sp.</td>
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<td>Hydropsyche sp.</td>
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<td>Cheumatopsyche sp.</td>
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<td>Arctopsyche grandis</td>
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<td>Hydropila sp.</td>
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<td>Ibytrichia sp.</td>
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<td>Oxycetis sp.</td>
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<td>Linnephilus sp.</td>
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<td>Hesperophylax sp.</td>
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<td>Oecetis sp.</td>
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<tr>
<td>Brachycerus sp.</td>
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<td>Lepidostoma sp.</td>
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<td>Microstoma sp.</td>
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<td>Helicopsyche sp.</td>
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<td>Cernotina sp.</td>
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<td>Oligophlebodes sp.</td>
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<td><strong>Diptera (true flies)</strong></td>
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<td>Radotanypus sp.</td>
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<td>Procladius sp.</td>
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<td>Thiemenannimyia sp.</td>
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<td>Diamesa sp.</td>
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<td>Pagastia sp.</td>
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<td>Potthastia sp.</td>
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<td>Odontomesa sp.</td>
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<td>Prodiamesa sp.</td>
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<td>Thiemenannimyia sp.</td>
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<td>Brilla sp.</td>
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<tr>
<td>Cricotopus spp.</td>
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<td>C. nostococladias</td>
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<td>Eukiefferiella sp.</td>
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<td>Heterotrissocladiis sp.</td>
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<tr>
<td>Hydrobaenus sp.</td>
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<tr>
<td>Orthocladiis spp.</td>
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<tr>
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<tr>
<td>Paraphaenocladiis sp.</td>
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<td>Psectrocladiis sp.</td>
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<tr>
<td>Pseudolimnophila sp.</td>
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<tr>
<td>Synorthocladiis sp.</td>
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<tr>
<td>Tvetenia sp.</td>
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<tr>
<td>Cryptochironomus sp.</td>
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<tr>
<td><strong>Chironomidae (midges)</strong></td>
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<tr>
<td>Microtendipes sp.</td>
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<td>Paracladopelma sp.</td>
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<td>Polypedilium sp.</td>
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<tr>
<td>Pseudochironomus sp.</td>
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<tr>
<td>Cladotanytarsus sp.</td>
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<td>Microspectra sp.</td>
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<td>Rheotanytarsus sp.</td>
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<td>Antocha sp.</td>
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<td>Dicranota sp.</td>
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<td>Hexatoma sp.</td>
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<td>Limonophilia sp.</td>
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<td>Tipula sp. 2</td>
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<td>Linnithiophila sp.</td>
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<td>Dixa sp.</td>
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<td>Simulium sp.</td>
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<td>Ceratopogonidae</td>
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<td>Tabanus sp.</td>
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<td>Cheilifer sp.</td>
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<td>Linnophora sp.</td>
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<td>Psychodidae</td>
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<td><strong>Coleoptera (beetles)</strong></td>
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<td>Dytsicidae</td>
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<td>Dubiraphia sp.</td>
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<td>Motobdella sedonensis</td>
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<td>Tubificidae</td>
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<td>Naididae</td>
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<td>Tricladida</td>
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<td><strong>Odonata (damselflies and dragonflies)</strong></td>
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<td>Amphipoda (scuds)</td>
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<td>Arachnida (spiders and mites)</td>
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<td>Mollusca (clams and snails)</td>
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<td>Annelida (segmented worms)</td>
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<td>Platyhelminthes (flatworms)</td>
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<tr>
<td>Nematomorpha (Gordian worm)</td>
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</table>

*The cpx. designates a species complex (a group of closely related species), where the exact demarcation between species is still being worked on by taxonomists.*
An Evaluation of Age-1 Steelhead Stocking Locations on a Minnesota Tributary to Lake Superior

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Published online: 08 Oct 2013.

To cite this article: Matthew C. Ward, Donald R. Schreiner & David F. Staples (2013) An Evaluation of Age-1 Steelhead Stocking Locations on a Minnesota Tributary to Lake Superior, North American Journal of Fisheries Management, 33:5, 1063-1070, DOI: 10.1080/02755947.2013.824936

To link to this article: http://dx.doi.org/10.1080/02755947.2013.824936
Management Brief

An Evaluation of Age-1 Steelhead Stocking Locations on a Minnesota Tributary to Lake Superior

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Abstract

Historically, less than 2% of steelhead *Oncorhynchus mykiss* stocked in river mouths on Minnesota tributaries to Lake Superior returned as adults. To investigate the influence of stocking location on adult return rates, similar proportions of age-1 steelhead were stocked in the mouth and throughout upstream reaches of the Knife River. A subset of steelhead stocked upstream were implanted with coded wire tags (CWT), which resulted in 18% of all fish stocked, regardless of location, possessing a CWT. A fish trap near the mouth of the river was used to sample emigrating age-0 through age-3 juveniles and returning adults. Of the steelhead stocked upstream 45% survived to emigrate. Electrofishing surveys and trap results indicated no steelhead remained in the river past age 2. No evidence was found that larger age-1 stocked steelhead displaced smaller age-1 wild steelhead. Only 12% of returning adults possessed CWTs, 6% less than the percentage stocked with CWTs (18%). Adult return rates for those stocked in the river mouth were 1.0% compared with 0.5% for those stocked upstream. Overall, stocking in the river mouth contributed 69% of the returning adults. Given these results, Minnesota fishery managers should continue to look for alternate ways to increase steelhead return rates if greater adult numbers are desired.

Throughout the past century, many populations of steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) in tributaries on the west coast of North America (Larson and Ward 1955; Leider et al. 1986; Smith et al. 2000) and on the Laurentian Great Lakes (Stauffer and Hansen 1969; Jones et al. 1993; Daugherty et al. 2003) continue to be supplemented or maintained by stocking age-1 steelhead. Steelhead fry also continue to be used to supplement populations throughout North America (Wentworth and LaBar 1984; Hume and Parkinson 1988; Close and Anderson 1992). Despite decades of stocking various life stages of steelhead, biologists continue to refine stocking strategies to maximize return rates (Tipping 1997; Negus et al. 2012).

Steelhead were first stocked into the Minnesota waters of Lake Superior in 1895 from the west coast of North America (MacCrimmon 1971). They have become naturalized and exhibit a lacustrine–adfluvial form (lake dwelling, ascending streams to spawn) of a potamodromous life history (migratory, but confined to freshwater; Gresswell 1997). Minnesota tributaries supported a robust self-sustaining steelhead fishery from the 1940s through the 1960s (Schreiner 2003), but angling pressure increased in the 1970s and 1980s, and catch rates declined. In response, the Minnesota Department of Natural Resources (MDNR) initiated several programs, which included stocking age-1 steelhead, to increase steelhead abundance and reestablish self-sustaining populations (Schreiner 1992, 2003). Age-1 steelhead were stocked in river mouths of six tributaries during 1990–2002. Two of the six tributaries had fish traps and annual spring creel surveys, which allowed for return rate estimates to be determined (Negus et al. 2012). Overall return rates to these two tributaries were less than 2% and were considered low

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Received February 12, 2013; accepted July 3, 2013
Published online October 4, 2013

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Steelhead stocked in Minnesota have the potential to not only return to other Minnesota tributaries, but also to tributaries in Wisconsin, Michigan, and Ontario. Straying of some returning adult steelhead that spent the first year of their life in a hatchery commonly occurs (Seelbach and Whelan 1988; Kenaston et al. 2001; Clarke et al. 2011) and can comprise substantial portions of spawning runs (Hansen and Stauffer 1971; Bartron et al. 2004). However, straying rates typically increase when age-1 steelhead are stocked in tributaries where their parents did not originate (Schroeder et al. 2001). When age-1 steelhead are stocked in tributaries from which their parents were captured, straying rates decrease as stocking distance increases upstream from the mouth (Schroeder et al. 2001). One goal of stocking steelhead upstream was to reduce straying.

In an era of reduced funding for resource management agencies, cost-effective stocking programs are critical (Negus et al. 2012). This study was the result of recommendations and funding by a local user group that desired greater numbers of adult steelhead to return to the Knife River. The overall goal of this study was to examine whether stocking location influenced the return rate of stocked steelhead. Objectives were to determine: (1) survival rates of age-1 steelhead stocked upstream until emigration to Lake Superior, (2) whether premature displacement of smaller wild age-1 steelhead occurred after stocking larger age-1 steelhead throughout upstream reaches, (3) whether adult return rates to the Knife River trap were different for age-1 steelhead stocked in the river mouth compared with those stocked upstream, and (4) whether straying to an adjacent Minnesota tributary differed between stocking treatments.

METHODS

Study area.—The mouth of the Knife River enters Lake Superior 30 km northeast of Duluth, Minnesota. The Knife River fish trap is located at river kilometer (rkm) 0.8 upstream from the mouth and has been in operation since 1996 (Figure 1). The trap facility contains an incline screen trap that samples fish migrating downstream and a separate trap that samples fish migrating upstream (Dexter and Schliep 2007). Stocking locations ranged from 7.9 to 27.2 rkm upstream from the Knife River fish trap. A similar fish trap is present at rkm 0.2 upstream from the mouth of the French River and has been in operation since 1970. The mouth of the French River enters Lake Superior 19 km northeast of Duluth. The French River Coldwater Hatchery (FRCWH) is located adjacent to the mouth of the French River and uses Lake Superior water. The hatchery discharges its filtered effluent just upstream from the trap. The effluent attracts some spawning adult steelhead that were reared at the hatchery (Negus 2003).

From 2002 to 2005, 35 pairs of wild, ripe, adult steelhead were collected annually at the Knife River trap in April and May, transported to the FRCWH, spawned, and returned to the Knife River. Fertilized eggs hatched in June, and fish were reared for 11 months. After 5 months, all steelhead were given a maxillary clip on alternating sides to designate year-class.
the same time, 37% of juveniles designated to be stocked in upstream reaches were implanted in the snout with a 1.1-mm CWT (Northwest Marine Technology). Each year, 200 of the coded-wire-tagged juveniles were examined after 30 d to determine CWT retention rates.

An annual quota of 40,000 fish were produced by the FR-CWH from 2003 to 2006 (2002–2005 year-classes) and stocked between late April and early May at 13 sites (Figure 1). The hatchery target size for stocking was 178 mm TL and 62 g, or “smolt size,” which indicated almost all stocked fish had attained or exceeded the minimum size (about 160 mm TL, 40 g) for smoltification to occur (Negus 2003). Upstream stocking sites were distributed throughout the watershed and ranged from 8.7 to 28 km upstream from the mouth. Similar abundances of age-1 steelhead were stocked at each of the 12 upstream sites. The downstream stocking site was 0.8 km up from the mouth and directly downstream from the trap. All 12 upstream sites were considered one treatment and were compared with the one downstream site, which was considered the other treatment. Four factors were taken into consideration when we determined stocking timing and location. These included having higher flows to increase emigration rates and minimize interactions with wild age-1 steelhead, stocking at a time that resulted in the highest return rates, and stocking downstream from headwater reaches to minimize interactions with native Brook Trout Salvelinus fontinalis. Poststocking mortality of steelhead stocked downstream from the trap was monitored daily by a creel census clerk who walked from the trap to the mouth throughout April and May. Similar monitoring did not occur upstream.

The trap was annually operated from ice-out through to ice formation. Fish captured were processed daily from early April through early July, and as needed until early November. The trap was used to assess poststocking survival and emigration timing of steelhead as they migrated to Lake Superior. Juveniles captured were examined for a maxillary clip, weighed, and measured, and scales were taken for age estimation.

During periods of low to moderate flows, the entire river flowed through the trap and capture efficiency was assumed to be 100%. However, under high flows when the entire river did not flow through the trap, four trials were conducted annually from 2003 to 2006 (N = 16) to determine efficiency. Trials consisted of collecting 100 age-1 stocked steelhead from the trap, marking them with a caudal fin clip, and returning them 300 m upstream from the trap. The numbers of age-1 stocked steelhead captured in the trap every day in which the entire river did not flow through the trap were estimated based on the average recapture rate of the four efficacy trials conducted that year. The estimation formula was: 

\[ N_{\text{sample}} = N_{\text{total}} \times p, \]

where \( N_{\text{total}} \) = total number emigrating, \( p \) = proportion caught in the trap, and \( N_{\text{sample}} \) = number of emigrants caught in the trap. These daily estimates were then added to the number of age-1 stocked steelhead sampled on all days, when the entire flow was going through the trap, to determine the total number of age-1 stocked steelhead that would survive and emigrate.

The trap was also used to monitor downstream movements of age-1 wild steelhead. To assess whether smaller age-1 wild steelhead may be prematurely displaced downstream by stocking larger age-1 steelhead throughout upstream reaches, we used a linear regression model to examine how a wild cohort’s emigration rate at age 1 was related to its overall abundance. For each wild cohort, overall abundance was calculated as the estimated number of wild emigrants to emigrate past the trap for the cohort over ages 1, 2, and 3. If higher wild cohort abundance was correlated with a higher wild age-1 emigration rate, then age-1 stocked steelhead could cause age-1 wild steelhead to have higher emigration rates by artificially increasing cohort abundance.

The trap was also used to monitor upstream and downstream movements of maxillary-clipped spawning adults. Adults were sampled from 2005 to 2012, which allowed sufficient time for all stocked fish to return for at least their initial spawning run (by age 6). Adult steelhead captured were counted, examined for a clip, had their scales taken for age estimation, and had a numerical T-bar anchor tag inserted, if one was not present, for individual identification. All adults were scanned with a handheld detector to determine whether a CWT was present and then released upstream of the trap to spawn.

The number of returning adults was estimated using annual mark–recapture estimates. As a result of high discharge rates, typically during the early portions of the spawning period from runoff, some adults migrating upstream were able to bypass the trap. Therefore, the efficiency of the trap to capture adults was calculated annually using the Lincoln–Peterson method (Van Den Avyle and Hayward 1999). The estimation formula was: 

\[ N = \frac{M \times C}{R} \]

where \( M \) = number of adults sampled migrating upstream prior to spawning, \( C \) = number of adults sampled migrating downstream after spawning, and \( R \) = number of adults sampled migrating upstream that were also sampled migrating downstream.

A \( Z \)-test was used to determine whether the percentage of marked adults (maxillary clipped and with CWTs) sampled by the trap was equal to the percentage of age-1 marked fish stocked (maxillary clipped and with CWTs). The percentage of stocked steelhead with a CWT for each year-class was a fixed parameter; i.e., there were a known number of marked (CWT) fish and thus no uncertainty concerning this parameter. In contrast, there were sampling errors in estimates of the percentage of marked (CWT) adults because not all adults were captured. For each stocked year-class, a \( Z \)-test using a normal approximation of the sampling distribution of the percent of returning adults was used to evaluate whether the percentage of returning adults sampled with a CWT was equal to the original percentage of steelhead stocked and marked with a CWT. A chi-square goodness-of-fit test was used to test for a difference in return rate across all year-classes. Adults with and without CWTs were assumed to be sampled in similar proportions.

Electrofishing surveys were used assess whether stocked fish remained upstream for 3 or 15 months poststocking, and if
so what size of stocked fish remained. From 2003 to 2007, backpack electrofishing surveys were conducted between late August and early September at seven of the upstream stocking sites and one additional site 1 rkm upstream from the trap. The length of each station was 35 times the mean stream width (Lyons 1992), which resulted in station lengths between 150 and 300 m. Three passes were conducted, and Zippen depletion estimates were used to quantify the number of stocked steelhead remaining (Van Den Avyle and Hayward 1999). All steelhead sampled were examined for maxillary clips, weighed, and measured, and scales were taken for age estimation. The other five upstream stocking sites were not electrofished as there was not enough time, and selected stations were assumed to represent all stocking sites.

The French River trap was used to assess whether straying rates to the French River differed between Knife River stocking treatments; a two-sample Z-test was used to test for a difference in the proportion of coded-wire-tagged fish between the two locations. The French River trap was in operation and fish were processed daily from ice-out through mid-June, or until spawning concluded. Adults captured were processed similarly to those captured at the Knife River trap.

RESULTS

Of the 164,126 age-1 steelhead stocked from 2003 to 2006, 77,550 were stocked throughout upstream reaches (Table 1). On average, 37% (range, 33–41%) of those stocked upstream were implanted with CWTs, which resulted in 18% (range, 15–19%) of all fish stocked possessing a CWT. These numbers and percentages were adjusted based on tests at the FRCWH for CWT retention (Table 1). On average the CWT loss rate was 1.4%, which resulted in an estimated 408 age-1 stocked steelhead not receiving CWTs, although they were supposed to. The mean annual stocking size was variable and ranged from 138 mm and 49 g to 189 mm and 76 g. The mean stocking date was also variable, because of the dependence on higher flows, and ranged from 24 April to 12 May.

Steelhead stocked upstream began entering the trap less than 24 h after being released in all study years, which indicated a rapid downstream movement of at least 10 rkm by some individuals. On average, 41% (range, 33–50%) of fish stocked upstream migrated to Lake Superior within 40 d of stocking (Table 1). The interval of 40 d poststocking was selected because 90% of those that were stocked and also emigrated did so within 40 d. An additional 4% (range, 1–8%) migrated during the remainder of the year in which they were stocked or the following year. On average, 55% (range, 43–60%) of fish stocked upstream were assumed to have died because no stocked steelhead older than age 2 were sampled in either the upstream electrofishing assessments or by the trap in subsequent years. Due to no observed mortalities between the downstream stocking site and the lake within 3 weeks of stocking, it was assumed 100% of fish stocked downstream survived to emigrate. Of the 96% (range, 86–100%) of stocked fish that emigrated within the first year they were stocked, it took an average of 24 d (mean annual range of 17–35 d) for a steelhead stocked upstream to emigrate.

Late summer electrofishing surveys at eight sites consistently sampled very low numbers of age-1 stocked steelhead that remained upstream 3 months poststocking. From 2003 to 2006, fewer than 15 age-1 steelhead were sampled at each station. No age-2 or older stocked steelhead were ever sampled (2004–2007), suggesting that very few, if any, became residents. The mean size of age-1 stocked steelhead sampled

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</tr>
</thead>
<tbody>
<tr>
<td>Year stocked</td>
<td>2003</td>
<td>2004</td>
<td>2005</td>
<td>2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean date stocked (month/day)</td>
<td>5/8</td>
<td>5/9</td>
<td>5/2</td>
<td>5/2</td>
<td>5/5</td>
<td></td>
</tr>
<tr>
<td>Mean length stocked (mm)</td>
<td>158</td>
<td>183</td>
<td>189</td>
<td>162</td>
<td>173</td>
<td></td>
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<tr>
<td>Mean weight stocked (g)</td>
<td>49</td>
<td>70</td>
<td>76</td>
<td>53</td>
<td>62</td>
<td></td>
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<tr>
<td>Number stocked</td>
<td>42,481</td>
<td>40,890</td>
<td>38,565</td>
<td>42,190</td>
<td>164,126</td>
<td></td>
</tr>
<tr>
<td>Number stocked upstream</td>
<td>19,653</td>
<td>19,224</td>
<td>17,864</td>
<td>20,809</td>
<td>77,550</td>
<td></td>
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<tr>
<td>Overall number with CWTs</td>
<td>8,134</td>
<td>7,564</td>
<td>5,917</td>
<td>7,082</td>
<td>28,717</td>
<td></td>
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<tr>
<td>Efficiency trial recapture rates (%)</td>
<td>63</td>
<td>67</td>
<td>62</td>
<td>53</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>Mean number of days to emigrate</td>
<td>35</td>
<td>17</td>
<td>25</td>
<td>21</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Number that emigrated</td>
<td>7,940</td>
<td>8,534</td>
<td>10,209</td>
<td>8,312</td>
<td>34,995</td>
<td></td>
</tr>
<tr>
<td>Number that emigrated within 40 d</td>
<td>6,570</td>
<td>8,024</td>
<td>8,834</td>
<td>8,146</td>
<td>31,574</td>
<td></td>
</tr>
</tbody>
</table>

aThese numbers have been adjusted based on tests at the French River Coldwater Hatchery for CWT retention.

bThe mean of four annual smolt trap efficiency trial recapture rates.

cRefers to those that emigrated in the year they were stocked.
during all electrofishing surveys was 168 mm TL and 42 g. The mean size of age-1 and age-2 stocked steelhead sampled by the trap was 202 mm TL and 74 g and 213 mm TL and 85 g, respectively. The mean size of wild age-1 steelhead sampled by the trap was 117 mm and 15 g. No evidence was found that larger age-1 stocked steelhead displaced smaller age-1 wild steelhead. The proportion of a cohort emigrating at age 1 for age-1 wild individuals was positively related to the cohort’s overall abundance, which explained 30% of the variation in observed emigration rates ($P = 0.06$; Figure 2).

The trap was 85% effective (range, 74–90%) at capturing adult steelhead during 2005–2012 based on annual Lincoln–Peterson estimates of trap efficiency. Throughout this study, an estimated 1,259 stocked steelhead returned as adults. From 2005 to 2012 a total of 760 different maxillary-clipped adults were sampled, and 12% possessed CWTs (Table 2). There was evidence that the percentage of marked adults (maxillary clipped and with CWTs) sampled by the trap was significantly different from the percentage of age-1 marked (maxillary clipped and with CWTs) fish that were stocked for the 2002 ($P < 0.001$), 2003 ($P = 0.05$), and 2004 ($P = 0.01$) year-classes, but there was no statistical difference for the 2005 year-class ($P = 0.18$). For the overall study, there was a significant difference in the observed annual percentage of adult marked fish compared with the percentage of marked fish at stocking ($\chi^2 = 41.2$, df = 3, $P < 0.001$).

Overall, 0.8% of all stocked steelhead returned to the Knife River as adults (Table 2). The return rate of those stocked upstream was estimated to be 0.5%, while the comparable return rate of those stocked at the mouth was 1.0%. The overall percent of adults that returned from upstream stockings (31%) was substantially less than that from downstream stockings (69%). Return rates of steelhead stocked in upstream reaches that survived to emigrate were 1.1%, which were similar to those for fish stocked in the mouth of the river (1.0%).

The French River trap captured 45 maxillary-clipped steelhead adults (i.e., fish that were initially stocked in the Knife River), of which five had CWTs (11.1%). The comparable percentage of adults with CWTs sampled at the Knife River trap was 11.7% (89/760). There was no significant difference between these proportions ($P = 0.90$); therefore, it appears

![FIGURE 2. The estimated number of naturally produced steelhead to emigrate past the Knife River trap for the 1997 through 2008 cohorts over ages 1, 2, and 3, compared with the proportion of those cohorts that emigrated at age 1. The years associated with data points denote cohorts.](image)

<table>
<thead>
<tr>
<th>Variable</th>
<th>2002</th>
<th>2003</th>
<th>2004</th>
<th>2005</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of adults sampled</td>
<td>231</td>
<td>85</td>
<td>335</td>
<td>109</td>
<td>760</td>
</tr>
<tr>
<td>Number of adults with CWTs</td>
<td>28</td>
<td>10</td>
<td>37</td>
<td>14</td>
<td>89</td>
</tr>
<tr>
<td>Percent adults with CWTs (%)</td>
<td>12.1</td>
<td>11.8</td>
<td>11.0</td>
<td>12.8</td>
<td>11.7</td>
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<tr>
<td>Difference in percent with CWTs (%)</td>
<td>7.0</td>
<td>6.7</td>
<td>4.3</td>
<td>4.0</td>
<td>5.8</td>
</tr>
<tr>
<td>Estimated number of adults</td>
<td>420</td>
<td>125</td>
<td>584</td>
<td>130</td>
<td>1,259</td>
</tr>
<tr>
<td>Estimated number of adults with CWTs</td>
<td>51</td>
<td>15</td>
<td>65</td>
<td>17</td>
<td>147</td>
</tr>
<tr>
<td>Return rate of upstream stocked fish (%)</td>
<td>0.6</td>
<td>0.2</td>
<td>1.1</td>
<td>0.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Return rate of downstream stocked fish (%)</td>
<td>1.3</td>
<td>0.4</td>
<td>1.9</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td>Overall return rate (%)</td>
<td>1.0</td>
<td>0.3</td>
<td>1.5</td>
<td>0.3</td>
<td>0.8</td>
</tr>
<tr>
<td>Return rate of upstream stocked fish that emigrated (%)</td>
<td>1.5</td>
<td>0.4</td>
<td>1.9</td>
<td>0.6</td>
<td>1.1</td>
</tr>
<tr>
<td>Percent adults from upstream stocking (%)</td>
<td>28</td>
<td>31</td>
<td>33</td>
<td>33</td>
<td>31</td>
</tr>
</tbody>
</table>

*This percentage is based on the estimated number of age-1 steelhead stocked in the upstream reaches that successfully migrated to Lake Superior.
straying rates from the Knife River to the French River did not differ between upstream and downstream stocking treatments.

**DISCUSSION**

Due to the high gradient of Minnesota tributaries and minimal groundwater contributions, base flow conditions occur quickly after spring runoff (Waters 1977). Therefore, age-1 steelhead in our study were stocked during the spring runoff period when higher flows were present to increase the rate at which stocked steelhead emigrated (Berggren and Filardo 1993) and to minimize interactions with wild age-1 steelhead (Vincent 1987; McMichael et al. 1999). Although no evidence was found that larger age-1 stocked steelhead displaced smaller age-1 wild steelhead in this study, there was evidence for higher age-1 emigration rates for wild cohorts with higher total abundance. Therefore, increased densities of similar-sized individuals suggest there is competition for size-specific food and preferable habitat. Increased emigration rates of wild juvenile steelhead have resulted from hatchery supplementation (Tatara et al. 2011), which attributed displacement to exceeding the carrying capacity (Cramer and Ackerman 2009).

Past research indicated age-1 steelhead stocked in late spring (mid-May to mid-June) returned at the highest rates, which coincided with the peak of wild steelhead smolt emigration (Wagner 1968; Negus et al. 2012). Therefore stocking steelhead in the Knife River took place as late as possible, but prior to the onset of base flow conditions. Base flows during the electrofishing portion of this study ranged from 0.2 to 3.0 m³/s and indicate how minimal the available habitat becomes.

The percentage of upstream stocked age-1 steelhead that survived to emigrate in our study (45%) was similar to the rate reported on another tributary to the Laurentian Great Lakes (48%; Seelbach 1987). Two studies on the west coast of North America also reported similar emigration rates (Muir et al. 2001, 38–53%; Johnson et al. 2010, 37–47%). Therefore, it does not appear as though the limitations in habitat, food resources, or both, which are characteristic of Minnesota tributaries to Lake Superior (Waters 1977), affected poststocking survival and emigration rates, while stocked fish remained upstream.

Electrofishing surveys and trap results indicate no stocked steelhead remained in the river past age 2. Therefore, we assumed all stocked fish that survived also emigrated and, so, assumed poststocking survival and emigration rates calculated at the trap were accurate. We also assumed that by sampling low abundances of age-1 stocked steelhead at all electrofishing stations, stocked fish migrated downstream at similar rates from all locations where fish were stocked. Similar to this study, no stocked individuals were sampled in electrofishing surveys on the Manistee River, Michigan, in early fall after May stockings, suggesting very few, if any, stocked fish became residents there (Seelbach 1987). However, some stocked age-1 steelhead have become residents on the west coast of North America (Wagner et al. 1963; McMichael et al. 1997). Results from these studies were probably influenced by stocking steelhead greater distances upstream in longer rivers with higher sustained flows. Results from our study were similar to past Knife River electrofishing assessments. While annually electrofishing between 10 and 16 stations throughout the Knife River watershed in late summer from 1973 to 2009, no stocked or wild age-4 or older steelhead were sampled, indicating residency rarely, if ever, occurs. The average size of age-1 stocked steelhead electrofished throughout upstream reaches was consistently smaller than the average size of age-1 stocked steelhead sampled at the trap, which indicates smaller stocked individuals probably remained upstream until attaining the necessary size to undergo smoltification (Negus 2003).

Higher return rates of steelhead stocked upstream were anticipated based on the assumption that imprinting and poststocking survival rates would be higher. However, upstream stockings only contributed 31% of returning adults, and return rates of steelhead stocked in the river mouth were two times higher than those stocked upstream. Research in British Columbia (Ward and Slaney 1990) and on a tributary to Lake Michigan (Black River: Hansen and Stauffer 1971) also demonstrated higher return rates for age-1 steelhead stocked near tributary mouths compared with those stocked farther upstream; although, other results in Oregon (Wagner 1969) and British Colombia (Slaney et al. 1993) were variable. Primary differences in return rates between the treatments in our study were due to higher in-stream mortality rates of fish stocked upstream, although upstream poststocking survival and emigration rates were similar to other studies. There was no difference between the return rates of age-1 steelhead stocked in upstream reaches that survived to emigrate and those of fish stocked in the mouth (1.1% versus 1.0%). Therefore, the factors that influenced survival of stocked steelhead after they migrated to Lake Superior and before they returned as adults were similar.

Overall return rates from this study (0.8%) were lower than those of age-1 steelhead stocked in other Great Lakes tributaries, which ranged between 1% and 10% (Hansen et al. 1990; Bartron et al. 2004). Return rates on the west coast of North America have typically ranged between 1% and 5% (Evenson and Ewing 1992; Tipping and Zajac 2010; Clarke et al. 2011), although can be between 6% and 12% (Larson and Ward 1955; Ward and Slaney 1990). A possible factor contributing to lower return rates along the Minnesota shore of Lake Superior when compared with other tributaries is the lack of transitional estuarine type habitat near tributary mouths. Estuaries near river mouths are instrumental in providing habitat (Quiñones and Mulligan 2005) and increasing survival and return rates of presmolt steelhead (Bond et al. 2008; Hayes et al. 2008). The bathymetry of Lake Superior along Minnesota drops off sharply (Negus et al. 2008) and does not provide estuarine type habitat. Therefore, steelhead emigrants have to quickly adapt to a lacustrine environment. Another possible factor contributing to lower return rates in this study was that stocked fish were smaller than had been requested in 2 of 4 years. Several studies have found higher return rates...
occurred when larger age-1 steelhead were stocked (Tipping 1997; Negus et al. 2012). Consequently, the return rates of the 2002 and 2005 year-classes potentially could have been higher if the mean size of stocked fish met the hatchery target size of 178 mm TL and 62 g, as requested (Negus 2003).

Quantifying straying rates to Lake Superior tributaries, other than the French River, was not feasible since there are no other traps where fish are routinely handled. Based on French River trap returns, there was no significant difference between the proportions of adults with CWTs observed at the French and Knife rivers (11.1% versus 11.7%, respectively). Therefore, straying rates to the French River did not appear to be different between stocking treatments. Wagner (1969) also concluded that age-1 steelhead stocked at downstream sites did not have a greater tendency to stray compared with those stocked upstream. Although straying to the French River was expected to occur to some extent due to hatchery effluent, returns of adults to the Knife River were substantially higher, indicating imprinting did occur. Feral Knife River broodstock were used to produce steelhead stocked in this study because straying rates decrease when age-1 individuals are stocked in tributaries where their parents originated (Schroeder et al. 2001).

Straying rates were also assessed during the 1990–2002 age-1 steelhead stockings by the MDNR. As a result of those stockings, strays from the five other rivers stocked comprised 2% (range, 0–5%) of adults that returned to the Knife River and 9% (range, 4–23%) of adults that returned to the French River. When accounting for low levels of straying in this study, overall return rates might have been slightly higher than 0.8%.

Because return rates of age-1 steelhead stocked in the mouth of the Knife River were two times higher than those stocked upstream, and fish stocked upstream risk displacing wild juveniles, we recommend not stocking age-1 steelhead in the upstream reaches of the Knife River. If stocking is proposed in the upstream reaches, we suggest evaluating the practice of stocking earlier life stages. Stocking earlier life stages will increase the likelihood of imprinting (Negus 2003). However, stocking individuals similar in size to their wild counterparts may also increase competition for habitat and size-specific food (Tatara 2003). Because straying to the French River was expected to occur, stocking treatments. Wagner (1969) also concluded that age-1 steelhead stocked downstream sites did not have a greater tendency to stray compared with those stocked upstream. Although straying to the French River was expected to occur to some extent due to hatchery effluent, returns of adults to the Knife River were substantially higher, indicating imprinting did occur. Feral Knife River broodstock were used to produce steelhead stocked in this study because straying rates decrease when age-1 individuals are stocked in tributaries where their parents originated (Schroeder et al. 2001).

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ACKNOWLEDGMENTS

Joe Ostazeski initiated this study. Fred Tureson, Mark Gottwald, and staff at the French River Coldwater Hatchery reared, marked, and tagged the age-1 steelhead. The Lake Superior Steelhead Association contributed 17% of rearing costs. The MDNR staff from Lake Superior and Duluth area offices stocked steelhead, operated the trap, and electrofished. This study was funded in part by the Federal Aid in Sport Fish Restoration (Dingell–Johnson) Program, D–J Project F29–R, Minnesota. We also thank Andy Carlson, Molly Negus, Pat Schmalz, Charles Anderson, Doug Schultz, Josh Blankenheim, Stephen Riley, and anonymous reviewers for providing edits to this paper.

REFERENCES


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