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EFFECTS OF SUBMERGENCE DEPTHS ON SWIMMING CAPACITY OF SEA LAMPREY

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ABSTRACT

Invasive sea lamprey (*Petromyzon marinus*) is a fish parasite that has damaged the Great Lakes ecosystem. In-stream barriers that prevent upstream passage during migration can help reduce populations of sea lamprey. Exploring their swimming kinematics will help us understand how lamprey navigate across barriers at various water depths. I recorded attempts of sea lampreys to cross wetted ramps varying in water depth from 1 to 7 cm and used video analysis to examine their swimming mode. I found that at the shallowest depth, amplitude and frequency of body undulations were increased, but swim speed was not. I conclude that swimming capacity was reduced in the shallowest treatment. My findings suggest that a lamprey barrier with shallow water could block sea lamprey but allow native fin-fish species to pass upstream.

INTRODUCTION

The Great Lakes contain 20% of the freshwater on Earth and support diverse and ecologically productive aquatic and terrestrial ecosystems. Improved transportation throughout the watershed has facilitated the introduction of non-indigenous species that have negatively affected freshwater lakes, rivers, and riparian zones throughout Michigan. An organism that has caused the decline of native, socioeconomically important fish species such as lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus*)
*clupeaformis* is the Atlantic sea lamprey (*Petromyzon marinus*). Sea lampreys are parasitic fish that use a sucker-like mouth to attach to the sides of fin-fish (McLaughlin et al., 2003). Food web disruptions caused by sea lamprey are common since they often devastate populations of apex predators (Cuhel et al., 2013).

To protect remaining native fish communities, an international, collaborative effort between government agencies and research institutions has focused on ecological management to reduce and potentially eliminate sea lamprey in the Great Lakes (Christie & Goddard, 2000). Although treatment of freshwater streams with chemical lampricides has been effective at reducing lamprey populations in certain areas, physical barriers are needed to reduce costs and harmful effects of lampricides on non-target organisms. Since sea lamprey are anadromous, the intentional fragmentation of aquatic ecosystems is often utilized to prevent access to spawning habitats and areas critical to other stages of their life history (Rahel, 2013).

A challenge for conservation biologists has been limiting the spread of undesirable species in their invaded ranges. In addition to lampricides and releases of sterile male lamprey, a current sea lamprey management strategy is a trapping program compatible with in-stream barriers (Dawson et al., 2017). Barriers may contain a fish passage device to allow fish to navigate around the barrier and continue upstream movement. Currently in use are weir-and-pool low-head barriers that allow passage of jumping fishes, but restrict movement of fish that cannot jump (Pratt et al., 2007). To minimize disturbance during the remainder of the year, many barriers operate seasonally and have increased crest heights during peak sea lamprey migration (McLaughlin et al., 2007). Ramps with vertical pegs in a uniform arrangement known as eel-ladder-style traps have effectively sorted sea lamprey from fin-fish, but further study is needed to improve overall trap efficiency (Reinhardt & Hrodey, 2014). In addition, dams that no longer serve their original purpose are often repurposed as sea lamprey barriers.

Physical layouts of barriers vary widely but most aim to reduce the connectivity of aquatic habitats on a local level (Rahel, 2013). Ecological fragmentation caused by barriers, however, can negatively affect native migratory fish by delaying or preventing their
migrations. Trap-and-sort areas allowing management personnel to separate sea lampreys from native fishes are often found at funnel traps and vertical-slot fishways, but automated fish sorting at barriers would reduce the need for manual sorting and improve human safety. An understanding of the behavior or swimming ability of sea lamprey and native fin-fish would provide insight into what differing swimming characteristics could be used to design a species-selective barrier that blocks sea lamprey, but allows passage to native fin-fish (Rahel, 2013; Reinhardt, 2010). A proof-of-concept study was conducted by Sherburne and Reinhardt (2016).

In contrast to carangiform or subcarangiform swimming of many native fin-fish, sea lamprey swim in the anguilliform mode characterized by left-right body wave undulations that increase in amplitude as they approach the caudal fin (Wiens & Nahon, 2012; Sfakiotakis et al., 1999). When fully submerged, anguilliform swimming in sea lamprey is less efficient than that of native, migratory Great Lakes fish (Katopodis et al., 1994; Tytell & Lauder, 2004) but its efficiency has not been studied thoroughly at the air/water interface or in partially submerged organisms. Analyses of basic kinematic parameters during aquatic locomotion may further our understanding of swimming in shallow water. The purpose of the present experiment was to investigate the effects of submergence depth on sea lamprey swimming ability. Sea lamprey swimming ability was examined by determining tail-beat frequencies, tail-beat amplitudes and swimming velocities of sea lampreys as they proceed across a fish passage device submerged at three depths. In this study, I hypothesize that shallow water will impede the swimming ability of sea lamprey. In the future, we will perform kinematic analyses on native fin-fish to compare swimming ability to that of sea lamprey.

**METHODS**

Adult migratory-phase sea lampreys (*Petromyzon marinus*) were collected in June 2016 from traps located in Michigan’s Ocqueoc and Cheboygan rivers and the Carp Lake Outlet, a tributary to Lake Michigan. Animals were transferred by the U.S. Fish and Wildlife Service to the Hammond Bay Biological Station in Millersburg, Michigan, where they were measured and
equipped with reflective fin clip tags. Lampreys were held in 500 gallon tanks containing 6-12 °C water pumped from Lake Huron by a flow-through system.

Sea lampreys were placed into the main fish passage device, which consisted of a 1 m x 0.3 m flattened surface, attached to a viewing platform. Two holding tanks were positioned on either side of the viewing platform to house the lampreys during trials. Lampreys began each trial in the downstream holding tank. A pump upstream of the viewing platform provided sufficient water flow. Plastic netting was adhered to the sides of the viewing platform channel to prevent animals from escaping. Depth of the fish passage device was controlled by adjusting the height of the viewing platform on the raceway. The submergence depths tested were 7 cm (fully submerged), 3 cm (partially submerged), and 1 cm (shallow depth).

Each trial lasted two hours and was filmed in darkness to simulate the conditions encountered by sea lamprey during their natural upstream migration. Sea lamprey swimming behavior was recorded at 90 frames per second under infrared lighting with an IR-sensitive video camera positioned above the center of the viewing platform. Dark markings every 0.1 m on the flattened viewing platform provided a scale, and each 0.1 m x 0.3 m segment was numbered 1-10, from left to right. The fin clip tagging arrangement allowed us to identify and monitor one untagged and three tagged individuals per trial.

Adobe Premier Pro was used to sort videos by submergence depth and to view them frame-by-frame on a digital monitor. Videos demonstrating erratic swimming were excluded and only those of animals swimming in a straight trajectory were analyzed. To correct for video playback distortion on either side of the viewing platform, distortion factors were calculated using the lengths and widths of each segment in three sections: left (segments 1-3), middle (segments 4-7) and right (segments 8-10). Segments were measured on-screen with a digital caliper and the average values of each section were compared to measurements of the physical fish passage device. At each section, three measurements were made. Swimming velocity was determined by counting the number of
Figure 1: Screen capture images of sea lamprey swimming. A. Location of tail-beat amplitude and tail-beat frequency measurements. B. Tip-of-snout location for velocity measurements.
frames needed for the lamprey’s tip of the snout to travel forward through a measured distance in one segment. A tailbeat cycle was defined as the tail moving from one side of the body to the other side, then returning to the same side in a propulsive wave. Tailbeat frequency was determined at each section by counting the number of frames required for the completion of one tailbeat cycle and comparing it to the duration. Tailbeat amplitude was calculated by measuring the distance between the maximum lateral displacements of the tail during a tailbeat cycle (Figure 1).

The effects of fish passage device submergence depth on body wave frequency and body wave relative amplitude (amplitude/body length) were determined using 1-way ANOVA. Statistical significance was assumed at p<0.05 for all analyses. Linear regressions were used to examine relationships between velocity and tail-beat frequencies and amplitudes (using VassarStats.net).

RESULTS

Tail-beat frequency and relative tail-beat amplitude (amplitude/body length) varied with fish passage device submergence depth (Figure 2 and Figure 3). The mean frequency of body waves was 2.54 Hz (±0.46 SD, n=7) in 1 cm submergence. In 3 cm, the mean frequency was 1.59 Hz (±0.32, n=14), while...
at 7 cm it was 1.41 Hz (±0.28, n=15). Mean relative tail-beat amplitude in 1 cm depth was 0.11 (±0.02, n=7). At 3 cm and 7 cm, mean relative amplitudes were 0.08 each (±0.02, n=14 and ±0.01, n=15). Tail-beat frequencies and relative tail-beat amplitudes were higher in the shallowest water (Tukey test, ANOVA $F_{2,33}=28.39$ p< 0.0001 and $F_{2,33}=5.91$, p= .0064, respectively).

Since ANOVA showed no significant effects of 3 cm and 7 cm submergence on tail-beat frequencies and relative amplitudes (Tukey tests, p> 0.05), the data for these two depths were then analyzed together to gain a larger sample size (n=29). When combined, a significant correlation was found between relative velocity (body length/s) and the product of wave frequency times relative wave amplitude ($r^2=0.151$, p= 0.037). At these depths, there was no correlation between frequency and relative velocity ($r^2 = 0.11$, p= 0.078), or relative amplitude and relative velocity ($r^2=0.025$, p= 0.4094), but there was a positive correlation between frequency and absolute velocity ($r^2=0.171$, p= .026). The product of relative amplitude and frequency was compared to relative velocity graphically, and revealed distinct clustering of data points corresponding to 1 cm submergence depth (Figure 4).

**Figure 3:** Relative amplitude (amplitude/body length) of sea lamprey body waves at various depths. The bars are means with ±SE.

**Figure 4:** Relative velocity (body length/s) of sea lamprey body waves at various depths. The bars are means with ±SE.
DISCUSSION

My investigation of anguilliform swimming ability in sea lampreys across a submerged fish passage device indicated that tail-beat frequency and tail-beat amplitude varied depending on submergence depth. At the shallowest depth, tail-beat amplitudes and tail-beat frequencies were higher than in 3 cm and 7 cm submergence, suggesting that sea lampreys compensate for lowered thrust by swimming with more exaggerated undulating movements. The results of this experiment contrast with a previous study comparing swimming kinematics of larval and young adult sea lampreys (McClellan et al., 2016). Although the present study exhibited similar absolute swim velocities to that of McClellan et al. (2016), our results showed lower relative velocities (body lengths/second) and lower tail-beat frequencies. Since the authors

Figure 4: Normalized swim velocity as a result of amplitude x frequency of body waves at three water depths.
evoked swimming in sea lamprey by administering an electrical stimulus, fish may have engaged in burst-like swimming, resulting in a faster swim speed than our lampreys, which swam leisurely across the platform between holding tanks. In addition, the smaller lampreys (120-150 mm) in their experiment could have displayed different swimming behaviors than fish used in our trials (420-540 mm). Overall, our study did not show a strong relationship between frequency and relative swim speeds (McClellan et al., 2016), but showed some of the expected positive correlations between velocity and body wave amplitude/speed. Research on locomotion of live fishes has revealed that amplitude and frequency are linearly correlated with a higher velocity (Tytell & Lauder, 2004; McClellan et al., 2016). In our experiment, however, higher frequency and higher amplitude were behavioral reactions to swimming minimally submerged in shallow water. By selecting 11 coordinate points on the bodies of sea lamprey, McClellan generated kinematic parameters using a computer program. In contrast, selecting a single point on the sea lamprey body for analyses of tail-beat frequencies and amplitudes may have contributed to high variability in manual data collection in our experiment, thus negatively influencing the recorded swimming velocities at the intermediate water depth.

We did not find any differences in body wave characteristics or swim velocities between partially submerged (3 cm) and fully submerged (7 cm) fish. It has been shown that some of a fish’s kinetic energy is lost as it is converted into potential energy in the form of surface waves when swimming at the air/water interface (Domenici & Kapoor, 2010; Webb et al., 1991). This process can increase the energy needed for a fish to sustain the same speed in shallow water, compared to swimming fully submerged (Blake, 2009). It is possible that I did not find such an effect due to the above-described shortcomings of my kinematic analysis.

Studies on anguilliform swimmers such as lamprey and eel have provided insight into fish locomotion and behavior. Increasingly, there is a need to incorporate behavioral information into fish passage mechanisms. Since widely-used lamprey control strategies like barriers may negatively affect native migratory fish and lampricides harm native silver lamprey (Ichthyomyzon...
unicuspis), it is important to gain knowledge of what swimming, morphological, or behavioral characteristics in fish can be exploited to successfully develop selective fish passage for ecological management of the Great Lakes. To better understand the ability of fish to pass through physical in-stream barriers, future studies will investigate kinematic parameters of native Great Lakes finfish and compare them to those observed in Atlantic sea lamprey.

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