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Similarities, Differences, and Unknowns in Biology and Management of Three Parasitic Lampreys of North America

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Similarities, Differences, and Unknowns in Biology and Management of Three Parasitic Lampreys of North America

ABSTRACT: Sea lampreys, *Petromyzon marinus*, are invasive to the Laurentian Great Lakes where they have decimated native fishes. Great Lakes sea lampreys have been subjected to control measures for several decades, and the drive to control them has led to major advances in understanding their biology and in informing management. In contrast, anadromous sea and Pacific (*Entosphenus tridentatus*) lampreys have co-evolved with their oceanic prey. Both of these anadromous lampreys are in decline, and a limited amount of information on their biology has stymied conservation. The tendency has been to make biological inferences about anadromous lampreys based on the Great Lakes sea lamprey without justifiable evidence. We identify areas in which key information is missing for the juvenile (parasitic feeding) phase and adult freshwater spawning migrations, and compare and contrast information for these lampreys. Our comparisons reveal major differences, some intriguing similarities, and key unknowns that will require empirical testing.

Similitudes, diferencias e incógnitas en la biología y manejo de tres lampreas parásitas en los Estados Unidos de Norteamérica

RESUMEN: la lamprea marina, *Petromyzon marinus*, es una especie invasiva de la región de los grandes lagos de los Estados Unidos de Norteamérica, en los cuales han diezmado las poblaciones de peces nativos. La lamprea marina de los grandes lagos ha sido sujeto de medidas de control por varias décadas y esta necesidad ha dado lugar a importantes avances en el entendimiento de su biología y manejo. En contraste, la lamprea anádroma y la del Pacífico (*Entosphenus tridentatus*) han co-evolucionado con sus presas oceánicas. Actualmente las poblaciones de ambas lampreas se encuentran en declive y la escasez de información sobre su biología ha interferido con su conservación. La tendencia ha sido hacer, sin evidencia que lo justifique, inferencias acerca de la lamprea del Pacífico sobre la base de lo que se conoce de la lamprea de los grandes lagos. Se identificaron áreas en las que se carece de información crítica de la fase juvenil (alimentación parasitaria) y de las migraciones reproductivas de los adultos y se comparó y contrastó información para estas lampreas. La comparación reveló diferencias significativas, algunas similitudes interesantes e interrogantes clave que demandarán de comprobación empírica.

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INTRODUCTION

Eleven parasitic lamprey species have been described in North America (Nelson et al. 2004), including the largest and most managed, the anadromous sea and Pacific lampreys (*Petromyzon marinus* and *Entosphenus tridentatus*, respectively), and the invasive sea lamprey (*P. marinus*) of the Laurentian Great Lakes. The remaining nine parasitic lamprey species have more restricted distributions, are generally smaller in body size (Nelson et al. 2004; Renaud et al. 2009), and are not actively managed to the same extent that sea and Pacific lampreys are. This review compares the biology and man-

agement of the anadromous and Great Lakes sea lampreys and the Pacific lamprey (Table 1).

The establishment of invasive sea lampreys in the upper Great Lakes by the mid-1940s was a major impetus for the creation of the Great Lakes Fishery Commission (GLFC). The GLFC initiated an international coordination and collaboration of research on the Great Lakes sea lamprey (Fetterolf 1980), which has led to a control program that has been called "...one of the largest and most intensive efforts to control a vertebrate predator ever attempted" (Smith 1980).

No organization similar to the GLFC exists to promote the conservation and management of native anadromous sea and Pacific lampreys across American and Canadian boundaries (although a conservation initiative has recently been designed for the Pacific lamprey, e.g., see Luzier et al. 2009). As a consequence, information on these anadromous lampreys is less extensive (Table 2), and managers have used the extensive published information on the invasive Great Lakes sea lamprey to infer the biology of anadromous sea and Pacific lampreys.

Such interferences may hinder research on anadromous lampreys and can result in flawed management. The goals of this paper are to: 1) compare and contrast the biology of the well-studied Great Lakes sea lamprey with that of the anadromous sea and Pacific lampreys of North America; 2) identify areas in which key information is missing; and 3) determine the extent to which information from the Great Lakes sea lamprey can be applied to the conservation of anadromous sea and Pacific lampreys. We begin with a brief examination of taxonomy, distribution, and the life cycle of these lampreys, and then focus on their juvenile (parasitic feeding) phase, upstream migration, and spawning. We then briefly examine differences in habitats and selection pressures experienced

by each of these lampreys, and conclude with lessons learned from our comparisons.

TAXONOMY AND DISTRIBUTION

The sea lamprey in North America consists of two forms: the adfluvial sea lamprey in the Great Lakes, and the anadromous form that occurs along the Atlantic seaboard (Figure 1). In contrast, the Pacific lamprey likely consists of only an anadromous form (Figure 1). All three of these lampreys are parasitic and semelparous, but each display different geographic distributions (Figure 2; Hubbs and Potter 1971; Scott and Crossman 1973) and belong to divergent taxa. The genera *Petromyzon* and *Entosphenus* both belong in the single family of northern hemisphere lampreys—Petromyzontidae—but morphological characters suggest that *Petromyzon* is one of the most ancestral lamprey genera, whereas *Entosphenus* is one of the more derived (Gill et al. 2003). Based on degree of mitochondrial DNA divergence, these genera are estimated to have diverged at least 9–13 million years ago (Docker et al. 1999). The American Fisheries Society Common and Scientific Names of Fishes supported synonymizing *Entosphenus* with *Lampetra* (Nelson et al. 2004), but the AFS Names of Fishes Committee is currently reviewing their decision and is expected to recognize *Entosphenus* as a valid genus (J. Nelson, University of Alberta, 2007 pers. comm.). At least five other *Entosphenus* species have been described in addition to the Pacific lamprey, whereas the sea lamprey is the sole species in its genus (Nelson et al. 2004).

The anadromous sea lamprey is native on both sides of the North Atlantic Ocean, from Labrador to the Gulf of Mexico in

Table 1. Summary of the status and threats to lampreys, benefits to humans, estimated ecosystem services, and management practices.

	Great Lakes sea lamprey	Anadromous sea lamprey	Anadromous Pacific lamprey
Invasive or native?	Invasive nuisance species ^a	Native	Native
Population trends	Variable ^b	Declining	Declining rapidly; petitioned to be listed under the ESA
Threats	Not applicable	Pollution, habitat degradation, obstacles to spawning habitat (dams)	Similar to anadromous sea lamprey
Benefits to humans	None realized	Scientific study	Food and ceremony for Native Americans ^c
Co-evolved with prey base?	No ^a	Yes	Yes
Estimated ecosystem services	Recycle stream nutrients and introduce lake-derived nutrients to watersheds; negatively impact native fish stocks	Recycle stream nutrients; introduce marine-derived nutrients to watersheds; salmonids ^c food source for freshwater, estuarine and marine animal	Similar to anadromous sea lamprey; predation buffer for native and endangered
Management practices	Control via larvicides, sterile male releases, man-made barriers to spawning grounds, and capture and removal of adults fish stocks	Creation of fishways to allow adults to pass dams	Modification of fishways to allow adults to pass dams; transplanting of adults to tributaries ^d

^aGenetic evidence suggest that the Lake Ontario population is indigenous, but this issue is not resolved (see text)

^bPopulation at or near target levels over last 10 years in Lake Ontario but numbers have generally been increasing in Lake Michigan (Larson et al. 2003; Lavis et al. 2003)

^cClose et al. 2002

^dClose et al. 2009

Table 2. Relative level of information available (None, Low, Moderate or High) for Great Lakes sea lamprey and anadromous sea and Pacific lampreys. Many of the references are comprehensive reviews of relevant studies, and citations provided here are not exhaustive.

Area of biology	Great Lakes sea lamprey	Anadromous sea lamprey	Anadromous Pacific lamprey	References
Survey, collection, and handling techniques	High	Low–Moderate	Low–Moderate	Moser et al. 2007
Basic biology (life history, feeding, reproduction)	High	Moderate	Low–Moderate	Applegate 1950; Scott and Crossman 1973; Docker 2006; SLIS 1, 2
Management	High	Low–Moderate	Low–Moderate	Kostow 2002; Moser and Close 2003; SLIS 1, 2
Abundance estimates of parasitic phase adults; bioenergetics and host impacts	High	None	None	SLIS 1, 2; Docker 2006
Upstream migration characteristics and swimming capacity	High	Moderate	Moderate	Moser and Mesa 2009; Reinhardt et al. 2009
Migration pheromone	High	None	Low	Sorensen and Hoye 2007; Robinson et al. 2009
Spawning pheromone	High	None	Moderate	Li et al. 2003, 2007; Johnson et al. 2009
Biology of maturation and spawning	High	Moderate to High	Low	Hardisty and Potter 1971; Scott and Crossman 1973; Beamish and Potter 1975; Sower 2003; Docker 2006; Mesa et al. 2010
Identification of reproductive hormones and receptors	High	High	Where known, likely similar to the other lampreys	Sower 2003; Silver et al. 2004; Freamat and Sower 2008; Kavanaugh et al. 2008; Sower et al. 2009; Bryan et al. 2006, 2008
Endocrine profiles during holding, migration, maturation and spawning	High	High	Moderate	Sower 1990; Bolduc and Sower 1992; Sower 2003; Sower et al. Submitted

the western Atlantic, and from northern Norway to the western Mediterranean in the northeast Atlantic (Hubbs and Potter 1971). Landlocked sea lamprey populations occur in the Great Lakes basin and other inland lakes in New York State and Vermont (Figure 2; Kraft et al. 2006). Landlocked sea lampreys are considered invasive within the Great Lakes; with the completion of the Welland Canal in 1820, they were able to bypass Niagara Falls and spread throughout the Great Lakes by 1946 (Smith 1971). Recent genetic evidence supports a natural post-Pleistocene colonization of Lake Ontario (Waldman et al. 2004, 2009; Bryan et al. 2005), but this conclusion is not universally accepted (see Eshenroder 2009) and the sea lamprey is still considered non-native in Lake Ontario for conservation and management purposes (Renaud et al. 2009). The Pacific lamprey occurs in oceanic waters and coastal rivers in Asia from Siberia to northern Japan, and in North America from the

Aleutian Islands, Alaska, to Baja California, Mexico (Figure 2; Renaud 2008), and they are native throughout their range.

LIFE CYCLE

The Great Lakes sea lamprey has been well-studied in comparison with anadromous sea and Pacific lampreys (Table 2). The commonalities of their life cycle are as follows: sea and Pacific lampreys develop as endogenous-feeding embryos (Piavis 1971; Meeuwig et al. 2005) before spending 3–8 years as filter-feeding larvae (ammonoetes) in soft stream sediments (Scott and Crossman 1973). During the late summer and early fall, a number of exogenous and endogenous signals cue transformation of the ammocoetes into macrophthalmia with functional eyes, sharp teeth, and silver body

Figure 1. Anadromous Pacific lamprey (top), anadromous (sea run) sea lamprey (middle), and Great Lakes sea lamprey (bottom) of North America. The illustration depicts the relative differences in body size among these three lampreys. (Illustration: Deian Moore)



coloration (Youson 2003). Macrophthalmia become entrained in the water column during freshets and appear to emigrate in a passive fashion (Applegate 1950; van de Wetering 1998) to the lake or ocean where they parasitize hosts. After 1–4 years (see below), they cease feeding and migrate back into freshwater streams to spawn and then die (F. W. H. Beamish 1980a; R. J. Beamish 1980).

In the following sections we compare and contrast two phases during which the biology of these three lampreys appears to differ: 1) the juvenile (parasitic feeding) phase; and 2) the adult (upstream migrating and spawning) phase. Where necessary, we supplement the information for anadromous sea lampreys of North America with information from anadromous sea lampreys from Europe.

Juvenile—parasitic phase

Juvenile anadromous sea and Pacific lampreys occasionally parasitize fish in fresh water during emigration from rearing areas to lakes or the ocean. Salmonids and clupeids appear to be common hosts of sea lampreys in freshwater systems entering the Atlantic Ocean (Potter and Beamish 1977; F. W. H. Beamish 1980a), and emigrating salmon smolts are not uncommon hosts of juvenile Pacific lamprey in the Columbia—Snake River system, some 630 river kilometers from the ocean (Setter et al. 2004). Freshwater parasitism en route to the ocean may be a function of long migratory distances (Hardisty and Potter 1971), perhaps providing transport or a replenishing source for low lipid reserves before entering the ocean (Potter and Beamish 1977). Some researchers have hypothesized that this feeding behavior can lead to adaptation to freshwater environments (Potter and Beamish 1977) or preparation for osmoregulation in sea water by sea lampreys (Hardisty and Potter 1971; F. W. H. Beamish 1980b).

The ability of parasitic sea lampreys to reside in fresh water appears to be a function of origin and body size: anadromous sea

lampreys osmoregulate better in sea water than Great Lakes sea lampreys, and large-bodied Great Lakes sea lampreys can osmoregulate better in sea water than small-bodied Great Lakes sea lampreys, likely a result of a smaller body-surface-to-volume ratio (F. W. H. Beamish 1980b). Therefore, colonization of the Great Lakes may have involved selection for small body size and changes in osmoregulatory abilities (F. W. H. Beamish 1980b).

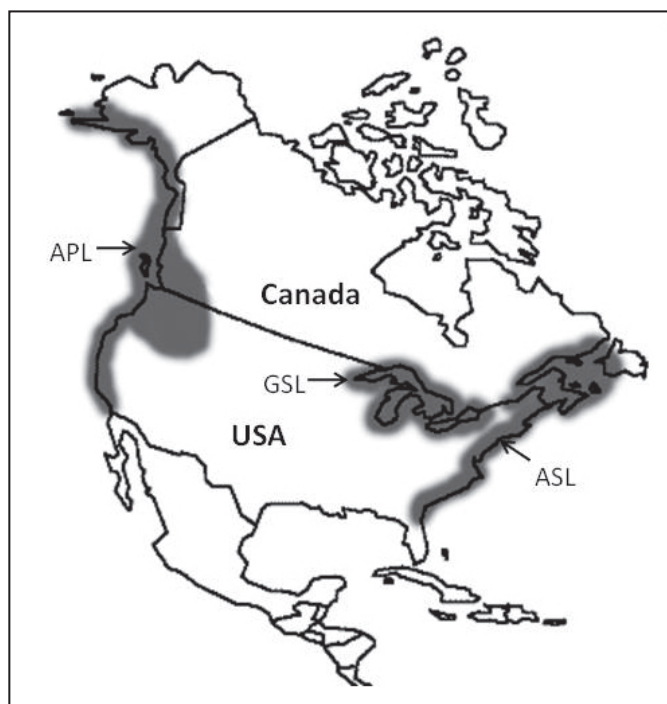
In contrast to the sea lamprey, several studies suggest that parasitic-phase Pacific lampreys cannot thrive in fresh water. Pacific lamprey populations have become extirpated after they were disconnected from the ocean through river impoundment (e.g., see Wallace and Ball 1979; Beamish and Northcote 1989), and juvenile Pacific lampreys held in the laboratory in fresh water fed poorly and ultimately died (Clarke and Beamish 1988). Populations of freshwater-resident Pacific lamprey have been reported (e.g., Moyle et al. 2009) but none are formally recognized. Some populations of lacustrine, non-migrating forms once considered to be dwarf races of Pacific lamprey have been elevated to species status (e.g., Bond and Kan 1973; Beamish 1982), and others (e.g., the Goose Lake population of Oregon) likely deserve species status (Moyle et al. 2009). Of the six described *Entosphenus* species, all but the Pacific lamprey occur solely in fresh water (Nelson et al. 2004). The lineage and taxonomy of these freshwater lampreys deserves further study, as the Pacific lamprey may speciate rapidly in fresh water.

The ocean phase of Pacific lampreys is estimated to be ~3.5 years, although this duration may only apply to moderate to large (250–500 mm) fish. Smaller returning adults probably have a parasitic phase < 3.5 years (R. J. Beamish 1980). Sea lampreys along the Atlantic seaboard likely spend ~2 years in the marine phase (23–28 months; F. W. H. Beamish 1980a), whereas sea lampreys in the Great Lakes generally have a shorter parasitic phase (12–20 months; Applegate 1950). The growth rate during the parasitic phase has been estimated at 0.65–0.79 g/day for sea lampreys in the Western Atlantic (F. W. H. Beamish 1980a) and 0.89 g/day for Great Lakes sea lampreys (Applegate 1950). Growth rate data are lacking for Pacific lampreys.

Sea and Pacific lampreys have similar attachment sites on host fishes, the majority of scars being ventrally- and anteriorly-located (reviewed in Cochran 1986). Adult salmon and adult gadiforms, in addition to a wide assortment of other commercially and ecologically important fishes, have been reported as hosts for both anadromous sea and Pacific lampreys (F. W. H. Beamish 1980a; R. J. Beamish 1980). In addition to fishes, various marine mammals have been reported as hosts for the Pacific lamprey (reviewed in Scott and Crossman 1973 and R. J. Beamish 1980), and parasitism of basking sharks (*Cetorhinus maximus*) by anadromous sea lampreys has also been observed (Wilkie et al. 2004). The Great Lakes sea lamprey feeds on a number of freshwater fish species, such as lake trout (*Salvelinus namaycush*), rainbow trout (*Oncorhynchus mykiss*), *Coregonus* spp., yellow perch (*Perca flavescens*), channel catfish (*Ictalurus punctatus*), carp (*Cyprinus carpio*), and others (Scott and Crossman 1973).

The degree of parasite-induced mortality in the ocean remains unknown, and such estimates require knowledge of abundance and host preferences for anadromous sea and Pacific lampreys. Parasite-induced mortality has been characterized in the Great Lakes (e.g., see Harvey et al. 2008; Madenjian et al. 2008; Table 2), and the large information base for Great Lakes sea lampreys allows modeling of bioenergetics and estimates of effects on host populations (e.g., see review by Docker 2006 and more recent work by Madenjian

Figure 2. Distribution of anadromous Pacific lamprey (APL), Great Lakes sea lamprey (GSL) and anadromous sea lamprey (ASL) in North America.



et al. 2008). Within the Great Lakes, the sea lamprey has decimated populations of indigenous fishes, although this appears not to have occurred in their natural range (Smith 1971). Likewise, no host decimations have been reported (since human observation of native lampreys began) for the Pacific lamprey or other parasitic lampreys, suggesting potential co-evolution of these parasitic lampreys with their hosts (Potter and Beamish 1977).

The comparisons we have made for the juvenile—parasitic life stage have revealed a surprising lack of detailed biological knowledge for anadromous sea and Pacific lampreys, particularly the degree of parasite-induced mortality in the ocean. More empirical data for growth rates and duration of this life stage is needed for anadromous sea and Pacific lampreys. It is also not known whether potential differences in feeding localities in the ocean might reveal differences in prey types, duration of parasitic feeding, and growth rates that might be greater within a species than between anadromous sea and Pacific lampreys. Finally, should differences in the biological characteristics of the parasitic life stage exist between anadromous sea and Pacific lampreys, such differences might be the result of differences in ecosystem health, stability, and productivity between the Atlantic and Pacific Oceans. Nevertheless, use of telemetry to track lampreys in the open ocean, in conjunction with tissue collection for stable isotope and proximate analyses, could provide information on geographical distributions, bioenergetic budgets, trophic niches, and host impacts.

Adult—non-feeding phase

Orientation and homing

At the end of the parasitic phase, sea and Pacific lampreys cease feeding and initiate their upstream migration (Scott and Crossman 1973). Research on returning Great Lakes sea lampreys

suggests that they orient to a larval (migratory) pheromone, which leads them to streams with quality spawning and rearing habitat (Sorensen and Hoye 2007; Wagner et al. 2009). The pheromone appears to work in concert with other factors, such as rheotaxis (Vrieze et al. 2010) and temperature (Binder and McDonald 2008) to control upstream migration by the lampreys to their spawning grounds. The sea lamprey migratory pheromone is composed of at least three separate bile acid compounds (Sorensen et al. 2005). The migratory pheromone does not appear to be species-specific (Fine et al. 2004), and a similar pheromone system exists in the Pacific lamprey (Robinson et al. 2009). However, Pacific lampreys seem to have a longer period of sensitivity to the major lamprey bile acids. Control of the Great Lakes sea lamprey has recently employed use of these pheromones to attract and trap upstream migrants (Wagner et al. 2006), and the pheromones may also be useful for attracting Pacific lampreys to suitable spawning habitat (Robinson et al. 2009).

A mark-recapture study found that Great Lakes sea lamprey returning to streams to spawn randomly distributed themselves among tributaries instead of returning solely to their natal streams (Bergstedt and Seelye 1995). Radio-tracking of displaced adult Pacific lampreys likewise suggests a lack of homing (Hatch and Whiteaker 2009), albeit with a much smaller sample size and over a relatively short study period (< 163 days) for fish that spend ≥ 1 year in fresh water prior to spawning (see “Overview and Timing of Upstream Migration,” below).

Genetic evidence likewise suggests that anadromous sea lampreys do not home to their natal streams. A relative homogeneity in microsatellite markers suggests panmixia along the Atlantic coast of North America (Bryan et al. 2005), although both mitochondrial (Rodríguez-Muñoz et al. 2004) and microsatellite (Bryan et al. 2005) markers show a lack of genetic exchange between North American and European sea lampreys. Within the Great Lakes, significant genetic differentiation was observed between sea lampreys in the lower versus the upper Great Lakes, but genetic differences among tributaries within a lake were observed only in Lake Erie. This may have been due to a lack of homogenous spawning habitat in and among tributaries rather than a result of homing (Bryan et al. 2005).

Do anadromous Pacific lamprey exhibit some sort of stock structure, whether it be homing to natal streams or via some other mechanism? The answer to this question is unresolved, due to the seemingly contradictory results of two separate studies that used different genetic tools and different collection methods. Although mitochondrial DNA markers have provided no evidence of population structure for Pacific lamprey ammocoetes collected from coastal streams from southern British Columbia to central California (Goodman et al. 2008), amplified fragment length polymorphisms (AFLPs) have provided evidence of weak stock structure in adults of this species from Japan, Alaska, the Pacific Northwest, and within the Pacific Northwest (Lin et al. 2008). It is unclear whether the lack of agreement between studies is a function of different genetic techniques and/or different sampling methods. Other genetic tools, such as microsatellite markers, may be necessary to delineate more nuanced genetic variability that might exist.

Native American tribes in the Pacific Northwest have collected Pacific lampreys from sources in the lower Columbia River Basin and transplanted these fish into formerly inhabited rivers in the hopes of reestablishing stocks (Close et al. 2009). The success of these efforts is contingent upon reproductive success of the fish and

a continued return of spawners to these rivers, but whether lamprey would return through natal homing or attraction to larval pheromones remains unknown.

Overview and timing of upstream migration

The upstream migration can be divided into three phases, using a slightly modified terminology from Robinson and Bayer (2005): 1) the initial migration; 2) pre-spawning holding; and 3) final migration/spawning. The duration and location of each of these phases often among the three lampreys (see Figure 3). Pacific lampreys generally spend ~1 year in fresh water before spawning (R. J. Beamish 1980; Chase 2001), but can reside in fresh water for as long as 2 years (Whyte et al. 1993; D. Hatch, Columbia River Inter-Tribal Fish Commission, 2007 pers. comm.). In contrast, Great Lakes and anadromous sea lampreys do not initiate upstream migration until ~4 months before they spawn, and they reside in the fluvial fan of the river mouth or estuary prior to entering the river (Applegate 1950; Figure 3). Although it is not known what proximate and ultimate factors have been selected for such a prolonged freshwater residency in Pacific lampreys, we hypothesize that it may be a function of the larger river systems on the west coast compared to those in the Great Lakes or along the Atlantic seaboard.

In the Pacific Northwest, sexually immature Pacific lampreys cease feeding and enter fresh water during April–June in the year prior to spawning (R. J. Beamish 1980), and begin their initial migration during July–September (Scott and Crossman 1973; Robinson and Bayer 2005). Pacific lampreys hide under stones while overwintering during October–March (Scott and Crossman 1973) before their final migration, nesting and spawning during April–July, after which they die (Scott and Crossman 1973; Brumo 2006). In interior Oregon, overwinter holding areas are relatively close to spawning locations (Figure 3; Robinson and Bayer 2005). In southern California, upstream migration and spawning occurs earlier than in Oregon and British Columbia (Chase 2001).

In sea lampreys, the initial migration occurs during the late winter in both the Great Lakes and Atlantic Ocean, and pre-spawning holding occurs near river mouths or in estuaries (Applegate 1950; Figure 3). Anadromous sea lampreys cease feeding around January and remain near shore. During mid to late May, migrants enter coastal rivers and travel to the spawning grounds about 1.5–2 months prior to spawning during late June–early July (Scott and Crossman 1973; Beamish and Potter 1975). However reproduction has been reported to occur as early as March in Virginia and Maryland and as late as September in New Brunswick (F. W. H. Beamish 1980a). In the Great Lakes sea lamprey, migration begins during April and the fish generally spawn during June and July (Applegate 1950; Manion and Hanson 1980).

Upstream migration and spawning of anadromous sea and Pacific lampreys therefore appears to occur earlier at lower latitudes, and this is likely also true of the Great Lakes sea lamprey. Photoperiod appears to play a role in stimulating the hypothalamic-pituitary-gonadal axis during maturation and spawning (Sower 2003). The timing of the spawning migration of anadromous sea lampreys has been concluded to be a function of distance to the spawning grounds, water temperature, and latitude (F. W. H. Beamish 1980a).

Swimming abilities of upstream migrants

Body size in lampreys is generally correlated with available prey resources and the distance of upstream migration (Hardisty and Potter 1971; R. J. Beamish 1980). Differences in the kinds of natural barriers encountered also appear to have shaped the body size, swimming performance, and behavior of these parasitic lampreys (Table 3), and large body size may also be important for Pacific lampreys, given the prolonged duration of their pre-spawning holding period. Anadromous sea and Pacific lampreys migrate longer distances and are larger than Great Lakes sea lampreys (Scott and Crossman 1973; F. W. H. Beamish 1980a; Kostow 2002; Table 3). Anadromous sea and Pacific lampreys also encounter large variations in salinity and current velocity and direction (i.e., reversing currents in tidal areas) during their upstream migration. Correlations between body size and migratory distance have also been suggested within the Pacific lamprey. For example, large body size has been reported in larger, more interior rivers like the Columbia River, whereas relatively small Pacific lampreys have been observed in coastal streams (Kan 1975; Kostow 2002), although it is not known if these differences are due to inherited characteristics which could signify some type of stock structure (Keefer et al. 2009a; see “Orientation and homing,” above).

Swimming performance in lampreys is largely a function of body size. Results from laboratory experiments with Great Lakes sea lampreys predicted that at 15°C and current velocities of 0.85 m/s, 400 mm long fish would be able to swim for only ~50 s, whereas those that were 500 mm long could swim three times longer (McAuley 1996). Similarly, the large anadromous sea lamprey, with a mean body length of 900 mm, had absolute swimming speeds faster than anadromous Pacific lampreys, with mean body length of 658 mm (Mesa et al. 2003; Almeida et al. 2007). However, when standardized for body size, temperature (15°C) and tag size (< 1% of the body mass of the fish), the critical swimming speeds for these two anadromous lampreys were similar (Pacific lamprey 1.1 BL/s, Mesa et al. 2003; sea lamprey 1.2 BL/s, Almeida et al. 2007). In both laboratory and field evaluations, Great Lakes sea lampreys and Pacific lampreys swam against velocities well above their critical swimming speed (> 2.7 m/s) by a saltatory “burst and attach” mode of swimming (McAuley 1996; Moser et al. 2002; Keefer et al. 2010). Anadromous sea lampreys also use this mode of swimming to negotiate difficult passage areas (Quintella et al. 2004).

The large body size, swimming speed, and swimming and climbing modes (see previous and below) of anadromous sea and Pacific lampreys may enable them to negotiate some large obstacles to reach upriver spawning sites. Obstacles to upstream migration of Pacific lampreys occur at natural waterfalls, low and high elevation dams, irrigation diversions (4), and probably also culverts. The characteristics common to these obstacles are a combination of rapid current velocity and the lack of sufficient attachment surfaces where the fish can hold and rest (Moser and Mesa 2009; Keefer et al. 2010). Obstacles to upstream migrating anadromous sea lampreys include moderate rapids and hydroelectric dams, whereas Great Lakes sea lampreys enter lower gradient streams with no natural obstacles (Table 3).

An important difference in the behavior of anadromous sea and Pacific lampreys when negotiating barriers is in their ability to “climb” vertically on a wetted surface. Pacific lampreys can climb vertical surfaces by attaching with their oral disc, contracting the body, and then releasing and reattaching a few centimeters higher

(Reinhardt et al. 2008); they are thus able to ascend continuous, perfectly-vertical, wetted surfaces > 1.7 m (Kemp et al. 2009). In fact, Pacific lampreys are capable of ascending the 12 m high Willamette Falls in the Willamette River, Oregon (4A and 4B); in the pre-dammed Columbia River, they would have encountered a raging 15 km series of rapids at historic Celilo Falls. In contrast, observations suggest that anadromous sea lampreys can ascend nearly-vertical barriers at heights of only 1.5–1.8 m (Scott and Crossman 1973), and Great Lakes sea lampreys are poorer climbers yet, being unable to ascend vertical heights greater than half of their body length (Reinhardt et al. 2009). To aid passage of Pacific lampreys at places where upstream passage is poor (e.g., dams), structures have been developed to take advantage of the climbing ability of Pacific lampreys by using steep ramps ($\leq 60^\circ$ angle) over which only a few centimeters of water flows (Moser and Mesa 2009).

Little is known about how hydraulic flow influences the behavior of migrating lampreys. Increases in stream discharge that occurs after rain or during the operation of hydroelectric dams can stimulate upstream migration in Great Lakes sea lampreys and anadromous sea and Pacific lampreys (Almeida et al. 2002; Keefer et al. 2009b; Binder et al. 2010).

Local flow characteristics may also influence lamprey behavior. For example, anadromous sea lampreys attracted to an Ice Harbor style of fishway at a dam were subsequently impeded from passing the dam due to adverse hydraulic conditions (Haro and Kynard 1997). Studies aimed at understanding how lampreys behave under various hydraulic conditions have the potential to predict migration routes, and would be beneficial for trapping and removal of Great Lakes sea lampreys, and for passing anadromous lampreys (Moser and Mesa 2009; Keefer et al. 2010).

Environmental cues to upstream migration

Lampreys are photophobic during their upstream migration and they migrate almost exclusively at night (Hardisty and Potter 1971). The Great Lakes sea lamprey (Kelso and Gardner 2000) and anadromous Pacific lamprey (Moser et al. 2002) (and presumably the anadromous sea lamprey), are most active within the first few hours following sunset. Lampreys avoid light during the day by hiding in deep pools, among large rocks, or within fallen brush and undercut banks (Kelso and Gardner 2000; Robinson and Bayer 2005; Binder and McDonald 2007). Despite this photophobia, however, there is some indication that lampreys may be attracted to light at night; traps were five times more attractive for Great Lakes sea lampreys when the entrances were lit with a flashlight (Purvis et al. 1985). More research is needed on the efficacy of light attraction for control of the Great Lakes sea lamprey, and for conservation of anadromous sea and Pacific lampreys.

Temperature modulates upstream migration behavior, general health, and sexual maturation in lampreys (Binder and McDonald 2008; Clemens et al. 2009; Keefer et al. 2009b). The springtime spawning migration of the Great Lakes sea lamprey begins after stream temperatures exceed 10°C (Applegate 1950); sudden increases in temperature tend to stimulate migratory activity, while sudden decreases halt migratory activity in this fish (Applegate 1950; Binder and McDonald 2008; Binder et al. 2010). The response to temperature appears similar in anadromous sea lampreys (F. W. H. Beamish 1980a). Similarly, Pacific lampreys are first detected in the Columbia River at River Kilometer 235 (non-tidal fresh water) in

May, when water temperature typically exceeds 11°C (Keefer et al. 2009b).

Rates of movement for Pacific lampreys increase during the summer as river discharge decreases and water temperatures rise (Moser et al. 2005; Keefer et al. 2009b), but slows in the fall when water temperature drops below 20°C (Robinson and Bayer 2005). Temperatures historically encountered during the entire migration for Great Lakes sea and coastal runs of anadromous Pacific lampreys are comparable: $\sim 5\text{--}20^\circ\text{C}$ (Applegate 1950; Kan 1975); whereas temperatures for anadromous sea lampreys are of a narrower temperature range: $15\text{--}21^\circ\text{C}$. Recently, however, temperatures $> 20^\circ\text{C}$ have been encountered by Pacific lampreys for prolonged periods of time in coastal and interior streams in the Pacific Northwest (Clemens et al. 2009). Similar prolonged warm water trends are also likely occurring within the geographical range of Great Lakes and anadromous sea lampreys, but Pacific lampreys are generally exposed to these river temperatures for much longer, owing to their prolonged freshwater residency (≥ 1 year versus a few months for sea lampreys). These warmer temperatures have been associated with significant, proportional decreases in body size and sexual maturation in Pacific lamprey during the following spring (Clemens et al. 2009). Effects of warmer temperatures on the maturation timing characteristics of Great Lakes and anadromous sea lampreys have not been investigated.

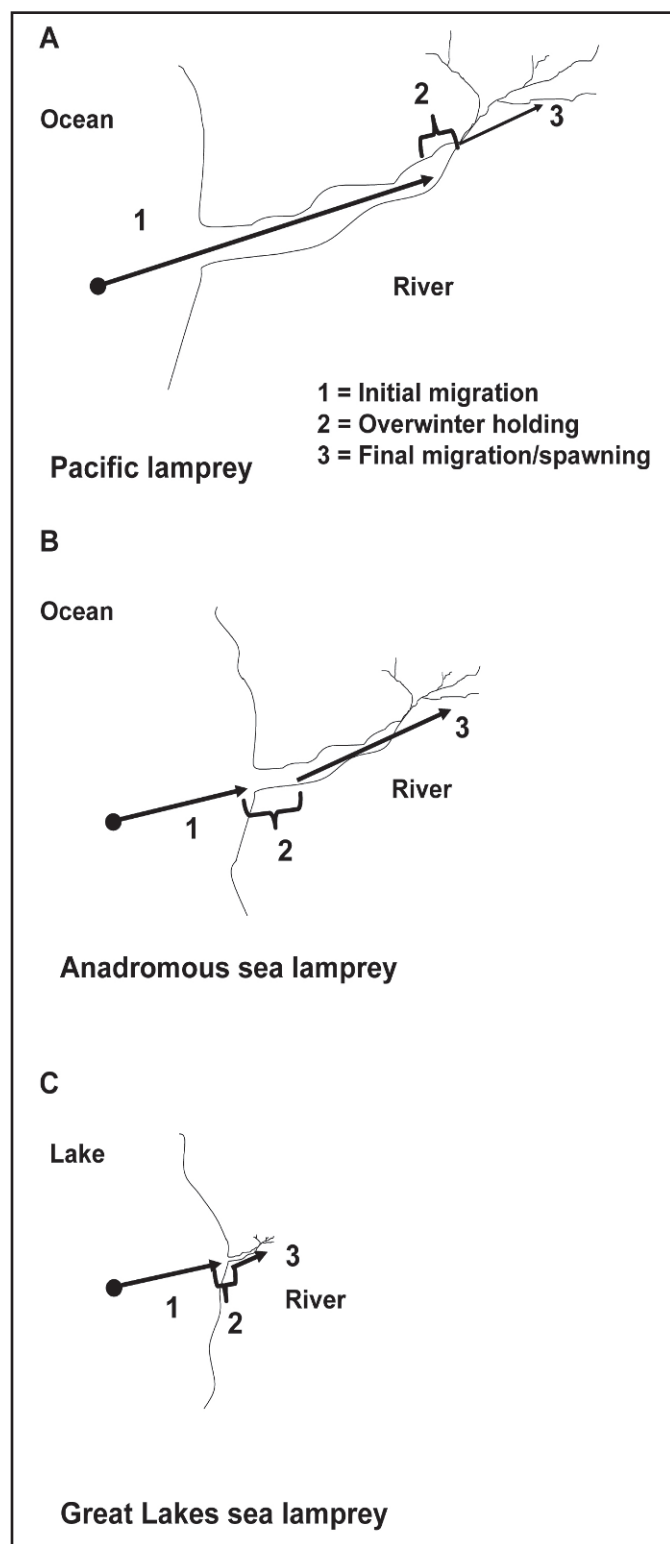
Sexual maturation, final migration, spawning, and death

All lampreys shrink considerably during their upstream migration. Anadromous sea lampreys decrease in body length by an estimated 19–24% between the initial migration and post-spawning (F. W. H. Beamish 1980a). Similarly, Pacific lampreys decrease in body length by an estimated 18–30% (R. J. Beamish 1980; Chase 2001). Great Lakes sea lampreys have the smallest decreases in body length, decreasing by an estimated 8–10% (O'Connor 2001). This smaller reduction in body length by the Great Lakes sea lamprey relative to the anadromous lampreys is likely related to the shorter migration distance (Figure 3). Reductions in body size are accompanied by a reduction in flesh quality and deterioration of organs to fuel sexual maturation (e.g., Larsen 1980; Clemens et al. 2009).

Lampreys are season- and temperature-responsive in the timing of their sexual maturation and reproduction (Sower 2003). Temperature regulation of migration and spawning behavior probably evolved in response to the strict thermal requirements of developing embryos (Piavis 1971). The thermal range for embryonic development of Great Lakes sea lampreys is between 15 and 25°C , with survival decreasing sharply as river temperatures deviated from the $\sim 18^\circ\text{C}$ optimum (Piavis 1971). The range is similar in anadromous sea lampreys ($15\text{--}23^\circ\text{C}$; Rodríguez-Muñoz et al. 2001), but survival across this temperature range is more consistent than in Great Lakes sea lampreys. The thermal range for embryonic development of Pacific lampreys is broader than for sea lampreys ($< 10\text{--}22^\circ\text{C}$; Meeuwig et al. 2005). This information on thermal ranges or embryonic development is from laboratories.

The spawning temperature for all three parasitic lampreys overlaps, although sea lampreys may have a higher peak spawning temperature than Pacific lampreys. Spawning of Great Lakes sea lampreys peaks at $\sim 14\text{--}18^\circ\text{C}$ (Scott and Crossman 1973; Manion and Hanson 1980), but has been observed at temperatures up to

Figure 3. Schematic comparison of the migration stages of the anadromous Pacific lamprey (A), anadromous sea lamprey (B), and Great Lakes sea lamprey (C) between the ocean or lake and river tributaries. The phases of the migration of the anadromous sea lamprey are thought to be similar to the Great Lakes sea lamprey. When the anadromous lamprey cease feeding about January, they are thought to be near shore. In May, anadromous sea lamprey begin to migrate into estuaries and then into freshwater streams. The relative migration distances amongst these lampreys are presented to scale. Note that the pre-holding migration and overwinter holding of the Pacific lamprey occur further up into the river system.



26°C (Manion and Hanson 1980). Anadromous sea lampreys in New Brunswick exhibit peak spawning at temperatures of 17–19°C (Beamish and Potter 1975) and in New Hampshire at ~18–21°C (Sower 2003). Spawning in Pacific lampreys has been observed at ~10–17°C, peaking at 13–16°C (Brumo 2006; Stone 2006). The apparent difference in peak spawning temperatures between sea and Pacific lampreys, however, may be due to fewer observations of Pacific lamprey spawning. The spawning season for Pacific lampreys ranges from March to July (Brumo 2006), similar to that reported for sea lampreys (F. W. H. Beamish 1980a), but—given its dependence on temperature—the spawning season varies considerably with latitude in both species (see “Overview and timing of upstream migration,” above).

Spawning behavior seems to be similar in sea and Pacific lampreys. Males generally arrive at the spawning grounds first where they construct nests in substrate composed of rubble, gravel, and sand on the upstream edge of riffles, in areas of “moderate” unidirectional flow (Applegate 1950; Scott and Crossman 1973; Manion and Hanson 1980). In sea lampreys, females also construct nests towards the end of the spawning season (Scott and Crossman 1973; Manion and Hanson 1980). During the spawning period, the lampreys are nearly blind, and the lampreys will spawn during daylight hours (Applegate 1950). Female sea and Pacific lampreys orient across the nest while the male initiates a “gliding-feeling” motion prior to attaching to the female’s head, wrapping around her, and squeezing the eggs out while fertilizing them (Scott and Crossman 1973). Genetic studies in the Great Lakes sea lamprey demonstrated that both sexes mate with more than one individual and matings with three or more individuals are common (see Docker 2006). These polygamous tendencies may be related to sex ratio (Scott and Crossman 1973; Manion and Hanson 1980), particularly as the result of sea lamprey control. Great Lakes sea lamprey populations have become highly female-biased following the initiation of sea lamprey control (Heinrich et al. 1980), and sex ratios may also vary during the season (Scott and Crossman 1973; Manion and Hanson 1980). However, much remains unknown about the mating systems of sea and Pacific lampreys under different conditions.

The total number of eggs is directly related to adult body size in lampreys. Accordingly, the large anadromous sea lamprey has the highest total fecundity, with an estimated mean fecundity of 171,589 to 210,228 eggs (reviewed in F. W. H. Beamish 1980a). The mean fecundity for the intermediate-sized Pacific lamprey ranges from 34,000 to 140,312 eggs (Scott and Crossman 1973; Kan 1975), whereas that of the relatively small Great Lakes sea lamprey ranges from 34,000 to 110,300 eggs (Scott and Crossman 1973). Further comparisons, such as the fecundity at spawning relative to the distance of the upstream migration, would be informative.

Gonadal development, reproduction and hormones

Reproductive physiology and endocrinology has been useful in informing control practices of the Great Lakes sea lamprey (e.g., the release of sterile males; see Sower 2003), and it may be useful for breeding and culturing of Pacific lampreys for seeding barren streams.

The maturation process begins during the parasitic feeding phase of lampreys, before they enter fresh water for their spawning migration. Although currently unknown, these maturation processes may occur more slowly during the prolonged spawning

Table 3. Comparisons of migratory distance, duration, and maximum total body length. Details are provided in the text.

Parameter	Great Lakes sea lamprey	Anadromous sea lamprey	Anadromous Pacific lamprey
Relative migration duration	Few months	Few months	≥ 1 yr
Maximum total body length	rarely > 700 mm	≤ 800–900 mm	rarely > 800 mm
Relative migratory distance	≤ 79 km	320–480 km	≤ 700 km
Swimming ability	Poor ^a	Comparable to anadromous Pacific lamprey ^b	Comparable to anadromous sea lamprey ^b
Obstacles	Low-head barrier dams	Rapids, hydroelectric dams	Waterfalls, hydroelectric dams
Climbing ability	Poor	Modest ^c	Exceptional

^a Direct comparisons of the swimming ability of Great Lakes sea lamprey are difficult to make with other lampreys because critical swimming speed has not been tested.

^b Details provided in the text.

^c Based on anecdotal observations noted in Scott and Crossman (1973). The climbing performance of anadromous sea lamprey has not been directly tested, as with Great Lakes sea lamprey and anadromous Pacific lamprey. (Reinhardt et al 2008 and 2009; Kempetal 2009).

migration of Pacific lampreys. In males, spermatogonia proliferate and develop into primary and secondary spermatocytes, and in females, vitellogenesis occurs (Sower 2003). The final maturation processes, resulting in mature eggs and sperm, occur during the non-feeding, upstream migration. Gonad development, reproduction, and reproductive hormones have been studied extensively in the anadromous and Great Lakes sea lampreys, and there appears to be little or no difference between them (Sower 2003; Bryan et al. 2008). Except for a recent study (Mesa et al. 2010), little is known of the reproductive physiology of Pacific lampreys; this leads us to invoke the null hypothesis that there is no difference between sea and Pacific lampreys in their reproductive physiology and endocrinology. Evidence for a few exceptions to this hypothesis, however are noted below.

Higher brain centers integrate environmental and sensory stimuli and relay this information to the hypothalamus of the brain. The hypothalamus controls reproduction through the release of gonadotropin-releasing hormone (GnRH). Changes in levels of GnRH in the brain are correlated with season (photoperiod and temperature; Sower 2003). There appear to be three isoforms of GnRH (GnRH-I, -II, and -III) that control sexual maturation and reproduction in lampreys (Sower 2003; Kavanaugh et al. 2008); GnRH-II was identified only recently (Kavanaugh et al. 2008). The GnRHs act on specific receptors located in the pituitary gland. In sea lampreys, one known gonadotropin is secreted from the pituitary in response to hypothalamic GnRHs, and this pituitary hormone is thought to act on one glycoprotein receptor in the gonad and one in the thyroid (Freamat et al. 2008; Sower et al. 2009) to influence steroidogenesis and gametogenesis. Various studies on the structure and function of the GnRHs in sea lampreys have established that this fish has a hypothalamic-pituitary-gonadal axis similar to all other vertebrates with a high conservation of the mechanisms of GnRH action (Sower 2003; Kavanaugh et al. 2008; Sower et al. 2009). The primary amino acid and cDNA sequences of the three isoforms of GnRH, the cDNA of one GnRH receptor, one pituitary gonadotropin- β -like protein, and several other brain and pituitary hormones/receptors have been identified for the sea lamprey (see Kavanaugh et al. 2008; Sower et al. 2009). The cDNA of lamprey GnRH-III has also been cloned for Pacific lamprey (Silver et al. 2004).

Seasonal and sex-specific changes of the three GnRHs during the final reproductive period suggest specific roles for each of the GnRHs in male and female lampreys. Several lines of evidence suggest that GnRH-III is the major form regulating final maturation in lampreys, whereas GnRH-I may influence spawning behaviour (see Sower 2003; Docker 2006). Levels of GnRH-I remain relatively low in female sea lampreys during their final maturation while GnRH-III is present in higher concentrations and undergoes significant increases during this period (Sower 2003). A possible function for GnRH-II is not yet known, although a recent study showed that its levels were elevated in male anadromous sea lampreys early in the season, dropped and then peaked in mid-season, and finally declined prior to spawning (Sower et al., submitted). In females, GnRH-II concentrations were elevated at the beginning of the season and then dropped and remained low during the rest of the season. More research is needed to fully understand the function of the three GnRHs in lampreys, and to determine if there are differences among lamprey species. Blood plasma concentrations of 15α -hydroxylated steroids (see below) increased in both sea and Pacific lampreys when GnRH was administered (Bryan et al. 2003; Young et al. 2004). These studies suggest that GnRH-III was more potent than GnRH-I in Pacific lampreys (Young et al. 2004), but only in some instances for sea lampreys (Young et al. 2004, but see Bryan et al. 2003). However, differences in study design and stage of maturation of the lampreys make these comparisons between sea and Pacific lampreys difficult, and more research is needed to clarify differences and similarities between sea and Pacific lampreys.

The gonadotropin secreted from the pituitary acts on the gonad, which produces sex steroids. The physiological role of these steroids has mostly been studied in the sea lamprey (reviewed in Bryan et al. 2008). In earlier studies, classical plasma steroid hormones such as estradiol were measured as indicators of gonad maturation and reproduction in both sexes of the sea lamprey (Table 2) and other lampreys (Bryan et al. 2008), and the role of estradiol in reproduction is further supported by the recent cloning of an estrogen-like receptor in sea lamprey (Thornton 2001). Estradiol, but not testosterone, appears to be a major steroid regulating reproductive maturation and function in both sexes of the sea lamprey (Sower 2003; Bryan et al. 2008) and Pacific lamprey (Mesa et al. 2010). However, many questions remain as to the type of steroids

Figure 4. Willamette Falls, Oregon (A and B); lowhead barrier dam in a tributary to the Great Lakes (C); irrigation diversion dam in a tributary to the Columbia River (D). (Photos: Benjamin Clemens, Stan van de Wetering, Thomas Binder, and Mary Moser.)



that are synthesized and their respective functions (Bryan et al. 2008). For example, there is growing evidence that all lampreys produce gonadal steroids that are different from those of other vertebrates, by possessing an additional hydroxyl group at the C15 position (Bryan et al. 2006, 2008). Furthermore, there is evidence that 15α -hydroxyprogesterone is a hormone in lampreys, and that androstenedione, a precursor to vertebrate androgens, is the main androgen (Bryan et al. 2008), but more research is required.

Mating pheromone

Spermiating male sea and Pacific lampreys attract ovulating females to nest sites with a mating pheromone that is released through the gills. The primary component of this pheromone is 3-keto-petromyzonol sulfate (3kPZS; Li et al. 2003; Robinson et al. 2009). This compound is attractive to ovulating females at concentrations as low as 10^{14} mol/L (Johnson et al. 2009). However, as studied in Great Lakes sea lampreys, 3kPZS alone does not retain ovulating females near the source, suggesting that other components of the mating pheromone evoke near-source search behavior (Siefkes et al. 2005; Johnson et al. 2009). Electrophysiological studies have demonstrated that Pacific lampreys are also sensitive to 3kPZS, albeit at much higher concentrations than detected by

sea lampreys (Robinson et al. 2009). A second component of the mating pheromone has been identified in sea lampreys (Li et al. 2003), but it is only detected by females at much higher concentrations than 3kPZS (Siefkes and Li 2004) and its function has not yet been tested.

The mating pheromone has recently been used to attract and trap females of the Great Lakes sea lamprey for removal (Johnson et al. 2009). The mating pheromone could potentially be used to attract Pacific lampreys with the goal of aiding upstream passage at dams and drawing the fish into barren streams.

SUMMARY AND CONCLUSIONS

We have reviewed the biology of the well-studied Great Lakes sea lamprey, an invasive pest, and compared this information with that of the anadromous sea and Pacific lampreys, which are of conservation concern. The key similarities, differences, and unknowns in the biology of these three parasitic lampreys are summarized in Table 4. The comparisons are necessarily generalized, and there are potentially myriad factors that might explain the biological differences, including phylogeny (e.g., at the level of genera or species),

Table 4. Similarities, differences and unknowns in the juvenile and adult phases among anadromous sea lamprey (ASL), Great Lakes sea lamprey (GSL), and anadromous Pacific lamprey (APL). Relevant citations are provided in the text.

	Similarities	Differences	Unknowns
Juvenile—parasitic phase	ASL, APL parasitize fish en route to ocean	APL cannot remain in fresh water; GSL can	Can all ASL stocks remain in fresh water?
	ASL, GSL, and APL attach to similar locations on prey	Body size of ASL > APL > GSL	Confirm that migration timing depends on latitude in GSL
	ASL and APL parasitize similar taxa in the ocean		Bioenergetics and host impacts of ASL, APL, growth rate data for APL
Adult—non-feeding phase: Initial upstream migration	Migration timing depends on latitude for ASL and APL	Body size of ASL > APL > GSL	Confirmation that no APL can remain in fresh water
	Photophobicity and cryptic behavior	ASL are able to ascend rapids; GSL cannot ascend wetted, vertical surfaces; APL are able to climb waterfalls	Evidence for lack of homing to natal streams in ASL or GSL; inconclusive for APL
	Tendency to become quiescent in water temperatures < 10°C; and to actively migrate upstream when temperatures > 20°C	Different swimming capacities, likely a function of differences in body size	Effectiveness of light to capture APL
Adult—non-feeding phase: Pre-spawning holding		*See differences in Figure 1 (Migration distance APL > ASL > GSL) APL can hold in fresh water for ≥1 year before spawning	
Adult—non-feeding phase: Final migration/spawning	Spawning characteristics and most secondary sexual characteristics	Male ASL and GSL exhibit prominent rope-like ridge anterior to first dorsal fin as they approach the spawning grounds, APL do not	Effect of sex ratio of mating systems in all Whether ASL and GSL enter river systems more sexually mature than APL Physiological characterization of maturation and bioenergetic status of APL

differences in environments (including selection pressures), and localized adaptations. Likewise, we do not know whether the similarities that we have found are due to evolutionary constraints on phylogeny and/or homoplasy.

In general, the large anadromous sea and Pacific lampreys, with their relatively long migratory distances, appear to have greater swimming abilities than the smaller Great Lakes sea lamprey. Anadromous sea and Pacific lampreys must negotiate hydroelectric dams and various man-made obstacles to access spawning grounds. The climbing abilities of anadromous sea lampreys are thought to be more modest, and climbing abilities of the Great Lakes sea lamprey are relatively poor. Pacific lampreys are adapted to the larger and more geologically-diverse rivers of the west coast of North America. Pacific lampreys exhibit a prolonged residence in fresh water prior to spawning and show exceptional climbing abilities. There are no natural obstacles to upstream migration for Great Lakes sea lampreys, and relatively low man-made obstacles have been used effectively to limit sea lamprey colonization of tributaries. In contrast to the Great Lakes sea lamprey, research on the

Pacific lamprey has focused on improving passage success at dams and other man-made structures.

All three lampreys discussed in this paper have similar maturation and reproduction timing that is modulated by water temperature and seasonal photoperiod, although again Pacific lampreys reside in fresh water for a much longer period of time prior to spawning than sea lampreys. Mean total fecundity is directly correlated with body size, with the large anadromous sea lampreys having the most eggs, and the small Great Lakes sea lampreys the fewest. Knowledge of the reproductive physiology of sea lampreys has helped in the development of a sterile male release program in the Great Lakes Basin. In comparison, knowledge of the reproductive physiology of Pacific lampreys is poorly known but could inform conservation scenarios aimed at culturing these fish for reintroduction into barren streams. The migratory and mating pheromones are relatively well known for sea lampreys, but have been studied comparatively little in the Pacific lamprey. Control of the Great Lakes sea lamprey has recently employed use of pheromones to attract and trap lampreys, whereas restoration of the Pacific lam-

prey might benefit from future use of pheromones for facilitating upstream passage over dams and into barren streams.

The extensive information base on the Great Lakes sea lamprey is a result of a management agency (the Great Lakes Fishery Commission) with a clear directive aimed at controlling this pest. By comparison, the relatively scant information available for anadromous sea and Pacific lampreys is a result of the lack of a similar organized effort to fund and coordinate research that can inform conservation of these imperiled fishes. Given these different goals for these North American parasitic lampreys, we wonder what basic or applied biological parameters have been ignored and will deserve more attention. Awareness of this bias in both the volume of the scientific literature and the goals behind this literature may aid intelligent, creative, and novel approaches to the management and conservation of sea and Pacific lampreys in North America. Some key similarities in biology do exist between anadromous sea and Pacific lampreys (Table 4), but these similarities should be used with caution. Likewise, differences between the invasive Great Lakes sea lamprey and the anadromous lampreys (Tables 1 and 4) cause us to question the appropriateness of using the vast amount of information garnered from Great Lakes sea lampreys as a useful surrogate for native anadromous sea and Pacific lampreys. Assumptions of reciprocal biology should be stated as explicit hypotheses that need to be vigorously tested to verify whether lessons learned from one lamprey species may be beneficial in the management or control of another.

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