Environmental Biology of Fishes (2006) 75:167–171
DOI 10.1007/s10641-005-4698-7

Swimming behaviour of juvenile Pacific lamprey, *Lampetra tridentata*

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Received 15 February 2005 Accepted 2 November 2005

Key words: hydroelectric dam passage, agnatha

Synopsis

We collected actively migrating juvenile Pacific lamprey *Lampetra tridentata* [Richardson, J. 1836. Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under the command of Sir John Franklin. R.N., Fauna Boreali-Americana, 327 pp.] from hydroelectric bypass facilities in the Columbia River and transferred them to the laboratory to study diel movement patterns and swimming ability. Volitional movement of lamprey was restricted mainly to night, with 94% of all swimming activity occurring during the 12 h dark period. Burst speed of juvenile lamprey (mean length 136 ± 5 mm SD) ranged from 56 to 94 cm s^{-1} with a mean of 71 ± 5 SD cm s^{-1} or an average speed of 5.2 s^{-1} body lengths (BL). Sustained swim speed for 5 min test intervals ranged from 0 to 46 cm s^{-1} with a median of 23 cm s^{-1}. Critical swimming speed was 36.0 ± 10.0 SD cm s^{-1} and 2.4 ± 0.6 SD BL s^{-1}. We found no significant relationship between fish length and critical swimming speed. These findings show that swimming performance of juvenile Pacific lamprey is low compared to anadromous teleosts. Their poor swimming ability provides a challenge when they encounter man-made structures and reservoirs during the freshwater migration interval downstream to the Pacific Ocean.

Introduction

Pacific lamprey (*Lampetra tridentata*) is the largest and most abundant lamprey species in the Snake and Columbia Rivers (Wydoski & Whitney 2003). They are parasitic as adults in the ocean, migrate into freshwater to spawn, and their larvae develop in the gravel–mud substrate for several years before migrating downstream as young adults. Principal spawning and rearing habitat of Pacific lamprey occur in tributary streams (Kan 1975), with use of the mainstem Columbia River corridor mainly limited to periods of adult and juvenile migration.

There has been a widespread decline in the number of Pacific lamprey returning to the Columbia River system since the 1960s. This decline has been attributed to various factors including habitat loss, water pollution, ocean conditions, and dam passage.[1] Operations at mainstem hydropower projects in the Columbia and Snake Rivers are a key concern because juvenile lamprey swim low in the water column during downstream migration (Long 1968) and are likely to encounter hydropower turbines. A related issue is impingement of juvenile lamprey on barrier screens placed at hydroelectric projects to bypass downstream migrant salmon and steelhead into

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[1] Close D.A., M. Fitzpatrick, H. Li, B. Parker, D. Hatch & G. James. 1995. Status report of the Pacific lamprey (*Lampetra tridentata*) in the Columbia River Basin. Prepared for the U.S. Department of Energy, Bonneville Power Administration, Portland, Oregon.

collection facilities.[2] Both issues may be related to lamprey swimming ability (Moursund et al. 2003). Additional information on their behaviour is important because of a recent petition to list all four species of lamprey in the Columbia River drainage for protection under the U.S. Endangered Species Act.

To address juvenile Pacific lamprey protection issues, we characterized their diel movement patterns and documented the sustained and burst swimming speeds of downstream migrants. Sustained and burst swimming may be used by lamprey when actively migrating, encountering engineered structures, and responding to predators. Knowledge of lamprey swimming behaviour can be used to develop mitigation strategies for downstream passage, including design of bypass systems at hydroelectric facilities and for irrigation diversion structures.

Materials and methods

Fish conditioning

We conducted laboratory tests in April and June 1999, 2000, and 2002 using juvenile lamprey obtained at diverted and trapped from bypass fish facilities at John Day and McNary Dams on the lower Columbia River. All specimens were actively migrating downstream and in Stage 7 of metamorphosis (Youson & Potter 1979). Test fish ranged from 110 to 165 mm in total length; their mean length was 136 ± 15 mm (SD). We held fish in a non-feeding state under experimental lighting and thermal conditions for 2–8 weeks prior to testing.

Diel behaviour

To observe group behaviour, we placed 20 fish in each of two 50 l glass tanks (94 cm wide × 63.5 cm deep × 47 cm high), supplied with 10°C river water at a flow rate of 20 l h^{-1}. We conducted tests under static hydraulic conditions with cobble substrate. The tank was top-lit with infrared lights (880 nm wavelength; 60 W) to record night-time swimming events. Tests were on a 12 h light-and-dark cycle with a 20 min transition period. We video-taped continuously over four consecutive days with a time-lapsed video tape recorder (0.6 s frame interval). We recorded the location and activity (i.e., whether fish were attached or swimming) of lamprey at 15 min intervals.

We also conducted tests with individuals to determine if the presence of other lamprey influenced fish response to light. We placed a single fish into 50 l glass tanks with cobble substrate and acclimated them for 12 h before testing. We documented their behaviour continuously over 24 h using time-lapsed video. We tested a total of 24 lamprey.

Swim speed

We measured burst speed of individual lamprey in still water (20 cm deep) in a 20 cm wide by 300 cm long Fiberglas trough. Water temperature was 12°C and the water depth was 10 cm. We initiated the test by placing a lamprey into the trough, allowing it to acclimate for 3 min, then inducing it to swim by squirting a stream of water at it through a pipette. Each fish was allowed to rest for 3 min before it was stimulated again. This process was repeated five times per fish for a total of 30 individual lamprey. Each swimming event covered a distance of ~100 cm. Video was collected at a 0.33 s frame interval using an overhead video camera. The maximum burst speed was determined as the fastest run measured within a 10-frame (0.33 s) interval. Mean burst speed was the mean of five individual lamprey trials. There was no evidence of habituation to the probe (i.e., no trend in swim speed over the five trials).

To measure sustained swim speed, we first had to deal with the general unwillingness of juvenile lamprey to volitionally swim in an open channel. We placed a 40 cm diameter × 115 cm long × 5 mm nylon mesh swim tube inside a 2200 l Brett-type respirometer (swim chamber) to form a conduit that lamprey could not attach to. The tube was then electrified with wire woven into the mesh to prevent fish from resting at the back of the tube. This setup allowed us to test lamprey that swam continuously. Voltage and current of the electrified

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[2] Hatch, D. & B. Parker. 1998. Lamprey research and restoration project. In Part (B) Abundance monitoring for Columbia and Snake Rivers of 1996 Annual Report. Prepared for U.S. Department of Energy, Bonneville Power Administration, Portland, Oregon.

portion were regulated to 5 V and 0.6 A DC. We placed individual lamprey in the swim tube at 0 cm s^{-1} for 15 min prior to testing. The starting water velocity for testing was 15 cm s^{-1}. Velocity was increased at 15 cm s^{-1} intervals every 5 min until lamprey became fatigued. The 5 min duration was based on range-finding tests where lamprey refused to swim volitionally for longer than 10 min. Fatigue was defined as when fish became impinged on the downstream part of the swim tube and could not free itself. Each test series consisted of 30 fish each during 1999 and 2002. We observed and recorded swimming behaviour at night using infrared light.

We calculated critical swimming speed (U_{crit}) using the formula of Brett (1964)

$$U_{\text{crit}} = u_1 + (t_{\text{i}}/t_{\text{ii}} \bullet u_{\text{ii}})$$

where u_1 is highest velocity maintained for the prescribed period (cm s^{-1}); u_{ii} is velocity increment (cm s^{-1}); t_1 is time (min) fish swam at the 'fatigue' velocity; t_{ii} is prescribed period of swimming (min). To determine if U_{crit} varied between the 2 years, we used a two-sample *t*-test because data were normally distributed.

Results

Diel behaviour

During group tests, volitional movement of juvenile lamprey was restricted mainly to night, with 94% of all swimming activity occurring during the 12 h dark period. Swimming activity was greatest in the early evening and gradually declined through the night (Figure 1). Fish had a strong preference for substrate, remaining near the bottom of test aquaria during daylight hours.

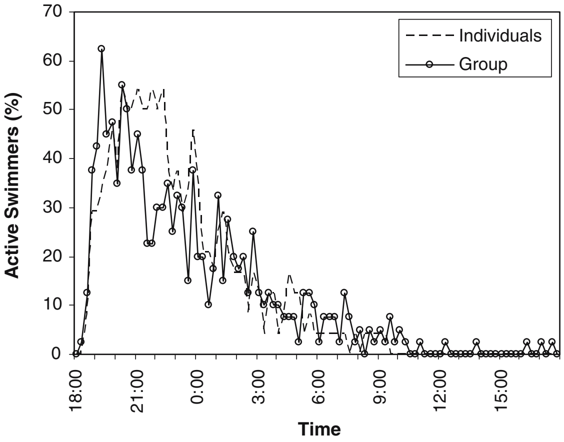

Figure 1. Diel activity patterns for juvenile Pacific lamprey, *Lampetra tridentata*, (all tests combined). The dark period begins at 18:00 h and ended at 06:00 h.

Typical behaviour for an individual lamprey was to attach during daylight hours, then to initiate swimming activity within 15 min of darkness. Swimming was not continuous. Of the 24 fish tested, 4 (16%) remained attached during the entire 12 h dark period. The remaining 20 fish swam an average of 3 h each during the dark period. The activity pattern of individual fish comported with that of groups (Figure 1).

Swim speed

There was no significant difference between years when swim speed data were compared either as body length (BL) s^{-1} ($p = 0.86$) or cm s^{-1} ($p = 0.63$); thus we pooled data. Burst speed of juvenile lamprey ranged from 55 to 94 cm s^{-1} with a mean of 71 ± 5 SD cm s^{-1} (Figure 2). This speed equated to an average speed of ~5.2 BL s^{-1}. There was no significant difference between fish length and either mean ($R^2 = 0.025$, $p = 0.40$) or maximum ($R^2 = 0.037$, $p = 0.31$) burst swimming speed of juvenile lamprey over the lengths tested.

Sustained swim speed ranged from 0 to 46 cm s^{-1} with a median of 23 cm s^{-1}. Swimming endurance decreased slightly as velocities were increased from 15 to 30 cm s^{-1}, then rapidly decreased at velocities of > 46 cm s^{-1}. The U_{crit} of juvenile lamprey was 36.0 ± 10.0 SD cm s^{-1} and 2.4 ± 0.6 SD BL s^{-1}. Within the range of sizes sampled, there was

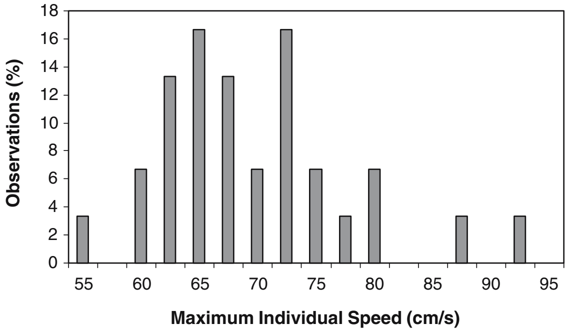

Figure 2. Distribution of burst speed values for individual Pacific lamprey, *Lampetra tridentata* ($n = 30$).

no significant relationship between the length of fish and their critical swimming speed (Durbin–Watson, $p = 0.94$, $R^2 = 0.0001$, 49 df).

Discussion

Juvenile Pacific lamprey were highly nocturnal during the laboratory studies, with $>90\%$ of their activity restricted to hours of darkness. This diel behaviour was consistent with movement patterns of downstream migrant juvenile Pacific lamprey passing hydroelectric dams in the lower Columbia River. For example, Long (1968) reported 62% of downstream migrating Pacific lamprey passed the Dalles Dam powerhouse at night. Potter & Huggins (1973) noted juvenile river lamprey, *L. fluviatilis*, also migrated downstream predominately at night. Adult Pacific lamprey migrate upstream in the Columbia River mainly at night (Moser & Close 2003).

Juvenile lamprey spent a high percentage of the time attached to objects during daylight hours. This behaviour suggests a need for them to manage energy reserves during downstream migration. Beamish (1974) speculated that absence of a hydrostatic organ required additional expenditure of energy by sea lamprey, *Petromyzon marinus*, to maintain their position in the water column. Having no pectoral fins and having a proportionately higher number of body segments involved in movement could also result in higher energetic costs (Webb 1975). For example, lamprey lack paired fins which produce upward lift forces for some non-teleosts (Alexander 1990). In addition, the reduced caudal fin of lampreys may not be well adapted for propulsion through the water column (Beamish 1974).

Given these limitations, it is not surprising that burst speeds of juvenile lamprey were low compared to most other fishes, particularly relative to body length. Elvers of American eel, *Anguilla rostrata*, a teleost having a similar anguilliform shape, have reported burst speeds of up to 7.5 BL s^{-1} (McCleave 1980) or almost 50% higher than juvenile lamprey. Both eel and lamprey swim by lateral undulatory movement (Sigvardt 1989). This style is thought to be relatively inefficient compared to other biomechanical modes of swimming (Lindsey 1978, Webb 1988). In contrast to eel, juvenile Pacific lamprey swim downstream or with the river current when migrating to the Pacific Ocean. Critical swim speeds of juvenile lamprey were only 40% of those reported by Mesa et al. (2003**)** for adult Pacific lamprey that migrate upstream to spawn.

The weak swimming ability of juvenile lamprey suggests they could be challenged by a lengthy migration to the Pacific Ocean. One issue is that 87% of riverine habitat in the Columbia River has been lost due to hydroelectric development (Dauble et al. 2003). Thus, juvenile lamprey must now migrate downstream through a series of slack-water reservoirs. These habitat alterations have lengthened the time required for juvenile salmon to get to the Pacific Ocean (Raymond 1979). Migration timing of juvenile lamprey would also be expected to be affected. A related issue is when juvenile lamprey encounter intake screens or other in-water structures at designed to collect debris or bypass fish at dams. For example, the mean burst speed of juvenile lamprey is less than the average perpendicular velocity (~1.0 m s^{-1}) at the face of some extended length submersible bar screens that divert juvenile salmonids from operating turbines on the lower Columbia River. Field observation has shown high rates of impingement under certain conditions (Moursund et al. 2003).

In conclusion, the early life history of juvenile Pacific lamprey evolved under a different set of conditions than what is now present in the Columbia River system. Changes to the aquatic ecosystem extend from the estuary to the Continental Divide. The ability of Pacific lamprey populations to respond to these changes is, in part, limited because of their poor swimming ability and should be considered in mitigation planning and/or population recovery strategies.

Acknowledgements

This study was funded by the U.S. Army Corps of Engineers, Portland District. Scott Abernethy and Robert Mueller provided able assistance in the laboratory. We also thank Mike Langeslay and Paul Ocker for their support.

References

Alexander, R.M. 1990. Size, speed, and buoyancy adaptations in aquatic animals. Am. Zool. 30: 189–196.

Beamish, F.W.H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. T. Am. Fish. Soc. 104: 355–358.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183–1226.

Dauble, D.D., T.P. Hanrahan, D.R. Geist & M.J. Parsley. 2003. Impacts of the Columbia River hydroelectric system on main-stem habitats of fall Chinook salmon. North Am. J. Fish. Manage. 23: 641–659.

Kan, T.T. 1975. Systematics, variation, distribution and biology of lampreys of the genus Lampetra in Oregon. Ph.D Thesis, Oregon State University, Corvallis, Oregon 194pp.

Lindsey, C.C. 1978. Form, function, and locomotory habits. *In*: W.S. Hoar & D.J. Randall, (eds), Fish Physiology, (Vol. 7), Academic Press, New York pp. 1–100.

Long, C.W. 1968. Diurnal movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fish. Bull. 66: 599–609.

McCleave, J.D. 1980. Swimming performance of European eel (*Anguilla anguilla* (L.)) elvers. J. Fish Biol. 16: 445–452.

Mesa, M.G., J.M. Bayer & J.G. Seelye. 2003. Swimming performance and physiological responses to exhaustive exercise in surgically tagged and untagged Pacific lampreys. T. Am. Fish. Soc. 132: 483–492.

Moser, M.L. & D.A. Close. 2003. Assessing Pacific lamprey status in the Columbia River basin. Northwest Sci. 77: 116–125.

Moursund, R.A., D.D. Dauble & M.J. Langeslay. 2003. Turbine intake diversion screens; investigating effects on Pacific lamprey. Hydro Rev. XXII(1): 40–46.

Potter, I.C. & R.J. Huggins. 1973. Observations on the morphology, behaviour, and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. (London). 169: 365–379.

Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. T. Am. Fish. Soc. 108: 505–529.

Richardson, J. 1836. The fish. *In*: Fauna Boreali-Americana; or the zoology of the northern parts of British America: Containing descriptions of the objects of natural history collected on the late northern land expeditions, under the command of Sir John Franklin. R.N., Fauna Boreali-Americana, 327 pp.

Sigvardt, K.A. 1989. Spinal mechanisms in the control of lamprey swimming. Am. Zool. 29: 19–35.

Youson, J.H. & I.C. Potter. 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 57: 1808–1817.

Webb, P.W. 1975. Hydrodynamics and energetics of fish propulsion. B. Fish. Res. Board Can. 190: 1–158.

Webb, P.W. 1988. Simple physical principles and vertebrate aquatic locomotion. Am. Zool. 28: 709–725.

Wydoski, R.S. & R.R. Whitney. 2003. Inland Fishes of Washington, 2nd edition, University of Washington Press, Seattle, Washington 322 pp.