Chapter 4
Life History Evolution in Lampreys: Alternative Migratory and Feeding Types

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Abstract Despite their highly conserved body plan and larval stage, adult life history type in lampreys diverges on two main axes related to migration and feeding. Of the 41–45 recognized lamprey species, 18 species feed parasitically after metamorphosis and their juvenile (sexually immature) feeding phase lasts from 3–4 months to 2–4 years. Nine of these species are exclusively freshwater resident; five are exclusively or almost exclusively anadromous, and four (sea lamprey, European river lamprey, Arctic lamprey, and, to a lesser extent, Pacific lamprey) are largely anadromous but with established freshwater populations. The other 23–27 described species are non-parasitic "brook" lampreys which remain within their natal streams. They initiate sexual maturation during metamorphosis, and, because the non-trophic periods of metamorphosis and sexual maturation are superimposed, the parasitic feeding phase is eliminated; this makes them the only vertebrates known to have non-trophic adults. Body size at maturity varies dramatically among life history types, ranging from ~110 to 150 mm total length (TL) in non-parasitic species to 800–900 mm TL in the anadromous sea lamprey. Freshwater forms are typically intermediate in size, although those that inhabit small systems may be no larger than non-parasitic lampreys and others (particularly the Great Lakes sea lamprey) are quite large. Some anadromous species (most notably European river lamprey, Pacific lamprey, and Arctic lamprey) show considerable intraspecific variation, consisting of typical large-bodied forms and dwarf or "praecox" forms that appear to feed at sea for a reduced period of time. Establishment in fresh water is more common in species that are consistently small-bodied or those with praecox forms. The only exceptions are the very small-bodied western river lamprey (mean TL at maturity ~200 mm), which does not produce freshwater parasitic forms (although it has given rise to innumerable non-parasitic freshwater populations), and the sea lamprey

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which, despite its very large size, has successfully colonized the Great Lakes. Abundant prey of a suitable size range is critical for establishment of freshwater parasitic populations. However, even with abundant prey, abandonment of anadromy is expected only under circumstances where decreases in mortality and the costs associated with migration make the reduction in size at maturity, and the accompanying reduction in fecundity, worthwhile. Pacific lamprey generally fail to establish when isolated above recently constructed barriers, likely because the reservoirs in which they have been isolated are relatively small and because they appear to osmoregulate poorly in fresh water. However, because colonization of fresh water appears to select for individuals "pre-adapted" to feed and grow to maturity in fresh water (i.e., relying on existing genetic variation within the source population), probability of establishment would likely increase with the number of founders. The existence of three closely related freshwater parasitic species suggests that Pacific lamprey successfully colonized fresh water in the past. Whether sea lamprey colonized Lake Ontario and Lake Champlain post-glacially or in historic times is debated. At present, the "invasion-by-canal" hypothesis appears to be the most convincing, but definitive resolution should be possible with genome-level analyses. Given the decimation of the Great Lakes ecosystem by sea lamprey, it is critical to be able to predict the potential for anadromous lampreys to become invasive in other freshwater systems. Migratory type is rarely considered a species-specific character unless it is accompanied by identifiable morphological differences. In contrast, variability in feeding type has long been considered a species-specific character because size-assortative mating was thought to result in reproductive isolation between parasitic and non-parasitic forms. However, not all parasitic and non-parasitic forms appear to be reproductively isolated, and different species show different degrees of divergence from their presumed parasitic ancestor. "Paired" non-parasitic species are defined as those that are morphologically similar to a particular parasitic species in all aspects other than body size, and "relict" brook lampreys are those that cannot be obviously paired with extant parasitic forms. However, molecular analyses have: (1) identified the closest extant parasitic relative to these relict species (although a few "orphan" species still remain, where identification of the closest living relative still sheds little light on the identity of the parasitic ancestor); (2) shown that the distinction between paired and relict species is sometimes unclear; and (3) demonstrated that there is also considerable variation among paired species in the degree to which they are morphologically and genetically differentiated from their parasitic ancestors. We review this "speciation continuum," particularly in European river and brook lamprey populations where recent genetic and genomic studies show significant gene flow between these species where they co-occur (i.e., refuting assumptions of complete reproductive isolation resulting from size-assortative mating) while also showing that there are genome-level differences between the feeding types (i.e., refuting the hypothesis of phenotypic plasticity). In sympatry, European river and brook lampreys appear to be partially reproductively isolated ecotypes that nevertheless maintain distinct phenotypes, because regions of the genome involved in reproductive isolation and local adaptation resist the homogenizing effect of introgression. Interestingly, the results of analyses used to reconstruct the demographic history of divergence in this species pair

are inconsistent with recent and rapid divergence in sympatry following the recent glacial retreat; rather, they support divergence in allopatry ~200,000–250,000 years ago and re-establishment of secondary contact ~90,000 years ago. Some loci have been identified that differ between the forms (e.g., the vasotocin and gonadotrophin-releasing hormone 2 precursor genes), but an understanding of the genetic basis of life history evolution in lampreys remains elusive. There appear to be strong parallels between factors that promote or constrain loss of anadromy in parasitic species (and reduction in duration of the feeding phase) and those that lead to or limit the evolution of non-parasitism (i.e., total elimination of the feeding phase). Smaller-bodied parasitic species have been far more prolific in producing non-parasitic derivatives than others; western river lamprey are already so small at maturity that "skipping" right to a non-parasitic form represents a more profitable trade-off between mortality and fecundity than freshwater parasitism. In contrast, there is a conspicuous absence of brook lamprey derivatives from the large-bodied sea, pouched, and Caspian lampreys. Our comparisons suggest that 300 mm TL (with a 10–12× reduction in fecundity) is the cut-off above which shifts to non-parasitism would not be beneficial. Therefore, we predict that Great Lakes sea lamprey is not an "intermediate" freshwater parasitic form that will give rise to a non-parasitic derivative, because complete elimination of the parasitic feeding phase would represent too large (~40×) a reduction in fecundity.

Keyword Ancestral life history type · Contemporary gene flow · Ecotypes · Ecological constraints · Evolution of metamorphosis · Fecundity · Genetic basis of life history type · Freshwater colonization · Invasive species · Life history trade-offs · Non-parasitism · Non-trophic adults · Osmoregulation · Parasitism · Partial anadromy · Reproductive isolation · Speciation · Species pairs

4.1 Introduction

Lampreys (order Petromyzontiformes) are one of the two surviving groups of jawless vertebrates. This small remnant group consists of three extant families and 10 genera. A total of 41 species were recognized by Potter et al. (2015); 37 species in the Northern Hemisphere are assigned to the family Petromyzontidae, and three and one species of Southern Hemisphere lampreys are allocated to Mordaciidae and Geotriidae, respectively. All lampreys have a protracted microphagous larval phase (generally lasting ~3–7 years) which is spent in fresh water (see Dawson et al. 2015) and culminates in a dramatic metamorphosis. During metamorphosis, all lampreys develop a suctorial oral disc and tongue-like piston (both of which bear teeth) and fully formed eyes, and they undergo a range of other anatomical, physiological, and biochemical changes (see Manzon et al. 2015; Potter et al. 2015).

Despite their highly conserved body plan and larval stage, lamprey life history type diverges at metamorphosis on two main axes related to migration and feeding. At the completion of metamorphosis, 18 species remain sexually immature and enter a trophic phase (the juvenile or parasitic feeding phase) in which they feed on the blood or tissue of predominantly actinopterygian fish hosts (see Chap. 3). The parasitic phase lasts between a few months and 2 or more years, with the duration varying among, and sometimes within, species. After the juvenile feeding phase, they embark on a non-trophic upstream migration (see Moser et al. 2015), undergo sexual maturation (see Chap. 1), spawn, and die (see Johnson et al. 2015). Nine of the parasitic species remain in fresh water, usually feeding in either large lakes or rivers (see Potter et al. 2015; Chap. 3). The remaining nine parasitic species are predominantly anadromous, that is, feeding in marine environments (see Chap. 3) before returning to fresh water to spawn. Mean size at maturity may be as small as ~125 mm total length (TL) in freshwater species like the Miller Lake lamprey *Entosphenus minimus* or as large as ~700 and ~900 mm in anadromous Pacific lamprey *En. tridentatus* and sea lamprey *Petromyzon marinus*, respectively.

Within parasitic species, there is also variation with respect to migratory type and duration of the feeding phase, and this intraspecific variation is often underappreciated. Migratory type is rarely considered a species-specific character unless it is accompanied by identifiable morphological differences (Potter et al. 2015). Three of the nine anadromous species (sea lamprey, Arctic lamprey *Lethenteron camtschaticum*, and European river lamprey *Lampetra fluviatilis*) have given rise to permanent freshwater-resident populations, and Pacific lamprey may have as well, although the propensity of this species to establish in fresh water appears more limited (Wallace and Ball 1978; Beamish and Northcote 1989). In another two species (western river lamprey *Lampetra ayresii* and short-headed lamprey *Mordacia mordax*), there are rare reports of at least some individuals remaining in fresh water throughout their life cycle. Even greater life history diversity within species is apparent when anadromous praecox forms are included. Praecox literally means “very early” (or premature or early onset) and is used to refer to lampreys that feed at sea, but presumably for a reduced period of time. Anadromous sea lamprey and pouched lamprey *Geotria australis* appear to be consistently large (i.e., without any known praecox forms), but Arctic, European river, and Pacific lampreys occur as both large “typical” forms and smaller praecox forms (e.g., Abou-Seedo and Potter 1979; Kucheryavyi et al. 2007). Within these species, taxonomic distinctions are rarely made between typical and praecox forms, and, in many cases, there is not even a clear dimorphism between the forms. In some rivers, bimodal distribution in the size of upstream-migrating European river lamprey can be used to distinguish typical and praecox forms (e.g., Abou-Seedo and Potter 1979), but often only a range of sizes (generally with differences among geographic regions) is evident. These differences are thought to be partly attributable to intraspecific differences in the duration of the marine feeding phase and differences in abundance and size of prey. These inter- and intraspecific differences are generally referred to as variation in migratory type, but where lampreys feed and for how long overlaps with the second axis of divergence, feeding.

Variability in feeding type per se, specifically parasitic versus non-parasitic types, has generally commanded more attention and appreciation than variation in migratory type. This “parting of the ways” observed at metamorphosis (Hardisty 2006) is more obviously dimorphic, and it has long commanded the interest of biologists (e.g., Loman 1912). Non-parasitic "brook" lampreys spend their entire life in fresh water. Like all lampreys, they enter a non-trophic metamorphosis at the end of the larval phase; however, unlike parasitic lampreys, they initiate sexual maturation during metamorphosis. As a result, the non-trophic periods of metamorphosis and sexual maturation are superimposed, and the juvenile (parasitic) feeding phase is eliminated. Lampreys are the only vertebrates known to have a non-trophic adult (Hendler and Dojiri 2009), which is likely another reason variability in feeding type has generally commanded more interest than variability in migratory type. In addition, conspicuous morphological differences distinguish non-parasitic adults from parasitic forms, with the most notable difference being adult body size. Adult brook lampreys will be smaller than the largest larvae, generally measuring ~110–150 mm TL at maturity (see Docker 2009). The morphological similarity between several pairs of non-parasitic and parasitic lampreys, and their often overlapping geographic distributions, led to suggestions that particular brook lamprey species evolved from a form similar to that of the extant parasitic lamprey (e.g., Hubbs 1925; Zanandrea 1959). Because it is generally thought that size-assortative mating would result in reproductive isolation between parasitic and non-parasitic forms (e.g., Hardisty and Potter 1971a; Beamish and Neville 1992), most lamprey taxonomists recognize feeding type as a species-specific character. There is past (e.g., Enequist 1937) and continuing (e.g., Artamonova et al. 2011) debate on this subject (i.e., are paired species "real" species?), but there is likely not a simple "one size fits all" answer to this question.

There is also lack of agreement regarding whether geographically disjunct non-parasitic derivatives of the same presumed ancestor constitute one or multiple species. Thus, although there is little or no dissent regarding the number of recognizable parasitic species (18), different taxonomies often vary in the number of non-parasitic species recognized. Many of the past debates have largely been resolved (e.g., that Pacific brook lamprey *Lampetra pacifica* is distinct from western brook lamprey *La. richardsoni*), and Potter et al. (2015) recognized 23 species of non-parasitic lampreys. However, there is continuing discussion whether three brook lamprey populations from Portugal are distinct species (the Nabão lamprey *Lampetra auremensis*, Costa de Prata lamprey *La. alavariensis*, and Sado lamprey *La. lusitanica*; Mateus et al. 2013a) or whether they are synonymous with European brook lamprey *Lampetra planeri* (Potter et al. 2015). Another new brook lamprey species named *Lampetra soljani*, which appears to be related to, but distinct from, the Po brook lamprey *Lampetra zanandreai*, was recently described from the southern Adriatic Sea basin (Tutman et al. 2017). Also, several genetically distinct populations may represent new species that have not yet been formally described (e.g., Yamazaki and Goto 1996, 1998; Yamazaki et al. 2006; Boguski et al. 2012). We do not attempt to definitively answer the question "exactly how many brook lamprey species are there?" We agree with previous authors (Potter et al. 2015; Tuniyev et al. 2016) that, for the sake of stability, lamprey taxonomy should not be hastily revised without full systematic examination, and, for the most part, we follow the taxonomy of Potter et al. (2015). However, we recognize the strengths and limitations of different species concepts (see Docker et al. 2015) and that the transition from parasitic ancestor to non-parasitic forms represents a continuum (Docker 2009) that is difficult to objectively partition. Thus, we mention these other newly described and as-yet-undescribed species here in an attempt to provide a fuller discussion regarding the transition process itself. Such discussion should help inform future decisions regarding species delimitation in lampreys (see Chap. 7).

In this chapter, we synthesize the available information regarding lamprey life history divergence on both migratory and feeding axes, and, by so doing, we attempt to offer some novel insights into life history evolution in these ancient vertebrates. We discuss the putative life history type of the ancestral lamprey and then attempt to provide a greater appreciation for the breadth of life history diversity in extant lampreys. We give an in-depth review of inter- and intraspecific variation with respect to migratory type within parasitic species, which we feel has been underappreciated in the past. We also continue earlier discussions (e.g., Hardisty and Potter 1971a; Potter 1980; Salewski 2003; Hardisty 2006; Docker 2009) on the evolution of non-parasitism in lampreys, particularly with respect to insights provided from recent genomic studies (e.g., Mateus et al. 2013b; Rougemont et al. 2017). In doing this, we intend to provide a broader view of life history diversity in lampreys than has been presented thus far and to move away from categorization of lampreys along two independent axes: anadromous or freshwater-resident and parasitic or non-parasitic. We extend the argument proposed by previous authors (e.g., Beamish 1985; Salewski 2003; Hardisty 2006) that variation in migratory type among and within parasitic species is the "jumping-off point" for the evolution of non-parasitism. The common factor in the transition from anadromy to freshwater residency and from parasitism to non-parasitism is a reduction in size at maturity and fecundity. Thus, strong parallels appear to exist between factors that promote or constrain loss of anadromy in parasitic species (and generally reduction in duration of the feeding phase) and those that lead to or limit the evolution of non-parasitism (i.e., total elimination of the feeding phase).

4.2 Life History of the Ancestral Lamprey

Among modern lampreys, parasitism is clearly the ancestral life history type. Modern non-parasitic species retain teeth on their oral disc (albeit generally reduced) and buccal glands that produce an anticoagulant necessary for parasitic feeding (see Docker 2009). However, this should not be interpreted as meaning that the earliest lampreys were necessarily parasitic (presumably parasitism originated after the evolution of fishes upon which they could feed) or that the only other alternative is that the ancestral lamprey life cycle was similar to that of modern non-parasitic lampreys (i.e., with an extended filter-feeding larval stage and an entirely non-trophic adult stage). Likewise, although anadromy is considered ancestral among modern lampreys in that anadromous species (most notably the sea lamprey) are known to colonize fresh water (see Sect. 4.3.3), this does not mean that the ancestral lamprey was anadromous or that the only other alternative is that it was entirely freshwater resident (i.e., the two options among extant lampreys). Furthermore, although all modern lampreys share a highly conserved larval stage, parting ways only at metamorphosis, this does not mean that the ancestral lamprey life history type included this larval stage. Here, we use the life history and morphology of extant non-vertebrate chordates, the limited lamprey fossil record, and interpretations of the external environment of the earliest fishes to make inferences regarding the evolution of metamorphosis and the characteristic larval ("ammocoete") stage in lampreys and to deduce the feeding and migratory type of early lampreys.

4.2.1 Evolution of Metamorphosis and the Prolonged Larval Stage

Many metazoan phyla undergo metamorphosis (i.e., indirect development), during which they undergo dramatic physiological, molecular, behavioral, and ecological changes as they transition from a larva to a morphologically distinct juvenile (Bishop et al. 2006; Paris and Laudet 2008; Laudet 2011). Metazoans that undergo metamorphosis include invertebrate taxa (e.g., insects, echinoderms), as well as the non-vertebrate chordates (cephalochordates and urochordates) and some vertebrate chordates (e.g., lampreys, eels, flatfishes, amphibians). Among all metazoans, there is clearly more than one origin of metamorphosis, but there is still debate whether metamorphosis evolved independently in those chordate lineages with it or whether it was an ancestral feature of all chordates. Considerable morphological diversity exhibited during metamorphosis in different chordate lineages has been used to support independent origins (Sly et al. 2003; Heyland et al. 2005). In contrast, Paris and Laudet (2008) suggested that the common role of a thyroid hormone-producing gland (the endostyle or thyroid gland) in the metamorphosis of all chordates—although sometimes in apparently different ways and by mechanisms not fully understood (see Manzon et al. 2015)—suggests an ancestral origin.

Whether the earliest vertebrates exhibited metamorphosis is also unknown. Some authors (e.g., Northcutt and Gans 1983; Mallatt 1984, 1985) suggested that the earliest vertebrates showed metamorphosis and that, like most extant non-vertebrate chordates, they had a pelagic larval stage and benthic adult stage. Northcutt and Gans (1983) suggested that the larvae were pelagic suspension feeders and the adults were benthic predators; in contrast, Mallatt (1984, 1985) suggested that the larvae were pelagic "raptorial" feeders (i.e., taking individual food particles from the water column) and the adults were benthic suspension feeders. However, hagfishes, the other extant ancient vertebrate lineage, are direct developers, meaning either: (1) indirect development was not a trait shared by the last common ancestor of hagfishes and lampreys, and lampreys since acquired the trait; or (2) hagfishes secondarily abandoned metamorphosis. It is now generally accepted that hagfishes and lampreys are each other's closest living relatives (rather than lampreys sharing an ancestor more recently with the gnathostomes, the jawed vertebrates; see Docker et al. 2015). However, they have still been separated for long periods of evolutionary time, having diverged ~486–444 million years ago (Ma; Kuraku and Kuratani 2006), and, despite retaining many ancestral vertebrate characteristics, both have become specialized in their own ways. Many hagfish features once thought to be primitive (e.g., their degenerate eyes) represent secondary losses associated with their deepsea habitat (see Docker et al. 2015). Thus, cyclostome monophyly alone does not allow us to distinguish between these two scenarios.

In this section, we address the questions: (1) did metamorphosis evolve in lampreys, or was it inherited from its early chordate or vertebrate ancestor? and (2) what was the body form of the earliest lamprey (i.e., which came first: the ammocoete or the adult)? Given the similarities in the body plans of modern lamprey larvae and cephalochordates (i.e., lancelets or amphioxi), lamprey larvae are often taken as representing the primitive early vertebrate bauplan (see Hardisty et al. 1989; Evans et al. 2018). Because extant cephalochordates undergo subtle metamorphosis, where the pelagic asymmetric larvae transform into benthic symmetric juveniles (Paris and Laudet 2008), one might assume that the earliest lampreys underwent a similar metamorphosis. However, several authors have concluded that early lampreys did not, in fact, metamorphose (e.g., Youson and Sower 2001; Chang et al. 2014), although there is a lack of agreement regarding the body form of lampreys prior to the evolution of metamorphosis. Youson and Sower (2001), whose argument has been termed the "larval-first" hypothesis by Evans et al. (2018), suggested that early lampreys were marine and probably resembled the larvae from which the urochordate larvaceans were derived. These authors proposed that metamorphosis (giving rise to a sedentary benthic adult) appeared later after entry into fresh water, where the iodide-concentrating efficiency of the endostyle was a critical factor in the evolution of metamorphosis (Youson and Sower 2001; Youson 2004). Diogo and Ziermann (2015), based on the anatomy and development of chordate cephalic muscles, concluded that the inferred adult muscles of the last common ancestor of vertebrates are strikingly similar to the condition that is present in the lamprey larva, and likewise support the suggestion that the adult lamprey phenotype is derived. However, the assumption that a blind protochordate-like stage is the ancestral lamprey body form is inconsistent with our understanding that the earliest vertebrates were characterized by a suite of advancements that included a cranium and pronounced cephalization and a set of highly specialized paired sense organs (including image-forming eyes and a lateral line; see Docker et al. 2015).

Also, the larval-first hypothesis is not concordant with the fossil evidence. To date, lamprey fossils mostly resemble very small modern lamprey juveniles or adults (i.e., following metamorphosis, when the lamprey is sexually immature or mature, respectively); evidence of animals resembling modern larval lampreys is not known before 125 Ma—although one that may have been a larva dates back to ~320 Ma (Chang et al. 2014). From the oldest fossils, which had not yet been discovered when Youson and Sower (2001) proposed that the earliest lampreys were likely larva-like, to the most recent, the known fossils of lampreys can briefly be described as follows:

- *Priscomyzon riniensis*, from upper Devonian marine or estuarine deposits (~360 Ma) in South Africa, had clearly developed eyes, a large oral disc, and circumoral teeth, but its TL was only 42 mm (Gess et al. 2006). Apart from its small size and differences in body proportions (e.g., an oral disc proportionately larger than in living lampreys), it looked astonishingly like modern juvenile or adult lampreys.

- *Hardistiella montanensis* from lower Carboniferous deposits (~320 Ma) in Montana resembled modern juvenile or adult lampreys less clearly (Janvier and Lund 1983). There was no evidence of an oral sucker, and instead, the mouth may have been surrounded by a simple oral hood similar to that of metamorphosing lampreys. The holotype measured ~115 mm TL. A 50-mm lamprey fossil from this same locality could be a larval lamprey, but poor preservation has prevented definitive identification (Lund and Janvier 1986). Another specimen (<100 mm TL) reported by Janvier et al. (2004) also showed no trace of preserved cranial cartilages (e.g., no piston or annular cartilages), but evidence of a "large, globulous" snout was taken as support for the presence of a sucking device.
- *Mayomyzon pickoensis* from upper Carboniferous (~280 Ma) deposits in Illinois (Bardack and Zangerl 1968, 1971) clearly possessed many of the morphological and anatomical characters of the adults of extant lampreys. Although an oral disc and circumoral dentition were not evident, an annular cartilage (which maintains the structural integrity of the oral disc), a piston cartilage (which implies the presence of a rasping tongue), and dorsolateral eyes were apparent. Again, however, the specimens were small; the holotype (which was a presumed adult) measured only 48 mm TL and presumed juvenile specimens measured 33–61 mm TL.
- *Mesomyzon mengae* from lower Cretaceous (~125 Ma) freshwater shale deposits in China had a well-developed oral disc and a long snout; it possessed ~80 myomeres, but was still relatively small (~85 mm TL). However, Chang et al. (2014) subsequently discovered well-preserved fossils of larval (40–67 mm TL) and metamorphosing (82–94 mm TL) *M. mengae*. The larval specimens looked "surprisingly modern," exhibiting tiny eyes, an oral hood and lower lip, and detritus in the gut. The fossils presumed to be metamorphosing lampreys had enlarged eyes and a thickened oral hood or pointed snout; an oral disc was not evident, but it was assumed that these individuals represented early stages of metamorphosis (see Manzon et al. 2015).

Therefore, the larval form and "three-phased" life cycle (i.e., with larval, metamorphosing, and adult stages) appear to be derived characters in lampreys. Chang et al. (2014) proposed that lampreys initially evolved without (or with at most a limited) larval period, and relied on the juvenile/adult form for all or the majority of their lives; they suggested that introduction (and subsequent lengthening) of the larval stage and metamorphosis came later. Evans et al. (2018) referred to this as the "juvenile-first" hypothesis. Hardisty et al. (1989) similarly indicated that, even if a larval phase had been present in early lampreys, it would have been of only short duration. The absence of clear larval lamprey fossils prior to 125 Ma, of course, does not rule out a considerably earlier origin, particularly given the fossil of a possible larval *H. montanensis* specimen from ~320 Ma. The fact that all extant lampreys share this highly similar triphasic life cycle suggests an origin that predates the separation of Northern and Southern Hemisphere lampreys. Using molecular data, Kuraku and Kuratani (2006) placed the divergence between the families Petromyzontidae and Geotriidae at 280–220 Ma, and the split between the two Southern Hemisphere families (Geotriidae and Mordaciidae) is assumed to have occurred at approximately the same time (Gill et al. 2003; Potter et al. 2015). This means that the modern lamprey life cycle had evolved by 280–220 Ma; otherwise, we would have to accept that it evolved independently in each lineage, which is not likely considering that the features of this life cycle are so highly conserved among all extant lampreys.

A third hypothesis has been proposed by Evans et al. (2018). Similar to the larval-first and juvenile-first hypotheses, Evans et al. (2018) suggested that the earliest lampreys were without a distinctive metamorphosis and only underwent gradual ontogenetic changes during development. However, Evans et al. (2018) suggested that initially early lampreys had a body form somewhat intermediate between that of modern larvae and modern juveniles/adults. In fossil specimens, the external (more obvious) features resemble the juvenile/adult form, but the position of the otic capsules and other features (more subtly) resemble modern lamprey larvae. They further proposed that, during the evolution of lampreys, the "larval" characters became segregated in the beginning of the life cycle and appearance of the "juvenile" characters was delayed; eventually, development of the juvenile characters was condensed into (and accelerated during) the distinct phase of metamorphosis following a progressively longer larval stage. Elongation of the larval stage and reactivation of development at metamorphosis is evident in modern lampreys in such processes as gonadal differentiation (e.g., with testicular differentiation delayed until the onset of metamorphosis; see Chap. 1) and eye development (which appears to "pause" after reaching a very immature stage before resuming near the end of the larval stage and at metamorphosis; Suzuki and Grillner 2018). Evans et al. (2018) termed their hypothesis the "condensation" hypothesis, in line with terminology used to describe the evolution of metamorphosis in other organisms (e.g., Schoch and Fröbisch 2006). Here, to contrast this hypothesis more explicitly to the "larval-first" and "juvenile-first" hypotheses, we refer to this hypothesis as the "segregation and specialization" hypothesis. Early lampreys were neither larva-like nor juvenile-like, but, over time, the larval and juvenile characters became segregated during development, which allowed each form to become more highly specialized. Colonization of fresh water (see Sect. 4.2.4) and exploitation of new trophic niches (see Sect. 4.2.2) may have selected for increasingly specialized larval and juvenile forms, respectively. A radical metamorphosis was required to effect the transition between these now distinctive periods, and the modern lamprey life history appeared. With the specialized larval and juvenile forms, each well-adapted to their respective environments, the growth potential of each period was maximized, enabling the large body size that now characterizes modern parasitic lampreys. As outlined above, evolution of this dramatic metamorphosis would have occurred at least 280–220 Ma.

As a final point when discussing the various hypotheses regarding the evolution of metamorphosis in lampreys, it should be noted that there is little or no support for a fourth hypothesis, the so-called "larval transfer hypothesis" (Williamson 2012). This hypothesis contends that lampreys and hagfishes had no larvae until an ancestor of modern lampreys acquired larvae by hybridizing with a cephalochordate; hagfishes, which never crossed with a cephalochordate, retained their direct development. Williamson's "long-cherished hypothesis" of a hybrid origin of other organisms with complex life cycles (e.g., Williamson 2001, 2009) has largely been discredited (e.g., Hart and Grosberg 2009; Minelli 2010).

Evans et al. (2018) reviewed the evolution of metamorphosis in two other groups of animals with complex life histories, insects and amphibians, and there are considerable similarities between the "condensation" or "segregation and specialization" hypothesis proposed for lampreys and the sequence of events that has been proposed for these other taxa. Early insect lineages did not undergo metamorphosis; instead, a continuous progression from egg to embryo to adult occurred (Truman and Riddiford 1999). Complete metamorphosis in insects evolved ~280–350 Ma and has largely been credited with fueling their dramatic radiation, because it presumably enabled stage-specific specializations to different habitats (Truman and Riddiford 1999; McMahon and Hayward 2016). Metamorphosis permitted the extreme adaptation of one stage for a particular role, such as dispersal, and allowed structures (e.g., wings) to be delayed in their appearance until needed (Truman and Riddiford 1999; Haug et al. 2016). Insect phylogeny shows a progression from groups that are ametabolous (no metamorphosis) to those that are hemimetabolous (partial metamorphosis, where there are more subtle differences from the younger stages to the adult, but not requiring a radical reshaping of the body at any time) to the most derived groups that are holometabolous (complete metamorphosis, with a radical change from a larva to the juvenile/adult) (Engel 2015). If we were to use the same terminology in lampreys, early lampreys appear to have been ametabolous and all modern lampreys are holometabolous; by the suggested "segregation and specialization" hypothesis, hemimetabolous might be an appropriate term to describe lampreys during the initial stages of segregation and specialization.

Early amphibians were also direct developers (Schoch 2009), and metamorphosis is thought to have evolved by ~300 Ma (Schoch and Fröbisch 2006). The development of juvenile characters was initially delayed but was then accelerated and condensed into the distinct phase of metamorphosis (Schoch 2009). As with insects and lampreys, this dramatic metamorphosis allows amphibian larvae and adults to efficiently exploit different resources, with amphibian larvae using suction feeding in an aquatic habitat and adults generally becoming adapted to the capture of terrestrial insects with tongue-supported feeding (Schoch 2009, 2014). However, unlike extant lampreys, some amphibians have since reduced or eliminated metamorphosis; some direct-developing frogs and salamanders show only vestiges of metamorphosis during early development, and other salamanders (e.g., axolotls, mudpuppies, some tiger salamanders) have eliminated metamorphosis completely, and retain larval characteristics and remain in aquatic habitats as adults (Johnson and Voss 2013).

Thus, although lampreys are often used as model ancient vertebrates, the life history type of extant lampreys appears not be representative of the earliest vertebrates. However, we have been able to make inferences only about the life cycle of early lampreys, but not necessarily the earliest lampreys. The lamprey and hagfish lineages are thought to have diverged ~486–444 Ma (Kuraku and Kuratani 2006), although this only indicates when they last shared a common ancestor and not necessarily the origin of lampreys per se. Considering the stability of lamprey morphology in the past 360 Ma, Janvier (2008) indicated that it would not be surprising if recognizable fossil lampreys "turned up" 50 or 100 Ma earlier. However, the above arguments do suggest that the dramatic metamorphosis that characterizes all modern lampreys was not present in the earliest known lampreys (~360 Ma), but had evolved by at least 280–220 Ma.

4.2.2 Origin of Parasitism

The earliest known fossil lamprey, *Priscomyzon riniensis* from ~360 Ma, had a large oral disc and circumoral teeth (Gess et al. 2006), but it was very small (42 mm TL). No oral disc was evident in *Mayomyzon pickoensis* from ~280 Ma, although the annular cartilage that supports the oral disc in extant lampreys is evident (Bardack and Zangerl 1968, 1971). Hardisty et al. (1989) suggested that the small size of *M. pickoensis* (48 mm TL in the adult holotype) and apparent lack of circumoral teeth made it unlikely that this species fed parasitically, and there was no evidence of parasitic feeding on other vertebrates in the deposit in which it was found. However, Hardisty et al. (1989) indicated that the presence of a piston cartilage suggests that it might have fed on carrion (as some extant lampreys do; see Chap. 3) or even browsed on surface algal films. As reviewed above, it appears that metamorphosis in lampreys had evolved by ~280–320 Ma, which permitted subsequent specialization and elongation of both the larval and juvenile forms (see Sect. 4.2.1). Thereafter, the juvenile form became fully specialized to take advantage of the newly diversifying jawed fish fauna, while the larval form became specialized to take advantage of newly hospitable freshwater environments (see Sect. 4.2.4).

We do not know on what the earliest parasitic lamprey would have fed, but, based on known hosts of extant lampreys (see Chap. 3), we would assume that they would have a general preference for fishes with few or small scales but that their tastes otherwise would have been rather catholic (meaning, in this context, "all-embracing" or "including a wide variety of things"). Some groups of armored jawless fishes are evident in the fossil record 488–443 Ma (Janvier 2007) and were diverse and abundant during the Devonian "Age of Fishes" (~419–359 Ma; Janvier 1996), but the armor likely limited lamprey feeding opportunities. Fossils of scales and dermal denticles indicate that cartilaginous fishes date back to ~455 Ma (Janvier 1996), but, notwithstanding the observation that sea lamprey may sometimes feed on sharks (Wilkie et al. 2004), cartilaginous fishes are not common hosts of modern parasitic lampreys. Thus, evolution of the ray-finned fishes ~439–383 Ma (class Actinopterygii, which includes sturgeons, paddlefishes, gars, bowfins, and teleosts) and diversification of some of the earliest extant teleost lineages ~333–286 Ma (Near et al. 2012) may have presented the first substantial parasitic feeding opportunities for juvenile lampreys. The salmoniform/esociform lineage (e.g., giving rise to salmonids and pikes) and clupeomorphs (e.g., herrings) arose and began diversifying by ~201–145 Ma and

252–201 Ma, respectively (Near et al. 2012). Clupeomorphs had a broad distribution in freshwater, marine, and brackish environments by 145–66 Ma (Vernygora et al. 2016). Hardisty et al. (1989) likewise concluded that suitable thin-scaled fishes similar to those used by modern lampreys to sustain rapid growth and attain large body size would not have been available before the end of the Carboniferous period (i.e., before ~299 Ma). Presumably, extension of the juvenile parasitic feeding phase occurred gradually, as growth opportunities increased, and perhaps with the evolution of anadromy, since larger body size might have been required to withstand the distance and rigor of upstream migrations (see Sect. 4.2.4). It is entirely feasible that this gradual extension of the juvenile feeding phase occurred independently in each lineage following separation of Northern and Southern Hemisphere lampreys, once the fundamental aspects of the modern lamprey life cycle that provided the capacity for growth were established.

With respect to the mode of feeding of the earliest parasitic lampreys, among modern parasitic lampreys, Potter and Hilliard (1987) concluded that blood feeding is ancestral. They argued that blood feeding would be less detrimental (to the hosts and thus, ultimately, to the lampreys which depend on them) in less productive waters. Blood is a renewable resource if the rate of feeding is not excessive relative to the size of the host, and the wounds would be smaller and less likely to be fatal. They concluded that flesh feeding came later, with access to smaller but more plentiful coastal fishes (e.g., herrings and other clupeids) or where lampreys travel farther offshore to feed in very productive waters (see Chap. 3; Sect. 4.4.2).

4.2.3 Origin of Non-parasitism

Even if the earliest lampreys were not parasitic (see Sect. 4.2.2), they did not resemble modern non-parasitic lampreys. Modern non-parasitic lampreys, which retain clear vestiges of the parasitic feeding mode, are derived from parasitic lampreys through a subsequent abandonment of the parasitic feeding phase (see Docker 2009). Non-parasitic derivatives of parasitic species are known in both hemispheres in two of the three extant families, Petromyzontidae and Mordaciidae. However, unlike the evolution of metamorphosis and the modern triphasic life cycle, the complexity and similarity of which would necessitate that it evolved once and was inherited in each of the extant families from their common ancestor, elimination of parasitic feeding can occur independently. In fact, even within the Petromyzontidae, non-parasitism has evolved independently in six of the eight genera and within genera as well (see Docker 2009; Sect. 4.6). In general, it is easier to lose complex traits than it is to acquire them because, from a strictly genetic point of view, most mutations are more likely to be degenerative than constructive (see Strathmann and Eernisse 1994; Gompel and Prud'homme 2009). Of course, evolution of non-parasitism in lampreys did not just involve a mutation that prevented feeding following metamorphosis; such mutations are unlikely to have been adaptive. The evolution of non-parasitism appears to have required a heterochronic shift in development that accelerated sexual maturation relative to metamorphosis (Docker 2009). We still know nothing regarding the genetic basis for this acceleration of sexual maturation or the extent to which the genetic changes are parallel among different independently derived species (see Sects. 4.6.3.3 and 4.6.3.4). However, for the most part, regardless of the genetic mechanism, we would expect acceleration of sexual maturation relative to metamorphosis to produce similar phenotypic results even when occurring independently. The non-trophic period of metamorphosis would merge with the non-trophic period of sexual maturation, resulting in elimination of the intervening juvenile feeding phase and eventual degeneration of the teeth and other structures associated with feeding (Docker 2009).

Nevertheless, apart from saying that non-parasitism did not need to evolve in the ancestor to all modern lampreys (i.e., before 280–220 Ma), we cannot say when the feeding phase was first eliminated. On the basis of mitochondrial DNA (mtDNA) sequence data, some of the oldest extant non-parasitic species are estimated to have diverged from any known parasitic species a few to several million years ago (e.g., least brook lamprey *Lampetra aepyptera* at least 2 Ma, and the Macedonia and Epirus brook lampreys *Eudontomyzon hellenicus* and *Eu. graecus* at least 5.5 Ma; see Sect. 4.6.2). However, given the increasing appreciation of the “non-clock-like” nature of mtDNA (see Galtier et al. 2009) and general concerns regarding the precision of molecular timescales (Graur and Martin 2004), these divergence times are very likely underestimates. In the least brook lamprey, Martin and White (2008) suggested that a vicariance event during the Pliocene (~5.3–2.6 Ma) produced strong phylogeographic structuring (see Sect. 4.6.2.3), which suggests that the species itself is considerably more than 2 million years old. Furthermore, these estimates do not represent the age of these species per se, only the approximate time since divergence from other extant species and certainly should not be interpreted as representing the first non-parasitic species. It has been suggested that non-parasitic species are more prone to extinction than parasitic species, because they typically show a more limited distribution and smaller populations (Spice et al. 2019). Older non-parasitic species will have become extinct but new ones will have evolved.

Despite the elimination of post-metamorphic feeding, all lampreys still undergo metamorphosis, unlike paedomorphic salamanders where elimination of metamorphosis has evolved rapidly and independently multiple times (Page et al. 2010; Johnson and Voss 2013). Metamorphosis in lampreys is energetically costly, requiring extensive remodeling of the body and subsequent maturation of the gonads while the lamprey is not feeding for 6–10 months (Docker 2009). Therefore, since it has been retained in all lampreys, it appears that the changes associated with metamorphosis are required, not just for parasitic feeding during the juvenile phase, but also for reproduction (Manzon et al. 2015). The oral disc that is a key feature of parasitic lampreys is also used by brook lampreys to attach to rocks during the short upstream migration, during nest building, and for attachment to mates during spawning (see Johnson et al. 2015). Other aspects of mate choice and reproduction may rely on adult sensory capabilities (Johnson et al. 2015). Youson and Sower (2001) suggested that a complex interplay between the thyroid and reproductive axes evolved during and subsequent to the evolution of metamorphosis in lampreys, and the two may not be easy to disentangle. There has been one report of apparent paedomorphism or neoteny in lampreys (Zanandrea 1957), but the general view is that true paedomorphism is not present in any extant lamprey species (Vladykov 1985). Zanandrea (1957) reported finding 12 Po brook lamprey larvae that showed well-developed ovaries with eggs that were in an advanced state of maturity. One larva had well-developed secondary sex characteristics (e.g., enlargement of the dorsal fins and urogenital papilla) and a transparent body wall through which the eggs could be seen. The endostyle and other larval features were still visible, and there was no evidence of any post-metamorphic features except for the well-developed ovary. However, artificial fertilization of the eggs was not attempted, so it is unknown if they were viable. The Po brook lamprey is considered to be an older "relict" non-parasitic species (see Sect. 4.6.2), so it is possible that the changes associated with the heterochronic shift in the timing of sexual maturation relative to metamorphosis produced rare individuals that began gonadal maturation in the absence of metamorphosis. However, there is no evidence that it could have successfully reproduced without completing a full metamorphosis.

4.2.4 Marine or Freshwater Origin of Lampreys

For decades, biologists and paleontologists have debated whether the vertebrates originated in the sea or in fresh water. This question is not trivial; differences between these two habitats would have involved much more than just the salt content of the water (i.e., it is not just a question of the osmoregulatory abilities of the earliest vertebrates), but also has profound ecological and evolutionary implications. When vertebrates arose (~500 Ma), the seas possessed a rich and diverse fauna while freshwater rivers and lakes are believed to have lacked multicellular animals and were rather unproductive (Halstead 1985). This would mean that, if the vertebrates originated in the sea, they would have evolved under conditions of diverse and abundant food supplies but with intense predation and competition. In fresh water, on the other hand, there would have been few predators or competitors, but food sources would have been limited to algae and other unicellular organisms (Griffith 1987, 1994). Arguments for a freshwater origin were based on some geological evidence suggesting that, at least in North America, early vertebrate fossils appeared to originate from freshwater localities, as well as the "naïve" suggestion that the streamlined shape of fish was a direct response to the flow of running waters and the "more sophisticated views" of Smith (1953) that the glomerular kidney evolved as a means of combating the problem of osmosis in fresh water (Halstead 1985). In fact, Romer (1955) concluded "I see no reason for serious consideration of a marine history for the early vertebrates." However, hagfishes also have a glomerular kidney, and it was subsequently concluded that the evolution of the glomerular kidney did not depend on a freshwater environment for its initial development (see Halstead 1985). For the most part, the argument has since been "conclusively settled in favor of a marine origin for the vertebrates," because all the non-vertebrate chordates (and hagfishes) are exclusively marine and the earliest vertebrate fossils come from marine environments (see Holland and Chen 2001; Janvier 2007). A third argument proposes that the early vertebrates were anadromous. Griffith (1987, 1994) suggested that marine "pre-vertebrates" invaded food-rich estuaries where, given the large fluctuations in salinity in these environments, they evolved osmoregulatory features that enabled reproduction in fresh water. Since fewer competitors would have been present in fresh water, it provided a safe haven from predators, although at the expense of growth. Slow-growing filter-feeding larvae developed in fresh water, and adults subsequently returned to sea to feed. Griffith (1987, 1994) argued that many of the characteristic vertebrate features (cephalization, paired sensory organs, complex endocrine system) could have evolved as a response to the demands of anadromous migrations and seasonal spawning. However, these are the same arguments given for a somewhat later invasion of fresh water by marine vertebrates (see below), and it is more likely that anadromy was a later addition to the repertoire of many fishes; evidence suggests that anadromy was acquired secondarily and independently within multiple lineages (McDowall 1988, 1993; Hardisty et al. 1989; Dodson et al. 2009).

Whether the earliest lampreys were marine, freshwater, or anadromous involves similar arguments. The earliest known fossil lamprey from ~360 Ma was recovered in marine or estuarine deposits (Gess et al. 2006). Fossils from ~320 Ma were also found in marine deposits (Janvier and Lund 1983), although a third specimen reported by Janvier et al. (2004) was found in an area that would have shown wide fluctuations in salinity ranging from brackish (slightly salty) to hypersaline conditions. *Mayomyzon pieckoensis* from ~280 Ma was recovered in a diverse collection of ~300 predominantly marine species, which suggests a coastal deltaic area of fluctuating marine and fresh waters (Bardack and Zangerl 1971). The fact that the lampreys were well preserved suggests a rapid death and burial in the area of deposition, but it cannot be determined with certainty whether they lived in fresh or marine waters. *Mesomyzon mengae* from ~125 Ma represented the first lamprey fossil from unambiguous freshwater deposits; it was found with other freshwater or terrestrial animals, and there was no indication that the area had any connection with the sea since the Triassic period (~250–200 Ma; Chang et al. 2006). The first (and only) definitive larval lamprey fossils were also recovered from these deposits (Chang et al. 2014; see Sect. 4.2.1).

However, Lutz (1975) suggested that lampreys evolved in fresh or brackish water based on their relatively low serum osmolality relative to marine fish species. The very low blood concentrations of Na^+ and Cl^- in larval lampreys in particular (and juveniles to a lesser extent) was used as support for a relatively long history of life in fresh water; Na^+ and Cl^- concentrations were similarly low in lungfishes and polypteroids (bichirs), which are "presumed never to have left freshwater" (Hardisty et al. 1989). It has also been argued that the early life stages of fish species survive best in the type of osmoregulatory environment ancestral to the group (see McDowall 1993), likewise suggesting a freshwater origin of lampreys since modern-day lamprey larvae are generally unable to osmoregulate in water with salinities higher than ~28% sea water (i.e., ~10 parts per thousand, ppt; see Dawson et al. 2015). Furthermore, Hardisty et al. (1989) argued that the small size of the earliest lampreys (see Sect. 4.2.1) would likely have imposed a greater osmotic stress in full-strength sea water, leading to the conclusion that early lampreys lived in a stable and predominantly freshwater or brackish environment.

Nevertheless, the above evidence and arguments are not entirely contradictory; the overlap appears to be the suggestion that the earliest lampreys occupied brackish environments. Janvier (2007) stressed that, during the Devonian (419–360 Ma), the continental margins were occupied by vast deltas and tidal flats, and that the environment of most fishes during this time (and probably earlier) was most likely comparable to present-day major tropical deltas and mangroves. Coastal deltaic areas would have been supplied by numerous slow flowing streams, and they would have provided diverse habitats with respect to salinity and depth (Hardisty et al. 1989). Furthermore, the reasoning made by Lutz (1975) cannot distinguish between evolution in fresh (or brackish) water and a subsequent long history of life in fresh water.

Thus, it appears that the earliest lampreys were likely marine, but they probably lived in coastal areas of fluctuating salinity that "prepared" them for subsequent invasion of fresh water following the development of terrestrial flora and more hospitable inland areas. The first true plants emerged onto land 470–425 Ma (Gibling and Davies 2012), and the earliest known trees date back to 385 Ma (Stein et al. 2007). The evolution of terrestrial plants led to the development of soils and terrestrial animal assemblages (Gibling and Davies 2012). Before this, inland streams and rivers would have been unproductive and, without stabilizing vegetation, extremely "flashy" (i.e., where water levels rise very quickly, making rivers prone to flooding). This timing is consistent with the suggestion that the larval stage and metamorphosis had evolved in lampreys by 280–220 Ma and may have been evident by ~320 Ma.

Early freshwater environments were relatively unproductive, but they also supported few predators, providing a "safe haven" for reproduction and rearing of early developmental stages. As suggested by Hardisty et al. (1989) and Evans et al. (2018), the development of the larval stage in the lamprey life cycle likely coincided with the invasion of fresh water, followed by subsequent specialization to the new environment. A pelagic larval stage would have been maladaptive in flowing water, for example, selecting for the evolution of the benthic (burrowing) larval stage. Subsequent elongation of the larval period would have taken advantage of the safe but relatively unproductive fresh waters, and size at metamorphosis approached that of at least some modern lampreys by ~125 Ma (see Sect. 4.2.1). Thus, metamorphosis in lampreys, insects, and amphibians appears to have evolved at similar times to take advantage of the opportunities presented by newly hospitable terrestrial or inland habitats.

The above discussion still does not address the question of whether, following colonization of fresh water for reproduction, early lampreys restricted their freshwater use to reproduction and rearing of the filter-feeding larval stage (i.e., were anadromous, returning to more productive marine coastal areas to feed as adults) or were entirely freshwater resident. Growth opportunities for the juvenile stage would clearly be better in the marine or estuarine environment (particularly given the especially depauperate nature of fresh waters at that time), but duration of the juvenile stage and size achieved during feeding at sea likely increased only gradually over time. Long feeding and spawning migrations characterized by some of the largest extant anadromous lamprey species were likely not a feature of the earliest anadromous lampreys. Based on plasma osmolalities of juvenile lampreys, Lutz (1975) and Hardisty et al. (1989) concluded that there has been a relatively recent origin of the marine feeding phase in lampreys. The freshwater lamprey genus *Ichthyomyzon* either evolved in fresh water or has been freshwater resident for long periods of evolutionary time (Bartels et al. 2012; see Sect. 4.3.2.4), but again this observation only allows us to determine that they have been in fresh water for a "relatively" long period. Regardless, the life history of the earliest lampreys that invaded fresh water was still not entirely similar to either extant anadromous or freshwater-resident parasitic lampreys. Despite their highly conserved body plan—which allows 360-Ma fossils to be immediately recognizable as lampreys—the above discussion indicates that there was likely a gradual transition in terms of life history from the earliest lampreys to those seen in modern forms and subsequent diversification in migratory and feeding types.

4.3 Variation in Migratory Type

Parasitic lampreys exhibit two basic migratory types, anadromous and freshwater-resident, and anadromous lampreys are sometimes divided into the large-bodied forms ("forma typica") and the smaller-bodied "forma praecox." Praecox lampreys are assumed to have a reduced marine phase relative to the typical form (e.g., Abou-Seedo and Potter 1979), although differences in the quantity or quality of available host fishes cannot be ruled out. The term praecox (not to be confused with *Mordacia praecox*, the non-parasitic precocious lamprey or Australian brook lamprey) has sometimes also been used to refer to freshwater-resident parasitic forms that are also generally smaller than anadromous forms (e.g., Hardisty 1986a; Maitland et al. 1994) or without distinction between small-bodied anadromous and freshwater forms (e.g., Berg 1948). Here, however, we use the term praecox to refer only to the smaller-bodied anadromous form. Some anadromous lampreys also appear to show considerable intraspecific variation with respect to migration timing (also known as run timing). Although some species show little intraspecific variation in the onset and duration of their upstream migration (e.g., sea lamprey and pouched lamprey appear to consistently enter fresh water 1–2 and 15–16 months, respectively, prior to spawning), others (e.g., Caspian and European river lampreys and, to some extent, Pacific lamprey) show variation among and within populations (see Moser et al. 2015; Chap. 1). For the non-anadromous lampreys, we use the term freshwater-resident to describe those that spend their entire life cycle within fresh water (i.e., excluding anadromous species that feed prior to or during outmigration to sea; see Sect. 4.3.4.4). Freshwater-resident populations (including all non-parasitic "brook" lampreys; see Sect. 4.6) are also sometimes referred to as potamodromous (i.e., showing directed movement within fresh water; Moser et al. 2015). The term "landlocked" is also frequently used, although many of these populations retain access to the sea, and, in some locations, freshwater and anadromous lampreys co-occur in a lake basin (e.g., European river lamprey in Lake Ladoga and Arctic lamprey in the Naknek River system; Sects. 4.3.4.2 and 4.3.4.3). In most cases, however, the majority of freshwater species or populations (e.g., sea lamprey in the Great Lakes, Arctic lamprey in Great Slave Lake) appear to be permanently freshwater resident without any individuals that go to sea. Whether or not the former cases represent polymorphism within a single population or spatially overlapping (but reproductively isolated and genetically determined) ecotypes has not yet been tested.

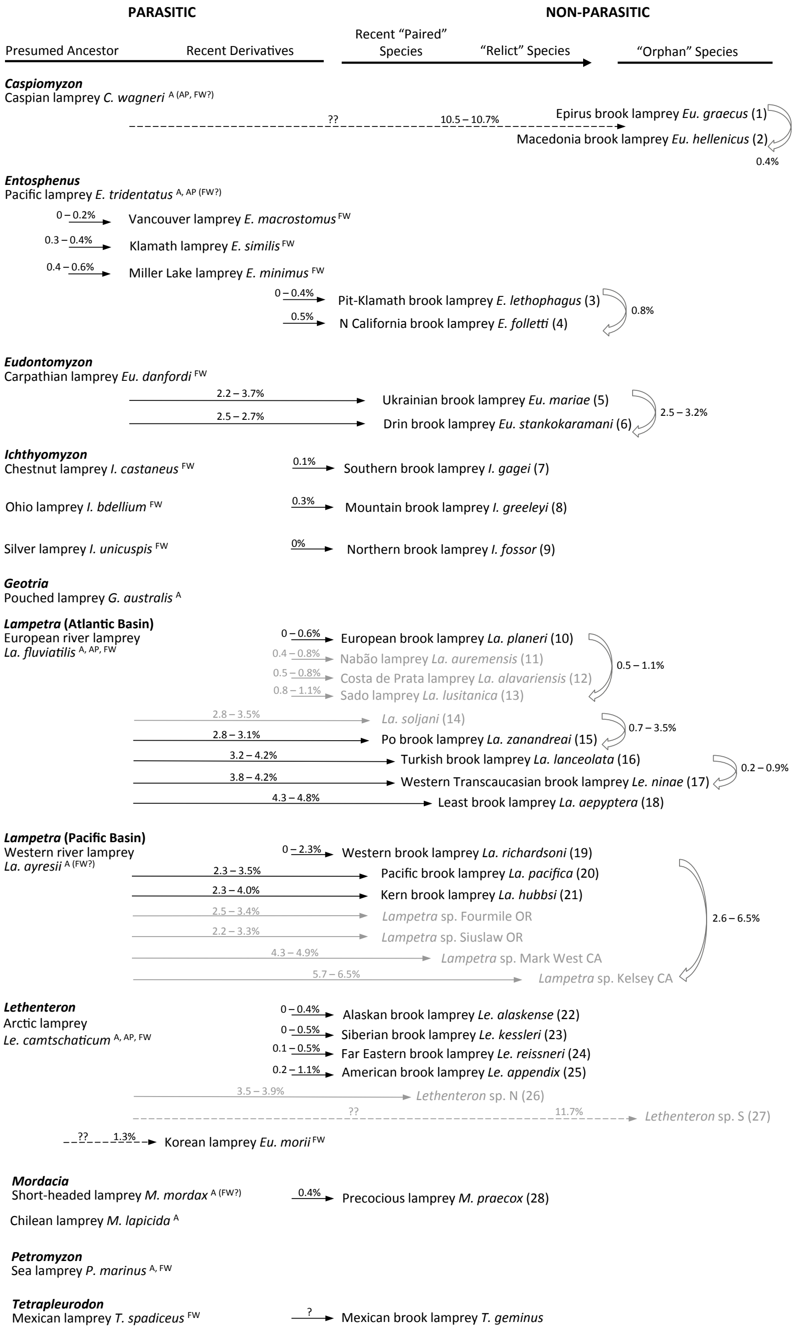
Of the 18 extant parasitic lamprey species, nine are exclusively freshwater resident and nine are largely anadromous, but with at least some reports of freshwater-resident populations in all but two of these species. Some of the freshwater-resident species and populations are clearly derived from anadromous species (e.g., the three freshwater-resident parasitic species in the genus *Entosphenus* and the Great Lakes sea lamprey); in constrast, others (e.g., species in the genus *Ichthyomyzon*) appear to have evolved in or been freshwater resident for long periods of evolutionary time (see Sect. 4.3.2.4). This section reviews these different migratory types in lampreys, with an emphasis on intraspecific variation in migratory type and features of the species or environments where the different types are found.

4.3.1 Exclusively Anadromous

Five lamprey species are exclusively or almost exclusively anadromous (Fig. 4.1). Rare or unconfirmed freshwater populations have been reported in three of these species (see Sect. 4.3.3), leaving only the pouched lamprey and Chilean lamprey *Mordacia lapicida* with no reports of freshwater-resident or praecox forms. The length ranges of fully grown individuals of these species are thus relatively narrow. At the commencement of their upstream migration, the majority of pouched lamprey typically measure 530–740 mm TL in Australia (Potter et al. 1983) and 445–570 mm in Chile (Neira 1984). Adults of the Chilean lamprey are reported to range in size from 278 to 313 mm (Neira 1984). Duration of the feeding phase is unknown in both species, but it is thought to be quite long in the pouched lamprey given its size (Renaud 2011; see Chap. 3).

4.3.2 Exclusively Freshwater

Nine parasitic lamprey species are exclusively freshwater resident, including: three species in the genus *Entosphenus*, which all appear to be recent derivatives of the anadromous Pacific lamprey; the Korean lamprey *Eudontomyzon morii* which, despite its current placement in the genus *Eudontomyzon*, may be an older freshwater derivative of the anadromous Arctic lamprey or an Arctic lamprey-like ancestor (see Sect. 4.3.2.2); and five species (Carpathian lamprey *Eu. danfordi*, silver lamprey


PARASITIC
NON-PARASITIC
Presumed Ancestor
Recent Derivatives
Recent "Paired" Species
"Relict" Species
"Orphan" Species
Caspiomyzon
Caspian lamprey C. wagneri A (AP, FW?)
??
10.5 – 10.7%
Epirus brook lamprey Eu. graecus (1)
Macedonia brook lamprey Eu. hellenicus (2)
0.4%
Entosphenus
Pacific lamprey E. tridentatus A, AP (FW?)
0 – 0.2%
Vancouver lamprey E. macrostomus FW
0.3 – 0.4%
Klamath lamprey E. similis FW
0.4 – 0.6%
Miller Lake lamprey E. minimus FW
0 – 0.4%
Pit-Klamath brook lamprey E. lethophagus (3)
0.5%
N California brook lamprey E. folletti (4)
0.8%
Eudontomyzon
Carpathian lamprey Eu. danfordi FW
2.2 – 3.7%
Ukrainian brook lamprey Eu. mariae (5)
2.5 – 2.7%
Drin brook lamprey Eu. stankokaramani (6)
2.5 – 3.2%
Ichthyomyzon
Chestnut lamprey I. castaneus FW
0.1%
Southern brook lamprey I. gagei (7)
Ohio lamprey I. bdellium FW
0.3%
Mountain brook lamprey I. greeleyi (8)
Silver lamprey I. unicuspis FW
0%
Northern brook lamprey I. fossor (9)
Geotria
Pouched lamprey G. australis A
Lampetra (Atlantic Basin)
European river lamprey La. fluviatilis A, AP, FW
0 – 0.6%
European brook lamprey La. planeri (10)
0.4 – 0.8%
Nabão lamprey La. auremensis (11)
0.5 – 0.8%
Costa de Prata lamprey La. alavariensis (12)
0.8 – 1.1%
Sado lamprey La. lusitanica (13)
0.5 – 1.1%
2.8 – 3.5%
La. soljani (14)
2.8 – 3.1%
Po brook lamprey La. zanandreai (15)
0.7 – 3.5%
3.2 – 4.2%
Turkish brook lamprey La. lanceolata (16)
3.8 – 4.2%
Western Transcaucasian brook lamprey Le. ninae (17)
0.2 – 0.9%
4.3 – 4.8%
Least brook lamprey La. aepyptera (18)
Lampetra (Pacific Basin)
Western river lamprey La. ayresii A (FW?)
0 – 2.3%
Western brook lamprey La. richardsoni (19)
2.3 – 3.5%
Pacific brook lamprey La. pacifica (20)
2.3 – 4.0%
Kern brook lamprey La. hubbsi (21)
2.5 – 3.4%
Lampetra sp. Fourmile OR
2.2 – 3.3%
Lampetra sp. Siuslaw OR
4.3 – 4.9%
Lampetra sp. Mark West CA
5.7 – 6.5%
Lampetra sp. Kelsey CA
2.6 – 6.5%
Lethenteron
Arctic lamprey Le. camtschaticum A, AP, FW
0 – 0.4%
Alaskan brook lamprey Le. alaskense (22)
0 – 0.5%
Siberian brook lamprey Le. kessleri (23)
0.1 – 0.5%
Far Eastern brook lamprey Le. reissneri (24)
0.2 – 1.1%
American brook lamprey Le. appendix (25)
3.5 – 3.9%
Lethenteron sp. N (26)
??
11.7%
Lethenteron sp. S (27)
??
1.3%
Korean lamprey Eu. morii FW
Mordacia
Short-headed lamprey M. mordax A (FW?)
0.4%
Precocious lamprey M. praecox (28)
Chilean lamprey M. lapicida A
Petromyzon
Sea lamprey P. marinus A, FW
Tetrapleurodon
Mexican lamprey T. spadiceus FW
?
Mexican brook lamprey T. geminus

◂**Fig. 4.1** Postulated relationships between freshwater-resident parasitic and non-parasitic species and their presumed ancestor in 10 genera of extant lampreys. The 41 species recognized by Potter et al. (2015) are shown in *black*; taxa not recognized by Potter et al. (2015) and new or tentative species that have not been formally described are given in *gray* (see Yamazaki et al. 2006; Boguski et al. 2012; Mateus et al. 2013a; Tutman et al. 2017). Presumed parasitic ancestors (as represented by 14 species in the contemporary fauna) are shown with recent exclusively freshwater parasitic derivatives (4 species) and recent (“paired”) and older (“relict”) non-parasitic (brook lamprey) derivatives (although, in some cases, the distinction between “paired” and “relict” species is not entirely clear; see Sect. 4.6.2.1; Fig. 4.2). Relict species whose parasitic counterparts in the contemporary fauna are particularly difficult to identify but whose affinities might be inferred from morphology (as indicated by current generic placement) or molecular data are also shown. Genetic divergence (Kimura’s two-parameter distance, K2P) between presumed parasitic ancestors and derivative species (and between multiple derivatives of the same presumed ancestor) is based on >300 cytochrome b gene sequences (>1,131 base pairs, bp) from GenBank, except for Northern California brook lamprey (where only 384 bp were available; Margaret F. Docker, unpublished data) and *Lampetra soljani* (where only cytochrome oxidase I sequence data was available, but where divergence at cytochrome oxidase I in these lamprey species was 0.75 times that of cytochrome b and adjusted accordingly); no sequence data was available for the Mexican lamprey. Migratory type (anadromous, anadromous praecox, and freshwater resident) is indicated (*A, AP, FW*) for parasitic species (see Sect. 4.3); numbers in parentheses after the name of each non-parasitic species are those referred to in Fig. 4.2

Ichthyomyzon unicuspis, chestnut lamprey *I. castaneus*, Ohio lamprey *I. bdellium*, and Mexican lamprey *Tetrapleurodon spadiceus*) from exclusively freshwater genera (Fig. 4.1). The duration of the parasitic feeding phase (and consequently body size) is reduced in these species relative to most anadromous forms.

4.3.2.1 Freshwater Parasitic *Entosphenus* Species

Mean and maximum TL of the three freshwater parasitic species of the genus *Entosphenus* are: 125 and 145 mm for Miller Lake lamprey (Bond and Kan 1973; Lorion et al. 2000) and 231 and 269 mm for Klamath lamprey *Entosphenus similis* (Vladykov and Kott 1979a), the two species found in the Klamath basin of Oregon and California; and 174 and 273 mm for the Vancouver or Cowichan lamprey *En. macrostomus* (Beamish 1982), which is endemic to the Cowichan Lake system on southeastern Vancouver Island, British Columbia. The particularly small size of the Miller Lake lamprey (presumably corresponding with the relatively small size of Miller Lake, 2.3 km^2) suggests a very brief post-metamorphic feeding period, and there have even been suggestions that some individuals do not feed at all (Bond and Kan 1973). Little is known about the feeding habits of the Klamath lamprey, but, given its size, it presumably feeds parasitically for no more than 1 year. The Vancouver lamprey also likely feeds for $\leq$1 year (see Chap. 3). All three species have been described as distinct taxa based on diagnostic morphological differences (see Renaud 2011; Potter et al. 2015), although low levels of genetic differentiation between these species and anadromous Pacific lamprey (Docker et al. 1999; Lorion et al. 2000; Lang et al. 2009; see Fig. 4.1) suggest that all are recent freshwater derivatives of the latter species. Kan and Bond (1981) proposed rapid speciation of the Miller Lake lamprey from Pacific lamprey or a Pacific lamprey-type ancestor following the eruption of Mount Mazama ~6,600 years ago that isolated Miller Lake from the Williamson drainage. Similarly, the Vancouver lamprey was likely established post-glacially with the formation of Cowichan Lake <15,000 years ago (see Taylor et al. 2012).

The Vancouver lamprey, endemic to Cowichan Lake (62 km^2), Mesachie Lake (0.6 km^2), and the interconnecting Bear Lake, is the best studied of these three species. Beamish (1982) described the Vancouver lamprey as a distinct taxon due to its smaller size and differences in body proportions, pigmentation, physiology, and spawning time and location. Most notably, the Vancouver lamprey is distinguished by its larger oral disc (which produces relatively large wounds on hosts that can be mistaken for attacks by Pacific lamprey), its ability to survive following metamorphosis in both fresh and salt water, and the fact that it spawns in the lake rather than tributary streams. During the parasitic feeding phase, Vancouver lamprey prey on a number of salmonid species found within the Cowichan system, including cutthroat trout *Oncorhynchus clarkii*, rainbow trout *O. mykiss*, coho salmon *O. kisutch*, Dolly Varden *Salvelinus malma*, and non-anadromous sockeye salmon or kokanee *O. nerka* (Beamish 1982, 2001; COSEWIC 2008). This species is not landlocked, but appears to be parapatric rather than sympatric with anadromous Pacific lamprey. Pacific lamprey are found in the Cowichan River downstream of Skutz Falls. A fishway at the falls was constructed in the 1950s to facilitate upstream passage of salmonids, but these falls were probably not a complete barrier to upstream movement by Pacific lamprey and other anadromous fishes (Taylor et al. 2012). However, there is no evidence that Pacific lamprey enter Cowichan Lake to spawn in its inlet tributaries, and, despite being indistinguishable in their cytochrome b gene sequences (Docker et al. 1999; Fig. 4.1), recent analysis using microsatellite DNA loci showed that Vancouver lamprey and Pacific lamprey in the Cowichan system represent distinct gene pools (Taylor et al. 2012).

Other potential freshwater parasitic *Entosphenus* forms have been reported that are sometimes referred to as non-anadromous Pacific lamprey populations but which may represent distinct but undescribed freshwater species. Hubbs (1925) suggested that the population in Goose Lake, a shallow alkaline lake in Oregon and California, represented a separate but unnamed race, and Moyle (2002) felt that this form should be considered a subspecies of Pacific lamprey. A non-migratory form of Pacific lamprey also occurs in the Sprague River and Upper Klamath Lake in the Klamath basin in Oregon (Hamilton et al. 2005), and it appears to be morphologically (e.g., in the number and structure of velar tentacles; Renaud 2011) and genetically (Lorion et al. 2000) distinct from other *Entosphenus* species. Both populations are presumably post-Pleistocene Pacific lamprey derivatives and not recently landlocked forms. Goose Lake formed from precipitation and melting glaciers at the end of the Pleistocene, and Upper Klamath Lake was also formed around this time when the much larger Lake Modoc receded and disappeared (Dicken and Dicken 1985). Non-anadromous Pacific lamprey-like populations have also been reported in three disjunct locations in southwestern British Columbia (Beamish 2001; see Sect. 4.3.4.1).

4.3.2.2 Korean Lamprey

The Korean lamprey from the Yalu River drainage in China and North Korea feeds in fresh water on small cypriniform fishes such as goldfish *Carassius auratus*, spine loach *Cobitis taenia*, and lake minnow *Rhynchocypris percnurus*. Maximum reported TL for this species is 279 mm, although adult size (i.e., following shrinkage prior to spawning; see Chap. 1) is typically ~150–200 mm (see Renaud 2011; Chap. 3). All other described species in the genus *Eudontomyzon* are freshwater resident (see Sect. 4.3.2.3), although there is debate regarding the generic placement (and hence the ancestor) of this species. Morphological phylogenies retain this species as sister to the Carpathian lamprey (Gill et al. 2003), but analyses using cytochrome b sequence data—albeit using a single metamorphosing individual—place Korean lamprey in the clade with *Lethenteron* (Lang et al. 2009). Given the disjunct distribution of the genus, Berg (1931) similarly suggested that the Korean lamprey evolved from the Arctic lamprey while the *Eudontomyzon* species in the Black Sea basin were derived from the European river lamprey. Cytochrome b gene sequences in Korean and Arctic lampreys differed by 1.3% (Kimura two-parameter, K2P, values; Lang et al. 2009; Li 2014). In comparison, Pacific lamprey and its three described freshwater derivatives differ by 0–0.6% in cytochrome b DNA sequence (Fig. 4.1), suggesting that the Korean lamprey is a somewhat older freshwater derivative. Although the precision of molecular clocks based on mtDNA sequence divergence has been debated (see Galtier et al. 2009), sequence data are useful for comparing relative divergence times between species.

4.3.2.3 Carpathian Lamprey

Carpathian lamprey feed for only 7–9 months (see Chap. 3). The maximum TL recorded during the feeding phase is 300 mm, although the largest mature adult recorded was only 207 mm and mean TL in different rivers ranged from 141 to 199 mm (Renaud and Holčík 1986). The Carpathian lamprey is an exclusively freshwater parasitic species (Potter et al. 2015), but the origin of this species and its presumed non-parasitic counterpart, the Ukrainian brook lamprey *Eudontomyzon mariae*, has been questioned. An extinct *Eudontomyzon* sp. nov. “migratory” lamprey from the Dniester, Dnieper and Don drainages in the Black Sea basin are included on the IUCN Red List of Threatened Species. Adults of this undescribed form were the target of fisheries during their autumn and spring migrations, but it is not known whether this lamprey fed at sea or entirely within fresh water (Kottelat et al. 2005; Freyhof and Kottelat 2008a). The absence of seawater-type mitochondria-rich cells (SW-MRCs, formerly known as chloride cells) in the gills of Ukrainian brook lamprey strongly suggests that this species did not evolve recently from an anadromous ancestor (Bartels et al. 2017), because non-parasitic (European brook lamprey, western brook lamprey, and American brook lamprey *Lethenteron appendix*) and freshwater parasitic (Great Lakes sea lamprey) species that are derived post-glacially from anadromous ancestors still develop SW-MRCs in their gills during metamorphosis (Youson and Freeman 1976; Youson and Beamish 1991; Bartels et al. 2011, 2015). However, further studies are needed to determine whether the Carpathian lamprey also lacks SW-MRCs, particularly since the Carpathian lamprey and Ukrainian brook lamprey are one of the very few lamprey species pairs studied that do not share cytochrome b haplotypes (e.g., Docker 2009; Lang et al. 2009; Fig. 4.1) and thus may not share the same recent evolutionary history as most paired species (see Sect. 4.6.3.1). Nevertheless, the cytochrome b network analysis performed by Bartels et al. (2017) suggests that the hypothetical ancestor of both Carpathian and Ukrainian brook lampreys was probably freshwater resident. Cytochrome b gene sequence in the Carpathian lamprey differed by 4.5–5.2% (K2P) from the European river lamprey, its closest extant anadromous relative.

4.3.2.4 Freshwater Parasitic *Ichthyomyzon* Species

Like other freshwater lampreys, adults of the three parasitic *Ichthyomyzon* species, the chestnut, Ohio, and silver lampreys, are smaller than most anadromous lampreys. Mean TL in the adults examined by Hubbs and Trautman (1937) were 189 mm for Ohio lamprey, 216 mm for chestnut lamprey, and 224 mm for silver lamprey, although maximum lengths of 279, 363, and 415 mm, respectively, have been reported during the feeding phase (see Chap. 3). Like other freshwater lampreys, the trophic phase is likely no more than ~1 year (Vladykov and Roy 1948; Hall 1963; Cochran et al. 2003). Access to large-bodied hosts (e.g., native and introduced salmonids, lake sturgeon *Acipenser fulvescens*, northern pike *Esox lucius*, muskellunge *E. masquinongy*, and American paddlefish *Polyodon spathula*) may permit the large size observed in some chestnut and silver lampreys relative to smaller-bodied freshwater lampreys such as the Miller Lake lamprey, Korean lamprey, and Carpathian lamprey (see Chap. 3). However, unlike most of the other freshwater lampreys discussed in this section, lampreys in the genus *Ichthyomyzon* likely evolved in fresh water or have been confined to fresh water for long periods of evolutionary time. Unlike lamprey species that were presumably derived post-glacially from an anadromous ancestor (see Sect. 4.3.2.3), silver and chestnut lampreys lack SW-MRCs in their gills (Bartels et al. 2012, 2015). This genus is confined to river systems and lakes in central and eastern North America at a considerable distance from the sea (Potter et al. 2015) and co-occurs in the large Mississippi River system with a number of ancient actinopterygian fishes also found only in fresh water (Hubbs and Potter 1971; Bartels et al. 2012). Phylogenetic analysis places *Ichthyomyzon* at or near the base of the phylogenetic tree of Northern Hemisphere lampreys, sister to *Petromyzon* with its anadromous and freshwater-resident sea lamprey (Gill et al. 2003; Lang et al. 2009). However, these two genera are not close relatives; cytochrome b gene sequences differ by ~14–15%. It appears that the genus *Ichthyomyzon* either evolved from a freshwater species that never possessed SW-MRCs, or SW-MRCs became lost in *Ichthyomyzon* during a long period of separation from an anadromous ancestor (Bartels et al. 2012, 2015).

4.3.2.5 Mexican Lamprey

Very little is known regarding the biology of the Mexican or Chapala lamprey. It is critically endangered but probably not yet extinct (Snoeks et al. 2009; Maitland et al. 2015). The reported range for adult TL (229–286 mm; Lyons et al. 1996) is comparable to that of most other freshwater parasitic species, although a parasitic feeding period of 2 years rather than $\leq$1 year has been suggested (see Chap. 3). Molecular studies (using cytochrome b sequence data from the presumably closely related Mexican brook lamprey *T. geminis*) place *Tetrapleurodon* as sister to *Entosphenus* (Lang et al. 2009); Mexican brook lamprey and anadromous Pacific lamprey cytochrome b gene sequences differ by 3.8%.

4.3.3 Anadromous Species with Rare Praecox or Freshwater Populations

Rare or unconfirmed freshwater populations have been reported in three of the 18 parasitic lamprey species, the Caspian lamprey *Caspiomyzon wagneri*, western river lamprey, and short-headed lamprey.

4.3.3.1 Caspian Lamprey

Berg (1948) reported two forms of the Caspian lamprey in the Volga Delta: a typical anadromous form where average TL ranged from 370 to 410 mm, with a maximum recorded TL of 553 mm, and smaller praecox individuals measuring 191–290 mm TL. The typical form underwent its spawning migration in November to March, and the praecox form was found migrating from mid-September to March. In contrast, in the European river lamprey, the typical form shows an earlier and more protracted migration (see Sect. 4.3.4.2). Berg (1948) also reported numerous praecox Caspian lamprey (250–370 mm) in the Sura River basin, a tributary to the Volga River. Freyhof and Kottelat (2008b) indicated that Caspian lamprey may have formed landlocked populations in reservoirs in the lower Volga River. The Volgograd and Saratov reservoirs (~3,120 and 1,830 km^2, respectively), constructed in 1958–1961 and 1955–1956, support dozens of fish species, including bream *Abramis brama*, European cisco or vendace *Coregonus albula*, burbot *Lota lota*, European perch *Perca fluviatilis*, and roach *Rutilus rutilus* (Ermolin 2010). Although no hosts of Caspian lamprey have been positively identified yet, these fishes are all preyed upon by other lamprey species (see Chap. 3). However, in the Saratov Reservoir, it appears that Caspian lamprey may now be extirpated. Ermolin (2010) reported that this species was found at low abundance in 1955–1967, decreased to very low abundance in 1969–1985, was represented by a solitary specimen in 1986–1995, and was not observed at all in 1996–2007. Construction of the Mingechaur Reservoir (605 km^2) on the Kura River in Azerbaijan in 1953 likewise appears to have resulted in loss of Caspian lamprey above the dam (Nazari et al. 2017), and this species also appears to have been extirpated from the Sura River following construction of the Cheboksary Reservoir (2,190 km^2) at its mouth in 1968–1986 (Ruchin et al. 2012). Since the Caspian Sea has a salinity approximately one-third that of most sea water, it would seem that an inability to osmoregulate at low salinities during the feeding phase would not hinder Caspian lamprey from establishing freshwater-resident populations (see Sect. 4.4.3). Most recent studies on the Caspian lamprey focus on those spawning in rivers in Iran, particularly in the Shirud River where TL ranges from 271 to 492 mm and in the Talar River where TL ranges from 295 to 428 mm (Nazari et al. 2017).

Differences in migration timing have been reported in Caspian lamprey from the Shirud River, with autumn migrants initiating upstream migration from mid-September to late October and spring migrants entering the river in mid-March to late April (Ahmadi et al. 2011; see Chap. 1). However, fall and spring migrants do not differ in size (Ahmadi et al. 2011), making it appear that the “premature migration” strategy shown by the fall migrants does not significantly cut short their growth opportunities at sea (see Quinn et al. 2016; Sect. 4.4.4).

4.3.3.2 Western River Lamprey

The western river lamprey or North American river lamprey is, on average, the smallest of the anadromous lampreys. Although a 324-mm individual was reported recently in the Columbia River estuary (Weitkamp et al. 2015), adult TL typically ranges from 168 to 236 mm, with a very narrow mean of 196–198 mm (Vladykov and Follett 1958; Beamish and Neville 1992; Weitkamp et al. 2015). The western river lamprey is considerably smaller than typical anadromous European river lamprey, with which it was considered conspecific until 1958 (although it is not as closely related as once thought; Docker et al. 1999; Lang et al. 2009; Li 2014), and it is even smaller than most praecox forms of the latter species (see Sect. 4.3.4.2). It could thus be argued that all western river lamprey correspond to the anadromous praecox type. Apparently, this species occurs only as widely separated populations, generally associated with larger estuarine systems (Moyle 2002; Boguski et al. 2012), and it feeds at sea for a single summer (3–4 months; R. J. Beamish 1980), compared with ~12 and 18 months for praecox and typical European river lamprey, respectively. Even “at sea” (e.g., in the Strait of Georgia), western river lamprey tend to remain in surface waters and are concentrated in the general vicinity of the larger rivers where salinity is reduced.

Despite what would seem as a “predisposition” for freshwater residency, western river lamprey—unlike the European river lamprey—appear to rarely, if ever, form freshwater-resident parasitic populations. Nevertheless, the western river lamprey or a western river lamprey-like ancestor has given rise to numerous freshwater non-parasitic derivatives (see Sects. 4.6.3.1 and 4.7). Some authors (e.g., Renaud 2011; Potter et al. 2014) have suggested that parasitic individuals produced within a western brook lamprey population on Vancouver Island may represent freshwater-resident western river lamprey (Beamish 1987; Beamish et al. 2016). However, unlike the freshwater-resident Vancouver lamprey which has retained its ability to osmoregulate in salt water (Beamish 1982), these parasitic variants (the so-called marifuga variety) are unable to osmoregulate in salt water (Beamish 1987). This and other features of these individuals suggest instead that they are western brook lamprey that show an “atavistic” reversal to the parasitic feeding type (see Docker 2009).

Beamish and Youson (1987) found that only 3% of western river lamprey held in the laboratory were able to feed and spawn entirely in fresh water, and there are only anecdotal suggestions of freshwater-resident populations of this species. Adult western river lamprey have been recorded in Lake Sammamish (19.8 km^2) and Lake Washington (88 km^2) in October and December, respectively, and the lamprey from Lake Washington was attached to and possibly feeding on a kokanee (Vladykov and Follett 1958). However, each record is represented by a single specimen (311 and 279 mm, respectively) and could represent individuals returning to fresh water to spawn following a marine feeding phase. Nevertheless, there are current reports of a healthy freshwater-resident western river lamprey population in Lake Washington, which may have become non-anadromous when the lake lost its natural connection with Puget Sound following construction of the Lake Washington Ship Canal in 1916 (Molly Hallock, Washington Department of Fish and Wildlife, Lacey, WA, personal communication, 2012). There are dozens of fish species in this lake, including coastal cutthroat trout, juvenile sockeye salmon, longfin smelt *Spirinchus thaleichthys*, and northern pikeminnow *Ptychocheilus oregonensis* (Quinn et al. 2012). There are also reports (in 1931 and 1959) of western river lamprey in Lake Cushman (United States Fish and Wildlife Service 2004), a lake that was expanded into a reservoir (16.2 km^2) after dam construction in 1924–1926. The 1931 specimen (Burke Museum Ichthyology Collection Catalog Number 1509) was collected in June by a commercial fisherman and could represent a remnant of the original anadromous population. Details of the 1959 specimen require verification; the only western river lamprey collected in 1959 in the Burke Museum Ichthyology Collection (Catalog Number 15726) was collected in March in the Yakima River in the Columbia River basin, below Easton Dam. A few transformed western river lamprey are collected each year at the Chandler Juvenile Fish Monitoring Facility in the lower Yakima River, but adult western river lamprey have never been observed here (Ralph Lampman, Yakama Nation, Fisheries Resources Management Program, Toppenish, WA, personal communication, 2018). Similarly, a single putative juvenile western river lamprey was recently reported above the John Day Dam, the third upriver mainstem dam on the Columbia River, but there is no evidence of an established freshwater population above the dam (Jolley et al. 2016). In both cases, it appears that these individuals (presumably captured during their outmigration to sea) have arisen from within the normally non-parasitic western brook lamprey populations upstream (see Sect. 4.6.3.3).

4.3.3.3 Short-Headed Lamprey

The short-headed lamprey is an anadromous species found in drainages and coastal waters in southeastern Australia. Individuals as large as ~500 mm have been reported during the feeding phase, and TL for adults at maturity is ~280–420 mm (Potter et al. 1968; see Chap. 3). In the Gippsland Lakes region of Victoria, this species is known to feed in fresh water on introduced brown trout *Salmo trutta,* black bream *Acanthopagrus butcheri*, and yellow-eyed mullet *Aldrichetta forsteri* during the summer and fall before going to sea; at sea, they appear to spend another 18 months feeding before returning to fresh water. However, there are also indications that a small population remains throughout the feeding phase in Lake Wellington, the largest (147 km^2) and least saline of the three lakes (Potter et al. 1968). Commercial fishermen report catching lamprey attached to yellow-eyed mullet in Lake Wellington throughout the year, but lamprey attached to black bream are reported in Lake Victoria (1.4 km^2) only during the summer months. Since the lakes have been completely cut off from the sea at times, Potter et al. (1968) considered it feasible that conditions existing in the Gippsland Lakes in the past led to the evolution of a form of short-headed lamprey which restricts its feeding to fresh or brackish water.

4.3.4 Anadromous Species with Established Praecox or Freshwater Populations

Praecox or freshwater populations appear to be more common and are certainly better known in the remaining four parasitic lamprey species: the Pacific, European river, Arctic, and sea lampreys. Compared to the other three species, there are few known freshwater-resident populations of Pacific lamprey, but this may be partly the result of many populations that are known having been described as distinct freshwater species (see Sect. 4.3.2.1). There are also relatively few freshwater-resident populations of sea lamprey (e.g., none are known from Europe), but, of course, where they do occur (i.e., in the Great Lakes, Finger Lakes, and Lake Champlain in North America), they have become very abundant and well established (see Chap. 5). Anadromous praecox (or dwarf) Pacific lamprey have been described from several locations, but no small-bodied anadromous sea lamprey are known. Praecox and freshwater-resident European river and Arctic lampreys are common.

4.3.4.1 Pacific Lamprey

The Pacific lamprey is typically large-bodied, although considerable geographic variation in body size has been reported. Over a broad scale, TL of spawning adults appears to be positively correlated with latitude and distance from the sea. Feeding phase individuals up to 850 mm TL have been captured in the Bering Sea (Orlov et al. 2008), and relatively large adults have been reported from large interior rivers within the Skeena River drainage in northern British Columbia and the Columbia River basin. In the Skeena River drainage, adult Pacific lamprey measuring 550–670 and 410–590 mm TL were reported in Babine Lake and Babine Creek, respectively, and adults ranged from 410 to 720 mm in the Bulkley River (R. J. Beamish 1980). In the Columbia River basin, Clemens et al. (2012) reported upstream migrants measuring 560–710 mm at Willamette Falls (235 river kilometers, rkm, upstream from the ocean), and migrants measuring ~710–810 mm TL have been observed in the Methow River, one of the most upstream spawning sites in the Columbia River drainage and accessible only to lamprey that are able to pass nine dams (John Crandall, Wild Fish Conservancy, Duvall, WA, personal communication, 2011). In the Umpqua River, on the Pacific coast, TL of upstream migrants has been recorded to be 415–644 mm (Lampman 2011), and the southernmost record of Pacific lamprey (from Revillagigedo Archipelago, Mexico) is that of a pre-spawning female measuring only 420 mm TL (Renaud 2008).

In contrast, Pacific lamprey appear to have smaller body sizes in small coastal streams or those draining into the Strait of Georgia (also known as the Salish Sea). Spawning migrants in four rivers on Vancouver Island draining east into the Strait of Georgia (Bonsall Creek and Qualicum, Chemainus, and Quinsam rivers) measured 130–380 mm TL. Those from three rivers on Vancouver Island draining west into the Pacific Ocean (Robertson Creek, Stamp River, and a tributary of Kennedy Lake) measured 220–510 mm TL (R. J. Beamish 1980). Smaller-bodied Pacific lamprey are also thought to occur in Duckabush River, which drains into Puget Sound. Similarly, Pacific lamprey in mainland rivers draining into the Strait of Georgia (i.e., the Salmon River, in the Lower Fraser Valley, and the Nicola River, a tributary of the Fraser River) appear to be considerably smaller than those in the Skeena and Columbia river systems; upstream migrants measuring only 193–214 mm and 273–453 mm were reported by Pletcher (1963) and Beamish and Levings (1991), respectively. Although not specifically described as praecox forms, these smaller-bodied anadromous Pacific lamprey are thought to spend less time feeding at sea. R. J. Beamish (1980) assumed that moderate to large lamprey spend up to 3.5 years feeding in salt water; minimum duration of the feeding phase has been estimated at 20 months (1.7 years). Given the range of sizes, there is not a clear distinction (i.e., based on a bimodal size distribution) between the typical and praecox forms; however, based on Pacific lamprey adults found in the Coquille River on the Oregon coast, Kostow (2002) considered mature individuals <370 mm TL to be the dwarf type and those >550 mm to constitute the typical form.

In addition to this variation in size at maturity, Pacific lamprey—at least in the Klamath River in California—show variation in migration timing. Although most populations appear to represent the typical "river-maturing" form (i.e., entering fresh water during the summer prior to spawning), Clemens et al. (2013) described an "ocean-maturing" form entering this river. These individuals are more sexually mature when they enter fresh water in late winter and likely spawn within weeks or months (see Chap. 1). However, unlike the European river lamprey in the Severn River, there is no apparent size difference associated with run timing (e.g., mean TL 609–625 mm for individuals entering in June–September and 612–618 mm for those entering in March–May; Parker 2018). Interestingly, Parker (2018) found that there was a genetic basis for these different ecotypes (see Sect. 4.4.3).

The wide variation in Pacific lamprey body size among rivers has often been used, reasonably so, as evidence of homing and local adaptation (e.g., Beamish and Withler 1986). There is now overwhelming evidence that migratory lampreys do not home to their natal streams (see Moser et al. 2015), but this does not mean that Pacific lamprey constitute a single panmictic population. Weak but significant genetic variation has been detected among widely separated populations, and evidence of isolation-by-distance suggests that limitations to their dispersal at sea prevent formation of an entirely homogenous population (Spice et al. 2012; Hess et al. 2013). Greater genetic differentiation among locations with dwarf or praecox forms suggests even more limited dispersal by smaller-bodied Pacific lamprey. This suggests that the praecox form may remain in estuarine or coastal areas, without the need or opportunity (i.e., because of a rich and/or less mobile prey base) to disperse more widely. Recent genomic studies have also indicated that there is a genetic basis for body size (Hess et al. 2013, 2014), and these individuals may represent a "jumping-off point" for the evolution of freshwater-resident parasitic and non-parasitic forms (see Hardisty 2006; Docker 2009; Sect. 4.7).

There have been several reports of freshwater-resident or landlocked Pacific lamprey, although it should be noted that some of the earlier reports of lacustrine forms once considered to be non-anadromous races of Pacific lamprey have since been elevated to species status (Bond and Kan 1973; Vladykov and Kott 1979a; Beamish 1982; see Sect. 4.3.2.1). These non-anadromous forms are thought to have arisen within the past 6,600–15,000 years, post-glacially in the case of the Vancouver lamprey and following the eruption of Mount Mazama in the case of the Miller Lake lamprey (see Sect. 4.3.2.1). Kan (1975) postulated that interior forms in Oregon and northern California were less affected by Pleistocene glaciation, but that non-anadromous forms arose and survived in large lakes when anadromous migrations were blocked off by the Cascade and Klamath mountain building. It is thought that some other non-anadromous populations (e.g., in Goose Lake and Upper Klamath Lake) likewise deserve recognition as distinct taxa.

More recently, there have been reports of a Pacific lamprey-like form or forms feeding parasitically in three disjunct lake systems in southwestern British Columbia: West Lake on Nelson Island, Village Bay Lake on Quadra Island, and two adjacent lakes (Ruby and Sakinaw lakes) on the Sechelt Peninsula (Beamish 2001; COSEWIC 2008). The freshwater lamprey in Ruby and Sakinaw lakes (~5 and 7 km^2, respectively) are the best studied. Although they shared cytochrome b DNA sequences with anadromous Pacific lamprey and Vancouver lamprey from the Cowichan lake system, analysis using microsatellite DNA markers showed that the lamprey in Ruby and Sakinaw lakes was distinct from the Vancouver lamprey and even more distinct from Pacific lamprey (Taylor et al. 2012). Although the taxonomic status of this population is still unresolved, there is good evidence that they feed in fresh water, including feeding on Sakinaw sockeye salmon, a stock that has been assessed as Endangered by the Committee on the Status of Wildlife in Canada, and perhaps also on small populations of coho salmon and chum salmon *Oncorhynchus keta* (COSEWIC 2016). Although much of the observed scarring in upstream-migrating and adult Sakinaw Lake sockeye salmon may be the result of parasitism by western river lamprey in the Strait of Georgia, there is also evidence of lamprey parasitism on sockeye fry and smolts within the lake (COSEWIC 2016). Other non-anadromous derivatives have been reported in British Columbia over the years (e.g., in the Columbia River, the Fraser River at Prince George, and Cultus Lake; McPhail and Lindsey 1970; Vladykov and Kott 1979a), but little is known about such lamprey and whether they, in fact, represent permanent freshwater-resident populations. There are also reports of Pacific lamprey in Grosvenor Lake and at the mouth of an unnamed creek in Brooks Lake in the Naknek River system in Alaska, but these reports were not substantiated by the extensive collections made by Heard (1966) when studying Arctic lamprey in this system. Lamprey remains have been reported in scat samples recovered from resident harbor seal *Phoca vitulina* in Iliamna Lake in Alaska. Although both Pacific and Arctic lampreys have been reported in the Kvichak River drainage (Hauser et al. 2008), these remains are likely from Arctic lamprey (see Sect. 4.3.4.3).

The freshwater derivatives of Pacific lamprey indicate that this species is capable of establishing in fresh water, although several reports of extirpations above dams suggest that not all populations or individuals are capable of doing so. Pacific lamprey were confined in Dworshak Reservoir (69 km^2) in the Columbia River basin in Idaho when dam construction was completed in September 1971 (Wallace and Ball 1978). Rainbow trout and kokanee were stocked into the impoundment in spring 1972 and 1973; during creel surveys in May 1973, 5% of the rainbow trout and kokanee were found to bear at least one lamprey scar, and this proportion increased to 16% by November 1973. However, incidence of scarring decreased to 4% in 1974 and <1% in 1975 and 1976, and no lamprey were directly observed after 1973. Beamish and Northcote (1989) reported a similar situation in Elsie Lake (6.7 km^2) on central Vancouver Island, following construction of five dams on the outlet of the lake in 1957–1959. Resident cutthroat and rainbow trout collected in the lake started showing evidence of lamprey scarring immediately after dam construction was complete in 1959. In this year, 74.5% of the trout had fresh wounds and 2.1% exhibited older wounds that were healing (Pletcher 1963). However, the small size of the wounds indicated that the lamprey probably grew very little during this time period, and, although the proportion of old scars increased from 1960 to 1963, there was a progressive decline in the proportion of fresh scars (to 0% in 1969, 1981, and 1987).

Likewise, Pacific lamprey appear to have been extirpated above barrier dams in the Willamette Basin in Oregon (Doug Larson and Matt Helstab, U.S. Forest Service, Middle Fork Ranger District, Westfir, OR, personal communication, 2017) after construction of two high-head flood control dams in the Middle Fork Willamette River in 1953 and 1954. Fish species in the resulting reservoirs (Dexter Reservoir and Lookout Point Reservoir, 4.2 and 17.6 km^2, respectively) included Pacific salmon *Oncorhynchus* spp., northern pikeminnow, and largescale sucker *Catostomus macrocheilus* (see Keefer et al. 2013). In 2001, however, six Pacific lamprey (two recently metamorphosed juveniles and four larvae) were captured during an

Environmental Protection Agency survey 4.8 km upstream of the uppermost dam. This would suggest that a small number of Pacific lamprey survived and reproduced upstream of the dams more than 45 years after their construction or that some escapement of anadromous lamprey occurred past the dams. Recent surveys have to date failed to detect additional Pacific lamprey at these sites, but investigation of this potential landlocked population is ongoing (Doug Larson and Matt Helstab, personal communication, 2017).

Extirpation of Pacific lamprey following confinement to fresh water is consistent with observations that post-metamorphic individuals held in fresh water in the laboratory fed poorly or not at all, and all ultimately died prior to maturation (Richards and Beamish 1981; Clarke and Beamish 1988). The ability to maintain blood sodium concentration in fresh water varied among lamprey from different source populations, with performance in fresh water (from best to worst) ranked as follows: Chemainus River > Puntledge River > Big Qualicum River > Kanaka Creek > Somass River > Babine River (Clarke and Beamish 1988). Chemainus, Puntledge, Big Qualicum, and Somass rivers are located on Vancouver Island; Kanaka Creek is a tributary of the Fraser River on the lower mainland of British Columbia, and the Babine River is located in northern British Columbia. Pacific lamprey from the Chemainus River survived in fresh water until July, but no Babine lamprey survived beyond mid-February. Survival in the laboratory was good in salt water (Beamish 1982). Thus, Clarke and Beamish (1988) concluded that confinement of Pacific lamprey in fresh water does not easily result in the formation of landlocked populations. Beamish and Northcote (1989) suggested that barriers to migration might select for a few individuals that genetically would be able to feed and grow to maturity in fresh water and that the chance of this happening would be higher if the size of the population was large (or if the founding population was naturally small-bodied or otherwise “predisposed” to freshwater residency; see Sect. 4.4.3). Beamish (1985) suggested that the genetic change required for Pacific lamprey to survive in fresh water is either extremely rare or requires a series of changes that are unlikely to occur immediately when faced with sudden barriers such as dams.

4.3.4.2 European River Lamprey

A wide range of sizes has been reported for anadromous European river lamprey, and there is evidence of geographical variation in size. Females at or near spawning in the Drwêca River in the Vistula River basin in northern Poland averaged 405 mm TL (337–462 mm; Witkowski and Ję̧sior 2000). Large size has also been reported among upstream-migrating European river lamprey in the River Meuse (>400 mm TL; Lanzing 1959) and in the Nemunas River in Lithuania (356–408 mm; Gaygalas and Matskevichyus 1968). This species seems to be somewhat smaller (mean TL for males and females was 310–320 mm and 320–340 mm, respectively; Berg 1948) in the River Neva, which flows into the Gulf of Finland, and even smaller in the U.K. In the Severn Estuary, mean TL in early upstream migrants was 290–306 mm in males and 301–318 in females (Hardisty and Huggins 1973), and average TL was ~300 mm near the end of the spawning run (Abou-Seedo and Potter 1979). In Scottish waters, TL of the anadromous form at or near spawning is ~300–350 mm TL (Hume 2013). Abou-Seedo and Potter (1979) suggested that the consistently larger size of European river lamprey in the Baltic and North seas, compared with those of the River Severn, indicates that feeding conditions in the former areas are probably better than they are in the region off the west coast of England. As with the western river lamprey, the European river lamprey may prefer water of reduced salinity (Bahr 1952), resulting in a more estuarine, coastal distribution, and more genetic variation among regions than wide-ranging, large-bodied lamprey species (Mateus et al. 2016; see Sect. 4.7.5).

The estimated duration of the marine trophic phase in typical European river lamprey is 18 months, from the spring of one year to the autumn of the next (Hardisty and Potter 1971b). In this form, the entire post-metamorphic period is thought to be ~2.5 years, including the non-trophic period following metamorphosis (i.e., migrating downstream in the fall, with growth over the first winter being minimal) and during upstream migration (starting in the fall prior to spawning; Abou-Seedo and Potter 1979). In addition to this typical form, a smaller praecox form with a presumably reduced marine trophic period has been identified in the River Neva (mean TL 225 mm) and Severn River (mean 240 mm) where, interestingly, the typical form is already smaller than elsewhere (Berg 1948; Abou-Seedo and Potter 1979). In both rivers, the praecox individuals formed a distinctly smaller size class alongside the typical form during upstream migration. Praecox European river lamprey (mean TL 249 mm) have also been reported in the River Bladnoch, which drains into the Solway Firth in southwestern Scotland (Hume 2013). In the Severn Estuary, the praecox form was less common than the typical form (comprising ~25% of all individuals), and it appeared to show differences in run timing, with a later and more contracted upstream migration. Typical anadromous individuals were occasionally found in the estuary as early as July and as late as April, with peak abundance generally in November; in contrast, the praecox form was present mainly between January and March. Abou-Seedo and Potter (1979) thus concluded that the praecox form spent ~12 months at sea, but, because it delayed its upstream migration until the winter or spring prior to spawning, its non-trophic period following metamorphosis lasts only 1.5 years. Therefore, the praecox form appears to reduce its post-metamorphic period by 1 year relative to the typical anadromous form but reduces the duration of feeding by only 6 months. In the River Neva, appreciable numbers of the praecox form were found in the delta in October and November, and Berg (1948) concluded that the praecox form began its upstream migration after feeding in the Gulf of Finland for <6 months. Other small-bodied European river lamprey (mean TL 220 and 240 mm for males and females, respectively) have been reported in the Narew River in western Belarus and northeastern Poland (Hardisty 1986a). These individuals were not identified specifically as the praecox form, but they likely would have had a reduced marine trophic phase relative to the large-bodied individuals in other tributaries of the Vistula River.

There are also several reports of small-bodied freshwater-resident European river lamprey populations, particularly in large lakes. Berg (1948) reported both large (up to 362 mm TL) and small (250–330 mm) European river lamprey in Lake Ladoga (~18,100 km^2) and Lake Onega (~9,700 km^2), the largest and second largest lakes in Europe, respectively. Lake Onega is connected to Lake Ladoga via the River Svir, and both lakes drain into the Gulf of Finland via the Neva River. Therefore, as with many other freshwater-resident populations, these European river lamprey were not landlocked; the larger form was presumably anadromous, and the smaller form was likely a freshwater-resident (lacustrine) form. However, it should be noted that the specimens examined by Berg (1948) were collected prior to construction of the first dam on the Svir River (1936), and now two dams present impassable barriers to anadromous river lamprey migrating upstream from the Baltic Sea and Lake Ladoga to Lake Onega. Nevertheless, the freshwater form still persists in these lakes. Tsimbalov et al. (2015) reported spawning-phase male and female lamprey measuring 202–241 mm and 200–247 mm TL, respectively, in the Lososinka River in the Lake Onega basin, and Kuznetsov et al. (2016) observed mature female lamprey measuring 264–348 mm TL in Lake Ladoga. Both lakes, particularly Lake Ladoga, have rich fish fauna, including freshwater Atlantic salmon *Salmo salar* populations (Ozerov et al. 2010) and other fishes (e.g., European perch, burbot, European cisco, and roach; Berezina and Strelnikova 2010). Berg (1948) found a large number of lamprey attached to European cisco. Lake Ladoga even supports a resident ringed seal population *Phoca hispida ladogensis* (Kunnasranta et al. 2001).

Small freshwater-resident European river lamprey (mean 200–225 mm TL) have also been reported in Lake Mjøsa in southern Norway (Berg 1948). Lake Mjøsa is the largest lake in Norway (365 km^2), as well as one of the deepest lakes in Europe, with at least 20 species of fish, including a fast-growing brown trout morph that can reach weights of >15 kg, northern pike, European perch, burbot, European smelt *Osmerus eperlanus*, European whitefish *Coregonus lavaretus*, and European cisco (Sandlund et al. 1987; Taugbol 1994; Mariussen et al. 2008). Freshwater-resident European river lamprey populations have also been reported in large lakes in the Vuoksi, Kymijoki, and Kokemaenjoki river drainages in Finland (Tuuainen et al. 1980).

Freshwater residency has also been demonstrated in European river lamprey inhabiting Lough Neagh in Northern Ireland (Goodwin et al. 2006). With a surface area of 390 km^2, it is the largest lake in the British Isles. Fishes within Lough Neagh have access to the sea, but all information suggests that all or most of the Lough Neagh river lamprey are non-anadromous. River lamprey are rarely caught in the River Bann downstream of the Lough Neagh outflow, and actively feeding lamprey (i.e., attached to pollan *Coregonus autumnalis* and with full guts) have been captured in the lough almost year-round (February to October). During this time, TL increased from 118 mm to a maximum of 391 mm. Scarring on pollan was first observed (at low incidence) in April and May and increased in late June and early July, although no fresh scars were evident in September or October. Multiple size classes were not present during the feeding phase, suggesting that this population feeds for ≤ 1 year in fresh water. Nevertheless, the size achieved by the end of the feeding phase indicates rapid growth during this year, making these individuals (mean 318 mm TL at maturity; Hume 2013) as large or larger than some of the praecox or even smaller-bodied typical anadromous European river lamprey that feed at sea for 1 or 1.5 years. Inger et al. (2010), using stable isotope analysis, subsequently confirmed that none of the 71 Lough Neagh river lamprey examined had fed in the marine environment. However, these authors identified brown trout and non-native bream as the main items in the river lamprey diet, with pollan representing the main food source only between May and July. This finding and the scarring data from Goodwin et al. (2006) suggest that river lamprey shift to larger fish species later in the year (see Chap. 3). Therefore, access to a range of prey sizes may be important in permitting these lamprey to reach a large size exclusively in fresh water.

The best-studied freshwater-resident European river lamprey is the population found in Loch Lomond (71 km^2) in Scotland. Loch Lomond contains the greatest number of fish species of any lake in Scotland. In addition to European river lamprey and European brook lamprey, and the occasional report of sea lamprey (see Sect. 4.3.4.4), Loch Lomond contains at least 12 other native fish species, including Atlantic salmon, brown trout, European whitefish (locally known as powan and sometimes recognized as *Coregonus clupeoides*), northern pike, roach, and European perch, and six non-native species (Maitland 1980; Hume et al. 2013a). Maitland (1980) found that brown trout, roach, and especially powan bore European river lamprey scars (with scars on 6, 5, and 45% of all individuals captured, respectively) and that 55% of the scarred powan had 2–8 scars each. Fresh wounds were recorded in May–November and were especially prevalent in July and August (Morris 1989; Maitland et al. 1994), that is, after they would normally outmigrate if they were anadromous. Maitland (1980) indicated that feeding river lamprey must be relatively common in most parts of the loch, because wounding rates were high on powan in all locations. However, it should be noted that Hume et al. (2013a) found that scarring on powan has become greatly reduced in recent years. In 2010, only 6% of powan had river lamprey scars, possibly as a result of declines in powan numbers following introduction of the ruffe *Gymnocephalus cernuus*.

The freshwater-resident European river lamprey in Loch Lomond, sometimes called a dwarf (Morris 1989) or praecox (Maitland et al. 1994) form, is not landlocked. Anadromous river lamprey can access the loch via the River Leven, which connects Loch Lomond to the Firth of Clyde via the River Clyde, and both forms spawn in the River Endrick, which flows into the eastern end of the loch (Morris 1989). The freshwater-resident form measures 155–257 mm TL during its upstream migration (Adams et al. 2008) and 164–197 mm (mean 185 mm) at spawning (Morris 1989), compared to 269–338 mm (mean 327 mm) in the anadromous form (Morris 1989; Adams et al. 2008; Hume 2013). Adams et al. (2008) used stable isotope analysis to show that the small and large lamprey size classes from the River Endrick corresponded to those feeding in fresh- and saltwater, respectively. Morris (1989) indicated that the freshwater form appears to feed for a few months compared to 15–18 months at sea for the typical anadromous form.

Morphological differences have been reported between the freshwater-resident and anadromous European river lamprey in Loch Lomond. The freshwater form has a bigger oral disc and eye, longer snout, and darker pigmentation (Morris 1989). Morris (1989) indicated that the freshwater form in Loch Lomond is in some ways intermediate between the normal forms of river and brook lampreys and suggested that it might represent an intermediate stage between these two species (see also Beamish 1985; Docker 2009; Sect. 4.7.3). However, there is evidence of temporal separation between forms, and some measurements and counts of the freshwater parasitic form were more extreme than either the anadromous river lamprey or brook lamprey; these observations suggest that the freshwater form is not a hybrid (Morris 1989). Furthermore, recent studies show that the freshwater form is more genetically differentiated from the anadromous and non-parasitic forms than either of these latter forms are from each other (Bracken et al. 2015; Hume et al. 2018), although there is evidence for ongoing gene flow among all three forms (Bracken et al. 2015).

4.3.4.3 Arctic Lamprey

Like the Pacific and European river lampreys, size at maturity in anadromous Arctic lamprey varies widely, and there appear to be geographical differences. Maximum TL during the feeding phase (790 mm) has been reported in the North Pacific Ocean (Orlov et al. 2014), and the largest size at, or approaching, maturation has been reported in southeastern Russia. Maximum TL at maturity was 625 mm (mean 505 mm) and 566 mm (mean 456 mm) in the Partizanskaya River (formerly known as the Suchan River) and the lower reaches of the Amur River, respectively (Bogaevskii 1949). In Japan, Yamazaki et al. (2001) reported maximum TL ranging from 400 to 442 mm at or near spawning, and in western Kamchatka, Russia, maximum TL of the typical anadromous form was 350 and 330 mm in males and females (with means of 293 and 279 mm, respectively; Kucheryavyi et al. 2007). Heard (1966) found that maximum TL of mature anadromous Arctic lamprey in southwestern Alaska was 311 mm TL (mean 253 mm), and they were even smaller (maximum and mean TL of 200 and 166 mm, respectively) on the southern Kuril Islands in the Western Pacific Ocean between Japan and the Kamchatka Peninsula (Sidorov and Pichugin 2005).

This latter population from the southern Kuril Islands could likely be described as a praecox anadromous form, although, given the range of sizes observed, the distinction between the typical and praecox forms is not entirely clear. Berg (1948) gave a brief description of a spent dwarf male Arctic lamprey (224 mm TL) from the mouth of the Kukhtui River, near the Sea of Okhotsk, and Kucheryavyi et al. (2007) explicitly described a praecox form in western Kamchatka (maximum and mean TL of 220 and 190 mm, respectively) that occurred alongside the typical anadromous form and a freshwater-resident non-parasitic form. The praecox form in western Kamchatka was less common (3% of all individuals) than the typical anadromous form (14%), and 92% of the praecox individuals were males, lending credence to the suggestion that life history transitions may occur more readily in males (see Docker 2009).

Duration of the feeding phase in this species can only be extrapolated from body size (see Chap. 3). However, given the range of sizes observed, there appears to be more intraspecific variation than in most other parasitic species, with the possible exception of the Pacific lamprey (see Sect. 4.3.4.1). Orlov et al. (2014) identified four size classes (150–320, 330–530, 540–650, and 660–800 mm) in Arctic lamprey captured in the North Pacific Ocean during the feeding phase, suggesting that individuals in this population feed at sea for up to 4 years. Presumably, populations with smaller sizes at maturity feed at sea for shorter periods of time, with those specifically identified as the praecox form having a marine trophic phase lasting for as little as several months to 1 year (Kucheryavyi et al. 2007). Nevertheless, given that we know relatively little about the marine feeding phase of lampreys, we cannot exclude the possibility that size differences are the result of differences in the quantity or quality of available host fishes. The anadromous sea lamprey can reach 700–800 mm TL in ≤ 2 years of feeding at sea (see Sect. 4.3.4.4); therefore, size at maturity (at least across species and potentially within species) may not be a reliable indicator of the duration of the feeding phase.

Freshwater-resident populations of Arctic lamprey have been reported in Asia and North America, but they are not known from Europe (Holčík 1986), and some freshwater-resident populations attributed to this species are apparently non-parasitic forms (Iwata and Hamada 1986; Kucheryavyi et al. 2007; Yamazaki et al. 1998, 2011; see Sect. 4.6.3.2). The best-studied populations where freshwater parasitism and permanent freshwater residency have been confirmed are in North America. The Naknek River system on the Alaska Peninsula consists of seven interconnected lakes, including Naknek Lake, which is the fifth largest lake in Alaska (584 km^2). Heard (1966) reported that both anadromous and freshwater-resident parasitic Arctic lamprey occurred in this system and that the freshwater-resident form was more common than the anadromous form. Lamprey were found feeding on sockeye salmon, rainbow trout, pygmy whitefish *Prosopium coulterii*, and threespine stickleback *Gasterosteus aculeatus* in July, August, and September. They measured 115–226 mm (mean 167 mm) TL during the feeding phase and 117–188 mm (mean 155 mm) at spawning. Vladykov and Kott (1978) subsequently re-examined 47 specimens (122–172 mm) from Heard (1966), as well as specimens obtained from other areas, and described these lamprey as a new non-parasitic species, the Alaskan brook lamprey *Lethenteron alaskense*. However, Heard (1966) did not find any recently metamorphosed individuals with maturing gonads and presented clear evidence of feeding in fresh water throughout the summer and fall. He suggested that individuals within this system might exhibit flexibility in feeding, remaining in the lake if there is an adequate source of prey or, alternatively, starting to feed on salmon smolts in fresh water and being carried to sea when they outmigrated. Arctic lamprey were observed attached to upstream-migrating rainbow trout and sockeye salmon congregating at the outlet to one of the lakes in this system in July and August, and Heard (1966) suggested that these lamprey had probably started to migrate from the lake but remained at the outlet upon finding a large concentration of prey. This would suggest that Arctic lamprey in this system are opportunistically freshwater resident, rather than representing a discrete freshwater population, and this population may represent one of the few cases of partial migration in lampreys. Partial migration refers to the resident–migratory dimorphism seen in many populations of other fish species and birds, for example, where some individuals in the population migrate and others remain resident (Olsson et al. 2006; Chapman et al. 2012). Other freshwater-resident lampreys, even those that co-occur with the anadromous form (e.g., European river lamprey in Loch Lomond; see Sect. 4.3.4.2), appear instead to represent distinct gene pools rather than belonging to a single polymorphic population.

Unlike Arctic lamprey in the Naknek system, the freshwater-resident Arctic lamprey population in Great Slave Lake (27,200 km^2) in the Northwest Territories in Canada is thought to represent a permanent freshwater population. Although not landlocked, anadromous lamprey in this system would need to migrate up the Mackenzie River, the longest river in Canada (1,740 km), to reach the lake. Arctic lamprey in this system have been found to prey on lake whitefish *Coregonus clupeaformis*, cisco *Coregonus* spp., inconnu *Stenodus leucichthys*, lake trout *Salvelinus namaycush*, longnose sucker *Catostomus catostomus*, and burbot (Nursall and Buchwald 1972). Specific size information was not given for the 112 feeding or spawning-phase lamprey collected, but body size in this population appears somewhat larger than in the Naknek River system; feeding phase juveniles collected in the north arm of Great Slave Lake in late August and September often exceeded 300 mm in TL, and size at spawning included a spent female measuring ~168 mm and a ripe male measuring 226 mm TL. No juvenile lamprey were collected in the winter fishery, leading Nursall and Buchwald (1972) to conclude that this population likely fed following metamorphosis for <6 months (i.e., from downstream migration in the spring to early fall).

Other freshwater-resident Arctic lamprey have been reported in Tatlmain Lake, a tributary to the Pelly River in the Yukon Territory, Canada, and in Iliamna Lake in southwest Alaska (McPhail and Lindsey 1970). Iliamna Lake is the largest lake in Alaska and the eighth largest lake in the U.S. (2,600 km^2) and has abundant salmonids (e.g., sockeye salmon, Arctic char *Salvelinus alpinus*, Dolly Varden) and other fishes presumably capable of supporting Arctic lamprey during the feeding phase (Foote and Brown 1998; Hauser et al. 2008; May-McNally et al. 2015). This lake drains into Bristol Bay via the Kvichak River, with no barriers preventing access to the sea, and the abundant prey base supports even a resident harbor seal population (Hauser et al. 2008). Lamprey remains identified as either Arctic lamprey or Pacific lamprey (the two species that have been reported in the Kvichak River drainage) were found in 27% of scat samples collected from these seal in July–August 2001, 2005, and 2006 (Hauser et al. 2008), indicating that lamprey were present in the lake after the time at which they would normally outmigrate. McPhail and Lindsey (1970) reported that lamprey up to 254 mm TL were recorded in the lake. Hauser et al. (2008) reported that they did not observe any sockeye salmon in the lake with lamprey attached, but directed studies targeting Arctic lamprey specifically are needed.

4.3.4.4 Sea Lamprey

The anadromous sea lamprey is the largest of all extant lampreys, and there are no known anadromous praecox populations. If there is geographic variation in size at maturity, it is more subtle than what has been observed in Pacific, European river, and Arctic lampreys. Given that TL has been estimated to shrink by up to 24.3% in females and 18.6% in males during the course of the spawning migration (F. W. H. Beamish 1980a; see Chap. 1), observed differences could be the result of individuals being measured at different points on their migration. Maximum TL during the feeding phase is recorded at 1,200 mm (see Chap. 3), and spawning migrants at or approaching 900 mm TL have been reported in Europe (e.g., Hardisty 1986b; Silva et al. 2013a; Rooney et al. 2015). Adults entering the Mulkear River in Ireland, for example, measured 616–913 mm TL (mean 760 mm; Rooney et al. 2015). In North America, upstream migrants averaged 743 and 729 mm TL in the St. Lawrence River in Quebec and St. John River in New Brunswick (ranges 666–841 and ~640–840), respectively (Vladykov 1951; Beamish and Potter 1975), and sea lamprey captured on the spawning grounds in the Terra Nova River in Newfoundland averaged 601 mm (530–687 mm; Dempson and Porter 1993). It is thought that sea lamprey feed at sea for 23–28 months (F. W. H. Beamish 1980a). Halliday (1991) found two size classes during the feeding phase in the northwest Atlantic (120–380 and 560–840 mm TL), which would likewise be consistent with a marine feeding phase lasting at least 2 years. However, Halliday (1991) could not rule out a 1.5-year juvenile feeding period, and a recent study conclusively showed that some individuals can reach large size in considerably less than 2 years. Silva et al. (2013a) captured a 895-mm upstream migrant in northwestern Spain that had been tagged on its downstream migration a mere 13.5 months previously, suggesting that it spent as little as 10.5 months feeding at sea.

Freshwater-resident sea lamprey are well known in the Laurentian Great Lakes, Lake Champlain, the Finger Lakes (Cayuga and Seneca lakes), and Oneida Lake (see Chap. 5). These lamprey grow larger than any other freshwater-resident parasitic lampreys and larger than many anadromous lampreys. MacKay and MacGillivray (1949) reported that the majority of upstream migrants in the Little Thessalon River (in the Lake Huron basin) in 1946 were ~610 mm TL, with a maximum TL of 762 mm. However, mean TL at maturity typically falls within the 395–500 mm range (e.g., Applegate 1950; Wigley 1959; Manion 1972; Johnson 1982; O'Connor 2001; Smith and Marsden 2007), and the maximum TL recorded in recent decades is ~570 mm (Johnson 1982). Duration of the parasitic feeding phase has been established at 12–20 months (Applegate 1950; Bergstedt and Swink 1995; see Sect. 4.5.3).

Although these sea lamprey populations are frequently referred to as "landlocked," until recently there were no physical barriers preventing movement between the Atlantic Ocean and Lake Ontario and the Finger Lakes (i.e., through the St. Lawrence River), and Lake Champlain likewise remains accessible from the Atlantic Ocean via the Richelieu River (Marsden and Langdon 2012; Eshenroder 2014). However, large-bodied sea lamprey of presumably marine origin have not been observed in Lake Ontario, and, with the strong downstream current, movement into Lake Ontario is thought to be unlikely (Eshenroder 2014). Construction of the Moses Saunders Power Dam on the St. Lawrence River in 1954–1958 would now further impede upstream migration of anadromous sea lamprey. Sea lamprey larvae are absent from any upper St. Lawrence tributaries (i.e., in the 160-km downstream portion from Lake Ontario to the Moses Saunders Power Dam), although parasitic-phase sea lamprey are sometimes attached to fish in the St. Lawrence River itself (Pearce et al. 1980). Sea lamprey populations in the lower St. Lawrence River are presumably anadromous, but possibly derive from Lake Champlain (Eshenroder 2014). Sea lamprey in Lake Erie and the upper Great Lakes are essentially landlocked. Although colonization past Niagara Falls was initially permitted through the Welland Ship Canal (see Chap. 5), present-day movement through the Niagara River or the Welland Canal is thought to be very limited, although not impossible (Larson et al. 2003; Kim and Mandrak 2016).

Thus, like the Arctic lamprey in Great Slave Lake, the sea lamprey in the Great Lakes, Lake Champlain, and Cayuga, Seneca and Oneida lakes represent permanent freshwater-resident populations. These lakes are also "great" in size and have a rich prey base (e.g., lake trout, lake whitefish, Pacific salmonids; see Chaps. 3 and 5). Surface area of the Great Lakes ranges from ~19,000 km^2 for Lake Ontario to >82,000 km^2 for Lake Superior; the surface area of Lake Champlain is ~1,300 km^2, and Oneida, Cayuga, and Seneca lakes range in area from 172 to 207 km^2. There is debate regarding the origin of sea lamprey in these lakes (i.e., whether they have been present in Lake Ontario and Lake Champlain since the last glacial retreat or whether they invaded via canals less than 200 years ago; see Sect. 4.5). Resolution of this debate will help determine whether colonization of fresh water required adaptation over time or whether access to abundant and large-bodied prey is the main determinant of whether sea lamprey can survive and indeed flourish entirely in fresh water (see Sect. 4.4).

Despite their rapid spread from Lake Ontario into Lake Erie and the upper Great Lakes in the 1920s and 1930s (see Chap. 5), sea lamprey do not appear to have spread farther into smaller inland lakes. However, a recent study by Johnson et al. (2016) indicates that, should they gain access, establishment might be possible if a sufficient prey base is available. These authors present evidence that a small number (<200) of sea lamprey may complete their life cycle in the Cheboygan River system, upstream of a dam intended to prevent spawning-phase sea lamprey access from Lake Huron. Despite this dam, the watershed remains infested with sea lamprey. A navigational lock on the dam was generally thought to permit escapement past the dam, but Holbrook et al. (2014) showed little or no escapement through the Cheboygan lock and dam during the 2011 spawning migration. There are four lakes upstream of the dam, the two largest of which—Mullet Lake (70 km^2) and Burt Lake (69 km^2)—contain fishable populations of northern pike, smallmouth bass *Micropterus dolomieu*, walleye *Sander vitreus*, yellow perch *Perca flavescens*, rainbow and brown trout, and a threatened population of lake sturgeon. Lamprey wounds on fish have been reported previously by local fishermen (Applegate 1950), and Johnson et al. (2016) confirmed the presence of lamprey wounds (the majority of which were classified as sea lamprey wounds rather than native silver lamprey wounds) on northern pike and rainbow trout in these lakes. Parasitic-phase sea lamprey captured in August (a few of which were attached to rainbow trout) measured 330–440 mm TL, indicating that sea lamprey feed substantially in these lakes long after they would normally outmigrate to Lake Huron. Johnson et al. (2016) also found adult sea lamprey in the upper river before the first lock opening in the spring, so unless they passed through the dam from Lake Huron by an unknown route, these individuals would have overwintered in the Cheboygan River system. Six unmarked spawning-phase sea lamprey captured in the upper river (and assumed to be from the inland population) averaged 459 mm TL, compared to 493 mm in marked sea lamprey of Lake Huron origin captured in the lower river. The difference in size suggests slightly lower growth rates within the Cheboygan River system, either due to differences in prey availability—although Johnson et al. (2016) indicated that these lakes are more productive than Lake Huron and likely have higher prey density—or due to more rapid cooling of Mullett and Burt lakes in the fall relative to Lake Huron.

No other freshwater-resident sea lamprey populations are known throughout the species' range. There are a growing number of accounts of freshwater feeding by anadromous sea lamprey, but all appear to represent transitory freshwater feeding prior to or during outmigration. However, these reports are worthy of discussion because at least a few individuals have been shown to reach appreciable sizes (250–410 mm TL) feeding either in rivers while en route to the sea or in lakes prior to outmigration. F. W. H. Beamish (1980a), for example, reported newly metamorphosed sea lamprey attached to alewife *Alosa pseudoharengus*, shad *A. sapidissima*, and white sucker *Catostomus commersonii* in the St. John River. These individuals were still reasonably small (mean 132–136 mm TL in mid- to late May, respectively), but condition factor ($CF = W/TL^3 \times 10^6$, where W is weight in g and TL is in mm) increased during this time (from 1.1 to 1.4 from mid- to late May). Furthermore, six individuals averaged 211 mm TL by mid-May, and two even larger sea lamprey (242–292 mm) were caught near the mouth of the river in early June. Feeding sea lamprey as large as 400 mm TL have been reported in rivers attached to anadromous fishes (e.g., Atlantic salmon, alewife, shad), but their occurrence is assumed to result from attacks initiated in marine or estuarine waters; sea lamprey juveniles found attached to the occasional non-anadromous fish species (lake trout, brook trout *Salvelinus fontinalis*) were always smaller (100–250 mm TL). Silva et al. (2013b) confirmed that feeding was initiated in fresh water when they observed outmigrating sea lamprey in two Spanish rivers attached to an exclusively freshwater cyprinid (northern straight-mouth nase *Pseudochondrostoma duriense*); they estimated that ~6% of this shoal-forming cyprinid had lamprey attached, and attachments or scarring were observed up to ~20 km from the upstream tidal limit. Silva et al. (2013c) suggested that 10–30% of all sea lamprey start feeding in the river, particularly on large anadromous fish species, and reported one individual attached to an Atlantic salmon measuring 315 mm TL. The other five sea lamprey that they found attached to anadromous brown trout or twaite shad *Alosa fallux* (20–40 km from the river mouth) measured 149–199 mm TL. Other downstream migrants (i.e., not attached to fish) measured 132–205 mm TL, suggesting that those at the upper end of the range had started feeding in fresh water as well. For comparison, newly metamorphosed sea lamprey feeding in the estuary measured 145–338 mm (mean 217 mm TL; Silva et al. 2013c). Recent observations by Baer et al. (2018) suggest a much lower incidence of in-river feeding by sea lamprey in the Rhine River in Germany, but indicate that those few individuals that do start feeding during outmigration can grow large. Only 28 of the 18,610 downstream migrants (0.15%) showed evidence of substantial feeding, but they measured 250–370 mm (mean 280 mm TL) compared to 90–190 mm for the remaining outmigrants. Over a dozen other fish species, including roach, bream, European perch, and zander *Sander lucioperca* occurred in this portion of the Rhine River. Unlike the previous studies, however, where most observations of in-river feeding were made near the river mouth, Baer et al. (2018) observed evidence of feeding 600 km upstream. These authors suggest that feeding in the river might increase in incidence as the lamprey move downstream.

Lacustrine feeding by anadromous sea lamprey prior to outmigration has also been observed. Davis (1967) reported sea lamprey feeding in Love Lake (2.7 km^2), Maine, where at least 17 teleost fish species occur. Virtually all newly metamorphosed sea lamprey outmigrated in November and December (98.4% in 1960–1961 when downstream movement was monitored between September and May), although a few downstream migrants were captured in February–May. Mean TL of outmigrants was 160 mm; the majority measured 140–175 mm TL, but 16.3% were larger than 175 mm, and the maximum reported was 234 mm TL. In 1960–1964, 85% of the landlocked Atlantic salmon captured had been attacked by newly transformed sea lamprey, and these salmon bore an average of 2.4 and a maximum of 8 wounds per fish. The incidence of fresh lamprey marks suggested that feeding occurred mainly in May–June and October–February. Only 5.1% of brook trout were observed with lamprey marks; marks were also observed on white perch *Morone americana*, white sucker, chain pickerel *Esox niger*, pumpkinseed *Lepomis gibbosus*, yellow perch, alewife, rainbow smelt *Osmerus mordax*, and other sea lamprey, but these marks were not necessarily indicative of successful feeding. Davis (1967) found no evidence of freshwater parasitism by sea lamprey in two other lakes in the East Machias River system downstream of Love Lake (4.8 and 1.2 km^2), but only Love Lake had a well-established population of landlocked Atlantic salmon. In Loch Lomond (71 km^2), Scotland, Atlantic salmon and brown trout occasionally carry lamprey scars that, based on their size and location, are likely caused by sea lamprey, and there are a few records of sea lamprey (up to 200 mm TL) attached to Atlantic salmon in this lake (Maitland 1980; Maitland et al. 1994). Two feeding sea lamprey (350 and 185 mm TL) were recovered on trout 9 and 18 years after construction of the Llandegefedd Reservoir in Wales in 1963 (1.7 km^2; Maitland et al. 1994). These individuals likely represented remnants of the original population, and there was no evidence of an established resident population once the offspring of the last anadromous sea lamprey died out. Likewise, a limited number of sea lamprey were observed feeding in two large reservoirs (Lakes Carrigadrohid and Iniscarra, 5.8 and 4.9 km^2, respectively) on the River Lee in Ireland in 1959–1965 following the construction of the reservoirs in 1957 (Kelly and King 2001). Subsequent monitoring in Iniscarra Reservoir has failed to show any additional evidence of sea lamprey feeding (King and O'Gorman 2018). Likewise, anadromous sea lamprey accidentally introduced into a reservoir above the Portodemouros Dam in northwestern Spain have been unable to form a self-sustaining population in fresh water (Silva et al. 2014). The reservoir, which has an area of 11 km^2, was formed in 1967 when the dam was built. In 2008, brown trout bearing sea lamprey wounds (including one with a 211-mm juvenile sea lamprey attached) were captured by anglers. Of 14 locations sampled across six tributaries of the reservoir, sea lamprey larvae were collected at only two locations 300 m downstream of a restaurant where groups of live adult lamprey showing reproductive behavior were held in nets within the river. There have been no other reports of sea lamprey in the reservoir, further suggesting that these captive individuals were the source of the parasites rather than a residual population that had been confined to fresh water since the building of the dam 40 years earlier.

Persistent freshwater feeding by sea lamprey has been reported in several other Irish lakes (i.e., year after year and over extended periods of the year). The largest individual recorded was 410 mm TL, but, again, there is no evidence that any individuals complete their life cycle in fresh water (King and O'Gorman 2018). Juvenile sea lamprey were reported feeding in Loughs Corrib (178 km^2), Conn (57 km^2), and Leane (19 km^2) in 1959–1965 and in Lough Derg (8.9 km^2) in 1996, and their continued presence in these lakes has been confirmed over the past decade. King and O'Gorman (2018) further reported feeding sea lamprey in two new locations, Muckross Lake (2.7 km^2) in 2009–2011 and Lough Gill (12.8 km^2) in 2011 and 2018. The majority of parasitic-phase individuals were collected during the annual brown trout angling season in May to early June, particularly in Loughs Derg and Conn, but juvenile feeding sea lamprey were collected by anglers in many months and a small number of sea lamprey that attached to open-water swimmers in Muckross Lake were collected in July–September. Sea lamprey attached to adult Atlantic salmon were observed in Loughs Conn and Leane, and attachments to pike and bream were also documented. Although many of the 79 juvenile sea lamprey collected when attached to fish were similar in size to the downstream migrants captured at the outflow from Lough Derg in January (~130–180 mm, mode 160 mm TL), 26.6% were >180 mm (up to ~250–280 mm in May–June), and two of them measured 400 and 410 mm TL (presumably from Muckross Lake later in the summer). King and O'Gorman (2018) found no evidence of "dwarf" sea lamprey in any tributary streams, arguing against the existence of self-sustaining freshwater populations.

Nevertheless, although sea lamprey appear not to readily become established in fresh water, the results of Johnson et al. (2016) suggest that colonization from the Great Lakes proper into other inland lakes is not impossible. Thus, preventing secondary spread to other inland lakes is a high priority (see Chap. 5). Johnson et al. (2016) also demonstrated that barriers to adult migration may not always be able to extirpate sea lamprey populations from upstream reaches if they have access to a sufficient prey base above the barriers. Similarly, dam removal on large streams such as the Black Sturgeon River in Ontario (McLaughlin et al. 2013) could expose large inland lakes to sea lamprey infestation that could result in parasitic feeding within these lakes (see Sect. 4.8.3).

4.4 Factors that Promote or Constrain Freshwater Residency in Parasitic Lampreys

Freshwater parasitic lampreys are said to have a restricted distribution relative to anadromous parasitic and freshwater non-parasitic lampreys, and it has been suggested that they represent an evolutionarily unstable and transitory form between anadromous parasitic and freshwater non-parasitic forms (Beamish 1985; Salewski 2003). Based on the above review, however, it could be argued that the distribution of freshwater lampreys is not particularly restricted, especially in North America where several species (e.g., chestnut and silver lampreys, Great Lakes sea lamprey) are abundant and well established in fresh water (see Sects. 4.3.2.4 and 4.3.4.4). Nevertheless, even if the freshwater parasitic life history type is not inherently unstable, it is apparent that specific ecological conditions are required for its evolution and persistence (Taylor et al. 2012). A minimum level of host fish acting as a forage base is clearly critical for the persistence of parasitic lampreys in fresh water, although the required minimum level apparently varies considerably among species. The ability of anadromous lampreys to colonize fresh water appears to be inversely related to their size (i.e., successful establishment is more likely for small-bodied lampreys) and directly related to availability of suitable prey (both in terms of abundance and size). However, different lamprey species may also show different genetic “predispositions” (e.g., related to osmoregulatory ability) to successful confinement in fresh water, and the “incentive” to abandon anadromy (i.e., related to life history trade-offs) will likely also differ between species and environments. Factors that constrain or promote freshwater residency in different species are, of course, not mutually exclusive. Body size and life history traits presumably also have a genetic basis (certainly among, if not within, species). The genetic basis of physiological and life history traits in lampreys is poorly understood, but recent advances in genomics in other fishes are beginning to identify genomic and transcriptomic differences between anadromous and freshwater forms (e.g., Czesny et al. 2012; Hale et al. 2013; Hecht et al. 2013) and will continue to contribute to our understanding of the genetic underpinnings of life history evolution (see Sect. 4.8.1).

4.4.1 Body Size

As shown by the above accounts (Sect. 4.3), all else being equal, establishment in fresh water is more common in small-bodied anadromous lamprey species or in large-bodied species in regions where dwarf or praecox forms have been reported. For example, at least six freshwater-resident populations of the smaller European river lamprey are known from western Russia, Norway, Finland, and the British Isles (see Sect. 4.3.4.2). In contrast, the large anadromous sea lamprey—although it can be seen feeding in fresh water during or prior to outmigration—appears not to have established any freshwater-resident populations in Europe (see Sect. 4.3.4.4). In this species, colonization of fresh water has only been successful in the Great Lakes and other large productive lakes in North America. Furthermore, the regions where lacustrine populations of European river lamprey have become established seem to be characterized by particularly small-bodied anadromous forms. Similarly, although some populations of Arctic lamprey reach appreciable sizes (e.g., in southeastern Russia), the only known freshwater-resident populations are in regions of Asia and North America where size at maturity of the anadromous population appears to be smaller (see Sect. 4.3.4.3). Likewise, the freshwater-resident *Entosphenus* species assumed to be post-glacial derivatives of the Pacific lamprey (see Sect. 4.3.2.1) and the few known non-anadromous Pacific lamprey populations generally occur in regions where smaller-bodied anadromous Pacific lamprey are known (see Sect. 4.3.4.1). Praecox Pacific lamprey tend to show more genetic differentiation among locations (i.e., more limited dispersal) than the larger anadromous form (Spice et al. 2012; Hess et al. 2013), and there appears to be a genetic basis for body size in this species (Hess et al. 2013, 2014). Thus, praecox individuals—by virtue of their smaller body size or other traits—could be genetically "predisposed" for freshwater colonization (see Sect. 4.4.3).

The only apparent exception to this pattern is the very small-bodied western river lamprey. Western river lamprey feed parasitically for only a few months, in estuaries (e.g., the Strait of Georgia) rather than at sea, and it could be argued that all individuals of this species constitute the praecox form (see Sect. 4.3.3.2). Therefore, we would predict that western river lamprey would be able to easily abandon anadromy. Nevertheless, there is only one report of a "healthy" non-anadromous population (in Lake Washington). However, the western river lamprey or a western river lamprey-like ancestor has given rise to numerous freshwater-resident non-parasitic lamprey populations (from Alaska to California), and perhaps this species, given its very small body size, readily abandons both anadromy and the parasitic feeding phase (see Sect. 4.7).

4.4.2 Prey Availability and Other Ecological Factors

Access to a sufficient prey base is clearly critical for the evolution and persistence of freshwater parasitic lampreys, but what qualifies as sufficient varies considerably among species. Small-bodied species that are exclusively freshwater resident can inhabit relatively small systems with small-bodied prey (e.g., the Miller Lake lamprey; Sect. 4.3.2.1), although others (e.g., silver and chestnut lampreys; Sect. 4.3.2.4) can grow quite large. Both prey abundance and prey size seem to be important. The consumption rate of large-bodied lampreys is high, and the host size necessary to support this consumption rate—particularly as the lampreys increase in size—can be limiting in fresh water (see Chap. 3). European river lamprey in Lough Neagh are estimated to feed in fresh water for only 1 year, but individuals in this population appear to grow as large or larger than some anadromous conspecifics that feed at sea for 1 or 1.5 years (see Sect. 4.3.4.2). Goodwin et al. (2006) showed that river lamprey in this lake shift to larger host species as they grow, and access to a range of prey sizes (and not just absolute prey biomass) may be important in fresh water.

It is no coincidence, of course, that large anadromous lampreys establish in large lakes only, generally where at least a dozen species of fish are present. Lough Neagh is the largest lake in the British Isles, and other lacustrine populations are known from lakes ranging in area from the size of Loch Lomond (71 km^2) to Lakes Onega and Ladoga (>9,700 km^2). The largest anadromous species, sea lamprey, has successfully established freshwater-resident populations in only the Laurentian Great Lakes (~19,000–82,000 km^2), Lake Champlain (~1,300 km^2), and Oneida, Cayuga, and Seneca lakes (172–207 km^2). It is not known if persistence in the smallest of these lakes is dependent on recruitment from or feeding opportunities in Lake Ontario. Likewise, sea lamprey appear to have become established upstream of a barrier in the Lake Huron basin, where they feed on prey in Mullet Lake (70 km^2) and Burt Lake (69 km^2) (Johnson et al. 2016; see Sect. 4.3.4.4). However, it is not known if the long-term persistence of this population depends on occasional recruitment from Lake Huron. Arctic lamprey, another relatively large-bodied anadromous species, has established freshwater-resident populations in large lakes (Great Slave Lake and Iliamna Lake, 27,200 km^2 and 2,600 km^2, respectively; see Sect. 4.3.4.3); in contrast, the Arctic lamprey in the Naknek River system (with a total lake surface area of ~700 km^2) might not be a permanent freshwater-resident population (Heard 1966). In the Naknek River system, individuals may feed opportunistically in fresh water, and there may be ongoing recruitment from the anadromous population.

Species for which few or no non-anadromous populations have been reported are generally those large-bodied species without access to large lakes. This includes the Pacific lamprey and pouched lamprey, and, to a lesser extent, the smaller-bodied western river and short-headed lampreys that share the respective ranges of these species. Compared to the three species discussed above, there are relatively few large lakes within the range of Pacific and western river lampreys, and the same is true for the Southern Hemisphere species. The small number of lamprey species in the Southern Hemisphere has been attributed to the general paucity of freshwater systems for spawning and larval rearing (Potter et al. 2015), and the shortage of large lakes in particular will limit freshwater parasitism. In Australia, natural freshwater lakes are rare due to the general absence of recent glaciation. Lake Wellington (147 km^2) appears to support a non-anadromous population of the smaller short-headed lamprey (see Sect. 4.3.3.3), but it is apparently not sufficiently large for the pouched lamprey.

There are more, but still relatively few, large lakes on the west coast of North America within the range of the Pacific lamprey. One of the largest lakes in this species' range in the contiguous United States (i.e., excluding Alaska) is Lake Roosevelt, which is a reservoir created in 1941 when the Columbia River was impounded by the Grand Coulee Dam. With a surface area of ~330 km^2, this lake is very small in comparison to the Laurentian Great Lakes and Great Slave Lake. The reservoir contains rainbow trout, kokanee, walleye, burbot, and smallmouth bass (Baldwin et al. 2003; Polacek et al. 2006), but there are no reports of Pacific lamprey becoming established following isolation above the dam. It is thus not surprising that large-bodied anadromous Pacific lamprey also failed to establish in the much smaller Dworshak

Reservoir and Elsie Lake (69 and 6.7 km^2, respectively; see Sect. 4.3.4.1). Lacustrine Pacific lamprey-like populations are known from Goose Lake (380 km^2) and Upper Klamath Lake (250 km^2), but these populations are likely of post-Pleistocene origin (see Sect. 4.3.2.1) and it is worth noting that Upper Klamath Lake is a remnant of the much larger Pluvial Lake Modoc, which at its largest, covered >2,600 km^2 (Dicken and Dicken 1985).

The largest lake within this species' range in British Columbia is Babine Lake (~480 km^2). Upstream-migrating anadromous Pacific lamprey were first recorded in this lake's tributaries in 1963, with the number increasing steadily by 1971, and the presence of larval Pacific lamprey was confirmed in many of the streams by the early 1980s (Farlinger and Beamish 1984). Thus, it appears that large-bodied anadromous Pacific lamprey (~480–690 mm TL; R. J. Beamish 1980) have only started accessing the system relatively recently, perhaps following removal of a major rock slide 65 km downstream of the lake (Farlinger and Beamish 1984). However, despite an unconfirmed report in 1977 of a lamprey feeding on a fish in Babine Lake (R. J. Beamish 1980), there are no documented reports of Pacific lamprey parasitizing freshwater fishes anywhere in the Skeena River drainage (Farlinger and Beamish 1984). The potential prey base in Babine Lake includes sockeye and coho salmon, rainbow trout and steelhead (i.e., anadromous rainbow trout), lake trout, and lake whitefish (Shortreed and Morton 2000). Whether a freshwater lamprey population could become established in this lake is unknown and should be monitored.

The western river lamprey likewise has access to relatively few large lakes within its range. It might be supposed that, given its very small body size, large lakes are not required. However, given the relative paucity of large lakes, but the abundance of spawning and larval rearing habitat in coastal systems, it may be more advantageous for this small-bodied species to bypass the parasitic feeding phase altogether and mature as a non-parasitic brook lamprey (see Sect. 4.7).

Although the above argument suggests that large-bodied anadromous lampreys should generally be capable of establishing non-anadromous populations in large productive lakes, isolation above dams appears not to have resulted in successful freshwater colonization in Caspian lamprey, even in very large reservoirs (1,830–3,120 km^2; see Sect. 4.3.3.1). As with Pacific lamprey, perhaps not all anadromous individuals are equally "prepared" for freshwater residency, and isolation of a relatively small number of individuals is insufficient for selection of a freshwater-resident phenotype (see Sect. 4.4.3).

However, feeding mode may also affect the ability of anadromous lampreys, particularly large-bodied ones, to succeed in fresh water. Potter and Hilliard (1987) proposed that blood feeding would have a selective advantage in freshwater environments, where a relatively restricted host population would be less likely to be decimated, especially if hosts are large enough to permit replacement of the blood lost during feeding. Furthermore, because wounds inflicted by blood-feeding lampreys are typically smaller than those caused by flesh-feeding species, they are less likely to be fatal. Therefore, the ability of sea lamprey to become established in the Great Lakes may be permitted in part by their blood-feeding mode. Mortalities are still observed, even among blood feeders (especially with Great Lakes sea lamprey, which are far larger than any other freshwater-resident lamprey), but sea lamprey behave more like a parasite than a predator (see Chap. 3). Likewise, chestnut and silver lampreys are blood feeders and have co-existed with their freshwater hosts for long periods of evolutionary time (e.g., Cochran and Lyons 2016). Potter and Hilliard (1987) suggested that flesh feeding, in contrast, evolved in lamprey populations which had access to estuarine and marine hosts with large, widespread populations. This would particularly be the case for small-bodied hosts that would provide only a small amount of blood and require the lamprey to frequently seek out new hosts (i.e., making blood feeding less efficient), but, given their abundance, they would not be easily depleted. The western river lamprey is categorized as a flesh feeder (Chap. 3), and, Beamish and Neville (1995) estimated that this species kills ~40–50 million Pacific salmon smolts per year and ~150–200 million Pacific herring *Clupea pallasii* >100 mm TL during its brief parasitic feeding phase as it enters the Strait of Georgia from the Fraser River. The Pacific lamprey is classified as a blood and flesh feeder (see Chap. 3). Both western river and Pacific lampreys are thus more likely to deplete their prey base in fresh water. The combined need for a particularly large prey base, but general lack of access to large lakes with a large prey base, may therefore explain why these two species have established few freshwater parasitic populations in contemporary time. The pouched lamprey is likewise a flesh feeder that travels farther offshore to feed in very productive waters (Potter and Hilliard 1987). Carrion feeding (e.g., by the exclusively freshwater-resident Carpathian lamprey) might also have a selective advantage in fresh water by reducing the pressure on local teleost populations (Potter and Hilliard 1987). Nevertheless, it does not appear that this presumed mode of feeding by the Caspian lamprey (see Chap. 3) helped it survive landlocking. Furthermore, the European river lamprey has successfully established in fresh water despite being a flesh feeder, and the Vancouver lamprey feeds on blood and flesh. However, both species are smaller-bodied than most of the blood-feeding freshwater species. Furthermore, although they probably inflict high mortality on their hosts (Beamish 1982; Potter and Hilliard 1987), the presence of fishes with healed scars (Goodwin et al. 2006; COSEWIC 2008) indicates that not all hosts succumb to their wounds, and a certain amount of host mortality would presumably be tolerated where prey are abundant.

As a final note regarding ecological constraints, it is also worth noting that, among other anadromous fishes, there is a greater tendency for populations at lower latitudes to become freshwater resident because fresh waters are more productive at these latitudes than ocean waters (Gross et al. 1988). In contrast, anadromous species tend to predominate in temperate regions, where the reverse is true. In lampreys, the majority of established freshwater parasitic populations are found at higher latitudes (i.e., the opposite of what would be expected). However, to explicitly test for the effect of latitude, we would need to control for other factors (e.g., the relative availability of large inland bodies of water and the presence of barrier dams), and we would also need to include freshwater-resident non-parasitic lampreys. Including brook lampreys, the expected pattern of fewer anadromous populations at low latitudes appears to hold (see Sect. 4.6).

4.4.3 Osmoregulatory Ability and Genetic Factors

Physiological constraints related to osmoregulation may limit the ability of some anadromous lampreys to colonize fresh water. It has been suggested that estuarine species such as European river lamprey prefer water of reduced salinity (Bahr 1952), and this may facilitate the transition of European river lamprey to fresh water. However, western river lamprey has likewise been thought to inhabit waters of lower salinity (R. J. Beamish 1980), but only one freshwater parasitic population has been reported, and this species appears to do poorly in fresh water during its parasitic feeding phase (see Sect. 4.3.3.2). Similarly, despite apparent adaptation to the very low salinity of the Caspian Sea (~one-third that of most sea water), Caspian lamprey do not appear to survive landlocking (see Sect. 4.3.3.1). Nevertheless, the failure of Pacific lamprey populations to survive above dams that prevent access to the sea is often attributed to their inability to osmoregulate in fresh water during the parasitic feeding phase (Clarke and Beamish 1988; see Sect. 4.3.4.1) and has been used to suggest that this species is ill-adapted for colonization of fresh water (e.g., Farlinger and Beamish 1984). By adaptation, we typically mean evolutionary change in a trait with a heritable basis (i.e., over the course of generations). This is different than acclimation or acclimatization, which is the adjustment of physiological traits (i.e., phenotypic flexibility within a single organism) to ambient environmental conditions in the laboratory or in nature, respectively (Piersma and Drent 2003). It is “notoriously difficult” to differentiate between adaptation and environmentally induced flexibility in wild populations because phenotypic variation could be the product of either mechanism or a combination of both (Laporte et al. 2016).

Invasion of fresh water by anadromous lampreys likely involves both adaptation and phenotypic flexibility. In populations suddenly isolated above a barrier, the immediate need to osmoregulate in fresh water during the feeding phase is likely met through a combination of selection on existing variation within the anadromous population and phenotypic flexibility within individuals. Existing variation and phenotypic flexibility allow initial survival; subsequent adaptation leads to further “improvements” and evolution of other traits that increase fitness in fresh water. In Pacific lamprey, some individuals or populations may be better adapted to freshwater feeding than others (i.e., based on existing genetic variation); in turn, feeding in fresh water may improve osmoregulatory ability (i.e., conferring phenotypic flexibility). Clarke and Beamish (1988) found that Pacific lamprey from different populations throughout British Columbia appeared to have different abilities to feed and survive in fresh water, and the ability may be inversely related to body size at maturity. Pacific lamprey from the Chemainus River (mean TL at maturity 270 mm) survived in fresh water until July, whereas no individuals from the Babine River (mean TL 480–640 mm) survived beyond mid-February (R. J. Beamish 1980; Clarke and Beamish 1988). These results are consistent with the suggestion above (Sect. 4.4.1) that anadromous lampreys from smaller-bodied source populations are the progenitors of freshwater-resident populations and species. However, the Pacific lamprey in this study fed poorly in fresh water, and plasma sodium concentrations were correlated with condition factor, suggesting that osmoregulatory failure may have resulted from, or at least been compounded by, depletion of body energy reserves. Hardisty et al. (1989) indicated that, because the blood and tissue of the lamprey's host fishes are isotonic with the internal milieu of the lamprey, feeding would be expected to ease the osmotic load. Ferreira-Martins et al. (2016) demonstrated that feeding on an isomotic meal helped anadromous sea lamprey compensate for ion gains from the seawater environment, and, in fresh water, feeding would be a source of ions (Wood and Bucking 2011). Failure of lampreys to feed during the parasitic phase would therefore compromise their osmoregulatory abilities.

R. J. Beamish and colleagues have suggested that confinement to fresh water might select for a few Pacific lamprey individuals that are genetically predisposed to feed and grow to maturity in fresh water, and the probability of this happening would likely be higher if the size of the population was large (Farlinger and Beamish 1984; Beamish and Northcote 1989). In this respect, Pacific lamprey may be similar to pink salmon *Oncorhynchus gorbuscha* and coho salmon. Pink salmon were previously thought to require salt water for completion of their life cycle, but they have nevertheless become firmly established in the Great Lakes following an accidental introduction into Lake Superior in 1956 (Emery 1981; Gharrett and Thomason 1987). Establishment of a freshwater-resident pink salmon population presumably involved differential survival of those individuals best adapted to fresh water, leading to strong and rapid selection. Non-anadromous coho salmon are also now common in the Great Lakes following introduction in the 1960s (Sandercock 1991), and there is recent evidence of "freshwater residualism" in coho salmon in two small lakes that drain into the Skeena River basin in British Columbia (Parkinson et al. 2016). To date, outside of the Great Lakes, only 15 coho salmon (11 of which were male) have been reported to reach maturity in fresh water (Parkinson et al. 2016). Freshwater residency outside of large lake systems is apparently rare for coho salmon, but rare does not mean impossible. Several authors (e.g., Hardisty 1969; Mathers and Beamish 1974; Beamish et al. 1978; F. W. H. Beamish 1980b) have suggested that colonization of the Great Lakes by anadromous sea lamprey involved selection for small individuals already predisposed for life in fresh water. However, if a relatively small number of sea lamprey colonized Lake Ontario in historical times via canals, this would imply that the genetic ability to osmoregulate in fresh water existed at higher levels within the anadromous population or that the relatively few were either "pre-adapted" (Briski et al. 2018) or "lucky" (see Sect. 4.5.3). Colonization of fresh water also may have involved selection for anadromous sea lamprey with accelerated gonadal development and reduced potential fecundity (Hardisty 1969; see Chap. 1), or these characteristics associated with existing freshwater-resident sea lamprey evolved rapidly following invasion.

Research into the genetic basis of life history traits in lampreys is still in its infancy. To date, however, loci correlating with body size and run timing have been identified in Pacific lamprey (Hess et al. 2013, 2014; Parker 2018), and some of the loci that differ between European river lamprey and European brook lamprey appear to be related to osmoregulation (i.e., rather than feeding type; see Sect. 4.6.3.3). Hess et al. (2014) found that body morphology, primarily TL of upstream migrants, was strongly associated with genetic variation at three single nucleotide polymorphism (SNP) loci (identified as *Etr_1806*, *Etr_4281*, and *Etr_5317*; Hess et al. 2013). The genetic mechanisms associated with these loci are likely complex, but Hess et al. (2013, 2014) have made some inferences regarding the function of the genes to which these SNPs were localized (i.e., when mapped to the sea lamprey reference genome; Smith et al. 2013). *Etr_1806* does not appear to localize within any described genes, but *Etr_4281* aligns with the human protocadherin related 15 (*PCDH15*) gene, which has an essential role in the maintenance of normal retinal and cochlear function, and *Etr_5317* localizes to the dymeclin (*DYM*) gene, which encodes a protein necessary for normal skeletal development and brain function in humans (Hess et al. 2013). Parker (2018) found that there was a strong correlation between run timing (i.e., whether anadromous Pacific lamprey were of the river-maturing or ocean-maturing ecotype; see Sect. 4.3.4.1) and two groups of linked loci. Individuals that were homozygous for the “ocean-maturing” allele at both linkage groups almost always had well-developed ovaries at the onset of their freshwater migration, but individuals that had at least one river-maturing allele in either linkage group had small ovaries. This means that the river-maturing ecotype carries standing genetic variation capable of producing both ecotypes (i.e., both dominant and recessive alleles), while the ocean-maturing ecotype carries a single (recessive) allele. The specific genes associated with these loci (represented by SNP loci *Etr_2878* and *Etr_2791*) have yet to be determined, but continuing improvements to the assembly and annotation of the sea lamprey genome (e.g., Smith et al. 2018) and growing genomic resources for other lamprey species will aid in these efforts.

4.4.4 Life History Trade-Offs

The above discussions largely revolve around factors that limit colonization of fresh water by anadromous lampreys. However, it is also possible—and, in fact, likely—that, in addition to these factors that constrain establishment in fresh water, there will also be factors that differentially promote freshwater residency. What constitutes sufficient “incentive” for lampreys to abandon anadromy will presumably vary among species. There has been considerable discussion regarding life history trade-offs in other anadromous and freshwater-resident fishes (e.g., Gross et al. 1988; Jonsson and Jonsson 1993, 2006; Fleming 1996; Klemetsen et al. 2003) and in parasitic and non-parasitic lampreys (e.g., Hardisty 2006; Docker 2009; see Sect. 4.7). Specifically, the reduction in fecundity in freshwater-resident lampreys (that results from reduced size at maturity) would require a compensatory reduction in mortality (resulting from generally shorter feeding and spawning migrations, reduced osmoregulatory costs, and reduced exposure to predators during a generally shorter feeding phase). Most non-anadromous lampreys are not actually “landlocked” (see Sect. 4.3); therefore, most appear not to be making the “best of a bad situation” by enduring fresh water when they are unable to feed at sea. Presumably, lampreys become parasitic in fresh water when they fare better in the freshwater system than they would in marine environments. Where the costs of anadromy outweigh its benefits or, conversely, where the benefits of freshwater residency outweigh its costs (e.g., in terms of lost growth opportunities at sea), freshwater residency should be favored. Large productive lakes at a considerable distance from the ocean (e.g., Great Slake Lake, the Great Lakes) would presumably favor freshwater residency; they offer access to a large, diverse prey base without the longer spawning migrations (see Moser et al. 2015). However, for large-bodied anadromous species, it likely becomes increasingly difficult for freshwater systems to sufficiently compensate for the loss of growth opportunities at sea. Across all populations and species of lampreys, fecundity increases approximately with the cubic power of length; thus as TL doubles, the number of eggs will increase by approximately an order of magnitude (see Chap. 1). Therefore, we would expect to see abandonment of anadromy only under circumstances where reduction of mortality and costs associated with migration make this decreased reproductive output worthwhile. For example, in sea lamprey, mean TL and fecundity are ~840 mm and 171,600 eggs in the North American anadromous population and ~440 mm and 70,000 in the Great Lakes (see Chap. 1 and references therein). This amounts to a 60% reduction in fecundity; presumably, this is an “acceptable loss” since growth conditions in the Great Lakes are very good and mortality rates during the shorter parasitic feeding and migratory stages are assumed to be lower. However, anadromy would presumably remain advantageous compared to feeding in small lakes or reservoirs where growth conditions are poor and reduction in fecundity could be 90–95% (e.g., if mean TL was reduced to 225–285 mm; see Chap. 1).

In contrast, the smaller-bodied anadromous lampreys have “less to lose” by abandoning anadromy. For example, large anadromous European river lamprey (mean TL ~400 mm) have an average fecundity of ~37,200, and freshwater-resident females (mean TL ~225 mm) produce an average of ~10,135 eggs (see Chap. 1 and references therein); this represents a >70% reduction in fecundity. However, there is virtually no difference in fecundity when comparing anadromous praecox (mean TL ~210 mm and 10,000 eggs) and freshwater-resident European river lamprey. Thus, for already small-bodied European river lamprey, abandoning anadromy would presumably reduce the costs and risks associated with the marine feeding phase, without sacrificing reproductive output. Likewise, for the Arctic lamprey, where large anadromous forms (TL 451–500 mm) produce ~102,000 eggs and freshwater-resident forms (TL 170–300 mm) produce ~21,400 eggs, colonization of fresh water by the large forms could result in an almost 80% reduction in fecundity. In contrast, abandonment of anadromy could be “a step up” for anadromous praecox Arctic lamprey (TL 280 mm and ~13,700 eggs). This is consistent with the general observation that freshwater forms arise in regions where smaller body sizes have been reported for anadromous lampreys (see Sect. 4.4.1).

The above argument depends on the relationship between body size and fecundity in female lampreys; whether or not male reproductive success is also related to size is not known. Large anadromous males would presumably have higher reproductive success than small freshwater males if strong size-assortative mating (Hardisty and Potter 1971b) ensures they mate with large anadromous females. However, sneak mating tactics have been observed in some lamprey species (e.g., Hume et al. 2013b) which would allow small males to fertilize at least some of the eggs of large females. Kucheryavyi et al. (2007) found that virtually all of the praecox anadromous form of Arctic lamprey in western Kamschatka were male, and they did not find size-assortative mating. The praecox males were observed to spawn jointly with the larger anadromous form but also with the even smaller non-parasitic form. In some other anadromous fishes, the dwarf or resident forms are entirely or predominantly male (e.g., Dalley et al. 1983; Heath et al. 1991), and Docker (2009) suggested that life history transitions in lampreys may occur more readily in males. However, with the exception of the praecox Arctic lamprey in western Kamschatka, male and female lampreys appear to abandon anadromy more or less equally.

Because lampreys are semelparous, it is relatively easy to quantify their lifetime reproductive success, at least in females, and the relationship between size at maturity and fecundity is reasonably well studied (see Chap. 1). However, the other life history variables "in the equation" (e.g., the costs associated with migrating to and from different environments and those associated with osmoregulating and feeding in different environments and for different durations) are more difficult to quantify. Costs of upstream migration in different anadromous and freshwater-resident populations can be estimated using an energetics approach (e.g., by calculating shrinkage or change in proximate body composition during migration; Beamish et al. 1979; R. J. Beamish 1980; Beamish 1982; see Chap. 1) or by comparing the length and duration of the spawning migration (see Moser et al. 2015). It should be noted, however, that the length and duration of upstream migration are not always correlated, and the apparent "paradox of premature migration" seen in anadromous salmonids is also observed in many lamprey species (Quinn et al. 2016). Some lamprey species, populations, or individuals (e.g., all pouched lamprey, most Pacific lamprey, some European river lamprey) enter fresh water 8–16 months prior to spawning, thus appearing to reduce their growth opportunities at sea, while others (e.g., anadromous and freshwater sea lamprey, ocean-maturing Pacific lamprey, and some praecox European lamprey) delay freshwater entry until 1–2 months before spawning. How these different strategies influence the relative benefits and costs of migration under different marine and freshwater conditions is unknown. Likewise, age-specific mortality rates are also difficult to quantify. Lampreys outmigrating to sea can significantly contribute to the diet of predatory fishes, birds, and pinnipeds (see Docker et al. 2015), but predation on downstream migrants in fresh water has not been quantified. Furthermore, although predation on juveniles is thought to be relatively low during the parasitic feeding phase (because the adults are well dispersed), predation on lampreys will often go undetected (Cochran 2009), and nothing is known of the age- or size-specific mortality rates during this stage (i.e., to balance the costs and benefits of delaying maturation for another year). More precise estimates of the relative cost and benefits of anadromy versus freshwater residency in different environments would be very informative.

4.5 Origin of Sea Lamprey in Lake Ontario and Lake Champlain

It is clear that sea lamprey invaded Lake Erie and the upper Great Lakes following completion of the Welland Canal in 1829 (or, perhaps more likely, following subsequent modifications in the early 1900s that resulted in the current Welland Ship Canal) which allowed them to bypass Niagara Falls (see Chap. 5). However, whether they are invasive or native to the Lake Ontario drainage (including the Finger Lakes and Oneida Lake)—that is, whether they entered in historic times (within the past 200 years through manmade canals) or prehistorically (as a result of post-Pleistocene natural colonization)—is still debated. Investigators have argued both for invasive (e.g., Aron and Smith 1971; Mandrak and Crossman 1992; Eshenroder 2009) and native (e.g., Hubbs and Lagler 1947; Wigley 1959; Bailey and Smith 1981; Daniels 2001; Waldman et al. 2004; Bryan et al. 2005) status. The origin of sea lamprey in Lake Champlain is similarly controversial (see Waldman et al. 2006; D'Aloia et al. 2015). Eshenroder (2009, 2014) thoroughly reviews the evidence for the competing "invasion-by-canal" and "native-but-rare" hypotheses and, in the 2014 paper in particular, argues very convincingly for the former hypothesis—or at least that sea lamprey were not present in Lake Ontario and Lake Champlain much before the 19th and 20th centuries, respectively. Nevertheless, it is also possible that sea lamprey adapted to fresh water following glacial retreat somewhere adjacent to these lake basins and then gained access to the Lake Ontario and Champlain basins in historical times. At present, support appears strongest for the "invasion-by-canal" hypothesis, but modern population genomic analyses may be able to conclusively resolve the issue. Resolution of this long-standing question will help us understand how quickly anadromous lampreys can become invasive in fresh water (e.g., whether colonization of fresh water requires gradual genetic change or whether it can happen almost immediately following access to large productive lakes).

4.5.1 Colonization in Historical Times: Invasion-by-Canal Hypothesis

The first record of sea lamprey in Lake Ontario is frequently dated to 1835, based on a diary description by the naturalist Charles Fothergill of a single adult said to have been collected in a creek just east of Toronto, Ontario (Lark 1973). Eshenroder (2014) reviewed the fisheries literature related to the earliest records of this species and concluded that this 1835 record is suspect. Although Fothergill's morphological description fits that of the sea lamprey, description of its natural history appears conflated with that of the American eel *Anguilla rostrata*, and Fothergill may have merely recorded information that he received second-hand and supplemented it with information taken from a textbook (Eshenroder 2014). Eshenroder (2014) concluded that the first credible report of sea lamprey in Lake Ontario was in 1888 when a parasitic-phase sea lamprey was found attached to a boat (Dymond et al. 1929). Eshenroder (2014) indicated that there were at least 13 instances when experts had the opportunity to encounter and report sea lamprey in the Lake Ontario drainage before 1888 but, with the exception of Fothergill's report 53 years previously, did not. The rare, smaller silver lamprey was reported twice in Lake Ontario before 1888. However, Waldman et al. (2009) noted that walleye, burbot, and yellow perch were not mentioned in earlier accounts despite having been present. Nevertheless, if sea lamprey were native, they likely would have been conspicuous in shallow tributary streams during their spawning runs, especially in streams blocked by mill dams, and scarring on frequently encountered host fishes (e.g., Atlantic salmon, lake trout, and lake whitefish) would have been noticed and commented upon (Eshenroder 2014). Thus, it is indeed hard to imagine that sea lamprey could have been present in Lake Ontario prior to the mid- to late 1800s and not be recorded.

The first credible account of sea lamprey in Cayuga Lake was an adult collected in 1875. Seven more were reported the following year, and over 1,000 adults were reported by 1886 (Eshenroder 2014). Zoologists at Cornell University were studying the fishes of Cayuga Lake at this time (Meek 1889) and presumably would have noticed and recorded sea lamprey had they been present much before this (Eshenroder 2014). Sea lamprey were apparently abundant in Seneca Lake by 1893 (Gage 1893) and were in Oneida Lake "near" 1894 (Gage 1928).

Eshenroder (2014) therefore concluded that sea lamprey entered the Lake Ontario drainage no earlier than the 1860s and quickly reached pest levels of abundance. This timeline is consistent with the time (~10 years) required for sea lamprey to reach pest proportions in Lake Ontario and the upper Great Lakes following colonization (Eshenroder and Amatangelo 2002). Eshenroder (2014) concluded that invasion of the Lake Ontario drainage was accomplished through the Erie Canal. This canal ran from Albany, New York on the Hudson River to Buffalo, New York on Lake Erie, thus allowing navigation between the Atlantic Ocean and the Great Lakes, and it also had an extensive network of lateral canals connecting to the Oswego River drainage and Lake Ontario. Anadromous sea lamprey once migrated reasonably far upstream in the Hudson River, probably at least as far as the mouth of the Mohawk River (Bigelow and Schroeder 1948). Daniels (2001) and Waldman et al. (2004) concluded that these 19th-century navigation canals would have been inhospitable to sea lamprey and would have had many barriers to passage. However, Eshenroder (2014) reviewed details of the construction and operation of the canal and suggested that completion of a dam and sloop lock on the Hudson River in 1823 could have diverted sea lamprey into the Erie Canal. He reasoned that the eastern section of the canal, with its high-quality water and directional current provided by feeder canals, would have facilitated upstream migration by adult lamprey. Even more likely, however, sea lamprey may have gained access in 1863 when a tributary of the Susquehanna River was diverted into the Oneida Lake drainage, creating a watershed breach between the Lake Ontario and Hudson River/Atlantic Ocean drainages (Eshenroder 2014). Water from the Susquehanna River drainage would have spilled directly into the Erie Canal or, under high-water conditions, spilled into Limestone Creek and eventually Oneida Lake. Sea lamprey spawning runs were known from the Susquehanna River drainage until it was occluded by construction of Conowingo Dam near its mouth in 1928 (F. W. H. Beamish 1980a; Waldman et al. 2009), and adults were observed in the upper reaches of the Susquehanna River "only a few miles south of Cayuga Lake" (Gage 1893). Larval pheromones in these upper reaches would have been diverted into the Erie Canal and could have served as an attractant to upstream-migrating sea lamprey at the canal's Hudson River entrance (Eshenroder 2014). Previous discussions regarding possible invasion routes into Lake Ontario (e.g., Aron and Smith 1971; Eshenroder 2009) were unaware of the watershed breach between the Susquehanna River and Lake Ontario drainages, but this later timing agrees well with the first reports and subsequent proliferation of sea lamprey in the Lake Ontario drainage in 1875–1888.

The "invasion-by-canals" hypothesis is consistent with arguments based on zoogeography. Mandrak and Crossman (1992), for example, classified sea lamprey as non-native to Lake Ontario, arguing that this species, if it dispersed into the St. Lawrence River and Lake Ontario basin during the Champlain Sea inundation (11,800–9,700 years ago), would have had the opportunity to colonize the Ottawa River and inland waters of eastern Ontario. Likewise, if it dispersed in the glacial lakes in the Ontario basin through the Susquehanna outlet 13,000–11,800 years ago, it would have had the opportunity to disperse into all the Great Lakes, because Niagara Falls was not established as a barrier to dispersal until ~12,500 years ago. Eshenroder (2009) briefly discussed two alternative versions of the non-native hypothesis to explain the belated appearance of sea lamprey in the Lake Ontario drainage. First, he suggested that extreme weather events could have caused a watershed breach between the Susquehanna River and Oneida Lake drainages or between the Mohawk River and Oneida Lake above the impassable falls. The divide, in several locations, is less than 2 km wide. Unusually heavy rains in 1818 breached the divide between the Mohawk River and Oneida Lake; due to the presence of two impassable falls, sea lamprey would not have been able to take advantage of this particular breach, but a similar breach above the impassable falls could have provided access. A second alternative to invasion via canals was human transplantation. Smith (1985) stated that Native Americans were not known to transplant fishes, but European colonists may have. Although there is no record of transplantation, sea lamprey were a popular food fish in Europe (see Docker et al. 2015), and larvae were used as bait and sometimes shipped to anglers at different locations (Daniels 2001).

In Lake Champlain, the first credible report of sea lamprey appears to date to 1929 (Greeley 1930). The literature related to records of sea lamprey in this lake is "long and convoluted" and is complicated by frequent revisions in taxonomy, interchangeable common names, and confusion regarding separate classifications for larval, juvenile, and adult lamprey of the same species (Eshenroder 2014). However, reviewing the literature, Eshenroder (2014) concluded that previous assumptions that sea lamprey were present in Lake Champlain since at least 1841 (Bryan et al. 2005) or 1894 (Waldman et al. 2006) were incorrect. The earliest report from 1841 (Thompson 1842) appears to have been a silver lamprey, and, as with the Lake Ontario basin, it is unlikely that spawning sea lamprey or sea lamprey scarring would have gone unnoticed had this species been native to Lake Champlain.

Eshenroder (2014) therefore concluded that anadromous sea lamprey colonized Lake Champlain via the Champlain Barge Canal, which opened in 1916. The Champlain Canal system connects the south end of Lake Champlain to the Hudson River, diverging from the Erie Canal just north of West Troy, New York. Eshenroder (2014) argued that the earlier Champlain Canals (i.e., the original 1825 Champlain Canal and the improved 1863 Champlain Canal) would not have permitted access to Lake Champlain. Instead, sea lamprey would have stayed in the Erie Canal, entered the Champlain Canal and migrated northward in the Mohawk River impoundment, or they would have continued northward in an artificial cut, remaining in the Hudson River. However, when the Champlain Barge Canal opened, sea lamprey migrating upstream in the Hudson River could have entered an artificial cut at Fort Edward, New York. At Fort Edward, a dam without locks (which has since been removed) would have blocked sea lamprey from further upstream migration and encouraged their entry into another artificial cut, allowing them to either swim back to the Hudson River or south to Lake Champlain.

4.5.2 *Post-glacial Colonization: Native-but-Rare Hypothesis*

Several authors have suggested that sea lamprey colonized the Lake Ontario drainage sometime after the retreat of the Laurentide ice sheet (e.g., Hubbs and Lagler 1947; Wigley 1959; Bailey and Smith 1981) by one of at least three hypothesized zoogeographic pathways (Waldman et al. 2004). These include colonization via Lake Ontario's present outlet, the St. Lawrence River (which has persisted for ~9,000 years), via temporary glacial outlets such as the Delaware-Susquehanna drainage (13,000–11,800 years ago), or via the Hudson-Mohawk system (12,500–12,000 years ago) (Underhill 1986; Mandrak and Crossman 1992; Wall and LaFleur 1995; Waldman et al. 2004). Similarly, a post-Pleistocene origin for sea lamprey in Lake Champlain has been suggested. Modern-day Lake Champlain, as well as the St. Lawrence and Ottawa River valleys, were once encompassed by the Champlain Sea, a temporary inlet of the Atlantic Ocean that was created during deglaciation ~11,800–9,700 years ago (Mandrak and Crossman 1992). Post-Pleistocene colonization by other anadromous fishes is known for Lake Ontario (e.g., Atlantic salmon, American eel, rainbow smelt; Mandrak and Crossman 1992) and Lake Champlain (e.g., Atlantic salmon, American eel; Marsden and Langdon 2012).

However, post-glacial colonization of Lakes Ontario and Champlain is inconsistent with historical records, and it is hard to imagine that sea lamprey could have been present much before the late 1800s in Lake Ontario and the early 1900s in Lake Champlain without having been observed (see Sect. 4.5.1). Nevertheless, some authors have suggested that sea lamprey went undetected for so long in these lakes because ecological conditions kept their numbers low; this is the "native, but rare" hypothesis (Waldman et al. 2009). Sea lamprey distribution and abundance, for example, may have been limited by the cooling and low productivity associated with the

"Little Ice Age" that lasted from the late 1500s to ~1850 (Patterson 1998). Warming and ecological changes associated with European settlement—for example, loss of the forest canopy and siltation as land was converted to farming or subsequently, as mill dams on tributaries were removed or deteriorated, thus opening up sea lamprey spawning habitat—may have served as a release for the previously small population (Waldman et al. 2004, 2009). It has likewise been suggested that fishing pressures (i.e., on Atlantic salmon and lake trout) and similar ecological changes from anthropogenic impacts initially depressed the native sea lamprey in Lake Champlain and then subsequently allowed it to increase to noticeable levels (Waldman et al. 2006; D'Aloia et al. 2015). In some cases, however, it appears that the onset of large-scale agricultural and clear-cutting practices may have suppressed, rather than released, the population (D'Aloia et al. 2015; see below). Furthermore, Eshenroder (2009) reasoned that it is unlikely that sea lamprey in Lake Ontario prior to the mid-1880s were significantly constrained by low temperatures and low productivity, because three large tributaries discharging into Lake Ontario were fed from lakes that should have generated nearly ideal temperatures for sea lamprey spawning (or at least comparable to, or warmer than, Lake Superior rivers currently infested with sea lamprey). He also argued that present-day Lake Superior is more oligotrophic and likely less productive than pre-1800s Lake Ontario (but it clearly still supports a large sea lamprey population), and abundant and not-yet-overfished populations of lake trout and deepwater ciscoes (*Coregonus* spp.) would have supported a large population of sea lamprey prior to the mid-1800s.

Genetic studies from the early 2000s have been used as support for post-Pleistocene colonization in both Lakes Ontario and Champlain. Studies using both mtDNA sequence data (Waldman et al. 2004, 2006, 2009) and microsatellite loci (Bryan et al. 2005) showed evidence for long-term vicariance (i.e., separation) of the freshwater and anadromous populations. These studies will be reviewed here briefly. Although they used the genetic markers available at the time, they are relatively limited compared to those now available and are generally no longer considered conclusive evidence of native status. Nevertheless, readers are referred to these influential papers and the rebuttal by Eshenroder (2009). In brief, these studies found significant genetic differentiation between sea lamprey in Lake Ontario or Lake Champlain and the Atlantic Ocean population. For example, Waldman et al. (2009) indicated that four of six haplotypes in the Lake Ontario population were rare (e.g., haplotype B) or absent (haplotype P) in the Atlantic population, and they argued that this was unlikely to have happened by stochastic lineage change in less than 200 years. A shift in haplotype frequency in rare alleles could have resulted from a founder effect (i.e., the loss of genetic variation that occurs when a new population is established from a larger population by a very small number of individuals), but founder effects normally result in the loss of rare alleles and haplotypes, not common ones (Waldman et al. 2009). Likewise, Bryan et al. (2005) found an allele that was exclusive to the Lake Ontario population and one that was represented only in the Lake Ontario and Lake Champlain populations, again suggesting that sea lamprey in these lakes have been separate from the Atlantic population for considerably longer than 200 years (i.e., that these exclusive alleles most likely evolved in the lake over thousands of years due to mutations that occurred during isolation since post-glacial colonization). Bryan et al. (2005) found statistical support for genetic bottlenecks (i.e., sharp reductions in population size) in Lake Ontario (and Cayuga Lake) sea lamprey populations, but not in Lake Champlain. These authors, as expected, also found evidence of sequential population bottlenecks as sea lamprey expanded into Lakes Erie, Huron, Michigan, and Superior, but they interpreted the bottlenecks seen in Lake Ontario and Cayuga Lake as possibly having been caused by environmental degradation during human settlement. Bryan et al. (2005) suggested multiple invasions of Lake Ontario and, using coalescence analysis, showed that colonization via the St. Lawrence River was more likely than via the Champlain Sea. Eshenroder (2009) argued that genetic differences between sea lamprey in Lakes Ontario and Champlain and the Atlantic population were likely the result of a recent genetic bottleneck at founding (rather than long-term residence followed by a recent bottleneck) and that the absence of rare alleles in the Atlantic population was likely due to a sampling artifact or recent declines in the Atlantic population. Haplotype P, for example, could have become extinct in the Atlantic since invasion of Lake Ontario in the late 1800s, or it might be restricted to, or more common in, regions not sampled by Waldman et al. (2004). Waldman et al. (2009) analyzed an expanded mtDNA data set that included samples representing most or all of the range of sea lamprey in the western Atlantic. They discovered three new haplotypes in the Atlantic population which, according to Eshenroder (2014), indicates that not all alleles existing in the Atlantic population have been recovered to date, but still failed to find haplotype P. Nevertheless, Waldman et al. (2009) estimated that the probability of obtaining the mtDNA results seen among the Lake Ontario specimens in less than 500 years of separation from the Atlantic population was considerably less than 1%.

Recently, D'Aloia et al. (2015) used additional genetic models to estimate the historical demography of sea lamprey in Lake Champlain, although with data comparable to the previous genetic studies, that is, with independently derived mtDNA sequence data and the summary statistics (i.e., rather than the complete microsatellite data set) from Bryan et al. (2005). These authors concluded that their results were most consistent with a post-Pleistocene origin of Lake Champlain sea lamprey. They identified an initial decline in effective population size which would have preceded the proposed invasion-by-canal hypothesis and a subsequent very recent population expansion (within the last 50 years). However, there was considerable uncertainty in both the magnitude and timing of these demographic events. For example, they dated the initial decline to ~400 years ago using BEAST analysis of the mtDNA data, but coalescent modeling of the microsatellite data suggested that the decline occurred ~1,230 years ago. D'Aloia et al. (2015) suggested that the initial decline, if ~400 years ago, could have been associated with land use and fishing pressure changes following European settlement. The very recent population expansion may have been associated with implementation of Atlantic salmon and lake trout stocking in the 1970s, following extirpation of these species in the basin in the mid- to late 1800s. D'Aloia et al. (2015) considered the alternative interpretation that the decline in effective population size and loss of genetic diversity might be the result of a founder event in the early 20th century, but, as discussed above, a recent founder event should lead to a loss of rare, not dominant, haplotypes. These genetic studies have provided some new insights into the demographic history of sea lamprey in Lake Ontario and Lake Champlain; it is hoped that definitive resolution will be possible with modern genome-level analyses (see Rougemont et al. 2017; Veale et al. 2018; Hohenlohe et al. 2019; see Chap. 7).

4.5.3 Morphological, Physiological, and Life History Differences

Morphological, physiological, and life history differences have been described between freshwater-resident sea lamprey and anadromous sea lamprey. For example, Gage (1893) reported that sea lamprey from Cayuga and Seneca lakes had a larger dorsal ridge (i.e., in sexually mature males), closer dorsal fins, a tendency for a greater number of cusps on the infraoral lamina, and differences in pigmentation relative to the Atlantic population. They are also considerably smaller (see Sect. 4.3.4.4), and Gage (1893) considered body size to be completely effective for reproductive isolation (see Sect. 4.6.3). He suggested that they be considered different species and thought that sea lamprey in the Finger Lakes had been separated from the Atlantic population since the end of the Pleistocene. However, it is not known whether body size has a significant heritable component or whether it is largely a plastic response to the freshwater environment. The transition to fresh water has involved a reduction in the duration of the parasitic phase from approximately 23–28 months (F. W. H. Beamish 1980a) to 12–20 months (Applegate 1950; Bergstedt and Swink 1995), but we do not know whether cessation of the feeding phase is triggered earlier in fresh water by environmental or endogenous cues (e.g., related to prey availability or growth rate) or whether reduction of the parasitic phase involved selection at the level of the genome. Bergstedt and Swink (1995) speculated that the large size of a few sea lamprey (~400–525 mm TL) collected in northern Lake Huron in April–May indicates that a small proportion of the population may feed parasitically for 2 years, but there is no proof of this (i.e., rather than representing unusually fast-growing individuals or those that started feeding earlier). Comparing mean TL during the parasitic feeding phase in anadromous and Great Lakes sea lamprey, Halliday (1991) suggested that the growth patterns are similar in both forms. Mean TL in Great Lakes sea lamprey in November (i.e., 1 year after metamorphosis and ~7–8 months prior to spawning) is ~430–475 mm (Applegate 1950; Bergstedt and Swink 1995), roughly comparable to the TL extrapolated for anadromous sea lamprey after their first year of feeding; Halliday (1991) estimated that TL increased from ~450 to 800 mm during their second year in the marine environment. An unpublished study by Roger A. Bergstedt at Hammond Bay Biological Station in Michigan (see Eshenroder 2009) suggested that Great Lakes sea lamprey showed better growth than anadromous sea lamprey when both were held in fresh water. When fed on white sucker in the laboratory, 92% of the Great Lakes sea lamprey grew compared to only

64% of the anadromous sea lamprey. However, although this might imply that the Great Lakes sea lamprey is better adapted to feeding in fresh water, the results were considered inconclusive because the anadromous lamprey may have been suffering from handling stress associated with the long transport from the Atlantic Ocean. Their corresponding performance in sea water was not assessed.

Apart from differences in the duration of the feeding phase, and the resulting differences in size at maturation and fecundity, there appear to be other differences in life history traits between the Great Lakes and anadromous sea lamprey. The best-studied differences are those associated with gonadal development during the larval stage and age and size at metamorphosis. There appears to be an acceleration of ovarian differentiation in the Great Lakes sea lamprey (i.e., occurring at 2–3 years of age versus when larvae are ~4–5 years old in the anadromous population; Hardisty 1969; Barker and Beamish 2000) and a concomitant reduction in potential (larval) fecundity (33,000–165,000 and 182,000–328,000 oocytes, respectively; Hardisty 1964, 1969, 1971; Barker et al. 1998; see Chap. 1). This acceleration of ovarian differentiation and reduction in potential fecundity is consistent with the shift seen following the transition from parasitic to non-parasitic lampreys (i.e., also with a reduction in size at maturity). This change in the phasing of oogenesis is assumed to have a genetic component because it happens during the larval phase, that is, prior to the divergent environmental influences experienced in the freshwater versus marine feeding phases (Hardisty 1964). Thus, if sea lamprey invaded the Great Lakes from the Atlantic Ocean in historical times (e.g., when a tributary of the Susquehanna River was diverted into the Oneida Lake drainage in 1863; see Sect. 4.5.1), it appears that changes in the timing of gonadogenesis and potential fecundity can evolve quickly in lampreys. Alternatively, as suggested by Hardisty (1971), differentiation of the “landlocked race” of sea lamprey may have involved selection for individuals who already exhibited low potential fecundity, reduced body size, and perhaps reduced osmoregulatory performance in salt water (see below). A non-parasitic form of Arctic lamprey arose in Japan following construction of a dam ~90 years previously (Yamazaki et al. 2011; see Sect. 4.6.3.2), but it is not known if there were corresponding changes to potential fecundity and the phasing of gonadogenesis similar to that observed in Great Lakes sea lamprey.

Differences in the size (and presumably age) at metamorphosis have also been reported. On average, sea lamprey in the Great Lakes appear to enter metamorphosis at a larger size than the anadromous form (~140 and 130 mm, respectively; Potter et al. 1978; Dawson et al. 2015; Manzon et al. 2015). However, there is considerable variation among and within populations, largely, or at least partially, attributable to variation in growth conditions (Dawson et al. 2015). Thus, it is not known if there has been selection (i.e., adaptation with a genetic basis) for a longer larval stage in the Great Lakes sea lamprey or whether most or all of the observed differences are the result of environmentally induced plasticity.

Physiological differences, mostly related to the ability of Great Lakes sea lamprey to osmoregulate in salt water during the parasitic feeding phase, have also been reported. Mathers and Beamish (1974) found that sea lamprey juveniles from Lake Ontario, when exposed to increasing concentrations of salt water (2 ppt per day), were able to osmoregulate up to concentrations of 16 ppt (where full-strength sea water is ~35 ppt). However, within 10 days at 26 ppt, over half of the small sea lamprey (mean TL 181 mm) had died, but all larger lamprey (mean TL 250 mm) survived for 15 days and were able to maintain their serum osmotic and ionic levels throughout this period. At 34 ppt, moderately large sea lamprey (mean TL 220–250 mm) were able to maintain serum osmotic and ionic levels for 4 days, but all had died by the ninth day. Only the largest category tested (mean TL 289 mm) survived at 34 ppt for 15 days with no mortality. As has been observed in other fishes (Fontaine 1930; Parry 1960), the reduced surface area-to-volume ratio in larger sea lamprey was likely an important factor in lowering their osmotic stress in salt water, although the relationship between body size and osmoregulatory ability is complicated by the fact that the surface area of the gill increases allometrically (Jonathan M. Wilson, Wilfrid Laurier University, Waterloo, ON, personal communication, 2018). Furthermore, Beamish et al. (1978) did not see a similar size effect in anadromous sea lamprey in salt water. Anadromous sea lamprey juveniles of all sizes (>135 mm) were able to osmoregulate between 0 and 35 ppt without mortality. In addition to greater survival rates, anadromous sea lamprey were better able to regulate serum osmolality at the higher salinities (26 and 34 ppt) than were small and large Great Lakes sea lamprey. For example, in the small anadromous individuals, serum osmolality at 34 ppt increased by less than 10% relative to that in fresh water, but it increased by ~25% in small Great Lakes sea lamprey (Beamish et al. 1978). Anadromous sea lamprey showed lower serum osmolality than landlocked sea lamprey at all salinities and large individuals had lower serum osmolality than small ones (Beamish et al. 1978). Anadromous sea lamprey juveniles, regardless of size, were able to regulate serum sodium levels in salt water more precisely than sea lamprey from Lake Ontario. It should be noted, however, that a more recent study—while also finding detectable differences in the inherent physiological capacity of landlocked and anadromous sea lamprey to osmoregulate in salt water—found that these differences were much more subtle than previously reported. Sea lamprey transformers from three landlocked populations (from Lakes Superior, Huron, and Champlain) showed survival rates ranging from ~40 to 100% (compared to ~90% for anadromous sea lamprey transformers) when held at 30 and 35 ppt for 30 days (Jessica L. Norstog and Stephen D. McCormick, University of Massachusetts, Amherst, MA and S. O. Conte Anadromous Fish Research Center, U.S. Geological Survey, Turners Falls, MA, personal communication, 2018). Survival rates between the landlocked and anadromous populations were not significantly different at 30 ppt, and only the Lake Champlain population showed significantly lower survival at 35 ppt. Unlike the studies above, these results suggest that even very small juvenile landlocked sea lamprey have robust salinity tolerance. Further research is required to clarify the contrasting results.

However, differences in osmoregulatory abilities between the anadromous and Great Lakes populations are not sufficient to conclusively resolve whether colonization was in historical or prehistoric times. The Vancouver lamprey, despite its presumed post-glacial origin, still retains the ability to osmoregulate in salt water (Beamish 1982). Landlocked sea lamprey still possess chloride cells (SW-MRCs) in their gills for osmoregulation in salt water during the feeding phase (Youson and Freeman 1976; see Sects. 4.3.2.3 and 4.3.2.4), but the retention of these cells does not distinguish between freshwater colonization that happened a few hundred years ago and a few thousand years ago (Bartels et al. 2012, 2015). Most salmonid populations that have been landlocked for several thousand years (i.e., post-glacially) do show decreased osmoregulatory ability in salt water (e.g., Staurnes et al. 1992; Nilsen et al. 2003), but other populations have shown no apparent decrease in this ability (e.g., McCormick et al. 1985; Nilsen et al. 2007). Conversely, there are examples where salmonid populations isolated above recently constructed barriers soon showed reduced ability to osmoregulate in salt water and reduced rates of smoltification (e.g., Thrower and Joyce 2004; Holecek et al. 2012). Moreover, there are multiple examples of rapid freshwater evolution in other fishes. Several populations of threespine stickleback, for example, have shown substantial changes in body shape and lateral plate phenotype within decades of freshwater colonization (e.g., Bell et al. 2004; Vamosi 2006; Gelmond et al. 2009; Aguirre and Bell 2012; Lescak et al. 2015). In fact, the results of Lescak et al. (2015) support the “intriguing hypothesis that most stickleback evolution in fresh water occurs within the first few decades after invasion.” In many cases, rapid adaptation to fresh water may be due to selection on pre-existing variation in the ancestral anadromous population (e.g., Colosimo et al. 2005; Barrett et al. 2008; Lescak et al. 2015; Nelson and Cresko 2018). Similarly in lampreys, several authors (e.g., Hardisty 1969; Mathers and Beamish 1974; Beamish et al. 1978; F. W. H. Beamish 1980b) have suggested that sea lamprey colonization of the Great Lakes might have involved selection for traits advantageous in fresh water (i.e., smaller body size, lower potential fecundity, and reduced osmoregulatory abilities in salt water).

4.5.4 Does It Matter?

The debate regarding the origin of sea lamprey in the Lake Ontario drainage (including the Finger Lakes and Oneida Lake) and Lake Champlain is often discussed in terms of the implications to the sea lamprey control program. For example, Waldman et al. (2004) suggested that sea lamprey control policies aimed toward intense suppression might need re-evaluation if sea lamprey are shown to be native to Lake Ontario. Determining whether there would be continued “social license” (i.e., acceptance within the local community and among stakeholders) for controlling a native species that is a significant pest would involve public consultation (see Chap. 7). Regardless, determining if the sea lamprey is native in these lake systems has other important management implications and will improve our understanding of life history evolution in lampreys. For example, it is important to understand how quickly sea lamprey (or other anadromous lampreys) can become invasive in fresh water and the genetic basis of this adaptation. Does adaptation to fresh water require gradual genetic change or can it happen rapidly? Clarifying the demographic history of colonization (e.g., identifying the initial number of founders) and the genetic changes associated with colonization also will be very informative. A review of the factors that promote and constrain freshwater residency in parasitic lampreys (see Sect. 4.4) emphasizes the need for a large prey base for establishment of sea lamprey in fresh water, but virtually nothing is known regarding the genetic basis of freshwater adaptation in lampreys. Did successful colonization of the Great Lakes depend on existing genetic variation within the anadromous population (i.e., “pre-selection” for individuals that already showed traits advantageous to survival in fresh water) or could any anadromous sea lamprey colonize fresh water if permitted access (see Sect. 4.8.3)?

4.6 Feeding Type Variation: Evolution of Non-parasitism

A non-trophic adult feeding phase is unknown in any group of vertebrates other than lampreys. Thus, the evolution of non-parasitism in lampreys and the relationship between closely related parasitic and non-parasitic forms have long interested biologists. Loman (1912), for example, recognized that European river and brook lampreys were morphologically similar, but he noted that the brook lamprey exhibited delayed metamorphosis and accelerated sexual maturation relative to the river lamprey. The morphological similarity between several other non-parasitic and parasitic lampreys was likewise recognized by Hubbs (1925), who suggested several cases in which a particular brook lamprey species had apparently evolved from a form similar to that of an extant parasitic lamprey. The term “paired species” was later coined by Zanandrea (1959). Vladykov and Kott (1979b) introduced the more general term “satellite species,” because there are several cases in which more than one brook lamprey (satellite) species has apparently been derived from a single parasitic (stem) species (see Potter 1980; Docker 2009).

In addition to the non-parasitic species that are paired with a parasitic counterpart, several so-called “relict” species have also been identified. Relict brook lampreys are non-parasitic species that occur at or near the extreme southern limits of distribution of the Northern Hemisphere lampreys and are generally those that cannot be unambiguously paired with an extant parasitic species (see Hubbs and Potter 1971; Docker et al. 1999; Potter et al. 2015). Much of the previous ambiguity of “who begat whom” has largely been removed through molecular phylogenetic studies (e.g., Docker et al. 1999; Lang et al. 2009; see Fig. 4.1), although it is now delineation between paired and relict species that is somewhat ambiguous. However, a better understanding of the apparent continuum between recently derived paired species and older relict species will be very informative. Non-parasitism has arisen independently in seven of the 10 extant lamprey genera—and often multiple times within each genus—with different non-parasitic species evolving at different times and in different locations (Hubbs and Potter 1971; Vladykov and Kott 1979b; Potter 1980; Docker 2009). By comparing the phenotypic, molecular, and ecological differences in parasitic–non-parasitic pairs that have only recently diverged (or are still in the process of diverging) to traits in progressively more differentiated relict species (i.e., those further down the pathway to non-parasitism), we can better understand the recurrent elimination of the adult feeding phase that is unique to lampreys.

4.6.1 Non-trophic Adults Unique Among Vertebrates

The characteristic elimination of the adult feeding phase in non-parasitic lampreys is unheard of in any other vertebrate. It is rare in animals in general, but it has been reported in a number of disparate insect and other invertebrate taxa (Hendler and Dojiri 2009; Benesh et al. 2013). All involve taxa with complex life cycles.

Among insects, non-trophic adults have been reported in eight of the ~120 families in the order Lepidoptera (butterflies and moths), two of the ~100 families in the order Hymenoptera (e.g., wasps, bees, and ants), seven of the ~160 families in the order Coleoptera (beetles), and seven of the ~150 families in the order Diptera (flies) (see Hendler and Dojiri 2009; Benesh et al. 2013). In the lepidopteran family Saturniidae (e.g., luna moth *Actia luna* and polyphemus moth *Antheraea polyphemus*), adults have vestigial mouthparts, lack functional digestive tracts, and generally live for <1 week following emergence from the pupa (Janzen 1984). Some species of geometer moths (family Geometridae) are similarly non-trophic as adults, and it has been proposed that loss of adult feeding is correlated with the evolution of flightlessness in forest habitats (Snäll et al. 2007). It has been suggested that, under conditions where female mobility lost its adaptive value (e.g., due to abundance of host plants for the larvae but scarcity of adult food in late summer), loss of wings—although preventing adult foraging, growth, and dispersal—allowed females to increase fecundity beyond the point at which egg loads would reduce flight performance. In the order Hymenoptera, a large number of species are parasitoids as larvae, and some feed on nectar or pollen as adults while the adults of other species do not feed at all (Benesh et al. 2013). The best-known insect order with non-trophic adults is likely Ephemeroptera (mayflies). Aptly named, the adult stage is very short lived (as short as 37 min in one species; Lancaster and Downes 2013), and its primary function is reproduction. Non-feeding adults have also been reported in species of the orders Plectoptera (stoneflies), Megaloptera (e.g., alderflies and fishflies), and Trichoptera (caddisflies) (Lancaster and Downes 2013). In some insect taxa (e.g., orders Strepsiptera and Embiidina), only males have evolved to be non-feeding, and, in many cases, their mouthparts are modified into mating appendages or sensory structures (Benesh et al. 2013 and references therein).

Non-trophic adults have also been reported in some crustaceans, all of which are parasitic as larvae: copepod species in the families Thaumatopsyllidae and Monstrillidae, isopods in the family Gnathiidae, and species in the subclass Tantulocarida. Likewise, horsehair or Gordian worms (phylum Nematomorpha), nematodes from the family Mermithidae, and ticks from the family Argasidae have non-feeding adults. In some barnacles and rotifers, only males are non-feeding as adults (Hendler and Dojiri 2009; Benesh et al. 2013 and references therein).

It thus appears that non-parasitic lampreys resemble these other species with complex life cycles, where the relatively long-lived larval stage is specialized for feeding and growth and the adult stage is specialized for reproduction (Hendler and Dojiri 2009; see Sect. 4.2.1). Benesh et al. (2013) proposed that the "no-growth strategy" should be found where "massive larval size can make adult growth superfluous" and showed theoretically that this counterintuitive strategy would be favored when the optimal larval size is greater than or equal to the optimal adult size for reproduction. It has already been suggested that non-parasitic lampreys evolve under conditions providing good larval growth opportunities (e.g., Kucheryayvi et al. 2007; Docker 2009). However, given the increase in fecundity achieved in lampreys with the inclusion of a parasitic feeding phase, it would be inaccurate to say that adult growth in lampreys is superfluous, although the trade-off between reduced mortality and reduced fecundity apparently makes it unnecessary under some conditions (see Sect. 4.7.4). It should be pointed out, however, that the duration of the non-trophic period in brook lampreys is appreciably longer (6–10 months) than that of invertebrate taxa with "ephemeral" non-feeding adult stages, even accounting for the shorter overall life cycle of the latter. Nevertheless, similarities and differences between non-parasitic lampreys and invertebrates with non-feeding adults could shed light on the mechanisms and selective pressures associated with elimination of the adult feeding phase.

4.6.2 Relict Species

"Relict" brook lampreys have been defined as non-parasitic species which cannot be obviously paired with extant parasitic forms and which have an extreme southerly distribution that seems to reflect their status as relicts of groups with a previously more widespread distribution (Hubbs and Potter 1971). Potter et al. (2015) recognized six relict species: the Po brook lamprey, least brook lamprey, Kern brook lamprey *Lampetra hubbsi*, Western Transcaucasian brook lamprey *Lethenteron ninae*, and Macedonia and Epirus brook lampreys. In each case, based on morphology, the identity of a possible parasitic ancestor has indeed been problematic, as evidenced by past or current uncertainty regarding generic placement (see Fig. 4.1; Sect. 4.6.2.3). However, molecular studies are helping to clarify the evolutionary history of many of these species although, in other cases, they are adding to the confusion. Mitochondrial DNA sequencing, for example, suggests that the Macedonia and Epirus brook lampreys are not closely related to any extant species, certainly none within the genus *Eudontomyzon*, while suggesting that other relict species are not as obviously "unpaired" as previously thought.

4.6.2.1 Older and More Divergent Brook Lamprey Species

With the inclusion of molecular data, the delineation between relict and "paired" species (i.e., non-parasitic species that are morphologically similar to a particular parasitic species in all aspects other than body size; Potter et al. 2015) has also become somewhat "fuzzier." These studies remind us that non-parasitism in lampreys has evolved independently at different times and in different locations (Hubbs and Potter 1971; Vladykov and Kott 1979b). Therefore, it is not surprising that there are different degrees of morphological and genetic divergence between a presumed parasitic ancestor and various non-parasitic derivatives (Fig. 4.1), and different brook lamprey species presumably represent different stages in the speciation process (Docker 2009).

We have tried to represent the different degrees of divergence between each non-parasitic species and its presumed ancestor (as best represented in the contemporary fauna) using a combination of differentiation at the mitochondrial cytochrome b gene (using Kimura's two-parameter distance, K2P) and reduction in the number of trunk myomeres (see Sect. 4.6.2.2) as proxies of time since divergence and degree of morphological divergence, respectively (Fig. 4.2). The non-parasitic species examined included the 23 brook lamprey species recognized by Potter et al. (2015), the three Portuguese species described by Mateus et al. (2013a), the recently described *Lampetra soljani* (Tutman et al. 2017), and the undescribed *Lethenteron* sp. N and sp. S (Yamazaki et al. 2006). Using this approach, non-parasitic species were divided into three categories:

(1) Species ($n = 8$) showing little or no genetic divergence ($\leq$0.4% K2P) and no reduction in number of trunk myomeres (i.e., 0–1.5 more trunk myomeres) compared to the presumed parasitic ancestors (see Sect. 4.6.3.1).
(2) Species ($n = 9$) showing intermediate genetic and/or morphological divergence (i.e., 0.2–2.9% K2P and 1–8.5 fewer myomeres) compared to the presumed parasitic ancestors (see Sect. 4.6.3.1).
(3) Species ($n = 11$) showing both higher genetic ($\geq$2.9% K2P) and morphological (2.5–13 fewer myomeres) divergence when compared to the most closely related extant parasitic species. This category includes the six relict species identified by Potter et al. (2015) plus the Turkish brook lamprey *Lampetra lanceolata*, the Pacific brook lamprey, *Lampetra soljani*, and *Lethenteron* sp. N and sp. S.

This third category therefore loosely corresponds with the relict species, but it is somewhat more inclusive. Potter et al. (2015) omitted Turkish brook lamprey from their list of relict species because, based on morphology (and confirmed with sequence data), it is probably derived from European river lamprey or a European river lamprey-like ancestor. However, molecular evidence suggests that this species is closely related to (or even conspecific) with the Western Transcausian brook lamprey (Li 2014; Tuniyev et al. 2016). Whether the two species are conspecific is not within the purview of this chapter, but, given the close relationship between the two, we decided to consider both (or neither) as relict species.

Likewise, Pacific brook lamprey was not considered a relict species by Potter et al. (2015), and its placement on Fig. 4.2 was somewhat intermediate between categories 1 and 2. Based on morphology, the Pacific brook lamprey is clearly a derivative of the western river lamprey or a western river lamprey-like ancestor. It is characterized by a low myomere count relative to western river lamprey, and, until recently, there was debate regarding whether it was distinct from or synonymous with western brook lamprey (see Reid et al. 2011; Potter et al. 2015). It is not found at the extreme southern distribution of Northern Hemisphere lampreys, but it appears restricted to the Columbia River basin, presumably south of the glacial margin during the Pleistocene (Reid et al. 2011). Furthermore, because Pacific brook lamprey showed sequence divergence from western river lamprey comparable to that of other relict species and their presumed ancestors, we include it here as an older non-parasitic derivative. It may not be a relict species by the definition of Hubbs and

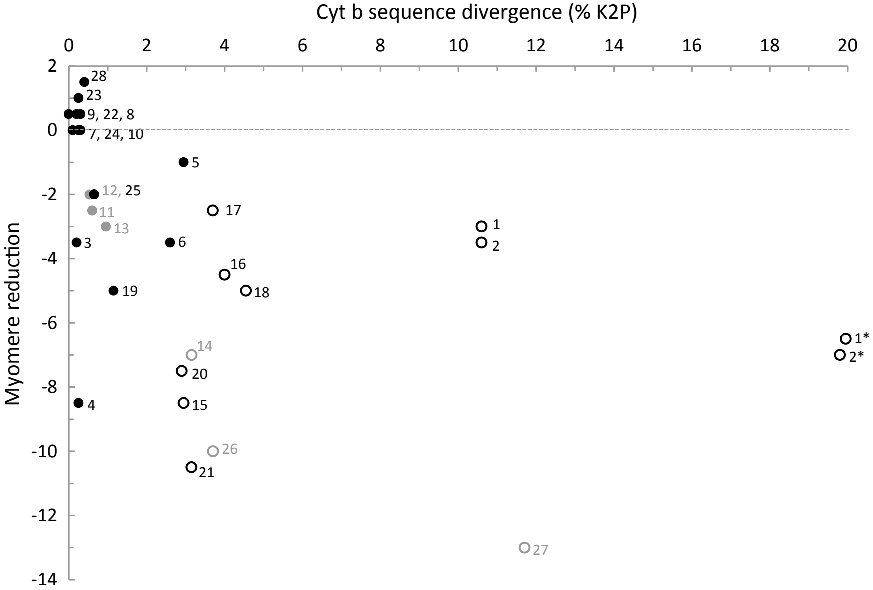


Fig. 4.2 Relationship between cytochrome b sequence divergence (Kimura's two-parameter distance, K2P) between non-parasitic lamprey species and their presumed parasitic ancestor and the extent to which the number of trunk myomeres has been reduced in the non-parasitic species. For sequence divergence, the mid-point in the known range is given (see Fig. 4.1); likewise, reduction in myomeres was calculated by subtracting the midpoint in the known myomere range for each non-parasitic species from that for the presumed ancestor. Myomere data were compiled from Seversmith (1953), Vladykov (1955), Vladykov and Kott (1976a, b, 1984), Yamazaki et al. (2006), Docker (2009), Naseka et al. (2009), Renaud and Economidis (2010), Reid et al. (2011), Renaud (2011), Mateus et al. (2013a), Renaud and Naseka (2015), Renaud et al. (2016), and Tutman et al. (2017); counts from larvae were used whenever possible. Numbers given as data labels apply to the non-parasitic lamprey species listed in Fig. 4.1; species recognized by Potter et al. (2015) are shown in *black*; other taxa or tentative species that have not been formally described are given in *gray*. *Closed circles* are those species considered here to be "paired" with their parasitic counterpart and *open circles* are considered "relict" species, although the distinction is not always clear (see Sect. 4.6.2.1). Species 1 and 2 (Macedonia and Epirus brook lampreys, *Eudontomyzon hellenicus* and *Eu. graecus*, respectively) are compared with both the Caspian lamprey *Caspiomyzon wagneri* with which they are most genetically similar and the Carpathian lamprey *Eu. danfordi* (*asterisk*) with which they are most similar morphologically

Potter (1971), but we feel that placing it in this category facilitates discussion related to the different stages in the evolution of non-parasitism. Boguski et al. (2012) found *Lampetra* sp. populations in Oregon and California that, based on cytochrome b gene sequence divergence from western river lamprey (or any known lamprey species), may also represent relict species. However, myomere counts (or other morphological characters) are not available for these populations.

Lethenteron sp. S has never been formally described (see Yamazaki et al. 2006), but its genetic distinctiveness and extreme reduction in number of trunk myomeres (relative to Arctic lamprey) suggest that it would also be considered a relict species. Yamazaki et al. (2006) suggested that it may be a descendent of the co-ancestor of *Lethenteron*, *Lampetra*, and *Entosphenus*. Based on its uncertain phylogenetic placement, we refer to it here as an "orphan" relict species to emphasize that it truly cannot be paired with an extant parasitic species. We likewise refer to the Macedonia and Epirus brook lampreys as "orphan" species because their putative parasitic ancestor cannot be identified (see Sect. 4.6.2.3).

Thus, whether we use the term "relict species" more loosely than originally defined or whether we merely refer to these as "older, more divergent brook lamprey species," category 3 includes brook lampreys with a relatively long separation from their parasitic ancestor. We recognize that this categorization is imperfect, since we are trying to divide a speciation continuum into discrete categories using only one gene and one morphological character as proxies of time since divergence. Caution needs to be exercised when relative divergence times are estimated from mtDNA sequence data alone, because genetic drift between isolated populations can obscure inferences (Galtier et al. 2009). Likewise, we also need to be aware that some species may show more rapid rates of morphological divergence due to drift or selection relative to morphologically conserved, but genetically divergent, populations. Furthermore, those species that are morphologically and/or genetically divergent from any known parasitic species may appear so due to extinction of their recent parasitic ancestor. However, these categories are useful for the purpose of trying to understand the sequence of changes involved in the evolution of non-parasitism. In particular, there appears to be a number of brook lamprey species within both North American and Eurasian *Lampetra* that show different degrees of genetic and morphological differentiation from the two (or a few closely related) parasitic ancestors (Fig. 4.1). In these two clades alone, different stages in the speciation process are represented within the contemporary fauna, and replication is provided among taxa.

4.6.2.2 Morphological Degeneracy in Relict Species

Despite their placement in different genera, relict brook lamprey species look rather similar. Over time, reduction in traits associated with parasitic feeding has occurred in the different species independently, allowing them to converge on a similar phenotype. Reduction in number of trunk myomeres (corresponding with smaller body size at maturity) is the easiest trait to quantify across taxa (hence its use in Fig. 4.2), but relict species are also characterized by more degenerate dentition and fewer velar tentacles (Hubbs and Potter 1971; Vladykov and Kott 1979b; Potter et al. 2015). Although Bond and Kan (Kan 1975; Bond and Kan 1986) suggested a latitudinal cline in trunk myomere counts, Goodman et al. (2009) and Reid et al. (2011) found no such pattern and concluded that any observed differences were taxonomic rather than latitudinal. The number of myomeres appears to remain unchanged or increase at speciation (i.e., in closely related non-parasitic species that are sympatric with their parasitic ancestor) but appears to decrease with time since divergence (Vladykov and Kott 1979b). Similarly, dentition in non-parasitic species appears to be more variable (e.g., in terms of number of teeth and cusps) in the initial stages of divergence but then becomes reduced over time (Hubbs and Potter 1971). The dentition of several of the relict species, most notably the least brook lamprey, is highly degenerate and contains only a few small, blunt teeth (Hubbs and Potter 1971; Potter et al. 2015). Thus, the long-standing difficulty in trying to pair the various relict species with extant parasitic forms based on morphology is not surprising.

The number, arrangement, and structure of papillae along the posterior margin of the gill pore in mature lampreys have recently been described as useful morphological characters for taxonomic discrimination in lampreys (Beamish 2010, 2016). There seems to be a general trend showing reduction in the number of marginal papillae in freshwater parasitic and non-parasitic species derived from an anadromous ancestor, and, as with number of myomeres and dentition, the extent of the loss appears correlated with presumed time since divergence. The trend is less obvious in the genus *Entosphenus*, where all derivative species are relatively recent, but is quite pronounced in North American *Lampetra*. In *Lampetra*, the number of marginal papillae decreased from 24–34 in western river lamprey to 27–29 in western brook lamprey, 8–12 in Pacific brook lamprey, and 6–13 in Kern brook lamprey (Beamish 2010). The function of these papillae is not known, but, because they increase in size at maturity, Beamish (2016) inferred that they may have some sensory function related to reproduction.

There may also be a progressive reduction in potential fecundity in non-parasitic species as they diverge from their parasitic ancestor. It has been suggested that recently derived non-parasitic species may still "atavistically" produce a large number of oocytes during the larval stage (i.e., in line with the high potential fecundity of their parasitic ancestor) and then reduce the number of oocytes prior to maturation (i.e., through atresia), so that fecundity at maturity is in line with their now-smaller adult body size (see Chap. 1). For example, Hardisty (1964) estimated that up to 90% of the larval oocytes in the recently derived European brook lamprey are lost to atresia. In contrast, the least brook lamprey is thought to experience little or no atresia, leading to the suggestion that natural selection in this relict species has had sufficient time to reduce the number of oocytes elaborated during the larval stage to a level that could reasonably be brought to maturity in the adult (Docker and Beamish 1991). However, there is debate whether extent of atresia is indeed correlated with time since divergence (see Docker 2009), likely due to the difficulties associated with accurately estimating potential fecundity and the relative dearth of such estimates (see Chap. 1).

Recent studies have started examining genome-level differences between the closely related European brook and river lampreys (Mateus et al. 2013b; Rougemont et al. 2017; Hume et al. 2018; see Sect. 4.6.3.3), but none have examined genomic differences between parasitic or recently derived non-parasitic species and the relict species. Such studies would help elucidate the genomic basis for the changes in morphological and life history characters observed at different stages in the transition from parasitism to non-parasitism.

4.6.2.3 Taxonomic Uncertainties in Relict Species

As indicated above, all the traditional relict species have presented— and sometimes continue to present—taxonomic uncertainties. Given their degenerate dentition, there has been uncertainty regarding generic placement as well as some confusion regarding species delimitation. For example, based on dentition, past authorities have sometimes placed the Po brook lamprey in the genus *Lethenteron* (see Potter et al. 2015); the least brook lamprey was once placed in the "provisional and noncommittal" genus *Okkelbergia* (Hubbs and Potter 1971), and the Kern brook lamprey was originally and until recently referred to the genus *Entosphenus* (see Docker et al. 1999; Potter et al. 2015). Molecular data have helped resolve many of these conflicts, identifying a putative parasitic ancestor, although it is interesting that the degree of divergence seen in the morphological characters is not always consistent with molecular distance. For example, the least brook lamprey is often seen as the "poster child" for degenerate dentition, but its genetic divergence from European river lamprey (4.3–4.8% K2P at the cytochrome b gene) is only moderately higher than that observed between the Turkish brook lamprey and European river lamprey (3.2–4.2%) and is considerably less than that inferred for the three "orphan" species (Figs. 4.1 and 4.2). Likewise, the Kern brook lamprey, despite its morphological distinctness from other *Lampetra* brook lampreys, particularly in terms of its dentition, was only moderately more divergent genetically from western river lamprey (2.3–4.0%) compared to the more morphologically conserved Pacific brook lamprey (2.3–3.5%).

The Western Transcaucasian brook lamprey, although originally and currently referred to the genus *Lethenteron*, likely belongs in the genus *Lampetra*. Based on re-examination of morphological characters, Tuniyev et al. (2016) concluded that features such as a tricuspid middle endolateral, low number of trunk myomeres, and absence of velar wings suggest that this species should be assigned to *Lampetra*. The Western Transcaucasian brook lamprey possesses a row of posterial teeth, which is typical for the genus *Lethenteron*, but Tuniyev et al. (2016) acknowledge that this characteristic may have evolved independently in *Lethenteron* and *Lampetra*. Mitochondrial DNA sequence data also place the Western Transcaucasian brook lamprey into the European *Lampetra* clade (Li 2014). However, we concur with the decision of Tuniyev et al. (2016) that reclassification should be delayed until a total evidence cladistic analysis (integrating both morphological and molecular characters) has been completed (see Chap. 7).

Cytochrome b gene sequences also show that the Western Transcaucasian brook lamprey is very closely related to the Turkish brook lamprey (Li 2014; 0.2–0.9% K2P). The two species are found in close geographic proximity to each other (the south and east Black Sea basins, respectively), and they are both no longer sympatric with European river lamprey (Naseka et al. 2009). We do not attempt to decide here whether these two species should be synonymized. What is relevant (i.e., what should be kept in mind when considering the recurrent evolution of non-parasitism in lampreys) is that these two brook lampreys may not represent independent non-parasitic derivatives of the European river lamprey or a European river lamprey-like ancestor. No satellite species is recognized as the ancestor of another satellite species (Vladykov and Kott 1979b), but, in cases like these, vicariance (i.e., geographical separation) following divergence from the common parasitic ancestor may be more likely than independent derivation from this ancestor. In a similar manner, *Lampetra soljani* from the southern Adriatic Sea basin appears closely related to the Po brook lamprey in terms of morphology (e.g., number of velar tentacles and trunk myomeres) and DNA sequence (0.7–3.5% K2P; Tutman et al. 2017). Several genetically divergent populations of *Lampetra* brook lampreys have been identified in Oregon and California (Boguski et al. 2012), but they have not been formally described. Again, we do not try to resolve here the taxonomic status of these species or populations, but we remind the reader that some now-distinct species or populations likely represent independent transitions to non-parasitism at different times and different locations but caution against assuming that all do without further study (see Sect. 4.6.3.4).

Vicariance leading to pronounced phylogeographic structure has been inferred in the least brook lamprey using mtDNA sequence data (i.e., suggesting evolution of non-parasitism followed by vicariance and not separate transitions to non-parasitism). Martin and White (2008) examined control region and NADH dehydrogenase subunit 3 (ND3) gene sequences in least brook lamprey from 21 populations in Maryland, Ohio, Missouri, North Carolina, Tennessee, Kentucky, Mississippi, and Alabama. They detected as many as 12 highly differentiated clades, differing in sequence by an average of 4.5% (range 2.5–9.0%), and their distribution corresponded to different drainages or parts of drainages. They detected distinct Atlantic coastal, Ohio River, and Obion-Mississippi drainage clades, but these three clades were embedded within the very diverse Gulf drainage clade. Given the lack of further resolution among the clades, Martin and White (2008) suggested that vicariance occurred over a relatively short time (e.g., as the result of rising sea levels during the Pliocene, 5.3–2.6 Ma). These authors suggested that the Obion-Mississippi drainage populations in Tennessee and Kentucky may represent an undescribed taxon, but this clade was not necessarily any more distinct than other clades. There has been debate over the years whether the least brook lamprey consists of a single or multiple species. Hubbs and Potter (1971) indicated that dentition in populations from the Atlantic Coastal Plain may be less degenerate than that from populations in the Gulf Coastal Plain. Vladykov et al. (1975) described some individuals from the Tennessee, Alabama, and Tombigbee river systems as a distinct species, *Lampetra meridionale* (separable from least brook lamprey within the same watersheds), although this species has since been synonymized with *Lampetra aepyptera* (Nelson et al. 2004).

Nevertheless, as many of the formerly ambiguous species (Kern brook lamprey, Po brook lamprey, Western Transcaucasian brook lamprey) are assigned to *Lampetra*, it is becoming increasing clear that the majority of brook lampreys appear to have originated from European and western river lampreys or now-extinct ancestors resembling these parasitic species. Characteristics of parasitic species that appear to promote evolution of non-parasitism are discussed in Sect. 4.7.

However, perhaps the most intriguing findings from molecular phylogenetic studies indicate that the Macedonia and Epirus brook lampreys are not closely related to any extant species within the genus *Eudontomyzon* and that the most closely related species is the Caspian lamprey (Lang et al. 2009). However, we agree with the conclusion of Renaud and Economidis (2010) that considering these two Greek non-parasitic species as sister to the Caspian lamprey is premature without a cladistic analysis that integrates multiple morphological and molecular characters. Furthermore, it is important to note that the molecular analysis suggests only that the Caspian lamprey is the closest living relative of these two species, not that it is a close relative and certainly not that it is the parasitic ancestor. The level of sequence divergence (10.5–10.7%) observed between these brook lampreys and the Caspian lamprey is substantial and comparable to some genus-level differences. For example, European river and Arctic lampreys (*Lampetra* and *Lethenteron*) differ at the cytochrome b gene by 8.2–9.7%, and Pacific and Arctic lampreys (*Entosphenus* and *Lethenteron*) differ by 9.9%. Note, however, that the Macedonia and Epirus brook lampreys are even more genetically divergent from other species within the genus *Eudontomyzon* (e.g., 19.4–20.3% divergent from the Carpathian lamprey). As with the Western Transcaucasian and Turkish brook lampreys, the Macedonia and Epirus brook lampreys are genetically similar to one another but exhibit morphological differences and have disjunct distributions, and it is unknown if they were derived independently from a recently extinct parasitic ancestor or if recent vicariant speciation followed divergence from a common ancestor.

4.6.3 *Paired Species: Update on the Update*

The concept of paired lamprey species has been discussed and reviewed by numerous authors over the years, including Hubbs (1925), Zanandrea (1959), Hardisty and Potter (1971a), Potter (1980), Salewski (2003), Hardisty (2006), and Docker (2009). In this section, we continue these discussions, in particular, providing an update on Docker (2009)'s "update on the paired species concept," and we attempt to clarify previous uncertainties or misconceptions resulting from earlier molecular phylogenetic studies. The lack of fixed differences in mtDNA sequence in many paired species, although rare among "good" vertebrate species (e.g., Johns and Avise 1998), is not in itself evidence for phenotypic plasticity (i.e., where the different feeding types are produced from a single genotype under the induction of an environmental cue). Conversely, demonstration of fixed genetic differences in some pairs does not indicate that these differences are species-level differences, nor can these findings be extrapolated to conclude that all paired species are distinct species. We review and update the "speciation continuum" discussed by Docker (2009), with a particular focus on the better-studied species pairs where recent population genetic and genomic studies both confirm that there are genome-level differences between the feeding types (and thus refute the hypothesis of phenotypic plasticity; Mateus et al. 2013b; Rougemont et al. 2017) and show significant gene flow between them where they co-occur (i.e., refuting suggestions of immediate reproductive isolation between feeding types; Rougemont et al. 2015, 2016, 2017). We do not try to answer conclusively the long-standing question "are paired species 'real' species?" (e.g., Salewski 2003; Docker 2009). Rather, we try to show the complexity of the issue and emphasize that there is not a universal "one size fits all" answer to this question (see Chap. 7). By appreciating that different species and populations represent different stages in the evolution of non-parasitism, we will better understand the process by which the parasitic feeding phase has been eliminated in different lamprey taxa. Taxonomic changes should only be made, if warranted, based on a more complete understanding of the process and its outcome in different pairs.

4.6.3.1 Not All Paired Species are Equivalent

Paired non-parasitic species are generally defined as those that are morphologically similar to a particular parasitic species in all aspects other than body size and that are assumed to have evolved from that parasitic species (Potter et al. 2015). However, it is becoming apparent that there are different degrees of morphological and genetic divergence between parasitic lampreys and their presumed non-parasitic derivatives (Fig. 4.1) with the distinction between paired and relict species sometimes unclear (see Sect. 4.6.2.1), and variation within each category becoming evident. Potter et al. (2015) considered 15 of the 23 recognized non-parasitic species as being paired with a congeneric parasitic species. An additional two species (Northern California brook lamprey *Entosphenus folletti* and Pit-Klamath brook lamprey *En. lethophagus*) also appear to be recent non-parasitic derivatives, but it is not clear whether Pacific lamprey or one of its freshwater parasitic derivatives (e.g., the Klamath lamprey) is the ancestor (Potter et al. 2015). Docker (2009) included 14 non-parasitic species as paired species. Three species considered paired species by Potter et al. (2015) were omitted from her list: Northern California and Pacific brook lampreys because they were, at the time, considered to be synonymous with Pit-Klamath and western brook lampreys, respectively, and Turkish brook lamprey, which Docker (2009) considered a relict species.

As outlined in Sect. 4.6.2.1, we have used here a combination of genetic divergence from the presumed parasitic ancestor and reduction in the number of trunk myomeres as proxies of time since divergence and degree of morphological divergence, respectively (Fig. 4.2 and references therein). To focus on the evolutionary processes rather than the taxonomy, we included the three Portuguese species described by Mateus et al. (2013a), the recently described *Lampetra soljani* (Tutman et al. 2017), and the undescribed *Lethenteron* sp. N and sp. S (Yamazaki et al. 2006). We found that these characters divided the extant non-parasitic "species" into three categories:

(1) Species (n = 8) showing little or no genetic divergence (≤0.4% K2P) and no reduction in number of trunk myomeres (i.e., 0–1.5 more trunk myomeres) compared to the presumed parasitic ancestors. This category includes non-parasitic species whose distributions are largely sympatric with that of their parasitic ancestor and who appear to have either diverged recently or still experience gene flow:

- the three *Ichthyomyzon* brook lamprey species (northern brook, southern brook, and mountain brook lampreys *I. fossor*, *I. gagei*, and *I. greeleyi*, respectively) which show no species-specific differences in mtDNA gene sequence compared to their respective parasitic ancestors (silver, chestnut, and Ohio lampreys; Docker et al. 2012: Ren et al. 2016) or even haplotype or allele frequency differences where they occur sympatrically (Docker et al. 2012), have virtually identical myomere counts (Hubbs and Trautman 1937), and appear to show considerably less reduction in dentition (in terms of number and sharpness of cusps or teeth) relative to more divergent non-parasitic species;
- the three non-parasitic derivatives of Arctic lamprey that occur within the range of the ancestor (Alaskan brook lamprey, Far Eastern brook lamprey *Lethenteron reissneri*, and Siberian brook lamprey *Le. kessleri;* Yamazaki et al. 2006; Renaud and Naseka 2015; Yamazaki and Goto 2016; Sutton 2017);
- European brook lamprey which, where it occurs sympatrically with the ancestral European river lamprey, usually shows evidence of contemporary gene flow (e.g., Rougemont et al. 2015, 2016, 2017; see Sect. 4.6.3.2);
- Australian brook lamprey.

(2) Species (n = 9) showing intermediate genetic divergence and/or trunk myomere reduction (i.e., 0.2–2.9% K2P and 1–8.5 fewer myomeres) compared to the presumed parasitic ancestors. This category includes non-parasitic species whose range no longer overlaps with that of their parasitic ancestor or where the parasitic ancestor appears to have a more restricted distribution within the range of the non-parasitic derivative:

- American brook lamprey, which is now allopatric with its Arctic lamprey ancestor and shows slightly more differentiation than the other descendants of this species (Li 2014);
- the three Portuguese brook lamprey species described by Mateus et al. (2013a), which likewise are no longer sympatric with the European river lamprey, and which show slight but species-specific differences in mtDNA sequence and slightly lower but overlapping trunk myomere counts (57–63 in the three brook lamprey species versus 58–67 in European river lamprey);
- Pit-Klamath and Northern California brook lampreys, which are genetically similar to, or indistinguishable from, the Pacific lamprey (assumed here, for

simplicity, to be the ancestor) but which have a reduced number of myomeres (i.e., 63–68 and 56–65, respectively) compared to Pacific lamprey (61–77; Vladykov and Kott 1976a; Docker 2009). However, if compared to the Klamath lamprey with 58–65 myomeres (Renaud 2011), these two species would be placed in category 1;

- Ukrainian brook lamprey and Drin brook lamprey *Eudontomyzon stankokaramani*, which show only a moderate reduction in number of myomeres (58–68 and 56–65, respectively) relative to the Carpathian lamprey (61–67; see Docker 2009), but >2% sequence divergence at the cytochrome b gene. These two species are more genetically distinct from their presumed ancestor than other paired species (Lang et al. 2009), although the widely distributed Ukrainian brook lamprey and Carpathian lamprey are still not reciprocally monophyletic (Levin et al. 2016);
- western brook lamprey, in which some populations (e.g., those in Alaska and British Columbia) are genetically indistinguishable from western river lamprey where their ranges overlap, but other populations (even excluding the four highly divergent populations from Oregon and California; Fig. 4.1) show increasingly greater divergence (up to 2.3%) from western river lamprey (Boguski et al. 2012). Number of trunk myomeres in this species also appears to differ among populations (Reid et al. 2011), although there are consistently fewer in western brook lamprey (57–67) relative to western river lamprey (63–71; Docker 2009; Reid et al. 2011).

(3) Species ($n = 11$) showing both higher genetic ($\geq$2.9% K2P) and morphological (2.5–13 fewer myomeres) divergence when compared to the most closely related extant parasitic species (see Sect. 4.6.2.1).

We recognize that this categorization is imperfect because we are trying to divide a speciation continuum into discrete categories using only one gene and one morphological character. However, the first two categories include most or all of the recognized paired brook lamprey species, and the third category roughly corresponds with the relict species (see Sect. 4.6.2.1). The Mexican brook lamprey would presumably fall into category 1 or 2; it was excluded from analysis here because cytochrome b gene sequence is not available for the parasitic Mexican lamprey (Lang et al. 2009), and myomere counts are not available for each species individually (Renaud 2011). Thus, by this approach, 18 brook lamprey species would be considered as paired (or recently derived) species, including 15 of the 17 species recognized by Potter et al. (2015)—all but the Turkish and Pacific brook lampreys which were placed into category 3—and the three Portuguese brook lamprey species. It is not our intention here to redefine the terms "paired" and "relict" species per se, but merely to facilitate discussion regarding steps in the evolution of non-parasitism.

A continuum is evident within the categories as well. In addition to variation in the degree to which different brook lamprey species have diverged from their parasitic ancestor, there are likely also differences among populations within species. Some apparent intraspecific differences may be the result of unrecognized diversity within nominal species. Some brook lampreys currently considered a single widely

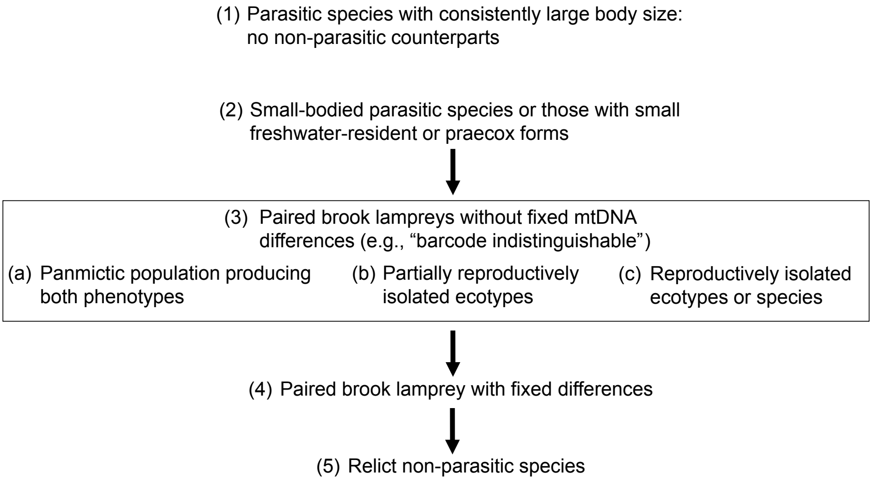


Fig. 4.3 Representation of speciation continuum seen in lampreys, ranging from (1) parasitic species with no non-parasitic counterparts to (5) relict non-parasitic species that have long diverged from a parasitic counterpart. Updated from Docker (2009) to more accurately show that (3) paired species lacking fixed differences in mitochondrial DNA (mtDNA) sequence may also include different species and populations at different stages of speciation; resolution among these subcategories are possible only with higher-resolution markers

distributed species may consist of different populations that evolved from the parasitic ancestor at different times (i.e., are polyphyletic; see Docker 2009) or that diverged as the result of vicariance following the evolution of non-parasitism (see Sect. 4.6.2.3). Spatially disjunct non-parasitic derivatives of the Arctic lamprey are traditionally recognized as four distinct species (or three, with Far Eastern and Siberian brook lampreys perhaps being synonymous; see Renaud and Naseka 2015; Yamazaki and Goto 2016), but different populations of other widespread species are often "lumped" together. Mateus et al. (2013a) described three evolutionarily distinct units within the European brook lamprey as distinct species, and more such populations (whether or not they are considered distinct Linnean species) may also exist (e.g., Pereira et al. 2014; see Chap. 7). Similar "splitting" might also be warranted in the widely distributed western brook lamprey (Boguski et al. 2012) and Ukrainian brook lamprey (Levin et al. 2016). A genetically divergent brook lamprey from the Aegean Sea basin, for example, may represent a tentative new species (Levin et al. 2016), and, as with other widespread non-parasitic species, the *Eudontomyzon* species complex requires further taxonomic examination.

In other cases, however, it is not merely a matter of phylogenetically distinct populations having escaped taxonomic notice to date. Different populations may be at different stages of divergence as the result of different demographic histories and different levels of contemporary gene flow. Within category 1, for example, further subdivision appears to exist that is not evident with mtDNA sequence data alone (Fig. 4.3):

(a) Panmictic populations producing both phenotypes: There have been reports of parasitic individuals arising within otherwise non-parasitic populations, most notably, the "giant" American brook lamprey in the Great Lakes (Manion and Purvis 1971; Cochran 2008) and the Morrison Creek lamprey on Vancouver Island (Beamish 1985, 1987; Beamish et al. 2016), as well as parasitic populations which apparently produce non-parasitic individuals (e.g., Kucheryavyi et al. 2007; Yamazaki et al. 2011; see Docker 2009). However, we do not yet know whether these polymorphic populations result from phenotypic plasticity or whether feeding type represents a genetically based polymorphism within a population with no barriers to interbreeding (see Sect. 4.6.3.3).

(b) Partially reproductively isolated ecotypes, where there is evidence of contemporary gene flow between sympatric parasitic and non-parasitic lampreys (e.g., at microsatellite loci), but genomic regions that consistently differ between the forms suggest a genetic basis to feeding type (e.g., Rougemont et al. 2015, 2017; see Sect. 4.6.3.2). Distinctly different phenotypes are maintained, even with extensive gene flow. These cases may represent the early stages of (incipient) speciation if there is selection against intermediate phenotypes, although it is not a foregone conclusion that full reproductive isolation would eventually result, nor is this evidence for divergence in sympatry (see Sect. 4.6.3.4).

(c) Reproductively isolated ecotypes (e.g., in parapatric populations), where there is a genetic basis to feeding type (Mateus et al. 2013b; Rougemont et al. 2017) and significant differentiation at microsatellite loci (e.g., Rougemont et al. 2015; Mateus et al. 2016) that indicates a lack of gene flow and separate evolutionary trajectories, but insufficient time has elapsed for morphological or genetic differences to become fixed.

The use of higher-resolution markers, especially non-neutral genome-wide markers, and modern population genetic and genomic analyses are allowing better resolution of these sub-categories. The remainder of this section will focus on reviewing these studies and their implications to our understanding of the evolution of non-parasitism in lampreys.

4.6.3.2 Incomplete Reproductive Isolation and Contemporary Gene Flow in Some Pairs

It has generally been thought that size-assortative mating would result in immediate reproductive isolation in most paired species (Hardisty and Potter 1971a; Beamish and Neville 1992) and that temporal, spatial, or behavioral isolation may further reduce or prevent gene flow (see Docker 2009). However, there is increasing evidence that size-assortative mating is an insufficient pre-zygotic barrier to hybridization and that reproductive isolation between paired species is not complete in sympatry. Previous reports of mixed-species spawning aggregations (Huggins and Thompson 1970; Kucheryavyi et al. 2007; Cochran et al. 2008) have been supported by further observations of paired species spawning together in the wild (Lasne et al. 2010).

Size-assortative mating may provide less of a barrier where size differences between species are relatively small (see Docker 2009; Rougemont et al. 2016), and, even with larger-bodied parasitic species, evidence of sneak (or satellite) male mating tactics may permit non-parasitic males to fertilize the eggs of large parasitic females. Satellite male mating behavior was reported previously within European and American brook lampreys (Malmqvist 1983; Cochran et al. 2008), and it has recently been demonstrated in mixed-species aggregations of European river and brook lampreys (Hume et al. 2013b). Lack of hybrid inviability in the early developmental stages (e.g., Piavis et al. 1970; Beamish and Neville 1992; see Docker 2009) has likewise been confirmed in recent studies (Hume et al. 2013c; Rougemont et al. 2015), showing lack of immediate and obvious post-zygotic reproductive isolation in paired species.

The study by Rougemont et al. (2015) was particularly interesting, because it used genetic parentage analysis to evaluate fertilization success when European river lamprey females ($n = 2$) were provided with simultaneous access to European brook ($n = 4$) and European river ($n = 2$) lamprey males. Reproductive success of the European brook lamprey males with European river lamprey females was relatively low, but it was not negligible. Of the 73 offspring assigned without ambiguity, 81% were sired by European river lamprey, and 19% were sired by European brook lamprey. Granted, without the presence of brook lamprey females, the proportion of interspecific matings may have been over-estimated if brook lamprey males were "forced" to mate with heterospecific females, and it is possible that some gamete mixing occurred during strict size-assortative mating. Nevertheless, the potential for substantial contemporary gene flow in sympatry was demonstrated. It is also interesting to speculate that, even with reduced fertilization success relative to European river lamprey males, siring 19% of the offspring from more fecund European river lamprey females (~20,000–35,000 eggs) could equate to higher reproductive success for European brook lamprey males (~3,800–6,650 offspring)—barring any selection against hybrids—than siring 100% of the offspring from less fecund European brook lamprey females (~1,500–2,000 eggs; see Chap. 1). However, we do not know if brook lamprey males could fertilize even close to all the eggs from a river lamprey female (i.e., whether sperm would be limited, whether they would be driven off by river lamprey males, or whether they would fail to induce female river lamprey to release their eggs). The relative testis size (the gonadosomatic index) of brook lamprey males is higher than that of parasitic species (10 and 4%, respectively), but, given the differences in body size, absolute testis size is still much greater in parasitic species (1.3 and 0.5 g in European river and brook lampreys, respectively; see Chap. 1).

Furthermore, "barring any selection against hybrids" is an important caveat. Many studies have demonstrated that the survival of hybrids between lamprey paired species is equivalent to that of pure individuals for the first few weeks following fertilization (e.g., Enequist 1937; Piavis et al. 1970), but there is virtually nothing known regarding possible selection against hybrids later in development. Only one study to date is known where hybrids between paired species were reared for more than a few weeks after hatch. Beamish and Neville (1992) reared hybrids between western river and western brook lampreys for 2.5 years, but, unfortunately, the experiment was terminated prior to metamorphosis. We therefore do not know what would happen in hybrids at metamorphosis (when the developmental trajectories of the parental species diverge so dramatically) or at spawning (e.g., in terms of mating behavior and viability). Furthermore, hybrid incompatibilities are best revealed in subsequent (F2) generations or in backcrosses (i.e., when the first generation, F1, hybrid is mated with one of parental species; Bierne et al. 2002, 2006). Therefore, it is clearly premature to suggest that there is no post-zygotic reproductive isolation in paired lamprey species. Evaluating the fitness of experimentally generated hybrids over at least two generations would be very difficult to accomplish entirely in the laboratory (see Chap. 2). However, Rougemont et al. (2017), using Restriction site Associated DNA Sequencing (RAD-Seq) to identify a small set of loci that were highly differentiated between European river and brook lampreys (40 of 8,962 SNPs; see Sect. 4.6.3.3), were able to identify putative hybrids among wild-caught individuals. Among 338 individuals genotyped, these authors found evidence of 22 hybrids (6.5%), 20–21 of which were F1 hybrids. The virtual absence of later-generation hybrids suggests some form of hybrid breakdown (e.g., reduced survival or fertility of the hybrids), and this warrants further study.

Nevertheless, behavioral studies showing the potential for interbreeding in paired species is consistent with recent population genetic studies that show contemporary gene flow in sympatry (e.g., Docker et al. 2012; Bracken et al. 2015; Rougemont et al. 2015). However, it is very important in such studies to distinguish between true sympatry, where the two species come into contact, and situations where they are found in the same basin or river systems but with no opportunity for contemporary gene flow (i.e., where they are parapatric). Using microsatellite loci, Docker et al. (2012) demonstrated a lack of significant genetic differentiation (F_{ST} 0) between silver and northern brook lampreys where they were collected from the same rivers in the Lake Huron basin, but the two species were significantly differentiated (F_{ST} 0.067) in the Lake Michigan basin where northern brook lamprey were collected almost exclusively from the eastern shores of the basin and silver lamprey were collected from the western arm of the lake. Similar patterns have been seen in recent studies investigating the level of gene flow between European river and brook lampreys from multiple locations in the British Isles and northern France that varied in their level of connectivity. Bracken et al. (2015) found evidence of ongoing gene flow between European river and brook lampreys where they occurred sympatrically (in the Loch Lomond basin, F_{ST} 0.019), but five parapatric populations (where brook lampreys were isolated above barriers to migration) showed higher levels of genetic differentiation (mean F_{ST} 0.073). Rougemont et al. (2015) sampled five sympatric and five parapatric European river and brook lamprey population pairs and likewise found little or no genetic differentiation where they occurred sympatrically (i.e., no significant genetic differentiation in one population, F_{ST} 0.008, and significant but low levels of differentiation in four populations, mean F_{ST} 0.055) and higher levels of differentiation (mean F_{ST} 0.113) in parapatry. The significant differentiation observed in all but one sympatric population argues against phenotypic plasticity in a completely panmictic population, but evidence of contemporary gene flow in sympatry shows that reproductive isolation is incomplete. Interestingly, in the one sympatric population in France (the Oir River population) where there was no significant genetic differentiation between the two forms, European river lamprey were much smaller (mean TL 225 mm) than at other sites (mean TL 303 mm). Rougemont et al. (2016) suggested that the smaller size difference between European river and brook lampreys in this river may have facilitated interbreeding of the two species.

Beamish et al. (2016) also presented evidence for gene flow in sympatry between the two forms of the western brook lamprey in Morrison Creek on Vancouver Island, where the normally non-parasitic population also produces a potentially parasitic "silver" form (Beamish 1985, 1987; see Docker 2009). Beamish et al. (2016) found no significant genetic differentiation between the forms (i.e., no evidence of even partial reproductive isolation).

Microsatellite loci provide much higher resolution than mtDNA loci (Selkoe and Toonen 2006). Even non-parasitic populations that appear to have been derived very recently show evidence of genetic differentiation at microsatellite loci when no longer in sympatry. Yamazaki et al. (2011) present evidence that non-parasitic lamprey populations have evolved from the anadromous Arctic lamprey in two rivers in the Agano River system in Japan when dam construction ~90 years ago isolated them from the anadromous population. These newly founded populations show strong genetic differentiation (F_{ST} 0.433–0.635) when compared to the parapatric Arctic lamprey, but a non-parasitic population that is not isolated above dams (i.e., is sympatric with the Arctic lamprey) was not significantly differentiated from Arctic lamprey.

Few examples exist of closely related parasitic and non-parasitic lampreys that show substantial barriers to gene flow in sympatry. One such example is the European river and brook lamprey pair in the Sorraia River in the Tagus River basin in southern Portugal (Mateus et al. 2016). Like all of the examples discussed in this section, this pair does not show species-specific differences in mtDNA sequence (Mateus et al. 2011), but significant and high levels of genetic differentiation (F_{ST} 0.317) have been demonstrated with the use of microsatellite loci (Mateus et al. 2016). This pair appears to be truly sympatric (i.e., collected from a common spawning site; Mateus et al. 2013b) but appears not to experience ongoing gene flow. The Tagus River basin is near the southern limit of distribution for European river and brook lampreys, and the climate here has been stable over longer periods of time than in the British Isles and northern France (Bracken et al. 2015; Rougemont et al. 2015). In northern Europe, recolonization following glacial retreat may have brought these species into contact before reproductive isolating mechanisms were fully established, enabling gene flow in sympatry (see Sect. 4.6.3.4). In contrast, reproductive isolating mechanisms may have had time to evolve in the Portuguese population. Evolutionary theory predicts that there will be selection for pre-zygotic reproductive isolating mechanisms when hybridization is maladaptive (Ortiz-Barrientos et al. 2009). Pre-zygotic reproductive isolation appears complete between *Lethenteron* sp. N and sp. S that occur sympatrically in the Gakko River in Japan (Yamazaki and Goto 2000, 2016). Although both species are non-parasitic (i.e., they are not paired species), they are genetically very divergent, and hybridization would presumably be maladaptive. Yamazaki and Goto (2016) observed no temporal isolation or size differences that would prevent interbreeding between these two non-parasitic species, but no mixed-species nests were observed (although communal single-species spawning was observed). The extent to which hybridization between closely related paired species might be maladaptive is unknown (see above).

Despite growing evidence for contemporary gene flow when paired parasitic and non-parasitic species occur sympatrically, at least in the more northerly parts of their range, it is important to recognize that they still maintain highly distinct phenotypes. Recent studies are showing that introgression at neutral markers (e.g., microsatellite loci) does not preclude differentiation at a restricted number of loci related to feeding type (see Sect. 4.6.3.3).

4.6.3.3 Genetic Basis of Feeding Type

Multiple phenotypes within a single species are common in a wide range of organisms. In some organisms, these do indeed represent phenotypic plasticity (i.e., polyphenisms) where the different phenotypes are produced from a single genotype under the induction of an environmental cue (e.g., Greene 1999; Hoffman and Pfenning 1999; Shine 2004; Podjasek et al. 2005). However, in many other cases (e.g., populations of rainbow trout where individuals adopt either a freshwater-resident or anadromous life history type), they appear to be (at least partially) genetically based polymorphisms (Hale et al. 2013; Hecht et al. 2013).

Phenotypic plasticity with respect to feeding type has been suggested in lampreys. For example, Kucheryavyi et al. (2007) suggested that larval growth conditions determine whether individuals in an Arctic lamprey population become parasitic or non-parasitic at metamorphosis. These authors proposed that individuals that accumulate a sufficient quantity of energy resources during the larval stage are able to mature without post-metamorphic feeding and become non-parasitic. A lack of species-specific differences in mtDNA gene sequence, although rare in vertebrates, is not evidence of phenotypic plasticity (see Docker 2009). Even the existence of polymorphic populations that appear panmictic (i.e., freely interbreeding, with no apparent barriers to gene flow) using microsatellite loci does not necessarily indicate that feeding type lacks a genetic basis. Mitochondrial and microsatellite markers are generally considered neutral markers (i.e., indicators of historical and recent or contemporary gene flow, respectively; Avise 2000; Selkoe and Toonen 2006), and introgression at neutral markers does not preclude differentiation at "genomic islands" related to feeding type (see below).

The western brook lamprey population in Morrison Creek on Vancouver Island produces both a potentially parasitic "silver" form and the typical non-parasitic form and appears to be panmictic (Beamish et al. 2016; see Sect. 4.6.3.2). However, we are not yet able to distinguish between phenotypic plasticity and a genetically based polymorphism within a freely interbreeding population. Interestingly, the abundance of the parasitic form has greatly diminished since the 1980s (i.e., comprising ~65% of the total catch in 1981 and 1987, but only 8% in 2011–2012). Over this time, the average length of the silver form has stayed the same (125 mm TL), but mean TL of the non-parasitic form has increased from 116 to 131 mm. Although we could argue that better growth during the larval stage permitted more individuals to mature without feeding, whether this shift in the proportion of the two phenotypes might be due to changes in the environmental cues inducing phenotype or selection on genetically based phenotypes is not resolvable at this point. Potentially parasitic individuals may "spontaneously" appear in other western brook lamprey populations. Jolley et al. (2016) reported capturing a western river lamprey outmigrant above the John Day Dam, the third upriver mainstem dam on the Columbia River located 348 rkm from the ocean, and a few transformed western river lamprey are collected each year in the lower Yakima River >530 km from the ocean (Ralph Lampman, Yakama Nation, Fisheries Resources Management Program, Toppenish, WA, personal communication, 2018). No freshwater-resident parasitic river lamprey have been observed in these areas, and the return of anadromous western river lamprey adults would be highly unlikely. However, we cannot distinguish between phenotypic plasticity and expression of an otherwise recessive genetic trait. Likewise, the appearance of a self-sustaining, non-migratory, non-parasitic population when anadromous Arctic lamprey are isolated above dams (Yamazaki et al. 2011) is not evidence of phenotypic plasticity, because existing genetic variation within the population cannot be excluded (see Sect. 4.6.3.4).

A few recent studies have found putative functional loci that differ between paired parasitic and non-parasitic species, providing evidence for a genetic basis for life history type. Yamazaki and Nagai (2013) found a significant signature of directional selection in a non-parasitic lamprey population that has been recently derived from the anadromous Arctic lamprey (see Sect. 4.6.3.2); one microsatellite locus exhibited a much higher degree of differentiation (F_{ST} 0.701–0.914) between life history types than the other six loci tested. This locus was estimated to be ~5,800 nucleotides from the vasotocin precursor gene, which plays an important role in osmoregulation. Yamazaki and Nagai (2013) thus suggested that there has been recent and strong natural selection related to the transition from anadromy to freshwater residency (i.e., that this particular difference was related to migratory rather than feeding type), and that selection was detected at the microsatellite locus due to a "hitchhiking effect" of the selective forces around the gene region.

In a groundbreaking study, Mateus et al. (2013b) used RAD-Seq to survey for genome-wide differences in European river and brook lampreys from the Sorraia River in Portugal. RAD-Seq is a reduced-representation genome sequencing strategy (i.e., rather than whole genome sequencing) designed to interrogate ~0.1–10% of the genome. Mateus et al. (2013b) recovered >8,000 polymorphic RAD loci and almost 14,700 SNPs. Of these, they found 166 loci fixed for different alleles between European river and brook lampreys (i.e., 166 species-specific differences in the genomes of these two species). This was the first study to show species-specific differences between European river and brook lampreys, at a time when the observation that most lamprey species pairs were "barcode indistinguishable" was sometimes interpreted as meaning that there were no genetic differences between paired species (see Docker 2009; Artamonova et al. 2011). However, a subsequent study by these authors showed that European river and brook lampreys from this population could also be differentiated at neutral microsatellite loci (F_{ST} 0.317; Mateus et al. 2016), suggesting that not all of the 166 fixed loci were necessarily correlated with life history type. With barriers to gene flow, genetic differentiation due to drift or selection on other traits would also be expected. Nevertheless, Mateus et al. (2013b) were able to link 12 of the 166 loci to genes that had been annotated in the sea lamprey genome (Smith et al. 2013): the vasotocin gene, the same gene implicated in migratory type adaptation by Yamazaki and Nagai (2013); gonadotrophin-releasing hormone 2 (GnRH2) precursor; four genes related to immune function; three genes related to axial patterning; a pineal gland-specific opsin; a voltage-gated sodium channel gene; and a tyrosine phosphate gene. Evidence of a species-specific SNP in the GnRH2 precursor was interesting, because GnRH is found at the top of the hypothalamic-pituitary axis in all vertebrates and is a key regulator of gonadal development and differentiation (Sower 2015), the timing of which differs between parasitic and non-parasitic lampreys (see Docker 2009; Chap. 1). Differences in genes related to axial patterning could potentially be related to differences in the number of trunk myomeres in parasitic and non-parasitic lampreys or other aspects of development related to the ultimate differences in adult body size (see Irvine et al. 2002; Childs 2013). The pineal gland-specific opsin gene may be an important regulator of the photosensitive pineal gland which is involved in the photoperiodic control of sexual maturation in adult lampreys (Joss 1973; Yokoyama and Zhang 1997) and which might play a role in metamorphosis (Cole and Youson 1981; see Manzon et al. 2015). Most of the 166 species-specific loci still remain to be annotated, but this preliminary list of candidates serves as a very important first step in identifying genes involved in evolution of the non-parasitic European brook lamprey from the parasitic anadromous European river lamprey.

In a subsequent study, Rougemont et al. (2017) likewise used RAD-Seq data from European river and brook lampreys, but they performed population genomic analyses using nine replicated pairs experiencing different degrees of gene flow (F_{ST} 0.008–0.189; Rougemont et al. 2015). This approach allowed these authors to disentangle the effects of selection from those of genetic drift. In sympatric pairs showing high genetic connectivity, most of the genome would be expected to show strong introgression (i.e., with little or no differentiation at neutral loci), and only regions of the genome involved in reproductive isolation and local adaptation would be expected to show strong differentiation. Rougemont et al. (2017) identified 40 SNPs that were highly differentiated between European river and brook lampreys (i.e., a small number of highly differentiated "genomic islands") amid a background or "sea" of less differentiated loci. Furthermore, 28 outlier loci (i.e., those most highly differentiated between life history types) were shared in the four population pairs showing high genetic connectivity, and this amount of sharing was higher than expected by chance alone. Homology searches for these outlier loci identified some of the same candidate genes as those found by Mateus et al. (2013b), that is, the GnRH2 precursor gene, the pineal gland-specific opsin gene, and genes involved in immunity and axial patterning. However, that these genes were correlated with the brook lamprey phenotype in multiple pairs is not necessarily the result of parallel and independent evolution in each pair. Rather, the apparent genetic parallelism is likely the result of a common history of divergence initiated in allopatry followed by secondary contact in the different populations. Secondary gene flow would have eroded past divergence at variable rates across the genome, but those loci associated with life history type appear to have resisted introgression (see Sect. 4.6.3.4).

In the above studies, feeding type and migratory type were always confounded, because the evolution of non-parasitism also involved a switch from anadromy to freshwater residency. In contrast, Hume et al. (2018) recently used RAD-Seq data to infer the demographic history of three life history types in Loch Lomond: anadromous European river lamprey, freshwater-resident European river lamprey, and European brook lamprey. In this manner, it might be possible to disentangle the effects of the anadromous to freshwater transition from the parasitic to non-parasitic transition. Outlier genes associated with the migratory type transition included those related to immune function (*nckap-1*; Zhou et al. 2017) and growth (*cd109*; Hockla et al. 2010), and genes broadly associated with embryonic development (e.g., *reck*, *scn4aa*, *rev31*; Wittschieben et al. 2000; Yamamoto et al. 2012) were implicated in the transition from parasitism to non-parasitism. This does not mean, of course, that the SNPs identified in these outlier genes are the causal mechanisms for the transition from an anadromous or freshwater-resident parasitic lamprey to a non-parasitic lamprey, but these three RAD-Seq studies serve as important first steps in elucidating the genetic mechanism of life history evolution in lampreys.

Although the above studies have refuted the hypothesis of phenotypic plasticity, at least in the European river and brook lampreys populations examined, the results of a 10-year study designed to test the heritability of feeding type in silver and northern brook lampreys deserves mention here (Neave et al. 2019). These authors tested for feeding type plasticity using two approaches. The first approach used a common garden experiment to determine if raising offspring from each species under common laboratory conditions would produce the parental phenotype regardless of conditions (suggesting a genetic component to feeding type) or induce the alternative feeding type (indicating phenotypic plasticity). The second approach used a transplant experiment to determine whether placing larvae of known parentage into streams which appear conducive to the development of the alternative feeding type (as determined by comparison of abiotic and biotic characteristics in streams inhabited by the two species) would result in production of the alternative feeding type. In short, 100% larval mortality by 3 months post-hatch in each of 3 years necessitated termination of the common garden experiment. In the transplant experiments, >12,000 larvae were stocked into 10 stream reaches in the Lake Huron basin, and post-metamorphic individuals of the alternative feeding type were recaptured 4–5 years later in two streams. However, transplantation was only permitted in streams already containing *Ichthyomyzon* larvae, and genetic parentage analysis indicated that the recovered individuals were not offspring of the original known-phenotype parents. Thus, phenotypic plasticity was not demonstrated. This was the first known study to attempt a common garden experiment or transplant study through metamorphosis. Even with improvements to artificial propagation procedures (see Chap. 2), a direct repeat of this study is likely not warranted, given the recent studies indicating a genetic basis to feeding type. However, rearing studies combined with a genomic approach could be powerful. For example, with the identification of specific loci associated with life history type, we could more easily study the phenotype and fate of hybrids. Of the 22 hybrids detected by Rougemont et al. (2017), 64% displayed the river lamprey phenotype, but whether this is due to inheritance patterns or selection against hybrids with the brook lamprey phenotype is unknown. Whether parasitic lamprey parents could produce non-parasitic offspring (e.g., if both parents possessed recessive genes for "non-parasitism") is likewise unknown.

Furthermore, although the emphasis to date has largely been on the morphological and developmental "parting of the ways" observed at metamorphosis, parasitic and non-parasitic lampreys show different developmental trajectories related to ovarian development, and these differences precede metamorphosis by several years (see Docker 2009). In most species studied to date, ovarian differentiation occurs at ~1 year of age in non-parasitic species and at 2–3+ years of age in parasitic species; the larger size at the onset of oogenesis in parasitic species is presumably responsible for the greater number of oocytes elaborated in these ultimately larger-bodied species (see Chap. 1). Thus, as suggested by Hardisty (1964) and Beamish and Thomas (1983), fecundity differences among species are very likely genetically based and largely determined at or before sex differentiation. Rearing offspring from paired species and hybrids through ovarian differentiation would shed light on the earliest point at which the developmental trajectories of paired species diverge, the genes involved in this process, and possible genetic incompatibilities in hybrids (see Mavarez et al. 2009; Renaut and Bernatchez 2011).

In addition, in recently diverged pairs or those experiencing gene flow, there may be a gradual (rather than immediate) acquisition of traits associated with non-parasitism. Despite the general observation that non-parasitic species initiate oogenesis earlier than their parasitic counterpart, a recent study by Spice and Docker (2014) suggested that some species are polymorphic with respect to timing of oogenesis and the resulting number of oocytes produced. In northern brook and chestnut lampreys, ovarian differentiation occurred in age classes I and II in both species (with no significant differences in the timing between species), and northern brook and chestnut lampreys had similar minimum oocyte counts. Granted, maximum oocyte counts were higher in chestnut lamprey larvae, a similar pattern observed by Neave et al. (2007) when comparing presumptive northern brook and silver lampreys, but these results suggest that all of the changes associated with the evolution of non-parasitism may not occur simultaneously. Changes in the phasing of gonadogenesis might not always coincide with the elimination of the parasitic feeding phase. Parasitic lamprey populations may already be polymorphic for this trait (i.e., with evolution of non-parasitism drawing on existing genetic variation within the population), or, conversely, selection for earlier ovarian differentiation and lower potential fecundity may follow the elimination of the parasitic feeding phase. The sequence of changes associated with the evolution of non-parasitism—and a better understanding of the mechanisms of life history evolution in lampreys—can be better resolved now with our improved understanding of where different species and populations fit on the continuum.

4.6.3.4 Demographic History of Divergence and Origin of Genetic Parallelism

Given the morphological similarity and lack of mtDNA sequence differentiation generally observed between lamprey species pairs in sympatry, particularly those in recently deglaciated regions, it is often assumed that divergence happened very recently (e.g., Hubbs and Potter 1971; Salewski 2003; Docker 2009). Although molecular phylogenetic studies that fail to find species-specific genetic differences and lack of reciprocal monophyly in sympatric pairs often add the caveat that genetic similarity may also result from introgression following secondary contact after divergence in allopatry (see Taylor 1999; Espanhol et al. 2007), this caveat is sometimes forgotten. Thus, it is often thought that most paired brook lamprey species have evolved from their parasitic ancestor in post-glacial times (e.g., Beamish and Withler 1986; Docker 2009), with the two distinct phenotypes rapidly differentiating in sympatry as a result of disruptive selection (Salewski 2003).

Previous studies have lacked the resolution to distinguish between primary, but recent or ongoing, divergence in sympatry and secondary gene flow following initial divergence in allopatry. However, recent studies by Rougemont et al. (2016, 2017) have used population genetic and genomic analyses to reconstruct the demographic history of divergence between European river and brook lampreys, and their results make us question past hypotheses regarding modes of speciation in lampreys. Using 13 microsatellite loci and an approximate Bayesian computational (ABC) approach combined with a random forest model, Rougemont et al. (2016) tested different scenarios of divergence in six replicated populations of European river and brook lampreys from northern France. These six pairs were all highly connected by gene flow: five populations were either truly sympatric or the two species were found in close proximity and not separated by permanent barriers to migration, and one population was parapatric but showed gene flow comparable to that of the sympatric populations. These authors statistically compared five alternative models for the divergence between each pair of species: (1) a model of panmixia (PAN) in which European river and brook lampreys within a population constitute a single gene pool; (2) a strict isolation model (SI) in which European river and brook lampreys diverged T_{DIV} years ago with no subsequent gene flow; (3) an ancient migration model (AM) in which European river and brook lampreys diverged T_{DIV} years ago but continued to experience gene flow up until T_{ISOL} years ago; (4) an isolation with migration model (IM) in which European river and brook lampreys diverged T_{DIV} years ago but continue to experience contemporary gene flow; and (5) a model of secondary contact (SC) after past isolation, where European river and brook lampreys diverged in allopatry T_{DIV} years ago and then started experiencing gene flow following secondary contact T_{SC} years ago (Fig. 4.4). The strict isolation (SI) and ancient migration (AM) models were both rejected for all six populations. Rejection of the SI model refutes the hypothesis that reproductive isolation between parasitic and non-parasitic lampreys would be immediate and complete as soon as elimination of the adult feeding phase produced differences in body size at maturity. Rejection of the AM model is consistent with the results showing that these populations are experiencing ongoing (contemporary) gene

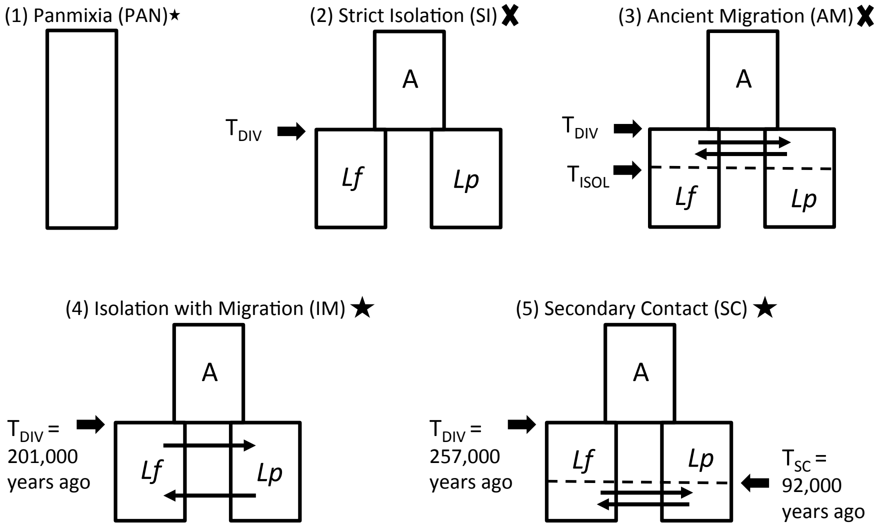


Fig. 4.4 Models of divergence between European river lamprey *Lampetra fluviatlis* (*Lf*) and European brook lamprey *La. planeri* (*Lp*) tested by Rougemont et al. (2016). T_{DIV} is number of generations since divergence; T_{ISOL} is generations since the two life history types stopped exchanging genes; T_{SC} is generations since the life history types entered into secondary contact following a period of isolation. PAN was the best-supported model for one of population (*asterisk*), and IM and SC were both well-supported models for five populations (*star*); SI and AM were rejected for all six populations (*X*). Estimates of T_{DIV} (expressed in years, assuming generation time of 5 years) and T_{SC} under the IM and SC models (median for the five populations) are given

flow; in fact, these populations were chosen because they were highly connected by gene flow. Of the remaining models, panmixia (PAN) was the best-supported model for one population; this was the Oir River population, where no significant genetic differentiation was previously found between the forms (Rougemont et al. 2015; see Sect. 4.6.3.2). Isolation with migration (IM) and secondary contact (SC) were the best-supported models in the remaining five populations, although it was not possible to distinguish between them. These two models could also not be ruled out in the Oir River population (at least not with neutral markers; see below).

The divergence time estimates generated by Rougemont et al. (2016) provided exciting insights into the tempo and mode of evolution in paired lamprey species. Assuming a generation time of 5 years for these species, these authors estimated that European river and brook lampreys in the five populations best characterized by the IM and SC models diverged on average 201,760 and 257,040 years ago, respectively (or 282,464 and 359,856 years ago, respectively, assuming a generation time of 7 years). This is completely inconsistent with recent and rapid divergence following the recent glacial retreats ~10,000–15,000 years ago. Even the bottom end of the 95% confidence interval from each of the individual populations (24,200 years ago) shows T_{DIV} higher than predicted if divergence occurred in post-glacial times. Also surprisingly, in the SC model, the median time at which gene flow resumed following secondary contact (T_{SC}) was 92,960 years ago. This suggests that not even secondary contact occurred in post-glacial times. The ancient secondary contact suggested by the T_{SC} estimate implies that the genetic signature of historical geographic isolation carried by neutral markers has been lost, which would explain the difficulty these authors experienced distinguishing between the SC and IM models (Rougemont et al. 2016). It also suggests that the period of isolation (i.e., between T_{DIV} ~200,000–250,000 years ago and T_{SC} ~90,000 years ago) was too short to allow genetic incompatibilities to accumulate and strong barriers to gene flow to develop.

However, with neutral markers, it can be difficult to distinguish between primary divergence (i.e., the SI, IM, or AM models) and secondary contact (SC), because both scenarios tend to converge to the same equilibrium (Bierne et al. 2013). Thus, Rougemont et al. (2017) subsequently used RAD-Seq data and a diffusion approximation approach to infer the demographic history of each of four sympatric and five parapatric European river–brook lamprey pairs. In all of the sympatric pairs, their analyses supported a model of secondary contact (SC) after initial divergence in allopatry (including the Oir River pair where their 2016 study suggested panmixia). In contrast, parapatric pairs have retained a signal of ancient migration (AM). The AM model was rejected in Rougemont et al. (2016) where only sympatric populations were included, but Rougemont et al. (2017) indicate that sympatric versus parapatric populations do not necessarily have radically different divergence histories; the signal of past secondary contact may have been lost or obscured in parapatric populations as result of recent drift.

In all nine pairs examined by Rougemont et al. (2017), models accounting for differential introgression among loci (i.e., incorporating heterogeneity in divergence along the genome) outperformed homogeneous migration models. As discussed above (see Sect. 4.6.3.3), there does not appear to be uniform gene flow across the genome; rather, regions of the genome involved in reproductive isolation and local adaptation appear to resist the homogenizing effect of introgression. Rougemont et al. (2017) found that 6–12% of loci in the most genetically connected pairs displayed a reduced effective migration rate between the life history types; during secondary contact, erosion of past genetic differentiation outside the direct vicinity of these "barrier loci" would result in low levels of genetic differentiation elsewhere in the genome. Only European river and brook lampreys have been studied to date using this approach, but the demographic histories of divergence should be tested in other paired species using this approach. Interestingly, Hubbs and Trautman (1937) suggested that the *Ichthyomyzon* brook lamprey species originated before the last glacial advance in North America, although Hubbs and Potter (1971) subsequently considered that a more recent origin was equally possible.

An extension of the "recent divergence in sympatry" hypothesis (although less explicit) is the assumption that widely distributed brook lamprey species evolved through this mechanism independently and repeatedly in disjunct locations (e.g., Beamish and Withler 1986; Docker 2009). Molecular phylogenetic analyses suggest that many widespread brook lamprey species are polyphyletic (i.e., derived from two or more ancestral sources), and their distribution in disjunct drainages separated by salt water argued against dispersal (at least via current connections) following a single brook lamprey origin. However, it is important to recognize that current connections between drainages do not reflect past connections. For example, stream capture can transfer some portion of an aquatic fauna into a new drainage, and rivers isolated from each other by marine or estuarine conditions can join farther out on the continental shelf if sea levels are lowered (Hughes et al. 2009). Furthermore, the current geographic distribution of contemporary species may not reflect the initial conditions of divergence (Bierne et al. 2011), and the results of Rougemont et al. (2016, 2017) remind us that repeated and independent evolution of non-parasitism in each location (i.e., in sympatry) or a single origin of each non-parasitic species in allopatry followed by subsequent brook lamprey dispersal are not the only two options. Their demographic models support divergence in allopatry, but with subsequent gene flow following secondary contact. Gene flow between the life history types in sympatry gives the erroneous appearance of divergence in sympatry and multiple independent and parallel origins of each brook lamprey species.

This point is worth emphasizing as we begin to explore the genetic basis of feeding type in lampreys, particularly with respect to understanding the extent to which the genetic changes are parallel among different species pairs and populations (e.g., whether they involve the same mutations in the same gene). There was considerable overlap in the list of genes that were highly differentiated between European river and brook lampreys in northern France and in southern Portugal (see Sect. 4.6.3.3). Is the apparent parallelism the result of parallel selection on standing genetic variation in the ancestral European river lamprey population, the result of a single speciation event in allopatry followed by dispersal, or the result of mutations occurring in these genes independently in disjunct locations? Rougemont et al. (2017) evaluated the extent of genetic parallelism among replicate European river and brook lamprey pairs in northern France, and they suggested that ancestral variation related to life history type arose in allopatry so that the “brook lamprey background” existed before the recent colonization of rivers. The brook lamprey phenotype may have arisen either through hybrid genotypes colonizing fresh water or through transport of alleles broken up by recombination and at low frequency in the river lamprey background into the freshwater populations. There would presumably be selection for the brook lamprey alleles in fresh water, and these rare alleles would be driven to high frequencies in multiple different rivers. This would be similar to the “transporter hypothesis” proposed by Schluter and Conte (2009) to explain the rapid and repeated evolution of multiple freshwater-resident threespine stickleback populations from the anadromous or marine form. Schluter and Conte (2009) proposed that ecological speciation has occurred multiple times in parallel when selection in freshwater environments repeatedly acts on standing genetic variation that is maintained in the marine population when freshwater-adapted alleles from elsewhere in the range are exported back into the marine population. In a similar manner, brook lamprey alleles are likely transported among disjunct rivers, mediated by the river lamprey which shows few barriers to gene flow among locations, at least within a region (Bracken et al. 2015; Rougemont et al. 2015; Mateus et al. 2016; see Sect. 4.7.5). Selection within each river on existing genetic variation would help account for the apparent rapidity of speciation (e.g., following northward range expansion and post-glacial colonization).

Further study is clearly required, but the results to date emphasize the need to avoid overly simple explanations or broad generalizations when trying to understand the evolution of non-parasitism in different lamprey species and throughout the range of each. It is unknown if all populations of a particular brook lamprey species share the same "brook lamprey background" derived from a single ancestral population, and the extent of genetic parallelism in different species pairs and different genera is likewise unknown. Even distantly related brook lampreys show obvious phenotypic parallelism, but whether their independent evolution has involved, for example, different mutations in the same genes or different genes in same developmental pathway (see Arendt and Reznick 2008), has yet to be explored.

4.7 Factors that Promote or Constrain Evolution of Non-parasitism

The conditions under which brook lampreys evolve have been reviewed previously by several authors (e.g., Salewski 2003; Hardisty 2006; Docker 2009). Two scenarios have generally been proposed: (1) that parasitic lampreys become non-parasitic in habitats where there is an insufficient prey base, perhaps as the result of barriers to migration that prevent access to the ocean or large lakes (e.g., as the result of glaciation and deglaciation events during the past 10,000–15,000 years); or (2) that parasitic lampreys become non-parasitic as the result of events that alter the relative benefits and costs of migration (e.g., Zanandrea 1959; Espanhol et al. 2007). The two options are not entirely mutually exclusive, although the first implies that non-parasitism evolved to "make the best of a bad situation" when post-metamorphic feeding was poor or not possible, and the second suggests that non-parasitism is a valid "choice" that, under certain conditions, confers greater (rather than merely adequate) fitness as a result of the trade-off between reduced fecundity and reduced mortality. Our intention in this section is not to repeat past reviews but, rather, to continue the discussion introduced in Sect. 4.4 regarding factors that promote and constrain freshwater residency in lampreys. Loss of anadromy almost invariably leads to a reduction in the duration of the parasitic feeding phase and size at maturity, and we contend that the complete elimination of the parasitic feeding phase is an extension of this process. The emphasis in this section will be less on the environmental conditions that might have promoted elimination of the parasitic feeding phase, and more on characteristics of parasitic lampreys that permitted or constrained evolution of brook lamprey derivatives. Some parasitic species are clearly much more prolific in terms of producing non-parasitic offshoots than others. Although there is not universal agreement on the "true" number of brook lamprey species, and there may never be an exact, objectively definable number (see Sect. 4.6.3; Chap. 7), it is apparent that the two anadromous parasitic *Lampetra* species are the "mothers" of many brook lampreys. At minimum, 35% of the 23 brook lamprey species recognized by Potter et al. (2015) are thought to be derived from the European and western river lampreys or European and western river lamprey-like ancestors (Fig. 4.1). At the other end of the spectrum, there is a conspicuous absence of brook lamprey derivatives from the large-bodied sea, pouched, and Caspian lampreys. The following discussion will largely try to address why there are no brook lamprey derivatives from this latter group, and we will speculate as to whether freshwater-resident sea lamprey might represent a "jumping-off point" for the evolution of non-parasitism.

4.7.1 Phylogenetic Constraints

Sea lamprey, pouched lamprey, and Caspian lamprey are each the sole species in their respective genera. Thus, the lack of brook lamprey derivatives from these species is potentially different from that of other parasitic species for which no non-parasitic derivatives have been described. No brook lamprey derivatives have been attributed to the Chilean lamprey, Korean lamprey, Vancouver lamprey, and perhaps the Klamath lamprey (depending on whether it or the Pacific lamprey is the ancestor to the two *Entosphenus* brook lamprey species; Sect. 4.6.3.1), but non-parasitic lampreys are found within each of these genera (see Fig. 4.1). Thus, "phylogenetic constraints" could potentially be used to explain the absence of non-parasitic lampreys in *Petromyzon*, *Geotria*, and *Caspiomyzon*—that is, that these lineages simply do not have the "wherewithal" to develop brook lampreys. However, *Petromyzon*, *Geotria*, and *Caspiomyzon* are well-distributed throughout the lamprey phylogenetic tree (based on both morphological and molecular characters) and are intermixed with the seven genera containing brook lamprey species (Potter et al. 2015). Brook lampreys are found in two of the three families of extant lampreys and, within the Petromyzontidae, in both or all three of the proposed subfamilies (Vladykov 1972; see Potter et al. 2015). In subfamily Petromyzontinae, all three parasitic species of *Ichthyomyzon* have given rise to brook lamprey derivatives, even if *Petromyzon* and *Caspiomyzon* have not. Phylogenetic constraint has been invoked in a variety of contexts, but as yet there is no consensus on its definition, and it was described by Alexander (1989) as "an argument of last resort." McKitrick (1993) defined phylogenetic constraint as "any result or component of the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage." Of course, we cannot rule out such a constraint. However, we argue below that, given their consistently large body size, evolution of non-parasitism would not be anticipated in these species (see Sect. 4.7.4). Thus, although there may be genetic constraints within each of the large-bodied species (see Sect. 4.7.5), we argue against phylogenetic constraints.

4.7.2 Ecological Constraints

Although the discussion of the factors that promote or constrain the evolution of non-parasitic lampreys often focuses on the ecological conditions under which non-parasitism arises, the dearth of non-parasitic species in some taxa appears not to be caused by lack of the appropriate ecological conditions. We recognize that the conditions under which even recent non-parasitic derivatives arose are not identical to conditions under which they are currently found, particularly if, as suggested by recent demographic analyses in European river and brook lampreys in northern France, divergence occurred in allopatry at least 202,000–257,000 years ago (Rougemont et al. 2016; see Sect. 4.6.3.4). However, those species that have no or few non-parasitic derivatives frequently overlap in their distribution with species that have given rise to non-parasitic derivatives. On either side of the Atlantic, anadromous sea lamprey co-occur in drainages with American brook lamprey (e.g., Aman et al. 2017; Evans 2017) and European river and brook lampreys (e.g., Maitland 1980; Taverny et al. 2012), and the Great Lakes sea lamprey overlaps in distribution with silver and chestnut lampreys, as well as northern brook and American brook lampreys (Renaud et al. 2009). The pouched lamprey co-occurs in Australian waters with short-headed lamprey which has given rise to a non-parasitic derivative. The Caspian lamprey has a more restricted distribution than the widespread sea and pouched lampreys but, nonetheless, overlaps somewhat in its distribution with *Eudontomyzon* brook lampreys (Levin and Holčík 2006; Potter et al. 2015; Levin et al. 2016).

There are clear ecological constraints related to the loss of anadromy in parasitic lampreys (see Sect. 4.4.2). Access to a sufficient prey base is obviously critical for the evolution and persistence of freshwater parasitic lampreys, and what constitutes sufficient varies considerably among species. The relative scarcity of large lakes within the range of the pouched lamprey, for example, may have prevented this species from establishing any freshwater-resident parasitic populations, but such constraints would not apply to the evolution of non-parasitism. Conversely, one could argue that non-parasitic species need to have a more productive larval environment to compensate for the lack of further growth following metamorphosis (Kucheryavyi et al. 2007). There is certainly a general trend showing that non-parasitic species typically have a longer larval stage and greater size at metamorphosis relative to their parasitic counterparts (Potter 1980; Hardisty 2006; Docker 2009), but duration of the larval stage and size at metamorphosis varies considerably among and within species. Large size at metamorphosis does not seem to be an absolute requirement for non-parasitic lampreys, nor is small size at metamorphosis the rule among parasitic species. Metamorphosing American brook lamprey as small as 100–109 mm TL have been reported (Hoff 1988), and sea lamprey average 130–140 mm TL at metamorphosis (Potter 1980). In contrast, pouched lamprey metamorphoses at relatively small sizes (~90–100 mm; Neira 1984; Potter and Hilliard 1986). Presumably, there is a lower size limit below which non-parasitic species would be unable to undergo both non-trophic metamorphosis and non-trophic sexual maturation. However, larval lampreys and post-metamorphic brook lampreys appear to be extremely energy efficient (Sutton and Bowen 1994; Beamish and Medland 1988; see Dawson et al. 2015), and it may be that the minimum size requirements for metamorphosis and sexual maturation in brook lampreys is not that much different than the minimum size requirements for metamorphosis and downstream migration in parasitic species. Differences may be apparent between the sexes (e.g., with larger size at metamorphosis being more important for female brook lampreys than for female parasitic lampreys; Docker 2009) and among some species or environments (e.g., where downstream migration is more arduous or the delay prior to parasitic feeding is longer), but it appears that brook lampreys should be able to persist anywhere that there is suitable spawning and rearing habitat for any lampreys. Even at high latitudes, brook lamprey larvae are able to grow well; Alaskan brook lamprey larvae as large as 144 mm TL were reported in the Martin River, Northwest Territories (61.924 °N; Renaud et al. 2016), and they were even larger (up to 214–215 mm TL) in the Chatanika and Chena rivers, Alaska (65.281 °N; Sutton 2017).

This is not to say that ecological conditions will not influence the relative costs and benefits of parasitism versus non-parasitism, but rather that evolution of non-parasitism does not appear to require particular ecological conditions. Certainly non-parasitic lampreys will be favored above barriers to migration that prevent access to a sufficient prey base, but the co-occurrence of parasitic and non-parasitic lampreys downstream of barriers in countless streams and rivers indicate that this is not the only factor to consider. Rather, it appears that non-parasitism represents an evolutionarily stable strategy in situations where the relative costs of migration and feeding outweigh their benefits. The balance of this trade-off will depend on ecological conditions, but it appears to vary considerably among species and even among populations or individuals (see Sect. 4.7.4).

4.7.3 Osmoregulatory Ability and the Importance of Freshwater Intermediates

It has been suggested that freshwater parasitic lampreys may be important intermediaries in the transition from anadromous parasitic to freshwater non-parasitic lampreys (Hubbs and Potter 1971; Beamish 1985; Salewski 2003; Hardisty 2006). Beamish (1985) reasoned that the many changes that must occur in this transition are too major to occur in a single step. Instead, he proposed that the first step in this evolutionary pathway was the ability to osmoregulate in fresh water during the parasitic feeding phase, possibly acquired as the result of gradual changes in salinity. By extension, one could argue that those parasitic species that are poorly adapted for feeding in a freshwater environment during the parasitic phase would be less likely to give rise to non-parasitic derivatives. However, an inability to osmoregulate during the juvenile feeding phase is not likely relevant once the juvenile feeding phase has been eliminated. Even anadromous lampreys exhibit a breakdown of their saltwater osmoregulatory mechanisms during upstream migration and sexual maturation (e.g., Pickering and Morris 1970; Beamish et al. 1978; Ferreira-Martins et al. 2016). Hence, elimination of the parasitic feeding phase should not require an intermediate freshwater form as means of adapting to fresh water during sexual maturation. Moreover, even though there is a general correlation between those parasitic species with freshwater forms and those that have given rise to non-parasitic derivatives, it is not absolute (Fig. 4.1). Most notably, freshwater-resident populations of western river lamprey are rare at best. Only one viable population has been reported (in Lake Washington; see Sect. 4.3.3.2), and yet this species has given rise to western brook lamprey in innumerable Pacific drainages from Alaska to California, and at least two older brook lamprey derivatives in Oregon and California.

Recent demographic reconstructions, using genome-wide markers in the three lamprey life history types from Loch Lomond (anadromous and freshwater-resident European river lamprey and European brook lamprey; see Sect. 4.3.4.2), compared 12 hypothetical evolutionary scenarios for divergence of the three forms, and the two models that were best supported both suggested a common ancestry for the two freshwater forms (Hume et al. 2018). These models suggested either a hybrid speciation scenario, by which hybridization between the freshwater and anadromous parasitic forms gave rise to the non-parasitic form, or a scenario by which the anadromous ancestor gave rise to both freshwater parasitic and non-parasitic forms. However, it is important to recognize that a linear progression was not supported (i.e., anadromous parasitic → freshwater parasitic → freshwater non-parasitic), and there was clear evidence of subsequent gene flow between the non-parasitic and anadromous parasitic forms (see Sect. 4.6.3.2). Interestingly, the freshwater parasitic form was more genetically differentiated from the anadromous and non-parasitic forms than either of these latter forms were from each other (Bracken et al. 2015; Hume et al. 2018), despite the two parasitic (river lamprey) forms being considered a single species distinct from the non-parasitic European brook lamprey.

4.7.4 Life History Trade-Offs

Life history theory seeks to explain the major demographic traits in an organism's life cycle (e.g., growth rate, age and size at maturity, number and size of offspring, age- and size-specific mortality rates) and understand the trade-offs and fitness consequences associated with the different traits. Lampreys are excellent models to study life history evolution; they show a highly conserved body plan but a diversity of life history types, and, because they are semelparous, lifetime reproductive success is easily quantifiable. As articulated by Hubbs and Potter (1971), brook lampreys and the largest anadromous forms represent two extreme forms of adaptation, exhibiting the range of life history trade-offs seen in lampreys. It has long been suggested that the viability of non-parasitic populations depends on low mortality resulting from the elimination of parasitic feeding and migration balancing the reduction in fecundity caused by the resulting decrease in size at maturity (Hubbs and Potter 1971; Potter 1980; Hardisty 2006; Docker 2009). At the other end of the spectrum, the large anadromous species combine maximum body size, wide-ranging migration, extended adult life (and presumably relatively high total mortality) with exceptionally high egg numbers. In the middle are the majority of parasitic species, those that are intermediate in body size (or, at least, with segments of their populations that are smaller bodied) and with more restricted migrations. Significantly, it is from this latter group that the vast majority of brook lampreys have been derived (Hubbs and Potter 1971). Thus, as suggested previously, it appears that selective constraints related to life history trade-offs have limited evolution of non-parasitism in the largest anadromous species and promoted their evolution in small-bodied parasitic species.

The latter group of parasitic species includes freshwater parasitic lampreys and the smaller anadromous lampreys. The smaller anadromous lampreys, given their need for a less extensive prey base than the very large anadromous lampreys, have generally been successful at colonizing fresh water (see Sects. 4.4.1 and 4.4.2). This gives the appearance of a correlation between the ability to feed parasitically in fresh water and the ability to give rise to non-parasitic forms, but the key appears to be reduced duration of the feeding phase and body size at maturity and not osmoregulatory ability. The anadromous sea lamprey is the largest extant lamprey (up to 800–900 mm TL at maturity) and has produced highly successful freshwater-resident populations (Sect. 4.3.4.4), but it has yielded no brook lampreys. In contrast, western river lamprey is the smallest anadromous lamprey (~200 mm TL at maturity); few or no parasitic populations have become established in fresh water (see Sect. 4.3.3.2), but this species has given rise to an abundance of brook lamprey populations.

The other two species with a conspicuous absence of brook lamprey derivatives or relatives are likewise those that are consistently large bodied (Fig. 4.5). In Australia, for example, pouched lamprey measure 530–740 mm TL at maturity, and no small-bodied forms are known (Potter et al. 1983). Small-bodied (praecox) anadromous Caspian lamprey have been reported, but they are apparently rare. Likewise, although there are reports of landlocked Caspian lamprey following dam construction, there is no evidence that they have become established in fresh water (see Sect. 4.3.3.1). Anadromous sea and pouched lampreys also tend to show more wide-ranging offshore feeding relative to smaller-bodied species (Potter et al. 2015). This suggests little limitation in terms of prey availability, so they would not have been under selection to reduce the duration of their parasitic feeding phase. For these large, ocean-going lampreys, the decrease in mortality rates that would accompany the shift to non-parasitism could not possibly offset the very drastic reduction in fecundity (Hardisty 2006). As discussed in Sect. 4.4.4, fecundity increases approximately with the cubic power of length, and reducing size at maturity from, for example, 600–800 mm TL to 120 mm TL would result in a reduction of fecundity from 149,240–342,690 to 1,430 eggs (Fig. 4.5; see Chap. 1), a reduction of more than 99%. The Caspian lamprey differs in having a more restricted distribution and more confined food resource than these other two large-bodied lampreys. However, its possible mode of carrion feeding (see Chap. 3) might have helped reduce the pressure on local host populations, so there was likewise little pressure for this species to reduce the duration of its feeding phase. The shift from a large-bodied parasitic form directly to a non-parasitic form would represent a significant reduction in fecundity.

In contrast, although Pacific and Arctic lampreys are also known to reach large sizes as the result of extended feeding at sea, both species show considerable intraspecific variation in size at maturity and duration of the parasitic feeding phase, and Pacific and Arctic lampreys are each recognized as having given rise to two or

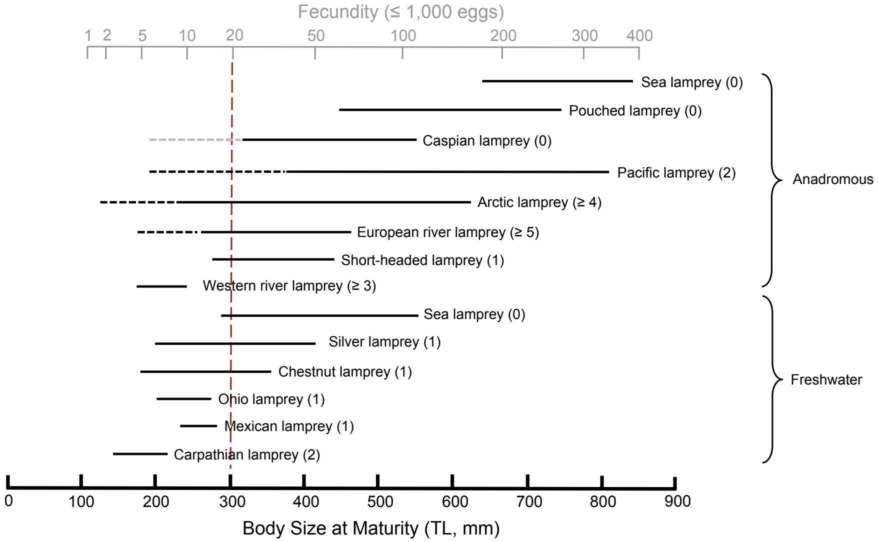


Fig. 4.5 Body size (total length, TL) at maturity for eight anadromous and six freshwater parasitic lamprey species and the number of extant non-parasitic lamprey species to which they are thought to have given rise (in *parentheses*, see Fig. 4.1). Size range at maturity is from Sect. 4.3, Docker (2009), and Chap. 1 (Table 1.11 and references therein); *black dotted lines* indicate size of well-characterized anadromous praecox or freshwater-resident individuals; *gray dotted line* indicates less well-known praecox populations. The relationship between mean fecundity and mean TL calculated across species and populations (see Chap. 1) was used to estimate total number of eggs produced by parasitic lampreys across this size range; mean fecundity for non-parasitic lampreys averages ~1,770 eggs. It appears that only parasitic species with at least some individuals smaller than ~300 mm TL at maturity (*red dotted line*) have given rise to non-parasitic species, resulting in a 10–12× reduction in fecundity

more non-parasitic species (Fig. 4.5). Hubbs and Potter (1971) described the Pacific lamprey as a "vast complex of very small to large forms." Praecox or dwarf anadromous populations are known in both Pacific and Arctic lampreys, and smaller-bodied freshwater-resident Arctic lamprey populations are also known (see Sects. 4.3.4.1 and 4.3.4.3). Compared to sea and pouched lampreys, these species feed more in coastal waters and at shallower depths, and they appear to show more limited dispersal at sea (Spice et al. 2012). Consequently, these species would be more vulnerable to declines in local fish stocks with a concomitant selection for the praecox form (see Sect. 4.4.2). These smaller-bodied individuals would then have been better poised to abandon parasitic feeding altogether than sea or pouched lampreys, with much more modest reductions in fecundity (Fig. 4.5).

Among the smaller anadromous species, the European river and western river lampreys have been particularly prolific, giving rise to at least five and three recognized brook lamprey species, respectively, and potentially many more (Fig. 4.1). European river lamprey, in addition to its typical anadromous form, also exists as even smaller-bodied praecox anadromous and freshwater forms (Sect. 4.3.4.2), and it could be argued that all western river lamprey correspond to an anadromous praecox form (Sect. 4.3.3.2). Freshwater parasitic species (with the exception of the landlocked sea lamprey) are likewise relatively small-bodied. The three parasitic *Ichthyomyzon* species, Carpathian lamprey, and Mexican lamprey generally feed parasitically for ≤1 year, and all have given rise to non-parasitic forms (Fig. 4.5). In these species, the reduction in fecundity resulting from elimination of the parasitic feeding phase will be limited. In the western river lamprey, for example, bypassing the brief parasitic feeding phase and the associated down- and upstream migrations results in a considerable reduction in exposure to predators (e.g., R. J. Beamish 1980; Roffe and Mate 1984; see Docker et al. 2015) with only a modest reduction in size at maturity and fecundity (Fig. 4.5). We thus suggest that western river lamprey rarely, if ever, establish viable freshwater parasitic populations, not because of osmoregulatory constraints, but rather as the result of selective constraints. Western river lamprey, even as anadromous parasites, are already so small at maturity that "skipping" right to a non-parasitic life history type represents a more profitable trade-off between mortality and fecundity than freshwater parasitism would.

Our comparisons indicate that all parasitic species that have given rise to non-parasitic derivatives have at least some individuals measuring ≤300 mm TL at maturity, and that those where large segments of the species are below this cut-off are more likely to have produced more brook lamprey derivatives. Not all parasitic species that are ≤300 mm TL have non-parasitic derivatives, but all that have non-parasitic derivatives are ≤300 mm TL. All parasitic lampreys that are ≤300 mm TL at maturity, and do not have known non-parasitic derivatives, belong to genera in which non-parasitic species are found. Chilean, Korean, Vancouver, and Klamath lampreys do not have known brook lamprey derivatives, but they belong to genera in which non-parasitic species are found, and our analysis suggests that they could give rise to non-parasitic derivatives. Hubbs and Potter (1971) indicated that *Mordacia* in Chile may have produced a brook lamprey in parallel to that observed in Australia, although there is no evidence that the Chilean lamprey has given rise to such a species (Potter and Strahan 1968).

Hardisty (2006) predicted that, in smaller parasitic species with lower levels of fecundity, the balance would be "more delicately poised" such that unstable environments that reduced feeding opportunities or increased mortality during the adult phase could tip the balance towards non-parasitism. The point at which the balance between reduced mortality and reduced fecundity tips in favor of non-parasitism is presumably subject to some variation, based on the relative costs and benefits of feeding and migration under different circumstances, but our comparison suggests that 300 mm TL (with a 10–12× reduction in fecundity) is the cut-off above which shifts to non-parasitism would not be beneficial. Mortality during the migratory and juvenile feeding stages in parasitic species has not been quantified, but we would predict that it is no more than 10–12× higher than that observed following metamorphosis in non-parasitic species.

Based on these comparisons, we predict that Great Lakes sea lamprey are not likely to give rise to a non-parasitic derivative, despite the occurrence of an "intermediate" freshwater parasitic form. Despite the consistently large size of anadromous sea lamprey, this species was apparently able to colonize fresh water because of the abundant prey resources and large size of the Great Lakes. Even in fresh water, size at maturity (mean TL ~395–500 mm) and fecundity (mean ~70,000 eggs; see Chap. 1) is still very high. Complete elimination of the parasitic feeding phase would represent too large (~40×) a reduction in fecundity.

4.7.5 Genetic Factors

Selective and genetic constraints on the evolution of non-parasitism are not mutually exclusive. Although it makes intuitive sense that the transition to non-parasitism would be disadvantageous to large-bodied, highly fecund species, we do not know if their presumably genetic propensity for consistently large size and a long, wide-ranging feeding phase would preclude evolution of non-parasitism. We know virtually nothing regarding the genetic factors governing differences in size at maturity among species or what factors regulate length of the feeding phase (see Moser et al. 2015). However, the above discussion suggests that the ranges in body size of fully grown anadromous sea and pouched lampreys (and perhaps Caspian lamprey, to a lesser extent) are genetically fixed, while species such as Pacific, Arctic, and European river lampreys show more intraspecific genetic variation in these traits. Recent genomic studies in Pacific lamprey have identified loci associated with intraspecific differences in size at maturity, and they appear to show regional heterogeneity associated with this trait (Hess et al. 2013, 2014). Population genetic studies suggest that sea lamprey on each side of the Atlantic constitute largely panmictic populations (Bryan et al. 2005), while evidence is accruing that Pacific, Arctic, and European river lampreys represent more heterogeneous gene pools. Lampreys do not home to their natal streams (see Moser et al. 2015), so there is no evidence of local adaptation to specific stream or river basins, but it appears that dispersal distance is related to body size and smaller-bodied anadromous lamprey typically show evidence of isolation by distance. This is the case in Pacific lamprey (Spice et al. 2012), and Rougemont et al. (2015) and Mateus et al. (2016) likewise found some genetic structuring among European river lamprey populations, at least among regions. In the Arctic lamprey from Japan and eastern Russia, significant genetic differences were found between three populations located in the northern part of the study area and the remaining nine more southerly populations; however, there was no significant isolation by distance, and there was evidence of gene flow among the populations (Yamazaki et al. 2014). Overall, it seems reasonable to infer that the regional differences in size at maturity that have been reported in Pacific, Arctic, and European river lampreys (Sect. 4.3.3) have some genetic basis and that evolution of non-parasitism involves further selection on individuals already predisposed to small size at maturity.

However, the additional genetic changes required for the complete elimination of the parasitic feeding phase are unknown. We do not know what factors prompt parasitic species to stop feeding and initiate sexual maturation (or vice versa, i.e., to initiate sexual maturation and thus stop feeding), and we certainly do not know what factors initiate sexual maturation without any parasitic feeding whatsoever. Whether the evolution of non-parasitism drew on existing (standing) genetic variation within these small-bodied parasitic lamprey populations or whether it depended on de novo mutations is unknown. With the new genomic technologies available, it is now possible to address some of these questions. Some candidate genes have been identified (see Sect. 4.6.3.3), but there is still considerable work required to understand the genetic and developmental changes associated with the evolution of non-parasitism.

Furthermore, whether other life history features associated with non-parasitism (e.g., earlier onset of gonadogenesis and lower potential fecundity) are also polymorphic in the ancestral parasitic population is unknown. The results from Spice and Docker (2014) suggest that some parasitic species are polymorphic with respect to the timing of oogenesis and the resulting number of oocytes produced (see Sect. 4.6.3.3; Chap. 1), and Hardisty (1964) suggested that non-parasitic forms may have evolved from an ancestral parasitic population whose fecundity was comparatively low. However, the more dramatic changes evident in non-parasitic species presumably evolved after establishment of fully non-parasitic populations, as the result of relaxation on selection for morphological (e.g., dentition, number of trunk myomeres; see Sect. 4.6.2.2) and developmental characters. The genetic basis of these traits is entirely unknown at present but will no doubt be elucidated in the future.

4.8 Conclusions

Early lampreys appear to have been small direct developers (i.e., with only gradual ontogenetic change occurring during development), with the characteristic larval "ammocoetes" stage and dramatic metamorphosis evolving later. The prolonged larval stage is now conserved among all extant lampreys, but there has been considerable diversification of life history types on two main axes related to post-metamorphic feeding and migration. The parasitic species delay sexual maturation until after the juvenile feeding phase, while the non-parasitic species initiate sexual maturation during metamorphosis and eliminate the parasitic feeding phase. All non-parasitic species are freshwater resident with the same post-metamorphic life span (~6–8 months) and similar body sizes (~110–150 mm TL) and fecundities (mean 1,770). In contrast, parasitic species are either anadromous or freshwater resident and vary widely in all three of these traits, presenting a continuum of trade-offs related to post-metamorphic growth opportunities that will increase an individual's reproductive output and the costs incurred while taking advantage of these opportunities. Duration of the parasitic feeding phase ranges from a single summer (3–4 months) to perhaps as much as 4 years, giving a post-metamorphic life span estimated to range from ~1.5–1.8 years to as much as ~4.5–5.8 years (i.e., accounting for the non-trophic periods of downstream and upstream migration). Body size at maturity ranges from ~125 mm in the freshwater Miller Lake lamprey to 800–900 mm in anadromous sea lamprey, and fecundity (which varies with the cubic power of TL) ranges from a few thousand to 150,000–300,000 eggs. The life history trade-offs associated with anadromy and freshwater residency have long been discussed in other fishes (e.g. Gross et al. 1988; Jonsson and Jonsson 1993, 2006; Fleming 1996), and those associated with the evolution of non-parasitism have been discussed in lampreys (e.g., Hubbs and Potter 1971; Potter 1980; Hardisty 2006). Nevertheless, there is much that we still do not know. Many of these knowledge gaps have been identified in the sections above. Here, we briefly highlight three of the overarching questions related to life history evolution in lampreys that remain to be answered; perhaps some of these questions will be answered by the next "update." Lampreys are becoming an important model for "evo-devo" research, helping to reconstruct some of the major events in the evolution of vertebrates (see Docker et al. 2015; McCauley et al. 2015; Chap. 6). With their conserved body form, but rich diversity of feeding and migratory types in replicate taxa, they are also an excellent model system for examining microevolutionary processes.

4.8.1 What are the Proximate Mechanisms Determining the Duration of the Parasitic Feeding Phase?

We do not yet know what factors prompt parasitic species to stop feeding and initiate sexual maturation or, conversely, to initiate sexual maturation and thus stop feeding. The relatively strict adherence to fixed maturation schedules in many lamprey species (e.g., anadromous sea lamprey and western river lamprey, most or all freshwater species) suggests that differences among species are "hardwired." However, intraspecific differences have been observed or inferred in other species (i.e., based on differences in size at maturation), and whether these differences have a genetic basis or whether cessation of the feeding phase is triggered by environmental or endogenous (e.g., body condition, growth rate) cues is unknown. In Pacific lamprey, the correlation between certain loci and body size (Hess et al. 2013, 2014) suggests at least some genetic component to size at maturity, but whether this is tied to differences in duration of the feeding phase or to other factors (e.g., metabolic efficiency, effectiveness in finding prey, habitat selection) is unknown. In sea lamprey, the transition to fresh water has involved a 1-year reduction in the duration of the parasitic phase (Bergstedt and Swink 1995), but whether this involved rapid evolution following colonization of large-bodied anadromous lamprey via canals, more gradual evolution following post-Pleistocene colonization, colonization via canals of smaller-bodied individuals already pre-adapted for feeding in a more confined environment, or phenotypic plasticity has yet to be resolved.

Factors controlling the onset of maturation have been studied in salmonids (e.g., to understand alternative male life history tactics and to reduce the incidence of precocious maturation in aquaculture settings; Paéz et al. 2011; Good and Davidson 2016). They are far from being fully understood, but it is clearly a complex situation. In Atlantic salmon, for example, the onset of maturation is governed by a variety of heritable, physiological, biochemical, and environmental cues and their interactions (Good and Davidson 2016). In one recent and exciting study, a single locus was found to have a highly significant role in age at maturation in Atlantic salmon (Ayllon et al. 2015). Four SNPs, including two mutations in the Vestigial Like Family Member 3 (*vgll3*) gene, explained 33–36% of the variation in age at maturation. Interestingly, a SNP in proximity to this gene in humans has been linked to age at puberty. Prince et al. (2017) found that premature migration in both Chinook salmon *Oncorhynchus tshawytscha* and steelhead was associated with mutations in the *GREB1L* locus, a paralog (i.e., arising during gene duplication) of the *GREB1* (Growth Regulating Estrogen Receptor Binding 1) gene. In a recent study in mice, *GREB1L* was found to be differentially regulated in neurons of the hypothalamic arcuate nucleus as a result of feeding versus fasting (Henry et al. 2015). Prince et al. (2017) suggested that the premature migration alleles arose from a single evolutionary event within each species and subsequently spread to other populations through straying and positive selection. Additional genomics studies are sure to further contribute to our understanding of the factors that control the onset of maturation in lampreys and other anadromous fishes.

4.8.2 What are the Proximate Mechanisms Underlying Non-parasitism?

When trying to unravel the genetic and developmental basis of non-parasitism in lampreys, it is harder to draw inspiration from genetic and genomic studies in other fishes. Since no other vertebrates are known to have a non-feeding adult stage, there would appear to be no obvious parallels to the evolution of non-parasitism. However, many other anadromous fishes (most conspicuously, semelparous Pacific salmon) cease feeding at sexual maturation. Because acceleration of sexual maturation at metamorphosis in brook lampreys results in the merging of metamorphosis with sexual maturation without an intervening feeding phase, non-parasitism may simply represent an extreme trade-off between size at maturity and mortality. Thus, the genetic mechanisms underlying this acceleration of sexual maturation may not be unique, and different life history trajectories (e.g., related to the phasing of gonadogenesis and differences in potential fecundity) may indeed be initiated well in advance of metamorphosis (Docker 2009; see Chap. 1). Pioneering genomic studies on different European river and brook lamprey populations have identified loci that differ between life history types (Mateus et al. 2013b; Rougemont et al. 2017; Hume et al. 2018), but interpretation of the results have been hampered by the difficulty in assigning a definitive function to these loci. Continuing improvements to the assembly and annotation of the sea lamprey genome (e.g., Smith et al. 2018) and developing genomic resources for other lamprey species will help these efforts. Furthermore, similar research in other species pairs will help determine the extent to which the genetic changes associated with non-parasitism are parallel among different independently derived species, and whether “brook lamprey alleles” exist (i.e., as standing genetic variation) within most parasitic lamprey populations. We predict that such alleles would be more common in those species or populations that most readily give rise to non-parasitic derivatives.

The “paired species problem” is definitely not unique to lampreys. A number of other postglacial fish species exhibit alternative migratory types or resource use polymorphisms that have arisen in parallel (within and among taxa) and fail to show reciprocal monophyly (see Taylor 1999; Docker 2009). Although taxonomic distinctions have been made between many of them in the past, most are now considered ecotypes of a single Linnaean species. This does not mean, of course, that ecotypes do not represent “evolutionarily significant units” (see Fraser and Bernatchez 2001) and certainly not that they are merely the product of phenotypic plasticity. There is now compelling evidence that European river and brook lampreys are partially reproductively isolated ecotypes (to variable degrees in different river systems) that nevertheless maintain distinct phenotypes in sympatry. However, we cannot assume that all paired species (or populations) will be the same, and it is important to avoid overly simplistic explanations. Major taxonomic revisions in lampreys at this point would be premature (see Chap. 7).

4.8.3 Can We Predict the Potential for Anadromous Lampreys to Become Invasive in Fresh Water?

In addition to its evolutionary significance, understanding the ease with which anadromous lampreys can become freshwater resident has important conservation and management implications. For example, large-bodied species of conservation concern (e.g., Pacific lamprey, anadromous sea lamprey, Caspian lamprey) are generally extirpated when dams prevent movement between upstream spawning habitats and the sea (see Maitland et al. 2015). This means that lamprey passage (e.g., Moser et al. 2015) or dam removal (e.g., Hogg et al. 2013) will be necessary when conservation is a priority. Alternatively, if a population is able to establish above the dams, selection will almost certainly lead to smaller-bodied, less fecund lampreys. Loss of anadromy is also detrimental where large-bodied anadromous forms are exploited for human harvest (e.g., Pacific lamprey by Native Americans) and through loss of marine-derived nutrients in freshwater systems (see Docker et al. 2015).

Conversely, successful establishment of anadromous lampreys in new inland water bodies could lead to serious management concerns, and it is important to be able to predict the potential for anadromous lampreys to become invasive in fresh water (i.e., which ones and where?). A non-anadromous Pacific lamprey-like form is already known to feed on an endangered sockeye salmon stock in Sakinaw Lake in British Columbia (COSEWIC 2016), and Farlinger and Beamish (1984) raised concerns regarding the possibility that Pacific lamprey could become freshwater resident in Babine Lake. If so, a major impact on salmon in this lake would likely result (see

Sect. 4.3.4.1). Establishment of both pink and coho salmon in the Great Lakes, despite previous views that these species require salt water for completion of their life cycle, makes it clear that we should “never say never” (see Sect. 4.4.3). Our discussions above and studies in other species suggest that standing genetic variation in the source population is important for rapid colonization of new environments and that the number of individuals that gain access to a new region will thus increase the chance of survival and establishment (e.g., Blackburn et al. 2015). Williamson (1996) coined the term “propagule pressure” (which incorporates estimates of the absolute number of individuals involved in any one invasion event and the number of such events) to predict species invasiveness. Although this suggests that a few large-bodied anadromous lampreys that undergo long migrations in manmade canals or are inadvertently transferred to fresh water would be unlikely to establish (i.e., if relying on freshwater alleles at relatively low frequency in the anadromous population), chances would increase if pre-adapted individuals show increased survival rates or preferential colonization (Briskie et al. 2017). Many anadromous lampreys appear capable of some parasitism in fresh water en route to sea (see Sect. 4.3.4.4), and some researchers have hypothesized that this feeding behavior can lead to adaptation to freshwater environments (Potter and Beamish 1977). Sea lamprey rapidly spread and soon reached pest proportions in the upper Great Lakes once access was permitted, and there is evidence of a secondary “landlocking” event in the upper Cheboygan River system (Johnson et al. 2016). Predicting the potential for further spread is important. Although sea lamprey depend on large productive lakes for establishment, there are several large inland lakes (e.g., Lake Nipigon in Ontario, 4,850 km^2) that could support sea lamprey if they were to gain access. Spread to Lakes Simcoe (745 km^2) and Winnebago (560 km^2), in Ontario and Wisconsin, respectively, is of particular concern. Two locks and a boat lift are the only obstacles on the Trent-Severn Canal between Lake Simcoe and Lake Huron, although they are maintained and operated to prevent movement of sea lamprey into Lake Simcoe. Lake Winnebago was connected to Lake Michigan via a chain of locks on the Fox River, but the lock system was closed in 1983 and a barrier was installed in 1988 (see Chap. 5). It is also important to ask if the likelihood of establishment in fresh water would increase with climate change or other ecosystem alterations (e.g., salmonid stocking or colonization by other invasive species). Expected climate-driven changes to the relative productivity of marine and freshwater systems, for example, are expected to alter the prevalence and distribution of anadromy in salmonids (Finstad and Hein 2012) and could similarly alter the relative benefits and costs of freshwater residency in lampreys.

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