Prolonged Swimming Performance of Northern Squawfish

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Abstract.—We determined the prolonged swimming performance of two size-classes of northern squawfish *Psycholellus oregonensis* at 12 and 18°C. The percentage of fish fatigued was positively related to water velocity and best described by an exponential model. At 12°C, the velocity at which 50% of the fish fatigued (FV50) was estimated to be 2.91 fork lengths per second (FL/s; 100 cm/s) for medium-sized fish (30–39 cm) and 2.45 FL/s (104 cm/s) for large fish (40–49 cm). At 18°C, estimated FV50 was 3.12 FL/s (107 cm/s) for medium fish and 2.65 FL/s (112 cm/s) for large fish. Rate of change in percent fatigue was affected by fish size and water temperature. Large fish fatigued at a higher rate than medium-sized fish; all fish fatigued faster at 12 than at 18°C. The mean times to fatigue at velocities of 102–115 cm/s ranged from 14 to 28 min and were not affected by fish size or water temperature. Our results indicate that water velocities from 100 to 130 cm/s may exclude or reduce predation by northern squawfish around juvenile salmonid bypass outfalls at Columbia River dams, at least during certain times of the year. We recommend that construction or modification of juvenile salmonid bypass facilities place the outfall in an area of high water velocity and distant from eddies, submerged cover, and littoral areas.

The northern squawfish *Psycholellus oregonensis* is a major predator on juvenile salmonids in a variety of waters (Jeppson and Platt 1959; Thompson and Tufts 1967; Poe et al. 1991). In the Columbia River, northern squawfish predation on juvenile salmonids is most intense in the tailrace areas downstream from dams (Poe et al. 1991), a scenario accurately predicted for riverine systems by Brown and Moyle (1981). Predation near dams is severe partly because prey are concentrated near juvenile fish bypass outfalls and may be less able to avoid predators because of passage-related disorientation, stress, or injury (Matthews et al. 1986; Maule et al. 1988).

Concern over the decline of many stocks of Pacific salmon *Oncorhynchus spp.* has led to efforts aimed at increasing juvenile salmonid survival, including a reduction in predation-related mortality. Although predator removal efforts are currently underway in the Columbia River, other methods designed to protect juvenile salmon as they migrate downstream might be as efficient, ecologically more prudent, and less costly. One method of protecting juvenile salmonids is the construction or improvement of fish bypass facilities, which help intercept fish in forebay areas, divert them away from turbines, and allow them relatively safe passage through the dam before they exit into the tailrace. Because northern squawfish appear to prefer low water velocities around bypass outfalls (Faler et al. 1988), a higher water velocity there might exclude them or reduce their numbers and thus decrease predation. Faler et al. (1988) found that radio-tagged northern squawfish did not use water velocities greater than 70 cm/s. However, their study did not fully address the swimming ability of northern squawfish in high water velocities.

Although the swimming performance of many fish species has been documented (see reviews by Beamish 1978 and Videler and Wardle 1991), Berry and Pimentel (1985) cautioned against using these data to predict the capabilities of unstudied species. Our objective, therefore, was to determine the endurance of northern squawfish at prolonged swimming speeds. Prolonged swimming speeds are those that a fish can maintain for up to 200 min before fatiguing (Beamish 1978). We also assessed the effects of fish size and water temperature on swimming performance. We anticipate that this information could aid in developing biological criteria for the location and operation of bypass systems for protecting juvenile salmonids from predation by northern squawfish.

Methods

Northern squawfish were captured as needed from the Columbia River by electrofishing, with a Merwin trap, and by angling and were transported to our laboratory. They were held outdoors under natural photoperiod in circular tanks (1.2 m in diameter, 0.8 m deep) that received well
water heated to ± 1°C of the selected experimental temperature. Water flow in the tanks produced a circular current for orientation. All fish were acclimated at least 1 week prior to testing and were fed to excess with live juvenile coho salmon _O. kisutch_. Fish showing signs of disease, injury, or other abnormalities were excluded from testing. Swimming tests were conducted from April through October in 1991 and 1992.

Swimming performance was measured in a stamina tunnel similar to that used by Thomas et al. (1964) and Berry and Pimentel (1985). The tunnel consisted of two 500-L reservoirs connected by two plexiglas pipes, one a return-flow pipe and the other a 0.2-m-diameter × 2.0-m-long swimming chamber. An electric pump recirculated water in the tunnel; motor speed was electronically controlled to produce a wide range of water velocities. We used linear regression to assess the relation between water velocity (measured in cm/s with a Pygmy flow meter) and motor speed. We then calculated the motor speed (Hz) necessary to produce a desired test velocity using the equation (N = 10, r² = 0.99):

\[ \text{Hz} = 0.381 + 0.533(\text{velocity}) \]

Fish were tested individually and encouraged to swim by manually operating electrified screens (5–10-V AC) located at each end of the swimming chamber. The upstream screen kept fish from remaining at the chamber entrance, whereas the downstream screen encouraged tiring fish to keep swimming. About 1.5 m of the middle of the swimming chamber was wrapped with black plastic except for the top, which allowed entrance of light from above. This isolated the fish from outside disturbance and provided an aid for its orientation.

The presence of a fish in the swimming chamber can cause a solid blocking effect, whereby the object blocking the flow through part of the tunnel cross section causes an increase in flow velocity around the object (Bell and Terhune 1970). To correct for this, we determined the cross-sectional area of a sample of our fish by cutting a fish at its thickest point, tracing an impression of the cut surface on blank paper, and measuring the area with a digitizer. We then established the relation between cross-sectional (XC) area and weight, using linear regression, as

\[ \text{XC} (\text{cm}^2) = 17.8 + 0.033(\text{weight, g}) \]

(N = 37, r² = 0.94). Because 98% of our fish exceeded 10% of the cross-sectional area of the chamber, we calculated corrected swimming velocities using the formula

\[ V_F = V_P[(1 + (\tau \lambda)) (A_p/A_t)^{1.5}], \]

where \( V_F \) = corrected velocity, \( V_P \) = test velocity, \( \tau = 0.8 \), \( \lambda = 0.7 \) length/thickness, \( A_p \) = maximum cross-sectional area of fish, and \( A_t \) = cross-sectional area of tunnel (Bell and Terhune 1970).

Swimming performance of northern squawfish was assessed at 12°C and 18°C for two size-groups, medium (30–39 cm fork length, FL) and large (40–49 cm FL). These temperatures represent the average water temperature in the Columbia River during the spring and summer juvenile salmonid migrations. The size-groups are representative of piscivorous northern squawfish in the Columbia River (Poe et al. 1991).

We used a test protocol similar to that of Berry and Pimentel (1985). The day before testing, three northern squawfish were selected randomly and transferred to an isolation tank; food was withheld from these fish to minimize the effect of feeding on standard metabolism (Beamish 1964; Bernatchez and Dodson 1985). The next morning, the tank was filled with water at the acclimation temperature of the fish. A single fish was netted from the isolation tank, rapidly measured to the nearest centimeter, and placed into the swimming chamber, where it was allowed to acclimate for 30 min at a water velocity of 0.75 fork lengths per second (FL/s). Following this acclimation, water velocity was gradually increased over about 5 min to a selected test velocity that ranged from 1.4 to 3.0 FL/s.

Test velocities were selected based on data we obtained from preliminary experiments. In this preliminary work, we subjected 13 fish to a range of velocities (based on velocities used by Berry and Pimentel 1985) and determined when swimming became very difficult or ceased completely. This procedure provided an approximate flow range that produced rapid fatigue. We chose 1.4 FL/s as the low end of the range because all fish could swim easily at this speed and we could divide the total range into enough increments to fully characterize fish performance. During the first year, we used data from test fish to increase the precision of the high end of the range.

Fish were tested for 120 min or until fatigued; sample size varied at each test velocity because of variability in performance. We defined a fish as fatigued when it became impinged on and would not leave the downstream screen despite several shocks. Following a test, swimming time was re-
corded, and fish were removed, sacrificed, and weighed to the nearest 25 g.

We used a "dose-response" approach to describe the relation between percentage of fish fatigued and water velocity for both size-groups and temperatures (Brett 1967). Scatter plots suggested that the relation between percent fatigue and water velocity was curvilinear. To provide a general description of this relation, we used an iterative, least-squares procedure to fit the exponential model

\[ y = b \cdot e^{mx}, \]

where \( y \) = percent fatigued, \( x \) = water velocity (FL/s), and \( b \) and \( m \) are coefficients. We estimated the velocity at which 50% of the fish fatigued (FV50) by refitting the data to a linear model. To do this, we added 1 to all percent fatigue values and transformed them to their natural logarithms. We then used simple linear regression to inversely predict water velocity at 50% fatigue. Standard deviations and the \( t \)-statistic were used to calculate 95% confidence limits for predicted water velocities (Neter et al. 1983).

To assess the effects of fish size and water temperature on percent fatigue, we did pairwise comparisons of homogeneity of slope for the linear regression equations (Zar 1984). We compared slopes for each temperature between fish size-groups and for each size-group between temperatures. Homogenous slopes would indicate that the rate of change in percent fatigue elicited by an increase in water velocity was similar between groups.

We calculated the mean time to fatigue for each group using the fatigue times from all individuals that fatigued at the two or three highest velocities tested. We expressed the water velocity for the mean fatigue time as the average of the velocities in which these fish had fatigued. A \( 2 \times 2 \) factorial analysis of variance was used to assess the effects of fish size and water temperature on mean fatigue time.

**Results**

We tested 345 fish; differences in size between large \( (N = 172; \text{average length } \pm \text{SE } = 43.5 \pm 0.2 \text{ cm}; \text{average weight } \pm \text{SE } = 976.6 \pm 15.7 \text{ g}) \) and medium \( (N = 173; 35.5 \pm 0.2 \text{ cm}; 530.8 \pm 11.4 \text{ g}) \) northern squawfish were significant (two-sample \( t \)-tests, \( P < 0.05 \)). The percentage of fish fatigued was positively related to water velocity and well described by the exponential model (Figure 1). Coefficients of determination for the four exponential curves ranged from 0.92 to 0.95. Estimates of FV50 values in FL/s for large fish were lower than those for medium fish, but when expressed in absolute speeds, swimming speed was positively related to fish size (Table 1).
TABLE 1.—Predicted water velocities at which 50% of fish fatigued (FV50) and their associated 95% confidence limits for northern squawfish during swimming performance tests. Values of FV50 are expressed in fork lengths (FL) per second and the equivalent absolute swimming speed. All velocities are corrected for solid blocking effects.

<table>
<thead>
<tr>
<th>Fish size</th>
<th>Temperature (°C)</th>
<th>FV50 (FL/s)</th>
<th>95% confidence limits (FL/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium</td>
<td>12</td>
<td>2.91</td>
<td>2.05–3.77</td>
</tr>
<tr>
<td>Medium</td>
<td>18</td>
<td>3.12</td>
<td>2.35–3.89</td>
</tr>
<tr>
<td>Large</td>
<td>18</td>
<td>2.45</td>
<td>2.13–2.77</td>
</tr>
<tr>
<td>Large</td>
<td>18</td>
<td>2.65</td>
<td>2.21–3.09</td>
</tr>
</tbody>
</table>

Both fish size and water temperature significantly influenced the rate of change in percent fatigue, because all pairwise comparisons indicated regression slopes were significantly different (Table 2). Large fish fatigued faster than medium fish at both temperatures and all fish fatigued faster at 12°C than at 18°C.

The mean times to fatigue for all fish ranged from 14 to 28 min and were not significantly (P > 0.05) affected by fish size or water temperature (Table 3).

Discussion

The prolonged swimming performance of northern squawfish, as expressed by our FV50 values, compares favorably with that of large Colorado squawfish *P. lucius* at 14 and 20°C (Berry and Pimentel 1985), indicating that the performances of comparable sizes of these congeners may be similar. The preference of Colorado squawfish for large riverine systems (Moyle 1976; Tyus et al. 1984) and their migratory behavior (Tyus 1990) might imply a swimming performance advantage when compared with the preference of northern squawfish for low-velocity microhabitats (Beamesderfer 1983; Faler et al. 1988). Indeed, the life history forms of several species that undertake frequent swimming (e.g., extended anadromous migrations) possess greater swimming capabilities than those of more sedentary populations (Tsuyuki and WillisCroft 1977; Taylor and McPhail 1985; Taylor and Foote 1991).

Because Colorado squawfish were (and still are) threatened with extinction, Berry and Pimentel (1985) had to use unexercised, hatchery-reared fish and they did not correct for solid blocking effects. Thus, the similarity in swimming performance between these two species might not adequately reflect their life history differences.

Although large fish fatigued at a higher rate than medium fish, this may in part reflect the limitations of the swimming chamber. As fish size increased, a greater proportion of the cross-sectional area of the chamber was occupied, which perhaps made large fish feel more restrained and less likely to perform adequately. However, we saw no evidence that the tunnel restricted fish movements and the diameter of our tunnel was the same as that used by Berry and Pimentel (1985), who swam larger fish than we did. Fish size is among the most

Table 2.—Least-squares regression equations for the relationships between percentage of northern squawfish fatigued (log,%) and water velocity at two temperatures and two fish size-classes. Water velocity is in fork lengths per second. Asterisks denote slopes (i.e., rates of fatigue) that differ significantly between groups. Values of the t-statistic are significant at P < 0.05*, P < 0.01**, or P < 0.001***.

<table>
<thead>
<tr>
<th>Group</th>
<th>Fish size</th>
<th>Temperature (°C)</th>
<th>Linear equation</th>
<th>N</th>
<th>r²</th>
<th>Slope comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Medium</td>
<td>12</td>
<td>log, (% fatigue) = -6.76 + 3.66· velocity</td>
<td>6</td>
<td>0.84</td>
<td>1 versus 3 5.27**</td>
</tr>
<tr>
<td>2</td>
<td>Medium</td>
<td>18</td>
<td>log, (% fatigue) = -5.36 + 2.97· velocity</td>
<td>7</td>
<td>0.87</td>
<td>1 versus 2 3.56*</td>
</tr>
<tr>
<td>3</td>
<td>Large</td>
<td>12</td>
<td>log, (% fatigue) = -7.55 + 4.68· velocity</td>
<td>5</td>
<td>0.96</td>
<td>2 versus 4 5.27**</td>
</tr>
<tr>
<td>4</td>
<td>Large</td>
<td>18</td>
<td>log, (% fatigue) = -6.03 + 3.76· velocity</td>
<td>6</td>
<td>0.91</td>
<td>3 versus 4 7.20***</td>
</tr>
</tbody>
</table>
important constraints on swimming performance and can directly affect endurance (Beamish 1978). The size (and temperature) effects we observed in our fish illustrate the importance of analyzing the data separately among groups. Compared to an analysis of pooled data, our approach resulted in more accurate curve fitting and estimates of FV50.

Northern squawfish demonstrated a better prolonged swimming performance at 18°C than at 12°C. The swimming performance of fish typically increases with water temperature (Brett 1967; Glova and McInerney 1977; Bernatchez and Dodson 1985) and peaks at an optimum temperature at which physiological functions are most efficient. As temperature increases, fish may have a greater oxygen uptake capacity (Bernatchez and Dodson 1985) or may show increases in metabolic rates or enzymatic processes (Brett 1967). Brown and Moyle (1981) stated that northern squawfish prefer water temperatures ranging from 16 to 22°C. Recent studies (Beyer et al. 1988; Vigg and Burley 1991) have shown that consumption and evacuation rates of northern squawfish peak near 21°C. This indicates an optimum temperature for northern squawfish greater than 18°C, so our data may underestimate their maximum swimming capability.

The mean fatigue times of our fish, in contrast to percent fatigue, were not influenced by fish size or water temperature. Other studies have shown fatigue times of other fishes to be significantly influenced by life history form (Tsuyuki and Williscroft 1977; Taylor and McPhail 1985), water temperature, water velocity, and fish size (Brett 1967; Bernatchez and Dodson 1985). Although further research is needed to fully understand the factors influencing northern squawfish fatigue time, the propensity of these fish to fatigue in a short period may have important implications for predator-prey interactions in fast-moving water.

Implications for Predator-Prey Interactions

Information on the swimming performances of fishes has been used for various management decisions, including assessments of the design of fish ladders (Collins et al. 1962; Slatick 1971), water intakes (Dorn et al. 1979), and culverts (Jones et al. 1974) and of the sublethal effects of pollutants (for a review see Beitinger and McCauley 1990). In the Columbia River, the use of high water velocities to exclude or limit predation by northern squawfish on salmonids in the area of dam bypass outfalls seems promising. Bypass outfalls could be located in areas with high water velocities, perhaps reducing the efficiency of predators. During juvenile salmonid migrations in spring and early summer, this scenario may already be working to some extent. During this period, water temperatures are low, flows are high, consumption rates by northern squawfish are relatively low (Vigg et al. 1991), and the swimming ability of these predators presumably is reduced. In addition to creating an area that excludes predators, high flows should also move juvenile salmonids downstream faster and keep them out of predator-inhabited eddies or littoral areas. As fish move downstream, predation rates by northern squawfish decrease (Vigg et al. 1991), perhaps because juvenile salmonids are dispersed and migrate in water offshore, near the surface, and at night (Brown and Moyle 1981).

During periods when river flows are low and thus do not fatigue the fish, the energetic benefits and costs of swimming may determine whether northern squawfish would inhabit areas around bypass outfalls. The metabolic costs associated with prolonged swimming speeds and maintaining position increase with water velocity and may involve aerobic and anaerobic processes (Beamish 1978; Faeay and Grossman 1990). The high energetic demands of a three-stage (approach, chase, and strike) predatory strategy (Harper and Blake 1988), which we believe typifies northern squawfish behavior, would also presumably increase directly with water velocity, perhaps precluding efficient feeding in areas of high water velocity. We recommend that the outfalls of new or modified bypass facilities for juvenile salmonids be sited in areas of high water velocity (e.g., 100–130 cm/s) and distant from eddies, submerged cover, and littoral areas.

Acknowledgments

We thank A. Murphy and T. McGuire for conducting some of the performance tests. J. Bloodgood for his exceptional technical assistance, and W. R. Nelson, B. Muir, T. Poe, and J. Zuboy for reviewing the manuscript. This work was funded by Bonneville Power Administration (contract DE-A179-88BP91964).

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Received December 21, 1992
Accepted June 21, 1993