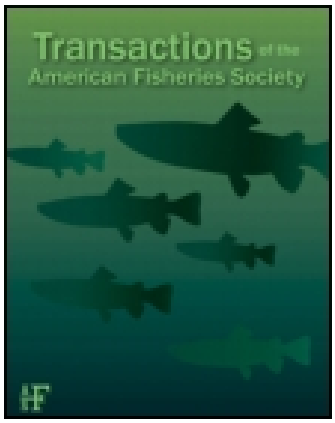

Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

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Published online: 09 Jan 2011.

To cite this article: Matthew G. Mesa , Jennifer M. Bayer & James G. Seelye (2003) Swimming Performance and Physiological Responses to Exhaustive Exercise in Radio-Tagged and Untagged Pacific Lampreys, Transactions of the American Fisheries Society, 132:3, 483-492, DOI: 10.1577/1548-8659(2003)132<0483:SPAPRT>2.0.CO;2

To link to this article: http://dx.doi.org/10.1577/1548-8659(2003)132<0483:SPAPRT>2.0.CO;2

Transactions of the American Fisheries Society 132:483–492, 2003
American Fisheries Society 2003

Swimming Performance and Physiological Responses to Exhaustive Exercise in Radio-Tagged and Untagged Pacific Lampreys

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Abstract.—Populations of Pacific lamprey *Lampetra tridentata* have declined in the Columbia River basin. One factor that may have contributed to this reduction in population size is an excessive use of energy by adult lampreys as they negotiate fishways at dams during spawning migrations. To gain an understanding of the performance capacity of Pacific lampreys, we estimated the critical swimming speed (U_{crit}) and documented physiological responses of radio-tagged and untagged adult lampreys exercised to exhaustion. The mean (±SD) U_{crit} of untagged lampreys was 86.2 ± 7.5 cm/s at 15°C, whereas the U_{crit} for radio-tagged lampreys was 81.5 ± 7.0 cm/s, a speed that was significantly lower than that of untagged fish. The physiological responses of tagged and untagged lampreys subjected to exhaustive exercise included decreases in blood pH of 0.3–0.5 units, a 40% decrease in muscle glycogen levels, a 22% increase in hematocrit for untagged fish only, and a 4- to 5-fold increase in muscle and a 40- to 100-fold increase in plasma lactate concentrations. These physiological changes were significant compared with resting control fish and usually returned to resting levels by 1–4 h after fatigue. Our estimates of U_{crit} for Pacific lampreys are the first quantitative measures of their swimming performance and suggest that these fish may have difficulty negotiating fishways at dams on the Columbia River, which can have water velocities approaching 2 m/s. Our physiological results indicate that tagged and untagged Pacific lampreys show similar metabolic dysfunction after exhaustive exercise but recover quickly from a single exposure to such a stressor.

Pacific lampreys *Lampetra tridentata* in the Columbia River basin have declined to remnant, pre-1940 population levels (Close et al. 1995). The ecological, economic, and cultural significance of this species is underestimated by most people; nevertheless, actions are currently being considered for their recovery (Close et al. 1995). One factor that could be detrimental to Pacific lamprey production is the amount of energy they expend negotiating upstream fish-passage facilities at dams. Recent research suggests that 50–60% of radio-tagged lampreys failed to pass the fishways at Bonneville Dam, the lowermost dam on the Columbia River (M. Moser, National Marine Fisheries Service, personal communication). However, detailed explanations and possible consequences of this behavior are lacking. Pacific lampreys enter streams up to 12 months before they spawn; they do not feed during this time and therefore have a finite amount of energy reserves for migration, sexual maturation, and spawning (Scott and Crossman 1973; Beamish 1980). An excessive use of energy in negotiating fishways during upstream migrations could hinder the physiological and behavioral processes necessary for sexual maturation and successful reproduction.

The possibility that adult Pacific lampreys use excessive amounts of energy during fishway passage seems high and is supported by several lines of reasoning. (1) Fishways at dams in the Columbia River basin have high water velocities and were originally designed to facilitate the passage of anadromous salmonids, a group of fish well known for their strong swimming capabilities. (2) Lampreys use an anguilliform swimming motion, which is considerably less efficient than the subcarangiform (burst-and-glide) motion used by salmonids. (3) Lampreys do not have swim bladders that allow them to maintain neutral buoyancy and must therefore swim constantly or hold fast to maintain position (Hardisty and Potter 1971). (4) Limited information on the swimming performance of sea lampreys *Petromyzon marinus* indicates that lampreys are poor swimmers compared with most teleosts (Beamish 1974; Hanson 1980; McCauley 1996).

During negotiation of fishways, lampreys may swim to exhaustion. Subjecting fish to exhaustive

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Received February 26, 2002; accepted October 8, 2002

exercise results in a variety of physiological disturbances, such as decreases in blood pH, increases in blood and muscle lactate levels, and changes in gas equilibria in the blood (Driedzic and Kiceniuk 1976; Wood et al. 1983; Cameron and Cech 1990; Pagnotta and Milligan 1991; Tufts 1991). Exhaustion may also result in the death of fish several hours after exercise (see review of early literature by Black 1958; Wood et al. 1983). Because physical stressors are known to alter several aspects of reproduction in fish (e.g., sex steroid levels, mean egg size, and fecundity; Pottinger 1999 and references therein), it seems probable that exposing fish to exhaustive exercise could have similar reproductive consequences. Thus, if lampreys negotiating fishways at dams are even occasionally swimming to exhaustion, the potential for physiological changes, altered reproductive performance, or even delayed mortality seems high.

The objectives of our study were to determine the critical swimming speed (U_{crit}) of radio-tagged and untagged Pacific lampreys and assess their physiological responses to exhaustive exercise. Because radiotelemetry is now commonly used in the Columbia River basin to study lamprey movements, we wanted to assess the influence of surgically implanted radio tags on these measures of performance. We expected our results to provide basic information on the physiological performance capacity of Pacific lampreys and insight into the difficulty they may be having negotiating fishways at dams.

Methods

Experimental lampreys.—Adult Pacific lampreys were collected from May to July 1999 and 2000 by using a metal trap (0.6 × 0.8 × 0.8 m) placed at the top of a weir in the north shore fish ladder at Bonneville Dam. For a complete description of the trap and its operation, see Moser et al. (2002). Lampreys were transported to our laboratory in Cook, Washington, and held in 1,400-L circular tanks provided with a continuous flow of water (about 4–6 L/min) from the Little White Salmon River. All water used for this research was heated to 15°C using a boiler system, and excess dissolved gases produced by heating were dissipated using air stones and packed columns. Automated water quality monitoring indicated that total dissolved gas levels ranged from 100% to 103%. We chose 15°C as our experimental temperature because it approximates average temperatures in the lower Columbia River during the upstream migration of lampreys. Lampreys were exposed to a simulated natural photoperiod produced by incandescent lights and timers, were not fed during any of our experiments (i.e., feeding does not occur during this life stage), and were held at least 2 weeks before experimentation.

Critical swimming speed tests.—Critical swimming speed tests on Pacific lampreys were conducted in two different years. In 1999, we conducted U_{crit} tests on untagged lampreys from September through early November. In 2000, from July through August, we tested fish that had a dummy radio transmitter surgically implanted in them. The cylindrical, epoxy transmitters were 29 mm long, 9 mm in diameter, and weighed 3.6 g in air; they had a plastic-coated antenna attached to one end. Because of logistics, timing constraints, and availability of transmitters, we were unable to swim tagged and untagged fish in the same year. For untagged fish, one lamprey was randomly selected from the holding tanks and anesthetized for 4 min in a 75 mg/L solution of buffered tricaine methanesulfonate (MS-222). Weight (g), total length (mm; TL), and maximum girth (mm) were then recorded. Lampreys in poor condition (based on qualitative observations of skin color and texture, wounds, or signs of disease) were not used in our tests. Surgical procedures were adapted from those commonly used in our laboratory (e.g., Adams et al. 1998) and are briefly described here. A fish was placed ventral side up in a foam lined, V-shaped trough, and its head and buccal pores were irrigated with a 50-mg/L solution of buffered MS-222. An incision was made and a shielded needle was used to puncture and send the transmitter antenna through the body wall. The transmitter was inserted into the body cavity and pushed anterior of the incision. The incision was closed with 3–4 simple interrupted sutures and the fish was placed in a small aquarium (50 cm long, 25 cm wide, 30 cm deep, total volume, 31 L) with flowing water. Surgeries were done in the early afternoon, and fish were allowed to recover overnight before starting the swim trials, which is consistent with ongoing field studies.

All swimming tests were conducted in a Blazka-type respirometer, which had a swimming portion that was 1.2 m long and an external diameter of 165 mm. A 1-hp motor was used to recirculate the water, and the tunnel was lined with plastic mesh (10 mm) to prohibit lampreys from holding fast. We used linear regression to determine the relation between motor speed and water velocity (measured with a pitot tube) for the tunnel with the mesh in place. The resulting equation (motor speed =

4.4364 [velocity] + 15.28; $N = 10$, $r^2 = 0.99$) was used to calculate the motor speed necessary to achieve a desired velocity.

Following measurement, an untagged lamprey was placed in the swim tunnel at a water velocity of 0.25 body lengths per second (BL/s) for 60 min. The day after surgery, one tagged fish was placed in the swim tunnel in the midmorning and another in the afternoon. For both tagged and untagged groups, after 60 min the water velocity was increased to 0.70 BL/s for 30 min and then increased by 10 cm/s every 30 min until the lamprey fatigued. Fatigue occurred when the lamprey became impinged on the downstream screen despite three successive attempts to dislodge it. Rapid changes in water velocity were used to encourage the lamprey to leave the downstream screen. After fatigue was confirmed, lampreys were rapidly removed from the swim tunnel and assigned to a postfatigue tissue sampling interval for our physiological study (see below). Critical swimming speed (cm/s) was calculated with the formula described by Beamish (1978). Two-sample *t*-tests were used to evaluate differences in mean total length, mean weight, and U_{crit} between the sexes within a group and between groups. Simple linear regression was used to examine the relation between total length and U_{crit} values.

Physiological responses to exhaustive exercise.—To assess the physiological responses of lampreys to exhaustive exercise, we obtained blood and muscle samples from individuals that successfully completed a U_{crit} test at selected time intervals after fatigue (4–6 fish/period). After a U_{crit} test, the lamprey was removed from the respirometer and either sampled immediately (time 0) or placed in darkened isolation aquaria. Because of the time it required to remove the lamprey from the swim tunnel, our time-0 sample was actually taken at 4–5 min after fatigue, which based on other research, may result in only minor elevations of the plasma and muscle factors we assayed (Wood 1991; Boutilier et al. 1993; Milligan 1996). Lampreys in the isolation aquaria were randomly assigned to a postfatigue sample time of 1, 4, 8, or 24 h, which is consistent with other studies assessing the responses of fish to exhaustion (e.g., Wood and Perry 1985; Wood 1991).

Sampled lampreys were placed in a 19-L bucket containing a lethal dose of buffered MS-222 (300 mg/L) but, before this were briefly preanesthetized in the isolation aquaria with 75 mg/L MS-222. When gill ventilation had ceased, lampreys were removed from the anesthetic and were bled (about 500 μL) from the caudal vasculature just posterior to the vent by using a 1.0-mL gastight Hamilton syringe and 24-gauge needle coated with a 50 IU/mL solution of ammonium heparin. Blood pH was measured immediately by injecting a small portion of the blood sample into a length of PE-50 capillary tubing connected to mini pH and reference electrodes (Microelectrodes, Inc., Bedford, New Hampshire). The electrodes were connected to a Corning model 314 pH meter that automatically corrected readings for temperature of the sample (15°C). We then injected a small sample of blood into a heparinized glass capillary tube to measure hematocrit by centrifugation and placed the remaining blood into a 400-μL centrifuge tube. Blood samples were centrifuged to obtain plasma, frozen at −80°C, and used to assay lactate and glucose. While blood was being processed, we removed a muscle sample (1 cm^2) from the side of each lamprey just below the origin of the first dorsal fin, wrapped it in aluminum foil, and flash froze it in liquid nitrogen. Muscle samples were stored in a freezer at −80°C and assayed later for lactate, glucose, and glycogen levels. To complete the sampling, we determined the sex of each lamprey by dissection and removed the dummy radio tag. We also sampled, in a manner identical to lampreys in isolation aquaria, a group of 18–20 control animals that had been rearing undisturbed in a 400-L tank for 2 weeks. This tank received a flow rate of about 4 L/min and water temperature was 15°C.

Plasma lactate and glucose concentrations were measured using commercial kit assays (Sigma Diagnostics, St. Louis, Missouri) that we modified for use with microplates. We processed muscle samples by placing a 100–200-mg piece of frozen muscle into a test tube containing 1.0-mL of ice-cold 6% perchloric acid. We then placed the test tube in a small beaker of ice water and homogenized the sample for several seconds using a Tissue Tearor, pulsing the device to prevent the sample from warming. Next, we added 10 μL of 3M K_2CO_3 and checked pH with test strips; we repeated this procedure until we obtained a sample pH of approximately 7.0. Samples were centrifuged for 15 min at 4,000 revolutions/min, and the resulting supernatant was used in the kit assays for lactate and glucose. To determine muscle glycogen, we added 25 μL of amyloglucosidase solution (1 mg/mL in citrate buffer) to each sample in the microplate 1 h before starting the glucose assay. Muscle glycogen was determined by subtracting the free glucose concentration from the concentration obtained after digestion with amy-

TABLE 1.—Mean (SD) total lengths, weights, and critical swimming speeds (U_{crit}) of Pacific lampreys that were untagged or surgically implanted with a dummy radio transmitter. Asterisks denote means that were significantly ($P < 0.05$) lower than corresponding means for untagged fish.

Group	Sample size	Total length (cm)	Weight (g)	U_{crit} (cm/s)
Untagged fish				
Total trials	24	63.2 (2.6)	383.2 (44.6)	86.2 (7.5)
Males	18	62.3 (2.2)	370.2 (39.5)	87.3 (7.5)
Females	6	65.9 (1.6)	422.2 (37.4)	82.9 (7.2)
Tagged fish				
Total trials	31	65.8 (3.4)	440.8 (57.5)	81.5 (7.0)*
Males	19	64.5 (2.7)	423.1 (44.0)	79.6 (7.1)*
Females	12	67.8 (3.4)	468.7 (66.6)	84.5 (5.7)

loglucosidase. For each sample period, we calculated mean values for all physiological variables and subjected them individually to analysis of variance (ANOVA). When the *F*-test was significant, we then used Dunnet's multiple comparison procedure to compare the means of fatigued fish at 0, 1, 4, 8, 12, and 24 h to the mean of resting control fish. Unless otherwise stated, the significance level for all tests was $\alpha = 0.05$.

Results

Critical Swimming Speed

In total, we attempted to swim 50 untagged lampreys for our U_{crit} tests. Of these, 24 successfully completed the test. Their mean lengths, weights, and U_{crit} estimates are shown in Table 1. In general, Pacific lampreys that successfully swam frequently searched for holdfasts and did not always orient to the current at low velocities. At progressively higher velocities, lampreys showed good rheotaxis and more directed swimming. All lampreys that did not complete a U_{crit} test showed aberrant behavior early during a test and seemed to concede to becoming impinged on the downstream screen. Differences in U_{crit} values were not significant between male and female lampreys ($t = -1.227$, $P = 0.2327$, df = 22), but females were significantly longer ($t = 3.606$, $P = 0.002$, df = 22) and weighed more ($t = 2.821$, $P = 0.010$, df = 22) than males. Simple linear regression indicated that the relation between total length and U_{crit} values was not significant for the range of lengths we tested ($r^2 = 0.15$, $P = 0.76$).

We attempted to estimate U_{crit} on a total of 48 radio-tagged lampreys. Of these, 31 fish successfully completed the test (Table 1). Based on our observations, the behavior of radio-tagged lampreys was similar to that of untagged fish and, in fact, we noted a lower failure rate in tagged than in untagged fish (i.e., 31 of 48 tagged fish completed the test versus 24 of 50 untagged fish). Differences in weight were not significant ($t = 2.304$, $P = 0.0286$, df = 29) between radio-tagged male and female lampreys. Although there were significant differences in length ($t = 2.980$, $P = 0.0058$, df = 29) between the male and female lampreys used in these tests, U_{crit} was not significantly related to total length ($F = 1.71$, $P = 0.3702$, df = 27).

Overall, the radio-tagged lampreys we used were significantly longer ($t = 3.06$, $P = 0.0035$, df = 53) and heavier ($t = 4.05$, $P = 0.0002$, df = 53) than the untagged fish. The mean U_{crit} of tagged fish (81.5 cm/s) was significantly lower than that of untagged fish (86.2 cm/s; $t = -2.37$, $P = 0.0213$, df = 53). Male tagged lampreys had a significantly lower mean U_{crit} (79.6 cm/s) than untagged males (87.3 cm/s; $t = -3.164$, $P = 0.0032$, df = 35), but females from the two groups did not differ in mean U_{crit} ($t = 0.492$, $P = 0.6294$, df = 16).

Physiological Responses

In untagged lampreys, blood pH dropped significantly ($P < 0.001$) right after completion of U_{crit} swimming tests but returned to levels similar to those of resting control fish for all other sample periods (Figure 1). Hematocrit in fatigued fish showed the opposite response, increasing significantly ($P < 0.01$) at time 0 and returning to values not different from controls for all other sample periods. Plasma glucose concentrations in lampreys subjected to U_{crit} swimming tests were highly variable among individuals and over time and did not differ between control and fatigued fish in any period. Plasma lactate concentrations were significantly ($P < 0.05$) elevated at 0 and 1 h after fatigue, but returned to levels not different from controls thereafter. Lactate concentrations showed relatively little variance, and the magnitude of maximum change at time 0 represented about a 40-fold increase.

In the muscle, lactic acid concentrations were significantly ($P < 0.01$) elevated immediately after fatigue but returned to levels similar to those of control fish by 1 h (Figure 2). The magnitude of maximum change represented about a 5-fold increase. Differences in muscle glucose levels were not significant between control fish and samples from fatigued fish in any period. In contrast, mus-

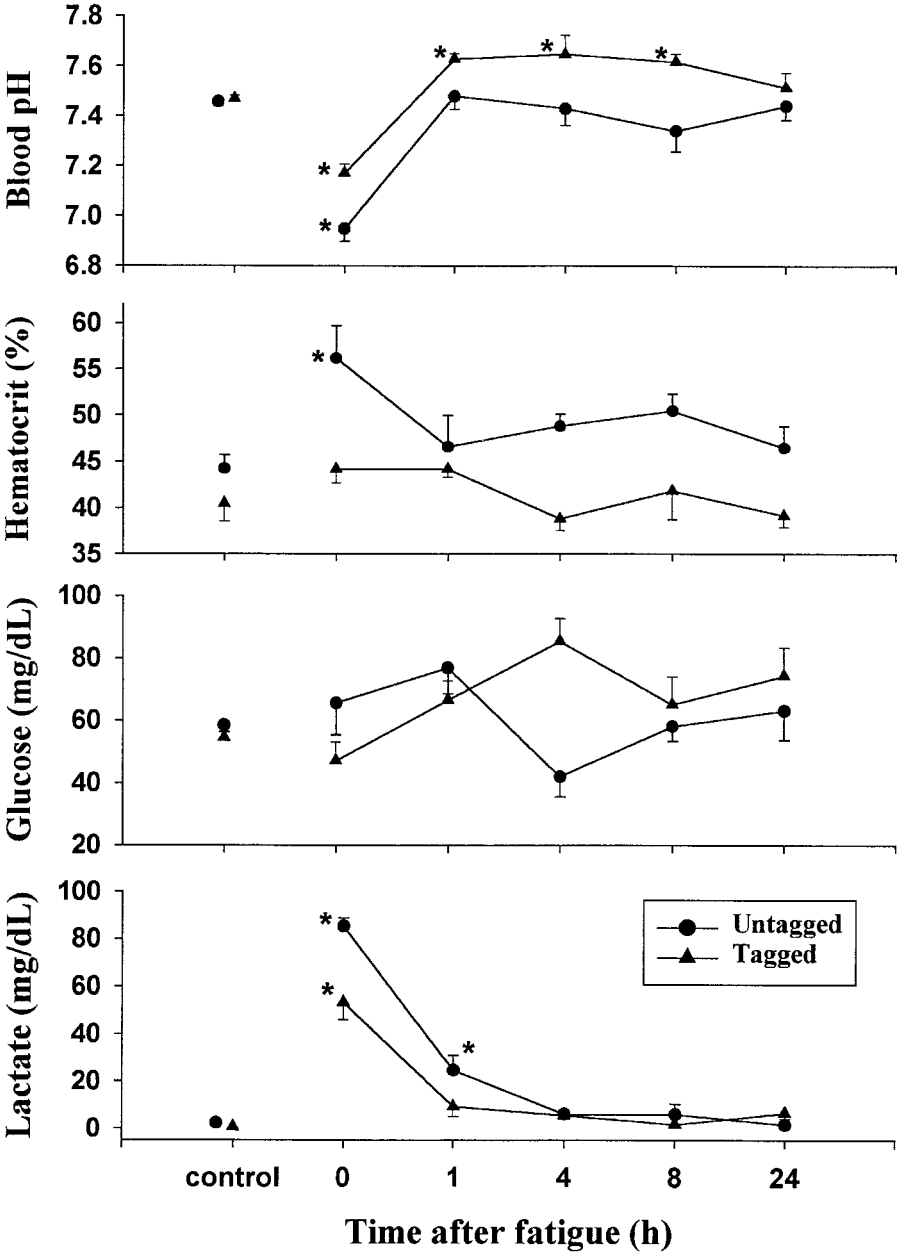

FIGURE 1.—Mean (±SE) blood pH, hematocrit, and concentrations of plasma glucose and lactate in untagged Pacific lampreys and those surgically tagged with radio transmitters after completing critical swimming speed tests leading to fatigue. Control samples are from groups of resting animals that were not exercised. Sample sizes were 4–6 fish/period for fatigued fish and 9–10 fish for control groups. Asterisks denote mean values that differed significantly ($P < 0.05$) from the control value of that group.

cle glycogen levels were significantly ($P < 0.01$) lower in exhausted fish for up to 1 h after fatigue and returned to levels similar to controls by 4 h. However, muscle glycogen concentrations from samples taken 4–24 h after fatigue, although not statistically different, were always about 10 μmol/g lower than the levels in resting fish.

In radio-tagged lampreys, blood pH in fatigued fish also dropped significantly ($P < 0.01$) relative to resting fish right after completion of U_{crit} swim-

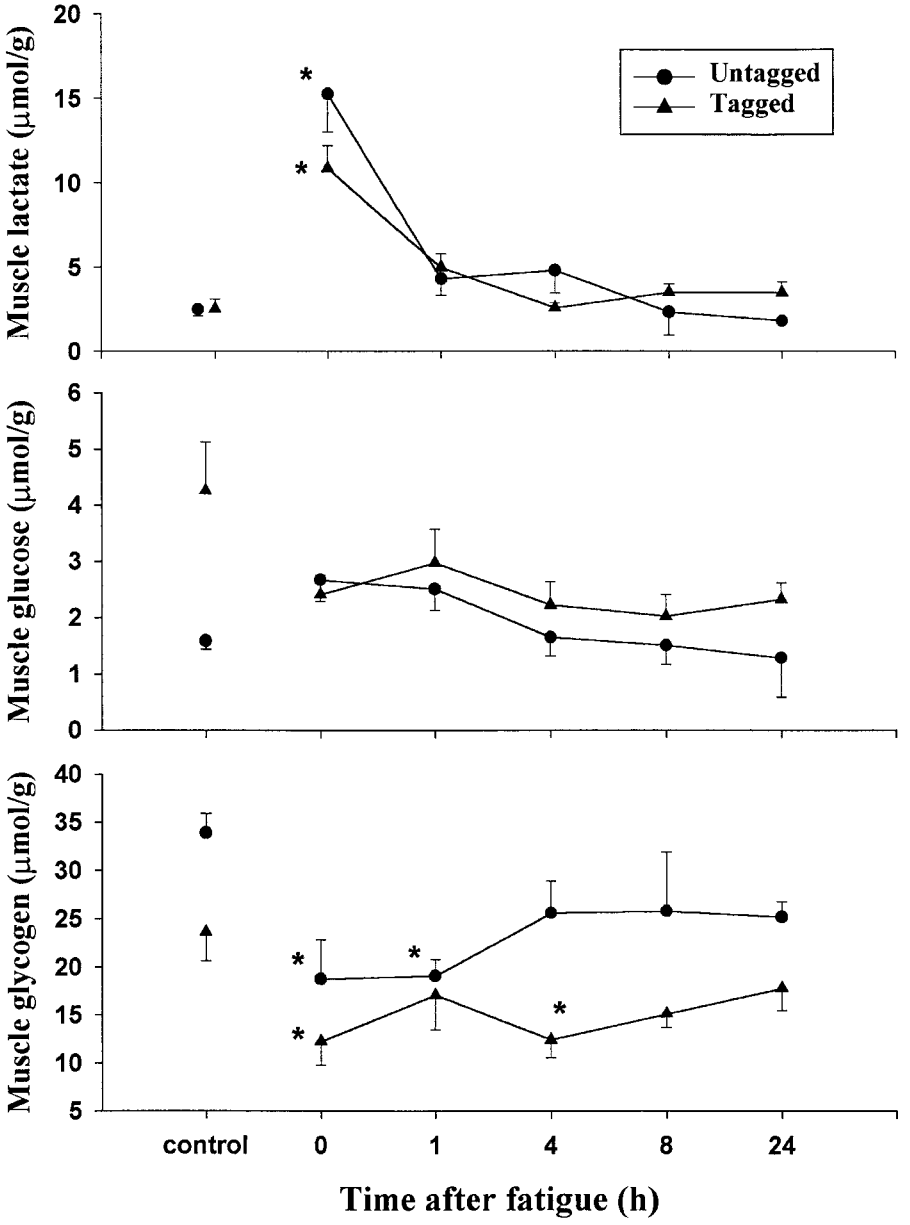

FIGURE 2.—Mean (±SE) muscle lactate, glucose, and glycogen levels in untagged and surgically tagged Pacific lampreys after completing critical swimming speed tests leading to fatigue. Control samples are from groups of resting animals that were not exercised. Sample sizes were 4–6 fish/period for fatigued fish and 9–10 fish for control groups. Asterisks denote mean values that differed significantly ($P < 0.05$) from the control value of that group.

ming tests (Figure 1). From 1 to 8 h after swimming, blood pH in fatigued fish increased and was significantly ($P < 0.05$) higher than the resting value but returned to a level similar to that of control fish at 24 h. Hematocrit in fatigued fish was slightly elevated for up to 1 h after swimming, but values at all periods never differed significantly from that of control fish. Like untagged fish, plasma glucose concentrations in radio-tagged lampreys subjected to U_{crit} swimming tests were highly variable among individuals and over time (Figure 1). Although glucose levels in fatigued fish

increased steadily for up to 4 h after swimming, differences were not significant between control fish and samples from fatigued fish in any period. Plasma lactate concentrations in radio-tagged fish were significantly ($P < 0.01$) elevated relative to controls immediately after fatigue but returned to levels not different from controls by 1 h (Figure 1). Lactate concentrations showed relatively little variance and the magnitude of maximum change at time 0 represented over a 100-fold increase.

In the muscle, lactic acid concentrations in fatigued radio-tagged fish showed a pattern similar to that seen in the plasma, becoming significantly ($P < 0.01$) elevated immediately after fatigue but returning to levels similar to those of control fish by 1 h (Figure 2). The magnitude of maximum change represented about a 4-fold increase. As in untagged fish, differences in muscle glucose levels were not significant between control fish and samples from radio-tagged fish in any period. In contrast, muscle glycogen levels were significantly ($P < 0.05$) lower in exercised fish at 0 and 4 h after fatigue but returned to levels similar to controls by 8 h. However, muscle glycogen concentrations from samples taken at 8 and 24 h after fatigue, although not statistically different, were always about 8–10 μmol/g lower than levels in resting fish.

Discussion

Our estimate of U_{crit} for untagged Pacific lampreys indicates that lampreys are poor swimmers compared with teleosts, and they may have difficulty negotiating fishways at dams in the Columbia River basin, which can have water velocities approaching 1.8–2.0 m/s. To our knowledge, our results are the first reported quantitative measures of the swimming performance of Pacific lampreys and represent an important benchmark towards understanding their basic biology and physiology. Critical swimming speed is a frequently used measure of swimming performance in fishes and has often been used to assess the effects of various stressors (Little and Finger 1990; Adams et al. 1998). Further, U_{crit} is presumed to be a relatively close measure of the maximum aerobic capacity of fish (Hammer 1995). Thus, at speeds close to or above U_{crit}, there is an increasing contribution by anaerobic metabolism to swimming performance. Although the highest levels of exercise performance are achieved anaerobically and can only last for brief periods, the consequences of forays into anaerobically fueled swimming performance and subsequent fatigue may be serious and include depletion of energy reserves, physiological dysfunction, and even death (Wood et al. 1983; Wang et al. 1994; Milligan 1996). Such consequences may be especially important for Pacific lampreys, which initiate their upstream migrations with a finite amount of energy reserves and thereafter cease to feed. Although our U_{crit} estimates for Pacific lampreys represent an important first step toward understanding their capacity for exercise, more information is needed on their use of saltatory swimming (i.e., holding fast combined with short, rapid swimming events). Information on continuous and saltatory swimming by Pacific lampreys would lead to a more complete understanding of the behavior and energetics of their upstream movements and seems prerequisite to assessing how strenuous their migration might be in the wild.

Surgically implanting a radio transmitter in the body cavity of adult Pacific lampreys had signficant but minor effects on their swimming performance as measured by U_{crit} tests. Other studies evaluating the effects of surgically implanted telemetry transmitters on swimming performance in fishes have shown mixed results, some reporting reduced swimming performance in tagged fish (Peake et al. 1997; Adams et al. 1998) and others reporting no effects (Mellas and Haynes 1985; Moore et al. 1990; Brown et al. 1999; Thorstad et al. 2000). Discrepancies between studies are at least partially due to species, size differences, and the ratio of transmitter to fish weight used. The tag ratio (i.e., [tag weight/fish weight] × 100) used in our study was commonly less than 1%. Overall, radio-tagged lampreys had a significantly lower mean U_{crit} (81.5 cm/s) than untagged fish (86.2 cm/s), the difference being manifested solely by the relatively poor performance of small-sized tagged males. Because none of the fish we used in our study were sexually mature, we consider the poor performance of small fish to be a size rather than gender effect. However, although we believe the difference in performance between tagged and untagged fish was due to a combination of surgery and fish-size effects, we cannot rule out the possibility of a time effect because we tested tagged and untagged fish in two different years. Nevertheless, we surmised that the influence of a year effect on our results would be minor for the following reasons: (1) all fish were collected from the same place during the same time in each year; (2) adult Pacific lampreys are sexually immature for nearly a full year after they start their upstream migration; (3) the majority of fish were tested between July and October in each year; (4) untagged

fish tested in September and October of 1999 had higher muscle glycogen levels than tagged fish tested in July and August of 2000, suggesting that differences in holding had minimal influence on energy reserves; and (5) there was no temporal trend in swimming performance for fish tested early in a year compared with those tested later. Regardless, we recommend that Pacific lampreys be at least 65 mm long (i.e., the size of the males used in our study) if they are to be surgically implanted with transmitters about the size we used. Because of the increasing popularity of radiotelemetry studies for assessing the behavior and physiology of fish in the wild, more research assessing the effects of tagging procedures on lampreys seems warranted.

The physiological responses of tagged and untagged lampreys subjected to exhaustive exercise included decreases in blood pH of 0.3–0.5 units, a 40% decrease in muscle glycogen levels, a 22% increase in hematocrit for untagged fish only, and increases in muscle (4–5-fold) and plasma lactate (40–100-fold) concentrations. These physiological changes were significant when compared with resting control fish and usually returned to resting levels within 1–4 h after fatigue. Our results indicate that failure of an individual to continue swimming towards the end of a test was a result of physiological fatigue and not due to a behavioral refusal to swim. Our results also indicate that Pacific lampreys can recover quickly from a single exposure to a U_{crit} test resulting in fatigue. However, we do not know how lampreys would respond to multiple bouts of exhaustive stress, which seem likely to occur in the wild.

The immediate drop in blood pH in tagged and untagged Pacific lampreys is within the range reported for more phylogenetically advanced teleosts and for sea lampreys subjected to exhaustive exercise (Wood 1991; Tufts 1991). Such a severe extracellular acidosis in the blood is usually attributed to increases in PCO_2 given off from tissues and increases in $[H^+]$ and [lactate] leaking from muscles. Although the blood pH of untagged lampreys recovered to a level similar to that of controls by 1 h (as observed in other fishes by Tufts 1991 and Wilkie et al. 1998), tagged fish overshot the pH of control fish and maintained elevated blood pH for up to 8 h after exercise. The reasons for elevated blood pH in tagged lampreys for several hours after exhaustive exercise are unknown but may be related to postsurgical effects or the development of a relative metabolic alkalosis after the initial recovery from exhaustion (Milligan et al. 2000).

The increase in hematocrit immediately after exhaustive exercise in our untagged lampreys is also fairly typical of fish subjected to exhaustion (Wood and Perry 1985). There are several possible contributing factors, including (1) a splenic release of red blood cells, (2) swelling of red blood cells, and (3) a hemoconcentration due to diuresis and plasma water moving into the intracellular compartment. This large fluid shift from the extracellular to the intracellular compartment is probably due to a large osmotic gradient within muscle cells created by a high concentration of lactate. The net effect of this increase in hematocrit, along with the typical increases in hemoglobin and plasma protein, is that the O_2- and CO_2-carrying capacities and buffer capacity of the blood are all enhanced (Wood and Perry 1985). That our radio-tagged fish showed no significant changes in hematocrit following exercise may be due to the trauma (shock) resulting from surgery (Summerfelt and Smith 1990), but the exact mechanisms involved remain unclear.

Plasma glucose concentrations in tagged and untagged Pacific lampreys showed no distinct trend after exposure to exhaustive stress, were highly variable among individuals, and never differed from control values. Other studies have also shown variability in plasma glucose levels in teleosts subjected to exhaustive exercise (Hammond and Hickman 1966; Pagnotta and Milligan 1991; Wang et al. 1994). Our findings contrast with those of Fitzpatrick et al. (1996) who found that glucose levels in Pacific lampreys were significantly elevated for various periods after a 5-min dewatering stress or surgical implantation of radio transmitters. They stated that they confirmed the use of plasma glucose as a clinical indicator of stress in Pacific lampreys, but our results do not completely support this evidence and suggest that the response of glucose in lampreys may be stressor dependent. This requires more study.

The response of plasma lactate to exhaustive exercise in Pacific lampreys was, in terms of the magnitude of maximum change, within the range reported for other species (Tufts 1991). Notably, after exhaustive exercise the untagged lampreys in our study had higher plasma [lactate] (about 10 mmol/L) than did sea lampreys (5.6 mmol/L; Tufts 1991), whereas our tagged lampreys had peak [lactate] similar to sea lampreys. All groups showed similar recovery dynamics and cleared lactate from the blood in about half the time reported for

rainbow trout *Oncorhynchus mykiss* following exhaustion (Wang et al. 1994; Milligan 1996). The reasons for our untagged fish having a peak [lactate] almost twice that of tagged fish and also having a longer recovery time are unknown, but we offer two possible explanations. (1) As with any of the physiological differences we observed between tagged and untagged fish, there may be unknown effects related to the trauma of surgery that affected the response of tagged animals to exhaustion. (2) Tagged fish, because they had a significantly lower U_{crit}, may not have achieved a similar state of exhaustion as untagged fish and perhaps produced less of a lactate load.

The responses of muscle lactate and glycogen to exhaustive exercise in our fish differed somewhat from the responses of other fish. For example, peak muscle [lactate] in our fish was lower and recovery of lactate levels was faster compared with other fish species subjected to exhaustive exercise (Wood 1991; Boutilier et al. 1993). Also, muscle [glycogen] in our fish remained low (though not always significantly) for 24 h following exercise, a result not commonly reported for other fishes. Such differences in muscle lactate and glycogen kinetics are at least partially due to the type of exhaustive stressor used in different studies (i.e., chasing fish to exhaustion versus swimming them to exhaustion). Most studies have chased fish to exhaustion, which has some psychological aspects of stress associated with it, results in fatigue within a few minutes, may require more anaerobic metabolism from fish than a U_{crit} test, and could therefore produce greater amounts of metabolites or different recovery dynamics. Because of (1) the different methodologies used, (2) the numerous factors that can influence the anaerobic capacity and recovery patterns in fish (Kieffer 2000), and (3) new information on the influence of easy swimming enhancing the physiological recovery of fish from fatigue (Milligan et al. 2000), there are still many opportunities for studying and comparing the responses of fish to exhaustive exercise.

In summary, adult Pacific lampreys had a mean critical swimming speed of about 85 cm/s, which suggests that they may have difficulty negotiating fishways with high current velocities. Surgically implanting radio transmitters elicited a small, but significant, decrease in their swimming performance. The physiological responses of tagged and untagged lampreys to exhaustive exercise were generally similar to those of teleosts and sea lampreys. Notable exceptions were that Pacific lampreys produced a relatively small amount of lactate in the muscle, restored plasma and muscle lactate to control levels within 1–2 h, and maintained low levels of muscle glycogen for up to 24 h after fatigue.

Acknowledgments

We are grateful for the technical and editorial assistance of Lisa Weiland. We thank personnel from the National Marine Fisheries Service for providing us with fish captured at Bonneville Dam. This research was funded by the U.S. Army Corps of Engineers under the administrative guidance of Mike Langeslay. Mention of trade names does not constitute endorsement by the U.S. government.

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