

## CHAPTER TWELVE

# THE POTENTIAL ROLES OF RIVER ENVIRONMENTS IN SELECTING FOR STREAM- AND OCEAN-MATURING PACIFIC LAMPREY, *ENTOSPHEMUS TRIDENTATUS* (GAIRDNER, 1836)

BENJAMIN CLEMENS, CARL SCHRECK,  
STACIA SOWER AND STAN VAN DE WETERING

### Introduction

Global climate change has been linked to rising water temperatures around the world (Kaushal et al. 2010; Mantua et al. 2010; van Vliet et al. 2013), and freshwater shortages are predicted to become increasingly problematic (Barnett et al. 2008). Global river temperatures are projected to increase by 1–2°C in the next 57–86 years, with some of the largest increases projected to occur in the United States (van Vliet et al. 2013). In addition, regional perturbations to watersheds can lead to increased air temperatures, relatively low river flows, and myriad other effects that can be exacerbated by climate change (Palmer et al. 2009; Kaushal et al. 2010). Dams can also exert indirect influences on aquatic biota via simplifying dynamic river processes, including flow regimes that can result in lowered water levels and the creation of reservoir-like conditions that can translate into relatively warm temperatures (Poff et al. 1997; Gregory & Li 2002; Poff et al. 2007).

An extensive and growing body of empirical and theoretical research exists for how warming of rivers can impact the physiology and ecology of salmonids (e.g., *Oncorhynchus* spp.; e.g., Rand et al. 2006; Crozier et al. 2008; Richter & Kolmes 2005; McCullough et al. 2009; Mantua et al. 2010; Beechie et al. 2012; Isaak et al. 2012). Comparatively little

information exists for how low flows and relatively warm water temperatures may affect the Pacific lamprey, *Entosphenus tridentatus*, an anadromous species that is sympatric with Pacific salmonids. We hope that this chapter will draw more attention to the effects of low river flows and high river temperatures on the upstream migrations and reproductive prospects of Pacific lamprey. Pacific lamprey have been classified as “highly vulnerable” to climate change, meaning that this species is “...approaching extinction and [is] likely to be re-categorized as critically vulnerable if their populations or ranges are diminished further” (Moyle et al. 2013).

This chapter synthesizes previous research with some new data examining associations of relatively warm summertime temperatures ( $\geq 20^{\circ}\text{C}$ ; and auto-correlated low river flows) with aspects of the upstream migration, the sexual maturation process, and identification of “ocean-maturing” and “stream-maturing” life history types of Pacific lamprey (Clemens et al. 2013). We refer to relatively warm temperatures as  $\geq 20^{\circ}\text{C}$  and relatively cool temperatures generally as being  $<20^{\circ}\text{C}$  and particularly as  $\leq 15^{\circ}\text{C}$ . The work synthesized in this chapter was born out of a combination of observations, monitoring, and experimental work. Though more research is needed to test the conceptual model we propose, we argue that it provides a parsimonious explanation for the existence of stream- and ocean-maturing Pacific lamprey. We hypothesize that relatively cool temperatures and high river flows may select *for* stream-maturing Pacific lamprey, whereas relatively warm summertime temperatures and low river flows may select *against* this life history, which reside in rivers for extended periods of time (a year or more) through factors that modulate metabolism and hence life and death, the propensity to migrate and sexually mature. Conversely, relatively warm summertime temperatures and low flow may select *for* ocean-maturing lamprey that may spend as little as several weeks in freshwater prior to spawning (Clemens et al. 2013).

Before proceeding, we wish to present two disclaimers and a counter to those disclaimers. First, most of what we discuss in this chapter is by way of correlation of patterns in the behavior and physiology of adult Pacific lamprey, with two particular aspects of its environment, temperature and river flow. Second, much of the work discussed herein stems from laboratory and field work conducted in the Willamette River Basin, Oregon (U.S.A.), with some work occurring elsewhere in Oregon, and some in the Klamath River estuary, in California (U.S.A.). This raises two concerns. One, we acknowledge that correlation does not necessarily equate with causation and we encourage more controlled experimentation

to improve understanding of behavioral and physiological mechanisms in Pacific lamprey (e.g., see synthesis on temperature and fishes by McCullough et al. 2009). Two, the scope of inference of our work in the strict sense is within these geographical locations. Regional genetic adaptations by Pacific lamprey (e.g., see Hess et al. 2013) to low river flows and relatively high summertime temperatures, if such adaptations exist, could present a caveat to this scope of inference. With this in mind, we counter that our hypothesis and prediction form a parsimonious, cohesive model that can explain much about the biological reactions of Pacific lamprey to the hydrological regimes they experience, and their population declines.

This chapter is divided into seven parts. In part one, we provide background on relative abundance of lampreys; life history diversity; and genetics, morphology, and stock structure. In part two, we review previous work on associations between river flow, water temperature, and migrations by Pacific lamprey to spawning areas. In part three, we review previous work and present some new data on associations between water temperature and sexual maturation in Pacific lamprey. In part four, we discuss association between relatively warm temperatures and atretic testes in males and skewing of sex ratios in favor of males. We also briefly discuss the role of disease in morbidity of Pacific lamprey. In part five, we briefly cover the association between water temperature and spawning in Pacific lamprey. In part six, we discuss relationships between water temperature and egg hatching, larval growth rates, and larval deformities in controlled laboratory studies. In part seven, we conclude with a recapitulation of our hypothesis that reduced river flows and increased water temperatures may form a strong selection factor against successful spawning by Pacific lamprey in the upper portion of watersheds. In the lower watersheds, the effects of warm water on Pacific lamprey may be more metabolically-taxing; and, through various means may result in unsuccessful reproduction. We predict that the mechanistic basis for this decoupling of successful reproduction in the upper portion of watersheds occurs via “controlling”, and in some cases “directive” or “lethal” factors (Fry 1971) that modulate metabolism and hence migration and sexual maturation.

## **Background**

There are approximately 41 species of lampreys, 18 of which are parasitic (Potter et al. 2015). One of these parasitic lampreys, the Pacific lamprey, is a relatively large, parasitic and anadromous fish that is found

throughout river drainages that have access to the Pacific Ocean, from Baja California to Alaska and Japan. Pacific lamprey reside as burrowing, filter-feeding larvae in fine-grained, fluvial substrates for up to six years before undergoing a metamorphic transition into parasitic juveniles that migrate to the ocean (Beamish & Levings 1991; van de Wetering 1998). Marine phase Pacific lamprey are estimated to spend up to 3.5 years in the ocean, where they feed as external parasites on teleost fishes and whales before returning to streams to spawn and then die (Beamish 1980; Clemens et al. 2010). In the Pacific Northwest, Pacific lamprey cease feeding in the ocean, return to freshwater during the spring (April–June), and begin their initial upstream migration during the summer (July–September) before their overwinter holding during October–March (Clemens et al. 2010). Pacific lamprey then mature, spawn, and die during April–July. During this year-long freshwater period as returning adults, Pacific lamprey experience a wide range of temperatures currently ranging from  $<5^{\circ}$  to above  $25^{\circ}\text{C}$ , as compared with a temperature range that may have been cooler about 40 years ago (Clemens et al. 2009; Clemens et al. 2010). The spawning period, however, is contingent upon temperature, photoperiod, and likely also with the migration distance to spawning grounds (Clemens et al. 2010). The spawning migration and spawning periods vary with latitude, being earlier in California than in the time periods noted above, which tends to hold for Oregon and then British Columbia as one proceeds northward (Clemens et al. 2010). Their prolonged freshwater adult residency without feeding, along with their capacity for extensive migration distances (up to 700 km; Clemens et al. 2010), raises many questions about the biology of Pacific lamprey, including their reproductive biology, and their adaptations to thermal regimes in river systems.

### ***Persistence and decline***

Lampreys, Petromyzontiformes, are some of the oldest vertebrates on earth, and they have changed very little since they appeared in the fossil record over  $\sim 300 - 500$  million years ago (Dawkins 2004; Janvier 2008; Helfman et al. 2009). Despite the persistence of lampreys through geologic time, lampreys worldwide have been undergoing severe declines, and river habitat degradation and barriers to spawning sites have been implicated (Renaud 1997). In North America, 10 of the 20 described lamprey species are vulnerable, threatened, endangered, or have imperiled populations (Jelks et al. 2008); and this is likely from the same causes described by some authors (Renaud 1997; Jelks et al. 2008).

Pacific lamprey abundance has declined significantly over the last 50 years in the Pacific Northwest of North America (CRITFC 2011). This decline has been attributed to the problems with lamprey populations in the northern hemisphere: declining habitat availability, quantity and quality, and barriers to upstream passage for spawning (Close et al. 1995; CRITFC 2011; Moyle et al. 2009) as well as barriers to downstream migration of larvae and juveniles (Moursund et al. 2003; CRITFC 2011). In fact, the results of the U.S. Fish and Wildlife Service's assessment indicate that much of the Pacific lamprey population(s) in the interior Columbia River Basin are "critically imperiled" or "possibly extinct" (Wang & Schaller 2015).

Native American tribes that use Pacific lamprey as a food, medicine and ceremonial and cultural resource have expressed great concern about the persistence of these fish (Close et al. 2002; CRITFC 2011; Petersen Lewis 2009). The state of Oregon has listed Pacific lamprey as a "sensitive" species at risk of extinction (Kostow 2002; ODFW 2006). In California, Pacific lamprey have been categorized as having a highly vulnerable baseline and as being highly vulnerable to climate change (Moyle et al. 2013). In 2003, a petition to list the Pacific lamprey as "threatened" or "endangered" under the Endangered Species Act was considered by the U.S. Fish and Wildlife Service, which concluded that insufficient evidence on biology, ecology, habitat needs and specific threats were available to list this fish (USFWS 2004).

### ***Life history diversity***

*"It is possible that Pacific lampreys within one stream system have more than one run...."* (Moyle 2002). Two "runs" of adult Pacific lamprey have been observed in some California rivers (Moyle et al. 2009), and a similar observation has been made in Cedar Creek, Washington, which enters the lower Columbia River just downstream from the Willamette River in Oregon. Two distinct pulses of returning adult *E. tridentatus* were observed over several years of monitoring: 1) an early pulse, occurring April–July and 2) a late pulse, occurring late August–November (Stone et al. 2001; Stone et al. 2002; Lê et al. 2004; Luzier & Silver 2005). It is not known whether these "runs" or "pulses" of Pacific lamprey represent "...a spring run that spawns immediately after the upstream migration and a fall run, which holds over and spawns the following spring" (Moyle 2002) or a spring run that was last years migrants and this year's spawners and a fall run that would spawn the following spring.

Native Americans from the Confederated Tribes of the Umatilla Indian Reservation noted a single migration lasting from spring through fall, of

which two morphotypes of Pacific lamprey were readily observed in the Umatilla River of northeast Oregon: 1) “short, brown eels” called “day eels”, and 2) “long, dark eels” called “night eels” (Close et al. 2004). Close et al. (2004) speculated that the day eels were animals that had overwintered and possibly spawned, whereas the night eels may have been recent migrants from the ocean. However, they were unable to rule out the possibility of two different life history types. Moyle (2002) also noted,

*“In the Trinity River (northern California), for example, there may be two distinct forms of Pacific lamprey, one smaller and paler than the other, that represent either separate runs or resident versus migratory individuals.”*

Recently, Clemens et al. (2013) described the maturation timing, associated phenotypic characteristics, and life history diversity of adult Pacific lamprey returning to Willamette Falls. They also collected recent migrants of Pacific lamprey as a reference to Pacific lamprey with unknown freshwater histories collected at Willamette Falls, 204 km from the Pacific Ocean. Recent migrants were collected at a location where they could be readily captured as they entered freshwater from the Pacific Ocean — at the mouth of the Klamath River (California). Using multivariate analyses of morphological measures and maturity via gonadal histology, they reported statistically-significant evidence to suggest that at least two life histories of Pacific lamprey exist. One life history is the typical “stream-maturing” life history that was described as *the* life history for Pacific lamprey over 35 years ago (Beamish 1980) that resides one year in freshwater before spawning. The other life history was identified from a small number of fish collected where the Klamath River mouth enters the Pacific Ocean. This life history includes maturing-mature fish, including females with oocytes in late vitellogenesis – early maturation stages and males with spermatocytes, spermatids, and spermatozoa. These lamprey appear to represent an “ocean-maturing” life history that may mature and spawn over the course of weeks (Clemens et al. 2013). This evidence seems to agree with Moyle’s hypothesis of the existence of more than one run in larger rivers (Moyle 2002). The relationship between genetic stock structure — or lack thereof — and life-history diversity in Pacific lamprey is not known.

### ***Genetics, morphology and stock structure***

Evidence from microsatellite markers (Spice et al. 2012) and single nucleotide polymorphisms (SNPs, Hess et al. 2013) suggests that, unlike

Pacific salmon (*Oncorhynchus* spp.), Pacific lamprey do not home to rivers in which they were born. Rather, the genetic evidence supports the hypothesis that they experience limited dispersal during their parasitic ocean phase (Spice et al. 2012). For example, these results indicated that along the Pacific Coast of North America, genetic samples from Pacific lamprey showed statistically-significant, albeit low genetic differentiation among locations; and significant, albeit weak isolation by geographical distance (Spice et al. 2012). Using genetic (SNPs) and phenotypic data (lipid content and behavioral migration patterns) in the Columbia River Basin, researchers have demonstrated that a particular genetic marker is associated with body size and lipid content, and a particular genetic marker is associated with migration distance and timing (Hess et al. 2014). These data suggest genetic selection for body size and migration distance. It is not known whether the life history diversity for Pacific lamprey (Clemens et al. 2013) is related to genetics, body size, and stock structure as described by Hess et al. (2014).

## **River flow and temperature: associations with the pre-spawning migration**

### ***Flow and adult migration***

During their upstream migration, lampreys are attracted to flow (Abou-Seedo & Potter 1979; Keefer et al. 2009; Clemens et al. 2012b) and decreases in flow to static or lentic conditions are not conducive to continued upstream migration (Daniels 2001). The number of European river Lamprey, *Lampetra fluviatilis*, captured at a power station in England was strongly related to an increase in river flow, although the authors of this study acknowledged that temperature may also have played a role in this relationship (Abou-Seedo & Potter 1979). Similarly, in a large radiotelemetry study in the Willamette River Basin, Pacific lamprey actively migrated further upstream when higher flows were available. These fish distributed throughout the mainstem more rapidly during a relatively high flow year. During the summer, when flows were low, and water temperatures high, the fish stopped migrating (Clemens et al. 2012a, 2012b).

### *Temperature and adult migration*

Although sea lamprey and Pacific lamprey are generally inactive at  $< 10^{\circ}\text{C}$  (Clemens et al. 2010), Pacific lamprey have been found to undergo some migratory activity at these low temperatures, and increase their activity as the water temperature warms beyond  $10^{\circ}\text{C}$  (Robinson & Bayer 2005; Starcevich et al. 2014).

The vast majority of migratory movements by Pacific lamprey in the Smith River, Oregon, during their pre-spawning migration occurred at temperatures  $< 20^{\circ}\text{C}$ , and migratory movements essentially ceased when water temperatures were  $> 20^{\circ}\text{C}$  (Starcevich et al. 2014).

Using radiotelemetry to track individual fish in the John Day River of interior Oregon, much of the initial upstream migration occurred between temperatures of  $\sim 27$  and  $18^{\circ}\text{C}$ ; the final migration to spawn between  $6$  and  $10^{\circ}\text{C}$ ; and spawning between  $10$  and  $15^{\circ}\text{C}$  (Robinson & Bayer 2005). However, as this temperature data was recorded from a single stationary site, these may not have been the actual temperatures that each fish experienced.

To understand the migration distances and timing during the initial or pre-spawning migration phase of adult Pacific lamprey, Clemens et al. (2012a) tracked radio-tagged fish throughout the Willamette Basin above Willamette Falls, Oregon, by airplane and recorded their location. Fish migrated primarily during the spring to early summer period before stopping during the remainder of summer, when peak river temperatures ( $\geq 20^{\circ}\text{C}$ ) occurred. These fish tended to remain stationary through the fall and winter. However, at least a few fish continued to migrate upstream after September, and the data therefore did not support the hypotheses that all fish would stop migrating during the summer. These results were consistent with a subsequent telemetry project in the same basin, in which many more fish were tagged and more fine-scale tracking occurred (Clemens et al. 2012b).

This slowing and stopping of upstream migration by Pacific lamprey during warm summer temperatures is an apparent contradiction to reports of increasing numbers of migrating lamprey with warm river temperatures at major dams. For instance, using fish counts at dams, Keefer et al. (2009) reported evidence to suggest that the pre-spawning migration of Pacific lamprey in the Columbia River occurred relatively early in years when river flow was low and water temperature high, and late when river flow was high and water temperature low. About 25% of the Pacific lamprey migrated upstream past the first dam on the Columbia River (Bonneville Dam) once water temperature reached  $17^{\circ}\text{C}$ ;  $\sim 50\%$  migrated upstream

once water temperature reached  $\sim 19^{\circ}\text{C}$ , and  $\sim 80\%$  migrated upstream once water temperature reached  $\sim 21\text{--}23^{\circ}\text{C}$ . Similarly, passage of radio-tagged Pacific lamprey at Willamette Falls increased dramatically during season highs of  $\sim 23^{\circ}\text{C}$  (Mesa et al. 2010). However, this difference in upstream migration behavior may be a function of compensatory responses to river flow and temperature at different locations in the Willamette (e.g., above or below Willamette Falls). The maximum breathing and heart rates for Pacific lamprey occurs at  $25^{\circ}\text{C}$  (the maximum temperature studied; Johansen et al. 1973), and incipient lethal levels for lampreys is  $\geq 28^{\circ}\text{C}$  (Potter & Beamish 1975; Macey & Potter 1978). Consequently these increases in upstream migratory activity by adult Pacific lamprey at Bonneville Dam in the Columbia River (Keefer et al. 2009) and at the Willamette Falls dam complex in the Willamette River (Mesa et al. 2010) may be an active response by the fish to escape warming temperatures of  $\sim 21\text{--}23^{\circ}\text{C}$ .

In a study that did not provide details, Lemons & Crawshaw (1978) reported that adult Pacific lamprey selected mean temperatures of  $16\text{--}17^{\circ}\text{C}$  in the laboratory. These temperatures are well within the range of temperatures at which Pacific lamprey have been reported to migrate (see Fig. 12-4, centerfold, page xxviii), and close to the mean temperature of peak migration of  $15^{\circ}\text{C}$  reported for other lamprey species (sea lamprey, *Petromyzon marinus*; Binder et al. 2010).

### **Temperature: associations with sexual maturation**

In anadromous lampreys, sexual maturation begins during the parasitic feeding phase. Final maturation leading to spawning occurs during the non-feeding, freshwater migration (Clemens et al. 2010). Sexual maturation in Pacific lamprey may be slower than in sea lamprey because some Pacific lamprey have prolonged migration in freshwater, both in terms of distance and duration (Clemens et al. 2010). During the maturation process, the lamprey brain integrates internal, sensory and environmental input and relays this information to the hypothalamus, which controls maturation and reproduction through release of gonadotropin-releasing hormones (GnRHs) that mediate the pituitary-gonadal axis (Sower 2003, 2015; Clemens et al. 2010). Accordingly, the synchronization of GnRHs with reproductive hormones (e.g.,  $17\beta$ -estradiol) should occur in a way that the lampreys will mature and spawn at a time and location conducive to successful reproduction. Seventeen-beta-estradiol ( $E_2$ ) is a major hormone regulating reproductive maturation and function in male and female lampreys (Sower 2003; Bryan et al. 2008;

Clemens et al. 2010). This hormone is released by the gonads of both sexes and stimulates a physiological cascade that results in the uptake of vitellogenin in maturing oocytes in females and the maturation of spermatogonia to undergo meiosis and eventually produce spermatozoa. Concentrations of  $E_2$  in the plasma have traditionally been used as an indicator of sexual maturation. Increases in  $E_2$  and GnRHs are associated with changes in photoperiod and warming river temperatures in sea lamprey (Sower 2003; Sower et al. 2011). In the laboratory, warm temperatures of 21.8°C (mean) during the summer were significantly associated with sexual maturation in 100% of Pacific lamprey the following spring (8–10 months later), whereas only 53% of the lamprey held at 13.6°C matured the following spring (Clemens et al. 2009). This line of evidence could suggest that warm summer temperatures are associated with high concentrations of  $E_2$  and expedited maturation timing in Pacific lamprey, and vice-versa.

***New data: 17 $\beta$ -estradiol and direct associations with temperature***

The physiological role of  $E_2$  during final sexual maturation has been studied primarily in the adult sea lamprey (Bryan et al. 2008; Clemens et al. 2010; Sower 2015). In Pacific lamprey, concentrations of plasma  $E_2$  were 0.5–2 ng \* ml<sup>-1</sup> in both sexes during fall – early spring, before peaking during mid-spring at 2–4 ng \* ml<sup>-1</sup> and decreasing during late spring. Concentrations of  $E_2$  were often higher in males than females, particularly during peak maturation in the spring (Mesa et al. 2009).

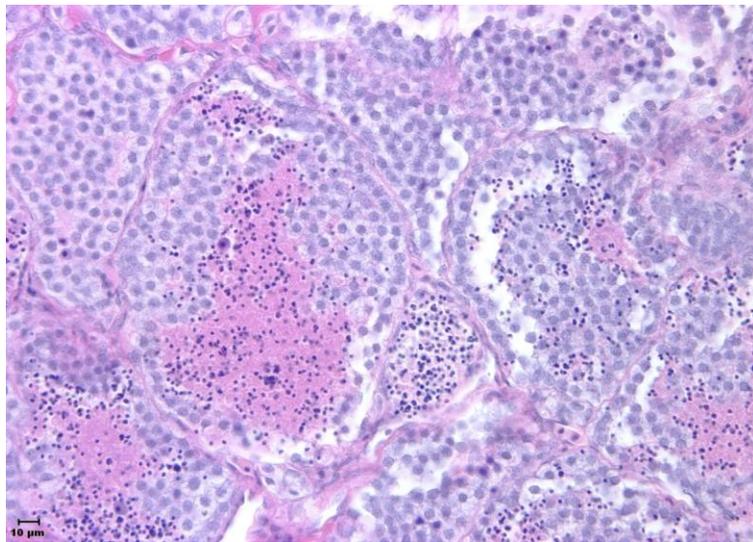
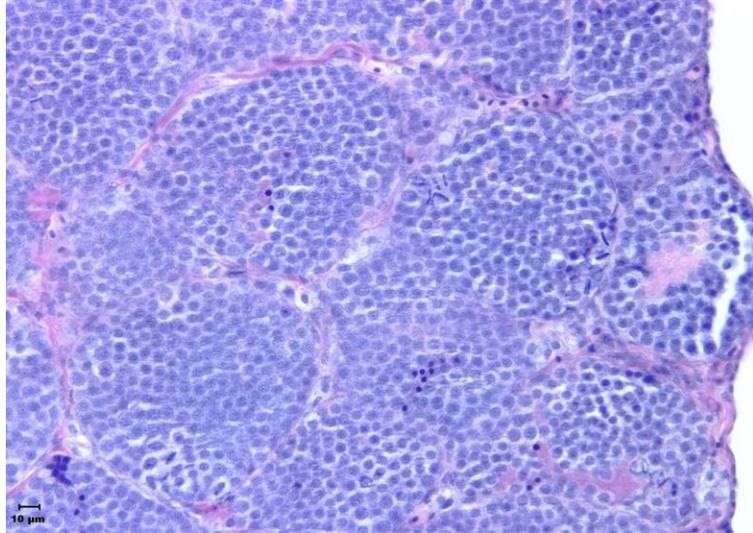
Our own results for Pacific lamprey collected during late summer at water temperatures of 21–22°C indicate a mean plasma  $E_2$  concentration of 0.66 ng \* ml<sup>-1</sup> (range: 0.12–3.13 ng \* ml<sup>-1</sup>; 47 immature fish; B.J. Clemens et al., unpublished manuscript), which overlaps the mean  $E_2$  values reported by Mesa et al. (2009). Particularly interesting is the overlap of our range with their fish that were undergoing final sexual maturation. By contrast, collecting lamprey from this same population and holding them for up to 1 month at a cooler temperature of ~14.5°C was associated with significantly lower concentrations of  $E_2$  for immature fish (mean: 0.17 ng \* ml<sup>-1</sup>, range: 0.13–0.39; N = 16; B.J. Clemens et al., unpublished manuscript). These results suggest that holding lamprey at temperatures that are cooler than the water they were initially collected from may reduce concentrations of  $E_2$  and vice versa.

## **Temperature: associations with morbidity that may preclude spawning**

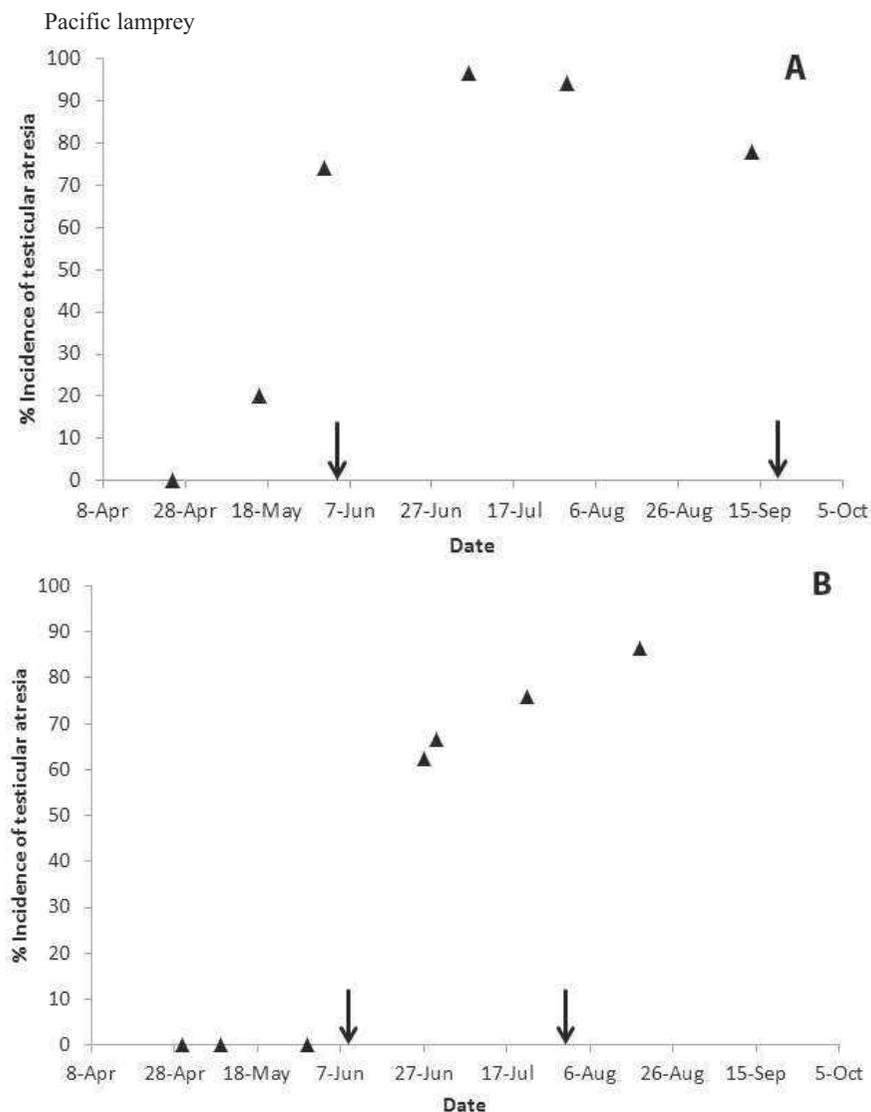
### *New data: testicular atresia and skewed sex ratios*

The following describes previously unpublished data on the incidence of testicular atresia in males, and skewing of sexes towards males, both coinciding with the onset of summertime, low river flows, and warm river temperatures ( $\geq 20^{\circ}\text{C}$ ). Adult Pacific lamprey were collected and sampled for physiological indices over time (at bi-weekly to monthly intervals) at Willamette Falls, Oregon. Fish were identified to sex, and measured and sampled for various morphological and physiological indices, including assessment of maturation status via gonad histology (Clemens et al. 2012c and 2013).

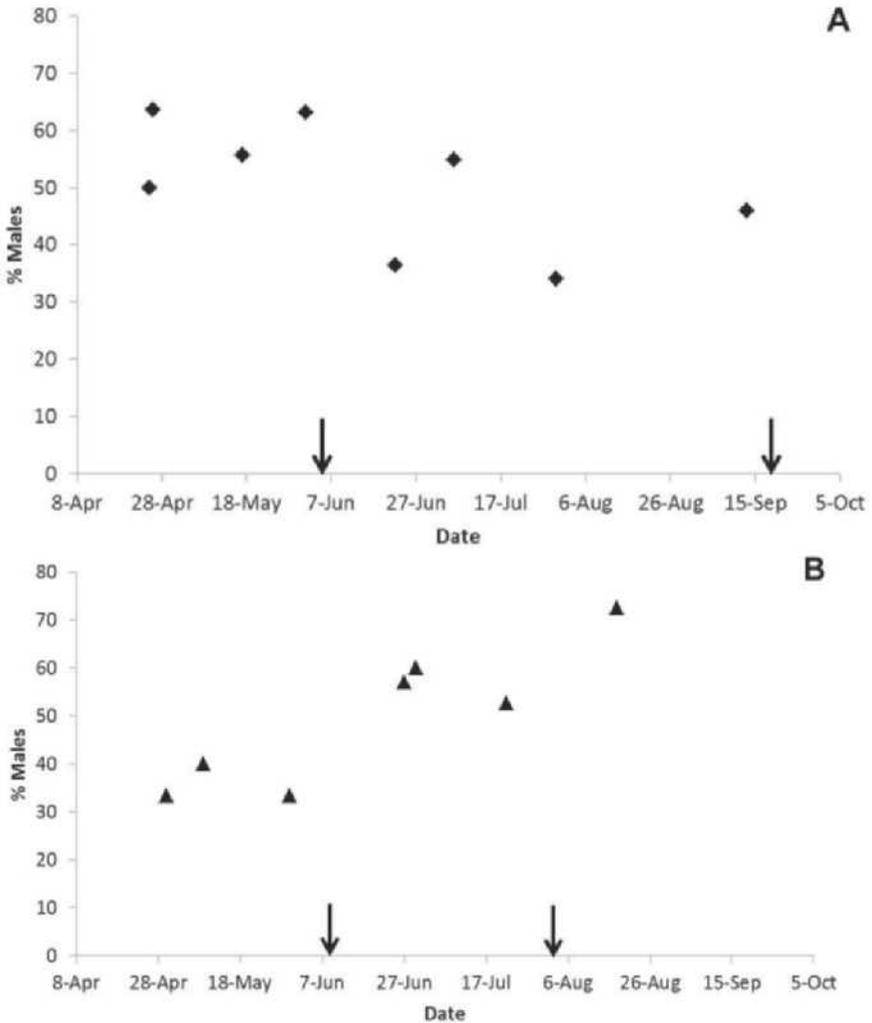
Pacific lamprey have a unimodal maturation timing at Willamette Falls between April and June, at water temperatures  $< 20^{\circ}\text{C}$ . Between July and mid-September, water temperatures at Willamette Falls peak at  $> 25^{\circ}\text{C}$ . This summer period coincides with evidence of relatively immature fish for both sexes (no early maturation stages for females and no obvious meiotic stages in males; Clemens 2011; Clemens et al. 2013). Immature males showed evidence of atretic testes (Fig. 12-1, centerfold, page xxvii) during July – September, as did the few mature males that occurred during early July. The level of incidence of testicular atresia for both 2007 and 2008 reached a peak during July – August (Fig. 12-2). By comparison modest incidence and individual level of oocyte atresia in females was observed (B. J. Clemens, unpublished data). Skewing in sex ratios towards a higher percentage of males by collection date, culminated in a 72.5% : 27.5% ratio of males to females, respectively, during August of 2008 (Fig. 12-3), the same collection date in which we observed hundreds of lamprey carcasses at Willamette Fall, an obvious fish kill when ambient river temperature was  $22.6^{\circ}\text{C}$  and the fish were stranded in small pools at the base of the falls. Both incidence of testicular atresia and the skewing of sex ratios towards males were pronounced during 2008 (Figs. 12-2 and 12-3), which may suggest that either females migrated away from this area or they perished. It is unknown if lamprey have the capability of regenerating atretic testes. Inter-annual variability in incidence of testicular atresia and sex ratios is apparent (Figs. 12-2 and 12-3).



**Figure 12-1.** Histology of testes of Pacific Lamprey showing spermatogonia, per Clemens et al. 2012c and 2013. (a). Normal, healthy looking testes. (b) Testes undergoing atresia.



**Figure 12-2.** Percentage of male Pacific lamprey showing testicular atresia over time at Willamette Falls, Oregon (U.S.A.) for (A) 2007 (N = 102 males) and (B) 2008 (N = 84 males). Vertical arrows on the x-axes indicate the start and end dates for when mean daily temperatures were  $\geq 20^{\circ}\text{C}$  at Willamette Falls. Note that the incidence of spermatozoa is found in April, peaks in May, and tails off in June (Clemens et al. 2013).



**Figure 12-3.** Percentage of male Pacific lamprey over time at Willamette Falls, Oregon (U.S.A.) during (A) 2007 ( $N = 213$  lamprey, across both sexes), and (B) 2008 ( $N = 147$  lamprey, across both sexes). Vertical arrows on the x-axes indicate the start and end dates for when mean daily temperatures were  $\geq 20^{\circ}\text{C}$  at Willamette Falls. Further information on collection methods and other measurements can be found in Clemens et al. (2013).

### ***Association of a pathogen with sexual maturation and death***

In fish health screening for pathogens, the primary concern was of the bacterium, *Aeromonas salmonicida*, which was detected in nine adult Pacific lamprey tested. These nine lamprey died following transfer to the upper portion of the Columbia Basin, to seed habitat blocked by dams (Ward et al. 2012). Recent data found an association between *A. salmonicida* and sexual maturation in Pacific lamprey. That research raised questions about whether *A. salmonicida* proliferates as a result of the maturation process or if the pathogen might kill the lamprey before they spawn (Clemens et al. 2009). Although warm water temperatures are correlated with *A. salmonicida* outbreaks in fishes, the laboratory study by Clemens et al. (2009) was not specifically designed to disentangle effects of temperature on incidence of this disease in Pacific lamprey from the sexual maturation process by these same fish — the maturation process itself being influenced by the warm test temperatures.

### **Temperature: association with spawning**

Pacific lamprey have been reported to spawn in natural streams at ~10–17°C, peaking at 13–16°C (Clemens et al. 2010; Starcevich et al. 2014). Further details on other habitat characteristics selected by Pacific lamprey for spawning can be found elsewhere (Stone 2006; Brumo et al. 2009; Gunckel et al. 2009; Clemens et al. 2010; Mayfield et al. 2014).

### **Temperature: relationships with hatching, larval growth and deformities**

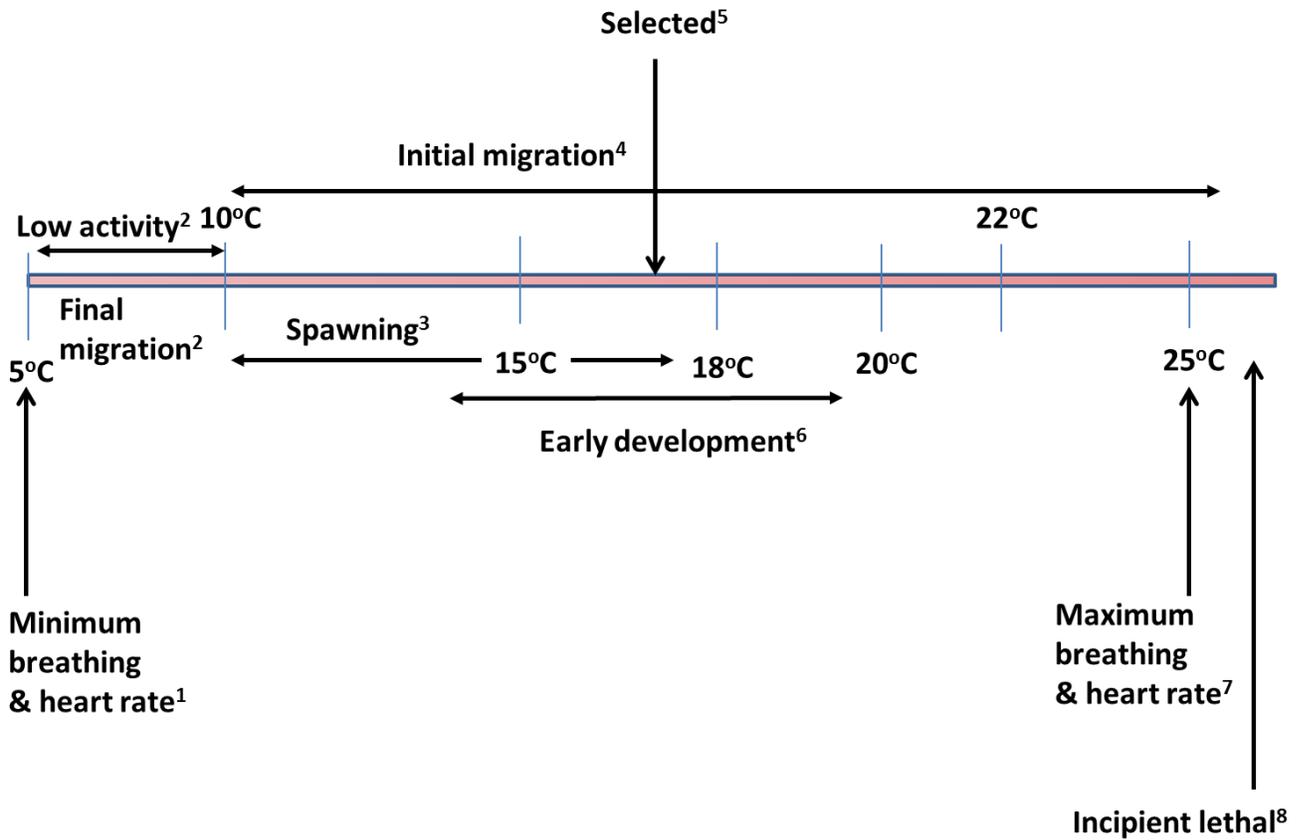
Water temperature is a significant factor in egg hatching and growth rates in larvae of the sea lamprey (Piavis 1971), and can be predicted via a derivation of the Arrhenius model, an exponential equation that can also be used to predict reaction rates, such as those through enzymatic and chemical reactions (Holmes 1990). The regulation of the spawning migration and spawning behavior in lampreys probably evolved as an adaptation to the thermal requirements of developing embryos (Clemens et al. 2010). Embryonic development in Pacific lamprey occurs within a relatively broad thermal range of <10–22°C. Maximum survival occurred at 18°C, and the highest incidence of developmental abnormalities occurred at 22°C. Of the temperatures tested (10, 14, 18, and 22°C), the most salubrious temperature for survival and development appeared to be 14°C. At this temperature, larval Pacific lamprey had the second highest

survival rate and the lowest incidence of developmental abnormalities (Meeuwig et al. 2005).

### **Recapitulation: hypothesis and predictions**

Adult Pacific lamprey appear to be most active across a temperature range of 10–23°C, with an apparent preferred temperature range of 13–17°C (Fig. 12-4, centerfold, page xxviii). The apparent preferred temperature range encompasses the selected range of temperatures by adults, the thermal window for upstream migration, the peak spawning temperatures, and a temperature at which relatively high embryonic survival and low incidence of deformities occurs (Fig. 12-4, centerfold, page xxviii). At temperatures  $\geq 20^\circ\text{C}$ , sexual maturation can be expedited; but disease, testicular atresia, and evidence of skewed sex ratios and decreased larval survival have been observed. Further, the maximum breathing and heart rates for Pacific lamprey occurs at 25°C (the maximum temperature studied; Johansen et al. 1973), and incipient lethal levels for five different larval lamprey species — and presumably Pacific lamprey — is  $\geq 28^\circ\text{C}$  (Potter & Beamish 1975; Macey & Potter 1978; Fig. 12-4, centerfold, page xxviii). The increases in upstream migratory activity by adult Pacific lamprey at major barriers (Keefer et al. 2009; Mesa et al. 2010) may therefore be an active response by the fish to escape warming temperatures of  $\sim 21\text{--}23^\circ\text{C}$ . By contrast, in the upper Willamette, Pacific lamprey either appear to migrate to an upper portion of the watershed that has temperatures  $< 20^\circ\text{C}$ , or they cease their upstream migrations. We provide an overall context for the thermal biology of Pacific lamprey across a range of temperatures in Fig. 12-4 (centerfold, page xxviii).

Pacific lamprey Pacific lamprey Pacific lamprey Pacific lamprey Pacific lamprey Our synthesis had lead us to hypothesize that the thermal histories of many adult Pacific lamprey could uncouple their spawn timing with optimal habitat characteristics that are synonymous with the upper portion of watersheds, including cool water temperatures ( $< 20^\circ\text{C}$ ; Fig. 12-4, centerfold, page xxviii) and optimum-sized substrates conducive to spawning, embryonic development and larval emergence, rearing and growth (Fig. 12-5, centerfold, page xxix; Meeuwig et al. 2005; Clemens et al. 2010). Based on the foregoing, we predict that high summer temperatures can act as a strong selection factor against stream-maturing Pacific lamprey; conversely this scenario may select for ocean-maturing Pacific lamprey. However it is not known whether the adult life history diversity for Pacific lamprey (Clemens et al. 2013) is related to genetics, body size, and stock structure as described by Hess et al. (2014).



**Figure 12-4 (next page).** Key biological processes of the Pacific Lamprey across life stages (with a focus on the final life stages) and the temperatures at which these processes occur.

<sup>1</sup> 5°C; Johansen et al. 1973

<sup>2</sup> < 10°C (low activity) Clemens et al. 2010; final migration 5–10°C Robinson & Bayer 2005; Starcevich et al. 2014

<sup>3</sup> 10–17°C (peak at 13–16°C) Clemens et al. 2010; Starcevich et al. 2014

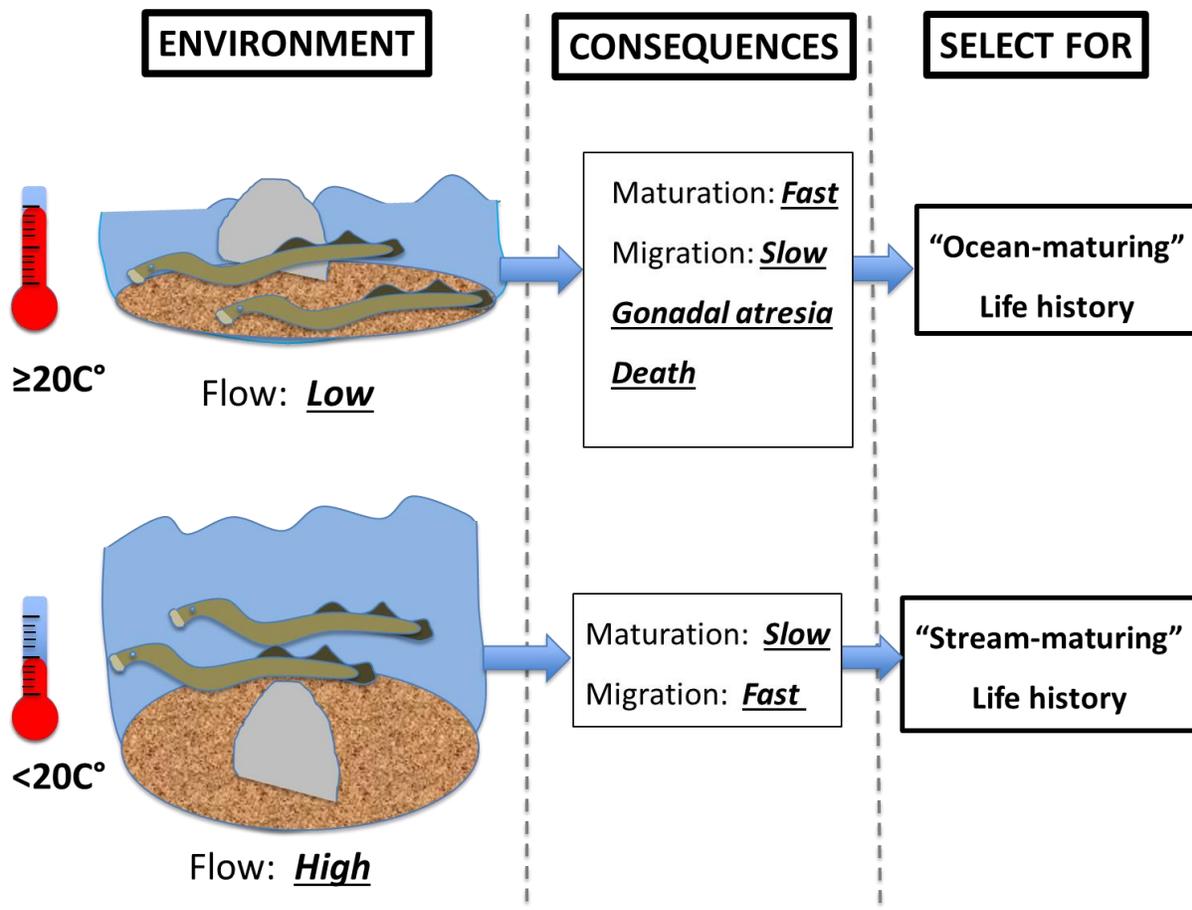
<sup>4</sup> 10–20°C; Clemens et al. 2012a and 2012b; Starcevich et al. 2013; ≥ 20°C; Robinson & Bayer 2005; Keefer et al. 2009; Mesa et al. 2010

<sup>5</sup> 16–17°C; Lemons & Crawshaw

<sup>6</sup> Meeuwig et al. 2005; Clemens et al. 2010

<sup>7</sup> 25°C; Johansen et al. 1973

<sup>8</sup> 28°C; Macey & Potter 1978; ≥ 28°C; Potter & Beamish 1975



**Figure 12-5.** Conceptual model of how water temperatures and flows may select for particular life history types in Pacific Lamprey. The top part of the model shows a scenario in which relatively warm summertime temperatures and low river flows may select *against* stream-maturing Pacific Lamprey (Clemens et al. 2013) that reside in freshwater for prolonged periods of time of up to and exceeding one year and may spawn in the upper portion of watersheds. Conversely, these conditions may select for ocean-maturing lamprey (Clemens et al. 2013). This model hypothesizes that relatively warm summer temperatures and low river flows may expedite the maturation of Pacific Lamprey while slowing their migration — does this lead to spawning relatively low in watersheds? In some incidences, the relatively warm summertime temperatures may cause mortality in females (which would explain skewing of sex ratios; figure 12-3), and gonad damage for males (testicular atresia; Figs. 12-1 and 12-2) — do these fish regenerate their gonads? The bottom part of the model shows a scenario in which relatively cool temperatures and high river flows may select *for* stream-maturing Pacific Lamprey.

It is interesting that the ocean-maturing life history has been identified out of the Klamath River Basin, a basin that: 1) has the highest diversity of lampreys (Kan 1975; Moyle 2002); 2) has a tributary (Trinity River) that is hypothesized to have two forms of Pacific lamprey (Moyle et al. 2002); and 3) is one of the most heavily impacted river systems in the Pacific Northwest, with several dams that form barriers to upstream migration, and numerous water quality problems (Levy 2003; Poff et al. 2003). This raises the question: did the inherent intra- and inter-species diversity of lampreys in the basin provide the template for this life history to evolve, and the impacted environment select for it? At this time, we do not have evidence that ocean-maturing life history of Pacific lamprey exists outside of the Klamath River Basin, but that is the only basin close to the estuary for which we were able to collect Pacific lamprey (Clemens et al. 2013). Adult Pacific lamprey have been collected by ourselves at Willamette Falls and by others at Bonneville Dam (234 km inland), yet these locations may be too far inland to find ocean-maturing Pacific lamprey. We offer two suggestions for research that could be done to test the hypotheses we have advanced for the role of the river environment in selecting for life history diversity in Pacific lamprey. The first suggestion includes monitoring Pacific lamprey across a large geographical swath of their distribution as they return to freshwater. If low river flows and warm summertime temperatures select for ocean maturation (as suggested in the Klamath River), we would expect a higher proportion of individuals maturing in the ocean further south (e.g., central California) and a lower further north (Washington). The second suggestion includes intensively monitoring Pacific lamprey across a particular river estuary like the Columbia. A challenge with this approach is finding a way to reliably collect fish representative of the population(s) at large. We have presented a conceptual hypothesis of how river environments, particularly river flows and temperatures, may select for stream- and ocean-maturing Pacific lamprey. Other ecological factors (e.g., in the ocean) outside the scope of this chapter may play significant roles in the selection of these life histories.

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