



Review

Synergizing basic and applied scientific approaches to help understand lamprey biology and support management actions

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ABSTRACT

Lampreys (Petromyzontiformes) are a key component of freshwater ecosystems throughout temperate parts of the world. Of the 44 described species of lamprey, the sea lamprey (*Petromyzon marinus*) is certainly the most commonly recognized. This species has expanded its range from the Atlantic Ocean basin where it is of conservation concern in North America and Europe into the Laurentian Great Lakes where it is subject to a large-scale international control program. Many other species of lamprey are imperiled and require management intervention to ensure their persistence. These management efforts range from routine assessment and monitoring to active or proposed restoration plans where they have been extirpated. Regardless of whether the goal is to control or conserve a given lamprey population, an understanding of their basic biology is paramount when generating and executing management plans. Here, we take a broad look across core aspects of biology (survival, foraging, and reproduction) that encompass challenges and opportunities in regard to future science-based management of lampreys. We attempt to synergize basic and applied research to highlight where these findings are most applicable to solving management problems and reveal knowledge gaps. We conclude by suggesting future research avenues and questions aimed to stimulate progress in both basic and applied lamprey research.

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Introduction

It is common in many scientific disciplines to recognize a distinction between basic and applied research; the former is typically theory-driven and involves hypothesis testing in the pursuit of fundamental understanding, the latter is prompted by the need to solve practical problems. However, basic research can be directed toward – and be motivated by – its ultimate application, just as applied research can be used to inform fundamental understanding. The resulting synergy of basic and applied scientific approaches can be profoundly informative. The need to control sea lamprey (*Petromyzon marinus*) in their invasive range within North America has provided ample opportunity to synergize basic and applied scientific approaches to support management actions. For example, two vulnerable periods of the life cycle were identified in the early years of investigations: the spawning migration of sub-adults, and the larval life stage. By exploiting the sea lamprey's upstream movement tendencies, barriers and weirs have been positioned low in river systems to trap sub-adults by directing waterflow through traps, which lampreys respond to through rheotaxis (Hrodey, 2021; Miehl, 2021). Similarly, it was discovered that 3-trifluoromethyl-4-nitrophenol (TFM) and 2',5-dichloro-4'-nitrosalicylanilide (niclosamide) were highly toxic to larval sea lamprey by disrupting oxidative phosphorylation in mitochondria, resulting in death within a few hours of exposure (Bircanu, 2021; Sullivan, 2021).

Supplementary control tactics and novel assessment protocols are now the focus of sea lamprey research efforts in the Great Lakes basin (Siefkes, 2021), including the application of semiochemicals (Fisette, 2021), use of environmental DNA (eDNA, Tkachuk and Dunn, 2020), and the potential for genetic manipulations (Ferreira-Martins, 2021; York et al., 2021). These, and other, management tactics have the potential to aid conservation and restoration initiatives for native lamprey species and further increase our understanding of lamprey biology. For example, we have recently gained greater insight into the reproductive ecology of pouched lamprey (*Geotria australis*) through a combination of telemetry and molecular ecological approaches. As a consequence, we have a better understanding of critical spawning habitat for pouched lamprey in New Zealand rivers (Baker et al., 2017), and have recognized a new cryptic species of southern hemisphere lamprey in Argentina that may require urgent assessment (Nardi et al., 2020; Riva-Rossi et al., 2020). Presently, lampreys are enjoying a renaissance as a focal organism in several geographic regions; and, in large part, this can be attributed to the intersection of basic and applied lamprey research (Docker et al., 2015; Docker and Hume, 2019).

Here, we take a broad look across areas of biology that encompass challenges and opportunities in regard to future science-based management. Many topics discussed herein are dealt with in-depth in separate contributions to this special issue (e.g., climate change, Wang, 2021; fish passage, Moser, 2021; and genetic control, Ferreira-Martins, 2021), and so we do not provide deep reviews of singular issues. Rather, we focus on three core aspects of biology (survival, foraging, and reproduction) and attempt to synthesize the literature across species. Our goal is to highlight aspects of basic lamprey biology useful in their management and

aim to inform three main groups: i) policy makers and practitioners that can benefit from the development of an agenda for scientific inquiry that meets information gaps, ii) funding agencies that can use it to support broad themes that have been identified as relevant by researchers, and iii) researchers that can better apply themselves to issues considered most relevant by managers and funding agencies.

Survival

Hatching to settlement – Taking lifetime fitness from zero to one

It is widely accepted that the early stages of development in fishes (eggs to larvae) are subject to extensive mortality, with survivorship influenced by an individual's phenotype that results in natural variation in recruitment to adult life stages (Pepin, 2015). In lampreys, pro-larvae (recently hatched) still derive energy from a yolk sac and remain vulnerable to environmental conditions and predation. This may, consequently, be a critical life stage in the management of lamprey populations as excessive mortality of pro-larvae could be a significant contributor regulating lamprey demographics. However, despite several decades of research into the culture of pro-larvae for research and restoration, our knowledge of the early weeks of lamprey life in the wild remains sparse (Moser et al., 2019). Thus, significant knowledge gaps remain if we hope to realize the ability to bolster populations of imperiled species, or design novel means to control invasive sea lamprey during this life stage.

Many northern hemisphere lampreys fertilize eggs in shallow gravel nests in swift running water (Johnson et al., 2015), however a significant proportion of fertilized eggs can be dispersed from these nests (Smith and Marsden, 2006) and drift up to 50 m downstream, becoming scattered throughout riffle habitats and depositional zones along stream margins (Silva et al., 2015). Hatching success is higher in substrates that contain greater proportions of gravel than silt (Silva et al., 2015), which may be due to higher dissolved oxygen being delivered to developing embryos through hyporheic exchange in areas proximal to spawning grounds (Smith and Marsden, 2006; Fixler, 2017). Furthermore, newly hatched pro-larvae appear incapable of burrowing and require existing interstitial spaces within which to hide (Aronsoo and Virkkala, 2013) meaning that survival rates may be lower for pro-larvae hatching on fine sand and silt. The requirement for extensive areas of suitable habitat for developing pro-larvae should therefore be considered when selecting stream reaches for habitat restoration or barrier mitigation. For example, if suitable spawning habitat is located too close to fine depositional materials downstream then survivorship of pro-larvae could be compromised. This is particularly important in highly fragmented rivers, where adult lampreys are restricted to the lower reaches and well-sorted gravels are typically scarce. The habitat requirements of pro-larvae of southern hemisphere lampreys are not known, and could be significantly different to northern hemisphere species. For example, pouched lamprey deposit adhesive egg masses beneath large boulders with adults remaining alive for several months after spawning (Baker et al., 2017; Paton et al., 2019), and larvae select rearing

habitats based on underlying rather than surficial substrate conditions (Kelso, 1993).

Mechanisms governing settlement of pro-larvae into suitable habitat are not well understood, but assumed to be passive (Moser et al., 2019). If pro-larvae drift downstream as passive particles, then as water velocity declines they will drop out of the water column in deeper pools and backwater areas. Yet there is evidence that pro-larval European river lamprey (*Lampetra fluviatilis*) select for fine-grained substrate patches (particles < 125 µm) among a range provided in the laboratory (Aronsoo and Virkkala, 2013). In addition, pro-larval sea lamprey are more likely to settle in habitat patches alongside full-siblings at probabilities higher than should be observed by chance (Derosier et al., 2007; Sard et al., 2020). This suggests settlement may not always be passive. Pro-larval sea lamprey have a pit on the head containing olfactory receptor cells at hatching (Zielinski, 1996); and, by 15 mm TL, there are dense concentrations of these cells in the olfactory epithelium (VanDenbossche et al., 1994). This arrangement is similar to juvenile and adult life stages (Kleerekoper and van Erkel, 1960; Zielinski, 1996) which respond to many odorants (Fisette, 2021). Zielinski (1996) suggested because pro-larvae rapidly develop a peripheral olfactory organ they may also use olfaction to recognize conspecifics and communicate with them. The development of the pro-larval olfactory system occurs coincident with the synthesis of bile in the liver (Piavis, 1971), and sub-adult sea lamprey use such bile products to guide migration into streams suitable for reproduction (Vrieze and Sorensen, 2001). Therefore, it is possible that pro-larvae could use these odors in a similar manner, as a cue to locate patches of suitable habitat in which to settle and begin feeding or as an indicator of occupied habitat to avoid.

Unlike other anadromous or adfluvial fishes, lampreys are not philopatric. Furthermore, larval lamprey development is exceptionally prolonged (typically 5–7 years, Dawson et al., 2015). Consequently, when adult lampreys deposit their offspring they do so alongside those of unrelated individuals from previous generations, all of which will be larger than pro-larvae. This could result in a competitive disadvantage for pro-larvae which must locate suitable rearing habitat that may already be occupied and gain access to sufficient food alongside larger individuals. Pro-larval survivorship could be improved in natal streams through the release of an alarm cue (Wagner et al., 2011) released from the tissues of dead adult lampreys following spawning. Potentially, this cue could stimulate older larvae from previous generations to begin downstream movement. If an alarm cue does stimulate larval movement, this would free up suitable early rearing habitat close to where spawning took place, reducing competition for resources and potentially improving early growth rates. However, in a laboratory study, larval sea lamprey reduced their drift rate in the presence of alarm cue, but it does suggest larvae can detect and respond to the cue (Wagner et al., 2016). It is unknown whether an alarm cue could induce downstream drift if applied over longer periods of exposure (days to weeks) in a stream which is more consistent with the rate of decay of lamprey bodies compared to exposure for several hours.

The potential reliance of pro-larval lamprey on olfaction, and the tendency to select for particular substrates, represent an opportunity to improve their management at a sensitive period of the life cycle. If alarm cue does induce drift in larvae, then it could be applied during suitable sampling windows (e.g., low flows) to assess the population using standard sampling methods (e.g., plankton nets). If semiochemicals do have an important role in governing settlement, then pro-larvae could be induced to move into manufactured habitat patches designed to improve or reduce natural survival. For example, creating ecological traps for invasive sea lamprey by attracting pro-larvae to highly silted stream

reaches where survival would be low. Additionally, semiochemicals and settlement substrates could be combined to collect pro-larvae for assessment (e.g., parentage analysis), for lure-and-kill tactics to control invasive sea lamprey, or to remove pro-larvae of endangered species for ex situ rearing. If pro-larval settlement is more passive in nature, then additional research could examine drifting capacity and indicate stream reaches to be targeted for habitat restoration. For example, improving access to spawning habitat for adults will not result in increased recruitment to the larval population if they are not sufficiently proximal to early larval rearing habitat. Knowledge of the interaction between pro-larval settlement behavior and stream geomorphology could aid in this regard.

Pro-larvae to metamorphosis – They mostly come at night, mostly

After they consume most of the yolk-sac, pro-larval lampreys begin dispersing downstream in a mass migration away from spawning and early developmental habitats and are referred to as larvae when they begin feeding exogenously. This movement is potentially driven by the need to locate suitable habitat in which to capture food because pro-larvae only initiate downstream movement when they can feed exogenously, and they do not do so when experimentally translocated to substrate with high organic content (Zvezdin et al., 2017). Pro-larvae emerge from stream substrates only during hours of darkness (<150 lx, equivalent to a very dark day) and do so in a highly synchronized manner (Brumo, 2006; Bull et al., 2018; Derosier, 2001; Kirillova et al., 2011; Pavlov et al., 2014; Zvezdin et al., 2017, 2016). The extent of movement can exceed distances of 150 m from nest sites (Derosier et al., 2007). That downstream movement of pro-larvae is both nocturnal and synchronized is indicative of visual-predator avoidance, and a common strategy employed by lampreys during other life stages undertaking mass migrations between habitats (juveniles and adults).

The rate of movement by pro-larval lampreys and its extent is influenced by stream characteristics such as gradient and depth as this alters water velocity. Given the small size of pro-larvae (~10 mm TL) and inability to swim in a directed manner, once within the water column they are unlikely to be able to resist even slow-moderate water velocities and so are likely to be transported downstream alongside other passive particles. This makes them vulnerable to capture gears such as plankton nets and available for routine assessment, ex situ rearing, translocation, etc. Electrofishing is an inefficient method to capture pro-larvae (Lasne et al., 2010; Silva et al., 2014) and so setting fine-mesh drift nets or ichthyoplankton cone nets flush with the substrate, close to or within the thalweg, and sited up to tens of meters downstream of known spawning habitat can be an effective approach (Brumo, 2006; Kirillova et al., 2011; Pavlov et al., 2014; Zvezdin et al., 2016, 2017).

Several protocols have been developed for the long-term assessment of larger larval lampreys (Harvey and Cowx, 2003; Slade et al., 2003). Moser et al. (2007) reviewed many of these and suggested guidelines. Although backpack electrofishing in shallow (<0.8 m) water is effective at revealing the presence of larvae within a habitat patch and is quantifiable, it is not always informative when considering distribution and demography within watersheds especially because larval habitat can be ephemeral in nature, shifting in response to fluctuating water levels and flow rates, and larvae could move with them, although this has not been quantified. Small larvae, which are informative with regards to recruitment and proximity to spawning grounds, are less likely to be captured during routine electrofishing surveys. Other types of habitat that can be occupied by larval lampreys, such as deep water stream reaches or lentic areas, may be equally important

as shallow habitats, yet they are often overlooked when monitoring plans are being devised because of their inherent sampling difficulties (Docker and Hume, 2019). Consequently, the standard approach to surveying larval lampreys should be altered as our knowledge of larval ecology grows.

Despite recent developments in methods to detect the presence of larval lampreys (e.g., eDNA, Ostberg et al., 2018), our general understanding of larval growth, survivorship, and habitat use lags behind that of the adult life stage. Recent studies have suggested that larval annual survival rate may be higher in deep water lacustrine habitat (Johnson et al., 2016; Jones et al., 2015) compared to shallow tributary streams (Irwin et al., 2012; Johnson et al., 2014; Jones et al., 2015, 2009). There is evidence to suggest that the mouths of large river systems are important for larval lampreys, perhaps due to catastrophic sediment scouring or the gradual downstream displacement of larvae via passive drift (Dawson et al., 2015; Harris and Jolley, 2016). If deep water habitation by larvae is a general trend then it has significant implications for lamprey management, as failing to assess these habitats will result in an incomplete picture of population health. This is important for invasive Great Lakes sea lamprey where treatment of deep water habitats with pesticides can be more costly and less efficient (Jubar, 2021). Similarly, for imperiled species inhabiting large rivers with barriers located low in the mainstem, these deep water areas may be the only habitat available. Dredging river mouths or mainstem large rivers for navigation could result in significant larval mortality and loss of habitat (Maitland et al., 2015). As large river mouths, estuaries, and the Great Lakes continue to be “cleaned up” following the industrial revolution, such habitats may become increasingly important to larval lamprey populations.

The out-migration – Are we there yet?

Downstream movement of recently metamorphosed lampreys is correlated with increasing stream discharge (Dawson et al., 2015; Sotola et al., 2018), and for most species there are peaks during fall and spring coincident with significant rainfall or snowmelt events (Applegate and Brynildon, 1952; Bradford et al., 2008; Goodman et al., 2015; Pavlov et al., 2017; Roby et al., 2011; Silva et al., 2013; Swink and Johnson, 2014). Downstream movement is synchronized within streams, with thousands of juveniles taking advantage of high flow rates to disperse en masse (Applegate and Brynildon, 1952; Marsden et al., 2004). For example, sampling juvenile Pacific lamprey (*Entosphenus tridentatus*) over 8 years in the Sacramento River, California, Goodman et al. (2015) found that 91% of days yielded catches of <2 individuals, while the daily maximum was >4000. Juvenile lampreys have a tendency to move within the thalweg of streams (Bracken and Lucas, 2013; Sotola et al., 2018), and this appears to be an active rather than passive process suggesting their movement tendency at this stage is a means of reducing energy expenditure by lowering transit times and/or reducing risk of predation (Goodman et al., 2015; Potter, 1980). Deng et al. (2018) tracked juvenile Pacific lamprey in the Columbia River using miniature acoustic tags and revealed that they preferred to travel at 80% of the water's depth and their distribution, although broad across the river channel, did shift as they travelled downstream. Tracking depth as they transit suggests juveniles were moving within a preferred zone of the river, but how they achieve this is not certain. In contrast, juvenile pouched lamprey migrating out of the Waikato River, New Zealand, were found to mostly travel at the river's surface (Empson and Meredith, 1987), indicating that again aspects of southern hemisphere lamprey biology may differ from those of northern hemisphere species. Meckley et al. (2017) speculate juvenile sea lamprey sample barometric pressure when relocating the coast following the cessation of feeding, but basic research is required to

understand how lampreys perceive changes in pressure. When they are not moving, juveniles will seek cover and attach to the substrate, so remaining close to the river bottom whilst travelling may provide higher encounter rates with suitable refuges.

In contrast to larvae and upstream migrating sub-adults, juvenile lampreys express reduced dermal photosensitivity (Binder et al., 2013; Johnson et al., 2019), but movement in natural streams is nonetheless typically restricted to hours of darkness (Goodman et al., 2015; Liedke et al., 2019; Miehls et al., 2019; Pavlov et al., 2017; Zvezdin et al., 2019) or in turbid conditions (Baer et al., 2018). A tendency to move within deeper water, in higher flow either in darkness or low visibility conditions suggests juvenile lampreys are avoiding visual predators such as fish, birds, and mammals during the out-migration. This same tendency renders juveniles difficult to manipulate or collect for management purposes (Evans, 2021). For example, guidance using DC electrical current was found to be capable of pushing up to 84% of juvenile sea lamprey from one side of an artificial raceway to the other (Johnson and Miehls, 2013), however, when water velocity increases this effectiveness declines substantially even at flow rates as low as 0.19 m s^{-1} , which are lower than those utilized by juveniles in nature (Johnson and Miehls, 2013; Miehls et al., 2017).

Developing an effective and consistent means of guiding out-migrating juveniles, using physical or non-physical approaches, will be an important achievement in lamprey management. Improving the survival of juveniles of vulnerable lamprey species could include preventing them from being impinged at water intake screens (Moser et al., 2015) or entrained by surface water diversions (Goodman et al., 2017; Liedke et al., 2019). Intentionally entraining juvenile sea lamprey in the Great Lakes could provide the ability to control or assess juveniles prior to the onset of feeding (Dennis III et al., 2016; Johnson and Miehls, 2013; Miehls et al., 2017). For example, Goodman et al. (2017) estimate the San Joaquin-Sacramento River Estuary water diversion, which bears an intake screen designed for salmonids, entrains 95% of juvenile Pacific and western river lamprey. However, with the installation of an intake screen with gaps that are narrower than the bodies of juvenile lampreys all juveniles could be successfully directed to a holding tank. It is also conceivable that the development of similar water abstraction techniques could capture large proportions of out-migrating juveniles for either conservation or control. During peak migratory periods, juvenile lampreys could be entrained in a diversion channel and river flow directed over collection screens or pools before being returned to the main channel.

Larval abundance – where'd everybody go?

Larval lamprey abundance is generally considered limited by the quantity and quality of available habitat within river systems (Slade et al., 2003), as well as the attractiveness of particular spawning streams to adults as a consequence of water quantity and the concentration of larval odor it carries (Morman et al., 1980; Mullett et al., 2003). But we lack a general appreciation of carrying capacity of larvae within rivers due to observed variation in larval abundance within and among streams and years. Without a clearer link between spawning habitat, adult abundance, fertilization success, larval habitat, and larval mortality, we lack the ability to make meaningful predictions regarding the number of larvae there “should” be. Developing predictive models of recruitment in response to environmental change and management actions is a staple of the sea lamprey control program in the Great Lakes, and managers of imperiled lamprey species would benefit from adopting a similar approach. Baseline data such as fecundity, operational sex ratios, extent of available spawning and larval habitat are available for several species already (e.g., Caspian lam-

prey, *Caspiomyzon wagneri* Ahmadi et al., 2011; Nazari and Abdoli, 2010; Pacific lamprey, CRITFC, 2011, Schultz et al., 2016; anadromous sea lamprey, Mateus et al., 2012; European river lamprey, Goodwin et al., 2009, 2008), and “rules of thumb” can be extended across ecologically similar species reducing initial effort (e.g., Dawson et al., 2015; Docker and Potter, 2019). Without considering factors that dynamically influence larval abundance, continuing to collect data regarding larval presence and distribution in watersheds appears to be of little value in an adaptive management framework.

Given the massive fecundity of adult females of anadromous lamprey species and availability of spawning habitat, large numbers of larvae are expected. For example, in the Garonne-Dordogne, a large river system in France, fishermen capture ~67,000 adults each year (Beaulaton et al., 2008). With an estimated fecundity of ~200,000 eggs per female (Docker et al., 2019), if all sea lamprey adults were to survive to reproduce then conservatively there is potential for 6.7 billion eggs going into this system annually. Similar numbers of adult sea lamprey are harvested in other large European rivers (e.g., Loire and Adour river systems in France, and Minho River, Portugal; Beaulaton et al., 2008). Despite this potential, in the UK (where abundance estimates for adult sea lamprey in rivers are lacking), “Favourable” conservation status for sea lamprey is conferred on streams containing larval densities as low as 0.1 m² at only 10% of sampled habitat patches (Cowx et al., 2009; Harvey and Cowx, 2003). Presumably, a large proportion of lamprey eggs are never fertilized, and/or mortality rates are exceedingly high within streams (natural or otherwise), but empirical data are lacking. Mortality rates in lampreys are likely highest during the first weeks of life, beginning with low hatching success of fertilized eggs. Low hatching rates have been attributed to poor fertilization efficiency and environmental variables such as temperature (Applegate, 1950; Manion, 1968; Meeuwig et al., 2005). Predation on eggs and pro-larvae is also suspected to be substantial (Arakawa and Lampman, 2020; Brumo, 2006; Moser et al., 2019; Silva et al., 2015; Smith and Marsden, 2006) although this has also not been quantified. Susceptibility to predation represents an opportunity to exert additional pressure on invasive sea lamprey populations in the Great Lakes, Finger Lakes, and Lake Champlain. The collapse of lake sturgeon (*Acipenser fulvescens*) and American eel (*Anguilla rostrata*) in the mid-19th Century preceded the sea lamprey population explosion, and this relaxed predation pressure, alongside other factors, may have facilitated their establishment in these lakes (Marsden and Langdon, 2012). It could be argued that restoring native predatory species to their former abundance will contribute to sea lamprey control, and holistic approaches such as this may reduce the cost and frequency of pesticide applications if they become self-sustaining.

Should pro-larvae avoid predation and successfully hatch and drift away from the nest, they quickly face another significant mortality bottleneck, the transition from endogenous to exogenous feeding. Larval gut contents contain large proportions of inorganic detritus, and larvae assimilate nutrients from both autochthonous and allochthonous material (Dias et al., 2019; Evans et al., 2018; Hayden et al., 2019). The gut microbiome could play an important role in early lamprey survival and the transition to parasitic feeding as it could assist in digestion. But the microbial community of the gut has not been well characterized, and its function is not understood. Larval lampreys can probably breakdown cellulose and lignin as detritus forms a major part of their diet. The microbiome of larval sea lamprey is more diverse than juvenile sea lamprey that feed solely on blood (Tetlock et al., 2012), and in pouched lamprey the microbiome correlates with the biota of the surrounding stream substrate and water column (Rogers et al., 1980). Con-

sequently, the gut microbiome may be acquired at the onset of exogenous feeding. Investigating this microbial community and its role in larval growth could result in procedural changes to improve culture of imperiled species and increase the success of stocking larvae to restore populations (Lampman, 2021; Moser et al., 2019). Furthermore, dysbiosis of the gut microbiome can result in disease manifestation as well as impaired growth and immunity (Kowalski et al., 2015), which may provide an opportunity to disrupt growth or metamorphosis of invasive sea lamprey to aid control efforts, if anti-biotics could be delivered to the gut. If antibiotics could retard larval sea lamprey growth rates, mortality rates could increase and the time to metamorphosis be extended allowing additional treatments with pesticides.

Misguided restoration – it’s a trap!

Several migratory species of lamprey remain the target of traditional and modern fisheries (Almeida, 2021). But in common with most diadromous fishes, these lampreys are captured in far smaller numbers compared to the early 20th Century. For example, estimating adult abundance based on mass of landings suggests declines >95% for some species (Cejko et al., 2016; Hokkaido Fish Hatchery, 2008; Kujawa et al., 2018, 2019). Aquaculture of European river lamprey has been an ongoing restoration effort in Latvia and Finland since the 1980’s to halt the species’ decline (Aronsoo, 2015; Birzaks and Abersons, 2011). However, despite stocking millions of pro-larvae annually over several decades there is no evidence of a positive effect on the numbers of returning adults, and survival of stocked pro-larvae appears to be low (Birzaks and Abersons, 2011). Reasons for the poor performance of restoration attempts by stocking pro-larvae range from unsuitable environmental conditions resulting in high mortality during dry summers to selecting unsuitable rearing habitats (Abersons, 2019). An alternative view is that the stocking of pro-larvae is directed at treating the symptom (low population sizes) and not the cause (e.g., barriers to migration, loss of spawning habitat, etc.) of lamprey declines (Aronsoo, 2015; Birzaks and Abersons, 2011; Docker and Hume, 2019). What use is generating millions of larvae if they cannot reach feeding grounds as juveniles, there is a lack of prey for juveniles in marine environments or higher mortality of juveniles en route, or sub-adults cannot return to spawning grounds because barriers impede them? Where barriers are known to be a principal bottleneck impeding restoration efforts, translocation of adults upstream, however, does appear to be a successful approach for some species. Both Pacific (Ward et al., 2012) and Miller Lake lampreys *Entosphenus minimus* (Clemens et al., 2017) have experienced an increase in the abundance of all life stages and extended their distribution, following translocation of adults and larvae.

Translocation is not a silver bullet to mitigate population declines though, as evidenced by the failure of such efforts to restore European river lamprey in Finland (Aronsoo, 2015; Hiltunen et al., 2013). Follow up assessments of the success of translocation efforts (e.g., spawner surveys, larval abundance estimates, parentage analysis of out-migrants) are key to ensure managers make well-informed decisions. In Finland, translocations have not been assessed, and presumably persist because large numbers of sub-adults continue to be captured at migration barriers each year. Aronsoo (2015) estimated that the three rivers in Finland where translocation of European river lamprey occurs produce 50% of Finland’s freshwater input to Bothnian Bay; therefore, it is possible they attract a very large proportion of European river lamprey seeking spawning grounds. These adult lamprey are then translocated into tributaries where the survival of their offspring is low. Absent a clearer understanding of the overall population size and the effectiveness of translocation as a management tactic in this

region, there is a real possibility the species has become a victim of an ecological trap of accidental design (Birzaks and Abersons, 2011).

Avoiding risk – The nose knows

Alarm cues are released from the tissues of injured organisms into the surrounding environment (e.g., after a predation event) where they can be detected by conspecifics which alter their behavior in response. For example, increasing vigilance, altering movement paths or rates, or fleeing. Sub-adult sea lamprey in the Great Lakes avoid areas activated by an alarm cue derived from the tissues of either decayed or freshly killed adults and larvae (Bals and Wagner, 2012; Wagner et al., 2011). This response is consistent in both laboratory experiments and field tests in natural streams (Di Rocco et al., 2016; Hume et al., 2015). When released in conjunction with attractive odors (e.g., migratory cue from larvae, 3kPZS from adults) semiochemicals could be used to manipulate sea lamprey during the spawning migration, for example pushing them toward traps and potentially luring them inside (Hume et al., 2020, 2015). So-called push-pull approaches like this could also be used to create or avoid ecological traps by encouraging lampreys to reproduce in streams with varying probabilities of offspring survival. However, alarm cue alone is unlikely to be of use in blocking stream access by sub-adult sea lamprey in the Great Lakes, as when presented bank-to-bank in a stream it does not prevent entry or subsequent upstream movement (Luhring et al., 2016). In sea lamprey, the response to the alarm cue appears to turn-off after a period of continuous exposure of ~4 h (Imre et al., 2016), and sub-adults hidden within refuge areas also fail to respond (Di Rocco et al., 2014). These findings require careful consideration of the circumstances under which repellent odors could be employed in management scenarios. For example, if used to chemically block a fishway in the Great Lakes to permit the passage of desirable species while preventing invasive sea lamprey from doing so, then care must be taken to ensure no sea lamprey are trapped in the channel where they might become continuously exposed or can seek refuge. Pulsing an alarm cue application in such circumstances, or limiting lamprey access to <4 h, might be a safer decision and similarly effective.

Lastly, the alarm cue may be phylogenetically conserved within northern hemisphere lampreys, as adult sea lamprey similarly respond, although generally less strongly, to the odor of dead conspecifics (Bals and Wagner, 2012; Byford et al., 2016; Hume and Wagner, 2018). It is not known if southern hemisphere lamprey exhibit an aversive response to the odor of dead conspecifics. However, if it can be established that other lamprey species elicit the same behavioral response to this cue as sea lamprey (e.g., Pacific lamprey, Porter et al., 2017), then the application of alarm cue could be extended to managing imperiled species. For example, guiding juveniles away from water intakes to reduce mortality; pushing sub-adults towards fishway entrances to improve passage rates; or aggregating them near river banks to enable accurate assessment using methodologies like dual-frequency identification sonar (DIDSON, McCann et al., 2018). A major challenge in extending initial basic research of lamprey behavioral ecology in response to odor cues into full-scale applications in management programs is characterizing the chemical nature of the reactive compounds. A first step in the process of characterization is the isolation and identification of the behaviorally reactive compounds themselves (e.g., Dissanayake et al., 2019, 2016), followed by their synthesis and subsequent field-testing. This process can take several years and is exacerbated by the fact that sub-adult lampreys are often only available for capture and behavioral study for a matter of weeks each year.

Foraging

Larval feeding – A moment on the lips, lifetime on the hips?

The growth rates of fishes is dependent on multiple factors, and these can be intrinsic (sex, age, and metabolic rate of individuals) or extrinsic (density of conspecifics) (Keeley, 2001), influenced by food quantity and quality, and the physio-chemical properties of water (Makori et al., 2017). Larval lampreys consume fragments of sestonic biofilm while they grow slowly over several years, and they naturally occur in high density aggregations within sediment patches that provide greatest concentrations of sestonic material (Dawson et al., 2015), suggesting access to these habitats is important. Several lines of evidence indicate larval lampreys experience some form of competition during their protracted development, but few hypotheses have been put forth and subsequently tested (Lamsa et al., 1980). In some streams newly colonized by invasive sea lamprey following pesticide treatment, there appears to be increased growth rates in the earliest year classes (Purvis, 1979; Weise and Pajos, 1998) and observations from the majority of growth rate studies indicate increased larval lamprey densities result in reduced growth rates (Mallatt, 1983; Malmqvist, 1983; Murdoch et al., 1992; Rodríguez-Muñoz et al., 2003; Swink, 1995). Physical disturbance via tactile stimulation under high density conditions has been hypothesized to result in reduced growth rate of larval lampreys (Bowen and Yap, 2018). Larvae could experience an energetic cost when stimulated to leave the sediment due to the movement of nearby larvae. The resultant search for less crowded conditions would reduce time spent actively feeding. More frequent disturbances, which are likely in high density habitat patches, proportionally reduce growth rates in disturbed individuals as a consequence of reduced gut fullness, altered selection of organic particles, and reduced assimilation rate of amino acids (Bowen and Yap, 2018; Swink, 1995).

Our understanding of how lamprey population dynamics are influenced by larval density is poor, but a key knowledge gap that could address several management issues (Hansen et al., 2016; Jones et al., 2003). For example, in regard to the control of invasive sea lamprey, variance in larval growth rates among streams necessitates continual assessment of each stream individually to accurately predict the timing of metamorphosis into the destructive juvenile life stage. An ability to predict the timing of this event, and how it varies spatially, is crucial to ensure cost-effective pesticide treatment of the largest larvae. Furthermore, the procurement of metamorphosed sea lamprey in the Great Lakes has been recognized as a fundamental infrastructure need to support ongoing and future control strategies (Docker and Hume, 2019), yet insights from artificial propagation of imperiled species suggests that density has a considerable negative effect during growth in an aquaculture setting (e.g. slow growth, reduced survivorship) and is a serious impediment (Moser et al., 2019). More basic research into larval ecology and their response to high density conditions could improve our ability and capacity to culture lampreys for restoration initiatives and research itself (Lampman, 2021).

Juvenile feeding – Greed might be good

Although much of juvenile lamprey ecology remains shrouded in mystery, for some species and populations we are beginning to reveal some critical foraging habitats. This could be exceedingly important in the future with some parasitic species already in decline and set to face additional threats in the coming decades (Lucas, 2021). For example, some marine areas such as near the eastern Aleutian Islands in the Bering Sea (Orlov et al., 2008;

Orlov and Baitaliuk, 2016), appear to support vast numbers of foraging juvenile Arctic (*Lethenteron camtschaticum*) and Pacific lampreys and may be key areas supporting multiple populations of different species. Recognizing and protecting these feeding grounds could be a significant step in managing juvenile lampreys. In Scotland, recent efforts to protect so-called Priority Marine Features (Tyler-Walters et al., 2016) extend protection to European river and sea lampreys on the UK's continental shelf through strict marine planning, site protection measures (Marine Protected Areas), and species-specific conservation measures (Howson et al., 2012). In addition to protecting marine habitats, freshwater habitats supporting lamprey juveniles should also be considered (e.g., via the European Union Habitats Directive (92/43/EEC)). Some parasitic lampreys, such as Vancouver lamprey (*Entosphenus macrostomus*), have very small geographic ranges and are at serious risk of extirpation or even extinction. Unfortunately, directed conservation ecology studies of such species are rare and we know little of their basic biology (e.g., Wade et al., 2018).

Juvenile lamprey are obligate parasites, meaning that the sole purpose of this life stage is to locate and attach to hosts. Their sensory ecology should reflect this biological imperative. Yet our knowledge of juvenile lamprey biology is limited (Hume, 2021; Quintella, 2021), and mechanisms of orientation and attachment to hosts are currently unknown. However, there is evidence that juvenile sea lamprey respond quickly to changes in prey abundance by switching hosts (Adams and Jones, 2021). Increasing our understanding of the link between juveniles and their hosts is a significant opportunity to synergize basic and applied approaches. Juvenile lamprey are highly mobile, have a well-developed olfactory system (Green et al., 2017), good visual acuity (Govardoskii et al., 2019), and innervated papillae on the oral disc (Renaud and Cochran, 2019). Based on these features, it is possible to generate a theoretical behavioral sequence that occurs during host location: general search of an area by swimming randomly; detection of host odor cues; increased movement rate and direction change toward host; host contact using odor, visual, and mechanical cues; feeding site selection facilitated by electrical stimuli; and then initiation of feeding. Particularly in regard to the control of invasive sea lamprey, demonstrating the sensory modalities important in the recognition of potential hosts is a critical knowledge gap, which if addressed could aid in developing novel control tactics for this life stage. For example, there could be potential for disrupting host location through attractants to Trojan hosts (e.g., lure-and-kill strategies). Additionally, parasitic lampreys tend to exploit a broad prey base, and this could be due to their ability to employ endocrine mimicry to remain undetected by hosts. When juvenile sea lamprey are exposed to teleost prey odor they produce host-specific peptides in their buccal gland secretions that may be used to evade host immunosuppression (Wong et al., 2012). Novel control tactics for this life stage could therefore also include manipulating the endocrine pathways in sea lamprey to prevent host-specific peptide production, which may increase the likelihood of host survival.

Reproduction

Chemical communication I – That new baby smell

Lampreys are strongly reliant on chemical communication, mediated by a finely adapted olfactory system, to complete their life cycle (Li et al., 2018a; Vrieze et al., 2010). This reliance on olfaction can be manipulated to achieve management outcomes, for example, to reduce adult abundance in support of sea lamprey control (Marsden and Siefkes, 2019) or guide imperiled species toward fishways in support of conservation objectives (Byford et al., 2016).

Chemical communication in sea lamprey is modulated by complex mixtures of behaviorally active and inactive components that function at specific ratios, and behavioral responses depend on the physiology and life stage detecting the cue, as well as the environment they occupy (Buchinger et al., 2019, 2015; Li et al., 2018a). However, there are still significant knowledge gaps in regard to lamprey chemical communication. Despite several decades of basic research resulting in the identification of multiple compounds, semiochemicals have not been incorporated into management strategies for any lamprey species.

Lampreys evaluate the suitability of spawning streams based on the presence of larval odors functioning as a migratory cue (Bjerselius et al., 2000; Buchinger et al., 2015; Teeter, 1980; Wagner et al., 2009). The attraction of sub-adult sea lamprey to an extract of larval odor is well documented (Bjerselius et al., 2000; Li et al., 2018a, 2018b; Moore and Schleen, 1980; Wagner et al., 2009); yet, many questions remain regarding identification of compounds and their function. For example, three components of larval odor (petromyzonol sulfate, petromyzosterol disulfate, and petromyzonamine disulfate) can attract sub-adult sea lamprey toward the odor source in the laboratory. However, tests with these same compounds in a stream found no observable attraction (Meckley et al., 2012). This contradiction in behavioral reactivity depending on environmental circumstance should be resolved. Other factors influence adult behavioral responses to the migratory cue, including: presence or absence of minor components (Li et al., 2013), maturational status of sub-adult lamprey (Brant et al., 2015a), the overall size (flow) and shape (including patterns in the relative sizes and numbers of confluences) of the main tributary (Neeson et al., 2011), stream temperature (Brant et al., 2015b), and the ratio of components administered into the stream (Li et al., 2018a). The full extract of the migratory cue remains most attractive to migrating sub-adult sea lamprey in field tests compared to individual components (Brant et al., 2015a, 2015b; Li et al., 2018a; Meckley et al., 2012). In such field tests, larval extract was shown to draw sub-adult sea lamprey to within 1 m² of the odor source (Brant et al., 2015a), a highly directed response that could be exploited.

The attractive response of sub-adult sea lamprey to larval odor has potential utility in several management scenarios. Should the compound(s) that elicit the attractive response be identified, sub-adult sea lamprey in their invasive range could be lured into spawning streams where larval survival is low or pesticide applications highly efficient. A consistently strong attractant could also have applications in “push-pull” scenarios, guiding sub-adult sea lamprey toward traps or assessment tools such as automated counting devices. Furthermore, it is not known how many lamprey species, besides sea lamprey, employ a migratory cue (Fine et al., 2004; Yun et al., 2011). For example, sub-adult European river lamprey are attracted to water conditioned with conspecific larvae when tested in a two-choice laboratory maze (Gaudron and Lucas, 2006). Do lampreys share cue components across species (Buchinger et al., 2019)? Should these knowledge gaps be resolved, larval odor could be used in the conservation of imperiled species by drawing sub-adults into prime spawning tributaries to boost survival, or toward fishways to increase encounter rates with these structures. Given the greater response of sub-adult sea lamprey to the complete larval odor, stocking of native lampreys in the Great Lakes above barriers is one potential novel means of luring an invasive species into an ecological trap, while simultaneously restoring populations of native species threatened by control operations.

Spawning migration – The in-crowd

Following the cessation of juvenile feeding, or completion of metamorphosis for nonparasitic lampreys, sub-adults begin a

return migration to the upstream reaches of rivers and streams to spawn. These movements may be extensive (100 s of km's) in the case of large-bodied anadromous species, moderate (10's of km's) for small-bodied anadromous and adfluvial species, or limited (<5 km) for brook lampreys (Moser et al., 2015). Consequently, lampreys will differentially be exposed to threats in the environment as they progress toward the spawning grounds. Significant threats currently recognized include pollution, barriers, poaching or legal exploitation, and reduced water quantity (Clemens, 2021; Lucas, 2021; Maitland et al., 2015). This period in the lamprey life cycle is probably the most well studied; therefore, here we will summarize only a few key biological traits of relevance to their management. Sub-adult lampreys utilize a range of sensory modalities while migrating upstream, including olfaction, hearing, and vision. The role of olfaction during the in-migration is discussed in-depth elsewhere (Fisette, 2021). Because the migration occurs during hours of darkness (Moser et al., 2015) sensitivity to light may hamper, or facilitate, management. For example, Caspian and European river lampreys are limited in their access to spawning habitats by exposure to light from bridges that sub-adults are unwilling to cross, particularly in shallow water (Aronsoo et al., 2015; Nazari et al., 2017). If such a response is consistent across species, negative phototaxis could be used to guide or block adult sea lamprey in the Great Lakes. However, evidence of the utility of light to guide juvenile or adult sea lamprey in the Great Lakes has been weak and often contrary to predictions (e.g., attraction to light; Johnson et al., 2019; Miehls et al., 2017; Stampelcoskie et al., 2012). Similar non-physical stimuli, applied singly or in combination, are being investigated for their ability to manage sub-adult sea lamprey, including aversion to CO₂ (Dennis III et al., 2016) and sound (Mickle et al., 2019; Miehls et al., 2017).

The movement tendencies of sub-adult lampreys are well recognized by communities that capture them in subsistence or commercial fisheries. In particular, fishermen regularly exploit sub-adult depth preferences in estuaries and lower river reaches by setting wide, bottom-oriented gears such as fyke nets, and the subsequent tendency to track slow flow through rapids by setting traps in stream margins to intercept them (Sjöberg, 2013, 2011; Araújo et al., 2016). Adopting similar adaptive tactics could be of great benefit to lamprey managers by deploying traps in response to the animal's changes in behavior instead of setting fixed position traps. Typically, however, the adult population of lampreys is not assessed in support of conservation initiatives (Lucas, 2021), and in the sea lamprey control program traps to estimate adult abundance suffer from poor and often highly variable efficiencies (Miehls et al., 2019). A frequent comment made of sub-adult lampreys is that they are "poor swimmers." Anguilliform fishes, such as lampreys, make long-distance migrations and can surmount the same natural obstacles (e.g., rapids, falls) as salmonids, but they do so in a different manner. For example, over long distances in slow flow anguilliform locomotion is more efficient than sub-carangiform (e.g., salmonid) locomotion (Quintella et al., 2009), and lampreys make use of a suctorial disc to pass areas of high flow using a high-performance saltatory, burst swim-attach movement (e.g., Almeida et al., 2007; Quintella et al., 2004). This movement is not restricted to large anadromous species. Even the relatively small (<200 mm TL) Carpathian lamprey (*Eudontomyzon mariae*) overcomes large rapids during its spawning migration (Talabishka et al., 2012). Therefore, managers should not consider natural areas of high flow or barriers to be impediments to lamprey migration; but, to be efficient, fishways should be engineered with lamprey behavior and capacity in mind (Moser, 2021; Zielinski and Freiburg, 2021).

Sub-adults of several migratory lampreys enter rivers and streams months in advance of spawning. For example, populations of Pacific, European river, Caspian, and pouched lampreys over-

winter prior to spawning (Abou-Seedo and Potter, 1979; Nazari et al., 2017; Potter et al., 1983; Robinson and Bayer, 2005). Suitable refuge habitats during this period of inactivity appear similar across species, frequently characterized by deep pools with large boulders and woody-debris (Aronsoo et al., 2015; Clemens et al., 2012; Kitson, 2012; Robinson and Bayer, 2005; Starcevich et al., 2014). Such habitats may be critical to ensure sub-adults survive until the spring warming period and the final movements to spawning grounds, but this remains uncertain (Keefer et al., 2020). It is important to recognize the value of over-wintering or refuge habitats to sub-adults, separate from gravel patches where spawning of sexually mature adults occurs in spring-summer (Moser, 2021). In particular, pouched lamprey have only been documented to spawn beneath boulders, bedrock, or other large substrates (Baker et al., 2017). Even in those species that do not over-winter (e.g., anadromous sea lamprey), sub-adults still seek out similar refuge habitats throughout the migration (Andrade et al., 2007), which is likely to reduce energy expenditure and predation risk (e.g., Boulêtreau et al., 2020). In general, lampreys will over-winter low in catchments when migrating long distances (e.g., > 100 kms, Robinson and Bayer, 2005) but may be more likely to hold closer to spawning grounds when migratory distances are constrained by barriers. The reasons underpinning the selection of particular refuge habitat remain an important knowledge gap to address if we are to adequately restore and protect habitats specifically for lampreys (Aronsoo et al., 2015; Clemens et al., 2012).

Chemical communication II – Smelled like victory

It has been recognized for centuries by sea lamprey fishermen in Europe that spermiating males attract ovulated females with a type of odor (Fontaine, 1938). A bile acid identified as a sex pheromone in sea lamprey (3-keto-petromyzonol-sulfate, 3kPZS) functions by drawing females to a nest occupied by a male for spawning (Johnson et al., 2009; Siefkes et al., 2005). 3kPZS also mediates a behavioral suite, including upstream movement, retention at the odor source, tail fanning at the odor source (to clear the nest substrate, Johnson et al., 2012), and can override environmental variables known to reduce upstream movement (Brant et al., 2015a). Similar to the response of sub-adult sea lamprey to the migratory cue, the behavioral response of mature sea lamprey to 3kPZS is influenced by biotic and abiotic factors we do not fully understand. Time of day (Walaszczyk et al., 2013), stream temperature (Binder and McDonald, 2008; Brant et al., 2015a), presence and concentration of alarm cue (Hume et al., 2020, 2015), internal state (Brant et al., 2015b), and the presence of additional pheromones (Buchinger et al., 2019, 2017) all modulate the sea lamprey response to sex pheromone components. The dependency of sea lamprey on pheromones to coordinate reproduction has also motivated researchers to block or interrupt pheromone-induced coordination in their invasive range (Li et al., 2007). Research into sex pheromone antagonists (pheromone-like compounds that bind to olfactory receptors and inhibit pheromone-induced behavior) in sea lamprey is underway (e.g., Buchinger et al., 2020). Antagonists may reduce the reproductive success of invasive sea lamprey populations by inhibiting pheromone reception in ovulated females (Johnson et al., 2006), thereby disrupting mate-seeking behavior.

More than 20 compounds have so far been identified and shown to be potent olfactory stimulants to sea lamprey in the Great Lakes, some of which are behaviorally active in either laboratory or stream tests (Li et al., 2018b). 3kPZS is considered the most promising single compound for integration into the integrated pest management of sea lamprey, and is the first pheromone registered for management purposes (Frederick, 2021). Increasing concentrations of 3kPZS can pull ovulated female sea lamprey past sources of

natural spermiating male odor (Johnson et al., 2009), but application of synthesized 3kPZS to barrier-integrated traps improves catches by only ~10% on average. The influence of 3kPZS on trap catches is far from clear (Johnson et al., 2020, 2013) but it does appear 3kPZS is most effective in wide streams (~40 m) with low conspecific abundance (<1000) (Johnson et al., 2020, 2015). But when employed alongside an alarm cue in a push–pull approach to trapping sub-adult sea lamprey, 3kPZS did not improve trap captures despite exceedingly high encounter rates with trap entrances at a barrier and in an open stream (Hume et al., 2020, 2015). Since SLIS II, use of sea lamprey semiochemicals in management has frequently been proposed in the form of redistribution, disruption, monitoring, repulsion, trapping, integration with barriers and traps, and integration with pesticides. Yet only pheromone-baited trapping using 3kPZS has been studied at a management scale thus far (Buchinger et al., 2015). Much basic research has been done to identify compounds, but comparatively fewer attempts have been made to develop semiochemical applications to address management problems. Promising semiochemicals identified, or suspected, to play key roles in lamprey life cycles should be more rapidly tested under a range of natural circumstances to establish their suitability for further development and integration into management plans.

Determining natal origins – there's no place like home

Knowledge of where juvenile and adult lampreys developed as larvae could be of major importance in a management context. For example, larval presence/absence data, although relatively cheap and simple to collect, does not account for differential mortality between sampling sites. Assumptions that every individual lamprey has the same odds of survival to the juvenile stage regardless of origin can obscure where the most important larval habitats reside. If it transpired that most individuals returning to spawn were derived from a single river in a broader region, we might conclude that river is of greater importance to a species' overall status, therefore that river should become the focus of increased attention. In regard to control of sea lamprey in the Great Lakes, this could result in changes to where pesticide treatments are applied or a “leaky” barrier repaired by providing an additional classification factor for streams. Because lampreys do not home to natal streams (e.g., Waldman et al., 2008), tagging studies are unlikely to be revealing in this instance, and also partly because of this molecular genetic differentiation within species is not always feasible (Mateus, 2021).

The discovery of a characteristic or trait pertaining to lamprey biology that remains consistent for juvenile and adult life stages, and that differs between streams, could be revealing in regard to determining natal origins. One candidate is microchemistry of the statolith, a small calcareous structure found in the head of a lamprey (homologous to teleost otoliths) that contains a range of trace elements and metals acquired from the environment (Brothers, 2003, 1998, 1987). Using statolith microchemistry on known origin larvae, the accuracy of assigning an individual sea lamprey larva to their stream of origin in the Great Lakes can be >80% (Brothers and Thresher, 2004; Hand et al., 2008). However, attributing an individual to a lake basin is less accurate (60%). No single stream could, therefore, be used to represent a broader geographic area given substantial within-lake variation (Hand et al., 2008). Variability in statolith microchemistry has important ramifications regarding its application across larger geographical areas with varied watersheds and geologies, such as occurs along the extent of a continent's coast. Whether or not a reduction in accuracy at larger spatial scales is apparent remains to be tested, but could be a boon for studies in areas encompassing varying geologies. For example, in Lake Champlain an average of only 57% of sea lamprey larvae from 12 streams

could be classified using statolith microchemistry, but when those same samples were coded with different geologies of the lake basin accuracy improved to 70% on average (Howe et al., 2013). The lower accuracy in Lake Champlain suggests this basin exhibits less varied stream chemistry compared with Great Lakes basins. Therefore, extending the statolith microchemistry approach across the coastline of a continent should encompass far greater geological variation than is observed in the Laurentian Great Lakes, perhaps allowing for some finer resolution of stock structuring in widespread anadromous species (Mateus, 2021).

One major challenge to using statolith microchemistry to determine natal origin of lampreys is that it does not appear capable of resolving adults to natal streams, even when those individuals are of known origin (Brothers and Thresher, 2004; Howe et al., 2013; Lockett et al., 2014). The process of metamorphosis decouples statolith microchemistry laid down during the larval stage, preventing accurate reassignment to natal streams in adults. Lockett et al. (2014, 2013) concluded that the concentration of Rubidium (Rb) is the most important element separating larvae from different streams (Brothers and Thresher, 2004; Hand et al., 2008; Howe et al., 2013). But Rb tends to increase during and/or after metamorphosis, rendering the element useless as a means of classifying adults to natal streams because there is mismatch between larval and adult readings. However, if this increase in Rb occurs in a consistent manner between sites, it remains possible that adult lamprey Rb concentrations could be used to estimate stream of origin. Other anatomical structures common to both larval and adult stages (e.g., eye lens) have yielded less promising classification rates thus far (50–55% on average; Evans, 2017). Attempts to classify adult lampreys to streams where they developed are burdened with substantial uncertainty and additional basic research will be required to validate its utility. In addition, due to the destructive nature of sampling otoliths this approach may not be tolerable in circumstances when imperiled lampreys are the species of interest.

Summary

By synergizing basic and applied approaches, we have made – and will continue to make – great strides in support of lamprey management in the coming decades. There is a rich history of attempting to solve the wicked problem of invasive sea lamprey in the Great Lakes, and that pressing need to solve a practical problem has resulted in a wealth of understanding regarding fundamental lamprey biology. In turn, many of the advances made in support of sea lamprey control in the Great Lakes have provided data with which to generate biological hypotheses to test in support of conserving imperiled lampreys elsewhere in the world, and vice versa. Yet substantial gaps in our knowledge remain, many of which can be tested using newly developed methodologies or may become more tractable in the near future (e.g., Docker and Hume, 2019; Lucas, 2021; Siefkes, 2021). In support of addressing these gaps, we have highlighted 15 areas of lamprey biology with example questions that could be pursued in the support of management actions (conservation or control). The following list is not intended to be exhaustive. Rather, it is based on the preceding review and the collective and diverse experiences of the authors in lamprey research and management in North America and Europe, as well as our interactions with delegates at SLIS III. This list reflects our conclusions regarding those opportunities most likely to positively impact lamprey management in the coming years.

- Early weeks of pro-larval development in streams. What cues are responsible for habitat selection by newly hatched larvae and how are they perceived? Estimate survival rates of wild vs stocked individuals.

- Response of larvae to olfactory stimuli. Do semiochemicals mediate intra- and interspecific interactions? Do semiochemicals mediate habitat selection?
- Movement ecology of larvae within river systems. Characterize use of deep water habitats. What is the response to dewatering or high flows, and how is this perceived or tolerated? Does residency time in habitat patches vary?
- Factors influencing larval abundance. Estimate survival rates of stocked vs wild individuals. Estimate carrying capacity of habitats.
- Factors influencing larval growth. Compare density-dependent effects of physical vs chemical stimuli. Is there competition for high quality food patches and how is this mediated? What is the effect of diet quality on the accumulation of lipids?
- Transition to parasitic feeding. What role does the gut microbiome play during the shift from filter-feeding to blood and flesh meals?
- Movement tendencies of juveniles during out-migration. Characterize response to changes in river flow, depth, and discharge. What are the triggers of mass movement and how are they perceived?
- Monitoring barrier mitigation efforts by assessing juveniles. Conduct parentage analysis to estimate spawner success and subsequent offspring survival following fish passage events or translocation.
- Identifying juvenile foraging habitats. What is the spatial distribution of juveniles at sea or in lakes? How do juveniles recognize and acquire prey? How do juveniles respond to changes in prey availability?
- Movement ecology of sub-adults within river systems. What is the response to natural vs synthetic semiochemicals, semiochemicals and environmental cues signaling competing risk, and congeneric semiochemicals? What is the response to changes in depth and flow? Is there evidence of social behavior or aggregation cues?
- Capacity and behavior of sub-adults to surmount barriers. How is anguilliform locomotion and suction used to exploit physical circumstances? Is there an allometric effect or do small and large lampreys behave differently?
- Habitat selection by sub-adults. Characterize over-wintering and refuge habitats.
- Monitoring barrier mitigation efforts by assessing adults. Conduct spawner surveys or track lampreys following fishway transit or translocation.
- Integrating semiochemicals with other adult management tactics. Guide spawners toward or away from select tributaries. Integrate semiochemicals with assessment tools such as automated counting devices or traps. Use odors for characterizing or monitoring timing and location of spawning.
- Determining natal origins of adults. Identify molecular or chemical markers to reconstruct origins of spawners.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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