Chapter 3
The Ecology of Larval and Metamorphosing Lampreys

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Abstract The life cycle of lampreys typically begins in streams where fertilized eggs hatch into small, wormlike larvae (ammocoetes) which burrow into soft stream bottoms where they filter feed on organic matter until the onset of metamorphosis. The relative importance of habitat variables can change with ammocoete size (and depending on the spatial scale measured), but habitat must provide adequate substrate for burrowing and a regular supply of the suspended organic matter upon which larval lampreys feed. Larval movement occurs significantly more often at higher densities and in warmer temperatures, and typically occurs in a downstream direction at night. Sex ratio of some lamprey species is often related to differences in larval density, with the proportion of males increasing with relative density. Larval mortality is thought to be high in the egg phase, immediately following hatching, and at metamorphosis. The duration of the larval period in the life cycle of lampreys has been found to vary among and within species, but generally ranges

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from 3 to 7 years. However, analyses of larval growth and duration of larval life have been hampered by the unreliability of age assessment methods for larval lampreys. Metamorphosis begins during the summer months, when water temperatures are the most favorable, and is completed by winter or early spring.

Keywords Age at metamorphosis · Feeding · Growth · Habitat · Larval density · Macrohabitat · Microhabitat · Movement · Sex ratio · Statolith

3.1 Introduction

Understanding the ecology and life history of larval and metamorphosing lampreys is important for the management of threatened or endangered lamprey species, as well as for control of the invasive sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes. The decline of many anadromous lamprey species (e.g., European river lamprey *Lampetra fluviatilis*, Pacific lamprey *Entosphenus tridentatus*, and sea lamprey in Europe) is often attributed to overharvest of adults and obstacles to their spawning migration (e.g., Almeida et al. 2002a, b; Mateus et al. 2012), but disruptions to larval habitat (e.g., pollution, irrigation and municipal water diversions, and other forms of habitat degradation) have also contributed to the decline of several species (e.g., Almeida et al. 2000; Luzier et al. 2011; see Chap. 8). Identifying—and protecting—critical larval habitat is thus necessary for species of conservation concern, whereas identifying—and targeting—critical larval habitat is necessary for sea lamprey control (see Marsden and Siefkes in press). Effective sea lamprey control also depends on accurately predicting larval growth and metamorphic rates in order to kill sea lamprey larvae in their natal streams before they become parasitic-phase juveniles (Christie et al. 2003; Hansen et al. 2003). Natural mortality is thought to be highest in early life and at metamorphosis, and studies of these life stages provide important information for both conservation and control.

In this chapter, we review ecological information regarding the larval stage of more than 20 of the approximately 40 recognized lamprey species worldwide (see Chaps. 1, 2 and 8). Following metamorphosis, 18 species are parasitic (in the ocean or in rivers or lakes) and the remaining species (the "brook lampreys") are nonparasitic (i.e., they do not feed at all following metamorphosis and become sexually mature, in their natal streams, within 6–10 months of metamorphosis; see Docker 2009). The ecology of the larval life stage, in contrast, seems more consistent among species.

A review of the ecology of the larval and metamorphosing stages of lampreys was provided by Hardisty and Potter (1971a, b), and subsequently updated by Potter (1980a). In recent years, however, targeted sampling for lampreys with improved electrofishing gear (especially in concert with efforts to monitor larval sea lamprey populations in the Great Lakes), statolith aging techniques, and the use of molecular markers have led to advances in our knowledge regarding larval abundance, distribution, habitat requirements, feeding, growth rates, duration of larval life, and possible compensatory mechanisms affecting growth, survival, and recruitment dynamics. This chapter therefore provides an updated synthesis of the ecology of the largely sedentary, stream-resident stage of the life cycle terminating with the outmigration of juveniles. The process of metamorphosis (e.g., the morphological and physiological changes that occur during metamorphosis, and the intrinsic and extrinsic factors triggering it) is covered in depth in another chapter (see Chap. 4). In our discussion, we will refer to larval lampreys (beginning after hatching and ending prior to metamorphosis) as larvae or ammocoetes. Lampreys that are in the process of metamorphosis are referred to as transformers, while lampreys that have completed metamorphosis but are not yet sexually mature will be referred to as juveniles. Lampreys that have reached sexual maturity will be referred to as adults. The chapter will focus on what we have learned about the ecology of larval and metamorphosing lampreys since 1980, including recently emerging topics and techniques which have advanced our knowledge.

3.2 Habitat

Although it has long been possible for "an experienced observer" to predict "with some accuracy" the location of larval lamprey populations within a river system (Hardisty and Potter 1971a), considerable efforts continue to be made to characterize, in precise physico-chemical terms, the essential features of larval lamprey habitat. The international control program for the invasive sea lamprey in the Laurentian Great Lakes ranks streams for lampricide treatment in part on electrofishing catches in the best available lamprey habitat; thus, the ability to define larval lamprey habitat is critical for successful sea lamprey control (Jones 2007). The need for conservation of many other lamprey species has resulted in calls for status assessment using standardized sampling methods, with the first step in assessing ammocoete abundance being the classification and quantification of habitat within the study area (Kirchhofer 1995; Harvey and Cowx 2003; Moser and Close 2003).

Larval lamprey distribution and abundance has long been studied at the microhabitat scale, and recent studies further quantify these factors and test the generality of previous observations in a range of lamprey species. These small-scale studies of larval lamprey habitat have been useful for developing a general understanding of the biology of lampreys. However, since the conservation and management of lamprey populations requires the ability to predict spatial patterns in larval abundance at several scales (Torgersen and Close 2004), other recent studies are evaluating lamprey abundance at multiple scales. Furthermore, examining how abundance is affected by factors on only one scale ignores the modifying effects of factors operating on other scales (Goodwin et al. 2008). Therefore, both microenvironmental and macroenvironmental factors are discussed below.

3.2.1 Microenvironmental Factors as Indicators of Ammocoete Habitat

Lamprey larvae generally occur in soft, burrowable substrates of fine sands, low current velocity, and some amount of organic detritus (e.g., Applegate 1950; Hardisty and Potter 1971a), and these qualitative observations form the basis of the habitat type classification used by sea lamprey control personnel and other lamprey biologists: Type I (preferred) habitat is located primarily in depositional zones and consists primarily of a mixture of sand and fine organic matter; Type II habitat (which is sometimes inhabited by larvae but at much lower densities) generally consists of shifting sand that may contain some gravel; and Type III (unacceptable) habitat consists of such substrates as hard packed gravel, hardpan clay, and bedrock (Slade et al. 2003). Mullett (1997) found that 93 % of sea lamprey larvae in Great Lakes tributaries were found in Type I habitat, and this qualitative classification system has become an effective tool in the assessment of larval lamprey habitat (e.g., Torgersen and Close 2004; Zerrenner and Marsden 2005; Neeson et al. 2007). Research continues, however, to quantify the microhabitat factors affecting lamprey distribution and abundance. Although multiple factors affect lamprey distribution and abundance in concert, those deemed to be most important are reviewed individually below. Water depth, water chemistry, and thermal and oxygen requirements are reviewed with macroenvironmental factors (Sect. 3.2.2).

3.2.1.1 Substrate Size and Depth

The availability of optimal substrate particle size is one of the most important factors limiting the distribution of larval lampreys (Hardisty 1979; Kainua and Valtonen 1980; Malmqvist 1980; Morman et al. 1980; Potter 1980a; Lee 1989; Young et al. 1990a, b; Todd and Kelso 1993; Beamish and Jebbink 1994; Ojutkangas et al. 1995; Beamish and Lowartz 1996; Sugiyama and Goto 2002; Goodwin et al. 2008; Table 3.1). As reviewed by Potter (1980a), Manion and McLain (1971) found sea lamprey larvae to be most abundant where 90 % of the substrate consisted of sand particles less than 0.5 mm in diameter. In the European brook lamprey *Lampetra planeri*, Malmqvist (1980) likewise observed only a small number of larvae where particle diameter exceeded 0.5 mm. More recent studies, in other species, have made similar observations. Potter et al. (1986) found density of larval pouched lamprey *Geotria australis* to be greatest in medium sand (0.2–0.6 mm diameter); in American brook lamprey *Lethenteron appendix*, larval density was related to the presence of medium-fine sand (0.15–0.25 mm: Beamish and Lowartz 1996). Beamish and Jebbink (1994) reported that abundance of southern brook lamprey *Ichthyomyzon gagei* was greatest when particles smaller than 0.15 and 1.0–2.0 mm in diameter represented at least 40 and 8 % dry weight of the substrate, respectively, and was lowest when the small particles represented less than 10 % dry weight of the substrate. Taverny et al. (2012) reported that sea lamprey and European river/brook lamprey larvae were found most frequently in fine/medium sand (0.05–0.6 mm diameter) and medium/coarse sand (0.2–2 mm diameter), respectively. In their study, 95 % of all ammocoetes (of both species) were collected in sandy substrate, and silt was generally absent or very low at these locations. In a laboratory study, larval least brook lamprey *Lampetra aepyptera* were given a choice of six equally-available substrate types; they selected fine sand (0.125–0.5 mm diameter) 52.2 % of the time (i.e., disproportionately to its availability; Smith et al. 2011). Although there may be subtle differences in preferred substrate particle size among species—for example, Goodwin et al. (2008) and Taverny et al. (2012) suggested that European river and brook lamprey larvae might be associated with somewhat coarser sands than other species—substrate requirements appear similar among species and, in fact, multiple species are often found at the same sites (Hardisty and Potter 1971a; Dawson and Jones 2009).

An appropriate river substrate is an essential environmental characteristic for the development of larval lampreys, not only because it allows burrow construction, but also because it helps to maintain a vital water flux. The detritivorous larvae depend on a unidirectional flow of water through their branchial chamber for the provision of food and exchange of respiratory gases and metabolic wastes (Hardisty and Potter 1971a). Fine sand (or the combination of particle sizes observed by Beamish and Jebbink 1994) appears to be optimal for burrow construction and water flow. Finer particles (e.g., clay and silt) are more compact and difficult to burrow into, and could potentially smother existing burrows or clog the gill lamellae of the ammocoetes. In contrast, large particles (e.g., coarse sand or gravel) could be too heavy for larvae to move or too large to be adequately held together by mucous secretions (Beamish and Jebbink 1994; Beamish and Lowartz 1996; Smith et al. 2011).

Protection from predators will also depend on the speed with which ammocoetes can burrow and on burrow depth, which will be affected by substrate composition and depth. Smith et al. (2012) demonstrated, in experimental trials, that depredation by yellow bullhead *Ameiurus natalis* was lowest where least brook lamprey larvae were able to burrow into fine sand; survival in fine sand averaged 80 % whereas survival averaged 58 % in coarse sand and only 4 % in silt/clay. Ammocoetes showed the slowest burrowing times in the silt/clay substrate and were observed swimming outside their burrows when provided only with this substrate. Burrowing times in larval sea and least brook lampreys are faster in fine sand compared to coarse sand (Quintella et al. 2007; Smith et al. 2012). Deeper burrows would also be expected to offer greater protection from predators, and the depth to which ammocoetes can burrow might be limited in silt/clay or coarse sand substrates and will, of course, be limited in more shallow substrates. European river and brook lamprey larvae in Northern Ireland were more abundant when sediment depth was > 11.5 cm (Goodwin et al. 2008). Sugiyama and Goto (2002) found that Far Eastern brook lamprey larvae *Lethenteron reissneri* were more likely to be found where substrate depth was > 2 cm, but noted in an experimental trial that only large larvae showed a significant preference for deeper substrate (see Sect. 3.2.3). Presumably, larger ammocoetes require deeper burrows to completely hide from predators.

3.2.1.2 Water Velocity

In most studies that have defined optimal ammocoete habitat on small spatial scales, substrate grain size and water velocity were the most important indicators of larval lamprey abundance (Malmqvist 1980; Beamish and Jebbink 1994; Beamish and Lowartz 1996; Almeida and Quintella 2002; Sugiyama and Goto 2002; Table 3.1), and the two factors, of course, are interrelated. The size of substrate particles that are eroded, transported, or deposited at a specific location depends upon local hydraulic conditions, primarily boundary shear stress (Allen 1984). Typical ammocoete habitat is an area protected from major fluctuations in water levels or stream flow, and where current velocity is usually slow. Such conditions are commonly found in eddies, backwaters, or at bends in a river, where accumulations of silt and sand provide suitable substrate for burrowing ammocoetes.

Areas of high abundances of pouched and landlocked sea lamprey larvae are normally found in regions of the river where current velocity is less than 0.03 m/s (Thomas 1962; Potter et al. 1986), and Thomas (1962) concluded that flow rates of 0.6–0.8 m/s represented an upper limit for sea lamprey larvae. The maximum near-bottom velocity where anadromous sea lamprey larvae occurred in the Gironde-Dordogne River basin did not exceed 0.3 m/s (Taverny et al. 2012). Optimal velocity for *Lampetra* larvae (i.e., European river or brook lamprey larvae) in the same river system was up to 0.05 m/s, but larvae occurred in sites where velocity was as high as 0.5 m/s (Taverny et al. 2012). These rates of flow are highly consistent with those from previous studies of European river lamprey in Finland, where larval habitat was characterized by water velocities ranging from 0.01–0.05 m/s to about 0.5 m/s (Kainua and Valtonen 1980). Small larvae were proportionally more numerous in habitats where the flow was rapid and, where larvae were found in shallow water, the rate of flow was almost constantly below 0.1 m/s (Kainua and Valtonen 1980). Stone and Barndt (2005) reported optimal velocities of 0–0.1 m/s for Pacific lamprey ammocoetes in a Washington stream. Torgersen and Close (2004) indicated that larval Pacific lamprey require habitat containing adequate flow that is sufficient to provide a stable food supply, but slow enough to allow sediment deposition required for burrowing. Habitats that supported larval Arctic lamprey *Lethenteron camtschaticum* were characterized as having predominantly silt or sand substrates with woody debris and slow flow (0.0–0.1 m/s) (Trent M. Sutton, University of Alaska, Fairbanks, AK, personal communication, 2011). Far Eastern brook lamprey larvae were positively associated with areas where water velocity was less than 0.1 m/s (Sugiyama and Goto 2002).

3.2.1.3 Organic Matter in the Sediment

Whereas substrate particle size and water velocity are consistently considered two of the most important fine-scale predictors of larval lamprey abundance, the importance of organic matter in the sediment is less clear. Organic detritus is generally deposited in areas of slow flow where accumulations of silt and sand provide suit-

Table 3.1 Summary of past research on larval lamprey habitat selection. Variables listed are those considered more important for adequate larval lamprey habitat at different spatial scales. (Adapted from Smith 2009)

Species	Variables	Study type	Reference
Entosphenus tridentatus, Pacific lamprey	Water depth/open riparian canopy/current (slow), pool habitats/substrate type	Field study	Torgersen and Close (2004)
Entosphenus tridentatus	Large scale: conductivity/dissolved oxygen/gradient Small scale: wetted width/percent fine sediment/canopy density/water velocity	Field study	Stone and Barndt (2005)
Entosphenus tridentatus	Substrate (fine-medium)/riparian shade	Field study	Claire et al. (2007)
Entosphenus macrostomus, Vancouver lamprey	Substrate (fine sediment on top of fine sand and small gravel, where overlaying silt < 10 cm)	Field study	Beamish and Wade (2008)[a]
Geotria australis, pouched lamprey	Substrate (particle size, depth)/organic material/chlorophyll α/shade/macrophyte roots/eddies, water velocity	Field study	Potter et al. (1986)
Geotria australis	Substrate/water depth	Field study	Kelso and Todd (1993)
Geotria australis	Substrate (fine sand)/shade/run habitat	Field study	Jellyman and Glova (2002)
Ichthyomyzon fossor, northern brook lamprey	Substrate (silt-sand)/current (slow)	Field study	Reighard and Cummins (1916)
Ichthyomyzon fossor	Substrate (fine sand)/organic debris	Field study	Leach (1940)
Ichthyomyzon fossor	Organic sediment	Field study	Yap and Bowen (2003)
Ichthyomyzon gagei, southern brook lamprey	Organic debris	Field study	Dendy and Scott (1953)
Ichthyomyzon gagei	Substrate (medium-fine sand)	Field study	Beamish and Jebbink (1994)
Lampetra aepyptera, least brook lamprey	Clay/silt/fine sand	Field study	Seversmith (1953)
Lampetra aepyptera	Substrate (fine sand)	Lab experiment	Smith et al. (2011)
Lampetra fluviatilis/*Lampetra planeri*, European river and brook lampreys	Substrate (coarse sand)/pH (≥ 8.2)	Field study	Goodwin et al. (2008)
Lampetra fluviatilis/*Lampetra planeri*	Substrate (coarse-medium sand)/water depth/current (slow)/macrophyte roots	Field study	Taverny et al. (2012)
Lampetra fluviatilis/*Lampetra planeri*	Altitude (< 170 m)/distance to coast (< 150 km)/substrate (> 70 % sand)/ maximum temperature of warmest month/precipitation of driest month	Field study	Ferreira et al. (2013)

Table 3.1 (continued)

Species	Variables	Study type	Reference
Lampetra planeri	Current (slow)/water depth (low)/substrate/chlorophyll α content (low)	Field study	Malmqvist (1980)
Larval lampreys in general	Stream gradient/substrate (silt-sand)/current (slow)/organic debris	Review	Hardisty and Potter (1971a)
Larval lampreys in general	Current (0.4–0.5 m/s)/substrate (silt and sand)	Field study	Hardisty (1979)
Lethenteron appendix, American brook lamprey	Substrate (medium-fine sand/organic content)	Field study	Beamish and Lowartz (1996)
Lethenteron appendix	Substrate (medium-fine sand)	Lab experiment	Lee (1989)
Lethenteron appendix	Substrate/distance from alluvial fans (close)/thermocline (above)/water depth (low)	Field study	Lee and Weise (1989)[a]
Lethenteron appendix	Substrate (medium-fine sand)	Field study	Mundahl et al. (2006)
Lethenteron camtschaticum, Arctic lamprey	50–150 mm TL: substrate hardness/DOM 10–50 mm TL: soft substrate/velocity	Field study	Shirakawa et al. (2009)
Lethenteron reissneri, Far Eastern brook lamprey	Substrate (fine sand-silt)/current (slow)/depth (shallow)	Field study, lab experiment	Sugiyama and Goto (2002)
Lethenteron reissneri	Substrate (medium-fine sand)	Field study	Yamazaki (2007)
Petromyzon marinus, sea lamprey	Substrate (medium-fine sand)	Lab experiment	Lee (1989)
Petromyzon marinus	Substrate (sand)	Field study	Young et al. (1990a)
Petromyzon marinus	Substrate (silt-sand)	Field study	Young et al. (1990b)
Petromyzon marinus	Substrate (sand)	Field study	Almeida and Quintella (2002)
Petromyzon marinus	Substrate/distance from stream mouth/slope of the lake	Field study	Fodale et al. (2003)[a]
Petromyzon marinus	Substrate (sand/fine organic matter)	Field study	Slade et al. (2003)
Petromyzon marinus	Geomorphic features (river slope, radius of curvature)	Field study	Neeson et al. (2007)
Petromyzon marinus	Substrate (fine-medium sand)/water depth (>2 m)/current (slow)/macrophyte roots	Field study	Taverny et al. (2012)

[a] lentic habitat

able substrate for burrowing ammocoetes and, in several studies (e.g., Shirakawa et al. 2009), larval abundance is related to substrate composition, water velocity, and dissolved organic material as predicted. Certainly, the presence of fine organic matter is one of the attributes of Type I (preferred) larval lamprey habitat (see Sect. 3.2.1). Potter et al. (1986) likewise found the presence of organic material in the substrate to be an important environmental variable predicting the density of larval pouched lamprey in three of their four seasonal models (i.e., in all seasons but winter). In their habitat selection study, Smith et al. (2011) found that—after their preference for fine sand—least brook lamprey larvae exhibited a secondary preference for an organic substrate (consisting of approximately 70 % decomposing leaves/stems and organic sediment particles and 30 % silt/fine sand). In contrast, Malmqvist (1980) found that water current, water depth, substrate size, and chlorophyll α content explained a large part of the variation in distribution of larval European brook lamprey, but found that organic content in the sediment did not improve his discriminant model. Organic content was not even correlated with larval density when simple linear regression was applied. Malmqvist (1980) thus suggested that the presence of organic material in the sediment is not a prerequisite for the larvae since they can ingest their food directly from the water column above the sediment. Sugiyama and Goto (2002) likewise found that habitat use by Far Eastern brook lamprey larvae was not influenced by the amount of fallen leaves. Rather than interpreting these findings to mean, however, that the presence of organic material in the sediment is not a prerequisite for larval lampreys, these authors suggested that the amount consumed by larvae is low relative to the amount generally present in larval streams (i.e., that organic detritus may exceed the necessary threshold to sustain larval growth in all but the most oligotrophic streams; see Sects. 3.2.1.4 and 3.3).

Although less well studied, there is also a lack of consensus on the relationship between chlorophyll α content of the sediment and larval abundance. Potter et al. (1986) found that substrate chlorophyll α content (presumably reflecting the relative amounts of diatoms and other microalgae in the sediment) contributed to their model in a positive manner in spring, summer, and autumn. This finding was not surprising to these authors, as diatoms and other microalgae form an important component of the diet of larval lampreys (see Sect. 3.3). In contrast, however, Malmqvist (1980) found a negative correlation between chlorophyll α content and larval abundance, and suggested that sites where chlorophyll α content is high may be subject to lowered oxygen levels at night as the result of increased algal respiration.

3.2.1.4 Patchiness at Small Spatial Scales

As expected, given the patchy distribution of the above features within and among river systems, ammocoetes are patchily distributed at both small and large spatial scales. At a small spatial scale, for example, Torgersen and Close (2004) found considerable variation in the occurrence of Pacific lamprey larvae among 1-m^2 quadrat samples distributed throughout a 55-km section of the Middle Fork John Day River, Oregon. At this scale, patchiness was associated with low water velocity and substrate type, as expected, and with channel morphology. Larval abundance was heterogenous across the stream channel, with over 80 % of the larvae being found along the stream margins. Several other studies have also reported ammocoetes aggregated at stream margin areas of fine silt and detritus (Farlinger and Beamish

1984; Brown and Moyle 1993; Roni 2002; Torgersen and Close 2004; Gunckel et al. 2009).

Patchiness at even finer scales has also been reported within habitat types. As expected, northern brook lamprey *Ichthyomyzon fossor* larvae in three oligotrophic Great Lakes tributaries were more abundant in Type I than Type II habitats (see Sect. 3.2.1), but they also showed a high degree of aggregation within habitat types (Yap and Bowen 2003). Within Type I habitats, larvae were generally aggregated at sites where obstacles to flow (e.g., stones or woody debris) caused localized accumulation of flocculent material (Yap and Bowen 2003); the authors referred to these sites as "Type Ia" habitat. These authors found that assimilation efficiency for organic matter and amino acids was higher in Type Ia habitat and that these larvae have higher condition factors (weight per length). Although the benefit of Type Ia habitats may not be as great in eutrophic streams (Yap and Bowen 2003), potential differences in habitat quality at such a fine scale are very interesting.

3.2.2 Macroenvironmental Factors as Indicators of Ammocoete Habitat

Patchiness is also evident at larger scales. Sea lamprey larvae, for example, have been detected in only 449 of the 5,747 (less than 8 %) Great Lakes tributaries (Morman et al. 1980; Heinrich et al. 2003; Larson et al. 2003; Lavis et al. 2003; Morse et al. 2003; Sullivan 2003), despite the widespread distribution of adults throughout the Great Lakes. In Portugal, Ferreira et al. (2013) found *Lampetra* sp. larvae in 8 of the 15 basins (53 %) and 60/401 sites (15 %) surveyed. Lamprey distribution is ultimately influenced, of course, by the interaction between small-scale and large-scale habitat variables, and more studies are beginning to examine the effect of such variables over a range of spatial scales. The existence of suitable microhabitats for ammocoete colonization is dependent on larger-scale processes (e.g., stream gradients determine the overall velocity of the current, the type of substrate particles that are deposited, and the accumulation of organic debris; Hardisty and Potter 1971a). Climatic factors (e.g., temperature) may limit lamprey distribution in some cases (particularly at the northern or southern limit of the species' distribution). Other variables such as water depth, proximity to adult spawning areas, and riparian canopy can also be important indicators of larval lamprey abundance on moderate to large spatial scales (Almeida and Quintella 2002; Torgersen and Close 2004).

3.2.2.1 Gradient and Other Geomorphic Variables

Broad-scale distribution patterns of larval lampreys have long been attributed to variation in channel gradient within and among streams (e.g., Baxter 1957), and Young et al. (1990a) suggested that gradient could serve as a useful "surrogate variable" for the suite of environmental factors that describe optimal larval habitat.

However, whereas measurements of substrate particle size and water velocity seem to be rather consistent among studies (see Sects. 3.2.1.1 and 3.2.1.2), stream gradients reported for different lamprey streams and species appear more variable. For example, stream gradient for sea lamprey streams in England was found to range between 5.0 and 14.5 m/km, which allowed for good spawning habitat in the upper reaches and depositional areas for larval habitats downstream (Baxter 1954). Stream gradients measured by Dawson and Jones (2009) in four sea lamprey-producing Great Lakes tributaries were found to fall within this range. Similarly, Hardisty (1986) reported average stream gradients of 17.7 and 8.3 m/km, respectively, for European brook lamprey in the upper reaches of the Jeziorka River in Poland and Ukrainian brook lamprey *Eudontomyzon mariae* in the lower reaches. However, there are also many reports of lampreys occurring in lower-gradient streams. For example, *Lampetra* larvae have been found in streams in Finland with average gradients of about 2 m/km (Hardisty 1986), and European brook lamprey in the River Yeo in England occur where the stream gradient is 1.9–3.8 m/km (Hardisty 1961a). In a western Washington stream, Stone and Barndt (2005) found that Pacific lamprey abundance per reach was negatively associated with stream gradient. There may, of course, be differences among species—Gunckel et al. (2009), for example, found that Pacific lamprey were more likely to occur in relatively wider, lower-elevation streams than were western brook lamprey *Lampetra richardsoni*—and it is becoming clear that the relationship between stream gradient and lamprey distribution will depend on the scale at which gradient is measured (Torgersen and Close 2004).

Neeson et al. (2007) attempted to predict the distribution of suitable larval sea lamprey habitat at several spatial scales using water surface slope (as measured in the field) and GIS-derived geomorphic values within the East Branch of the Chagrin River, Ohio. Of the five geomorphic variables tested, field-measured slope and GIS-derived radius of curvature influenced the probability that a stream segment would contain suitable ammocoete habitat (i.e., Type I or Type II habitat; see Sect. 3.2.1) at a stream segment length of 50 m. Organic content was significantly higher in low-slope (≥ 0.005 or 5 m/km) areas compared to high-slope (>0.005) areas. GIS-estimated slopes were not sufficiently accurate at this scale, so the final model included only radius of curvature (to allow habitat categorization using only GIS). At longer stream segment lengths (100, 200, 300 m), however, no relationships between geomorphic variables and presence of ammocoete habitat were observed (Neeson et al. 2007). Fine sediments accumulate immediately downstream of sharp bends, which is consistent with radius of curvature affecting habitat characteristics only on a local scale. In terms of slope, Neeson et al. (2007) suggested that, at coarse scales, alternating channel units of varying slope (e.g., pools and riffles) would obscure a finer-scale association between slope and habitat. In contrast, Torgersen and Close (2004) suggested that the relative influence of channel gradient as a predictor of Pacific lamprey larval abundance might increase at larger spatial scales because of changes in bedform morphology at the stream segment or network scale. These authors found that channel gradient corresponded with large-scale larval abundance patterns, but was not an important predictor of adundance after accounting for water depth and extent of the riparian canopy (see Sects. 3.2.2.1 and 3.2.2.3).

Ferreira et al. (2013) likewise found that GIS-derived slope did not improve the performance of their model predicting the distribution of European river and brook lamprey larvae in Portugal at a macrospatial scale. However, in this study, altitude was the strongest predictor of larval distribution, and altitude is generally correlated with gradient or slope. Predicted occurrence of larvae peaked at low altitudes (<170 m), before tailing off at higher elevations. The two other geomorphological variables that explained most of the variation in the distribution of these species was distance to coast and percentage of sand (at a resolution of 1 km^2). The distance upriver at which larval abundance peaked varied, depending on the size of the river basins, but was within 150 km from the coast. Microhabitat characteristics that are favorable for larval lampreys (e.g., low current velocity, preferred substrate) are more prevalent in the downstream reaches of the rivers. Neeson et al. (2012a) similarly found that distance to the river mouth was an important geomorphic predictor of the prevalence of preferred substrate habitat of Great Lakes sea lamprey in the Lower Peninsula of Michigan. In most cases, distance to the river mouth was negatively related to preferred substrate habitat, reflecting the increasing gradient in particle size from a river's mouth to its headwaters. These authors also found that distance to the nearest upstream dam or lake was likewise negatively related to preferred subtrate habitat, reflecting the general lack of fine sediments found below impounded lakes and, to a lesser degree, natural lakes (Neeson et al. 2012a).

Barriers to migration are also more prevalent with increasing distance from the river mouth. Goodwin et al. (2008) found that abundance of European river and brook lamprey larvae was inversely related to the distance upstream and the number of potential barriers, at least at the catchment level. At smaller (microhabitat) scales, larval abundance was most associated with substrate particle size and depth and, at the larger (regional) scale, abundance was associated with stream pH (see Sect. 3.2.2.4).

3.2.2.2 Water Depth

The association between water depth and larval abundance may also differ depending on the spatial scale considered. Previous studies suggest that the most favorable habitat conditions are usually found in shallow water near the edge of the river (Hardisty and Potter 1971a; Malmqvist 1980). Several recent studies likewise report maximum larval abundance or occupancy in shallower waters: Sugiyama and Goto (2002), for example, found more Far Eastern brook lamprey larvae where water depth was <30 cm; Stone and Barndt (2005) generally found Pacific lamprey ammocoetes in areas where water depth was 70 cm deep; and Taverny et al. (2012) found that European river and/or European brook lamprey larvae preferentially used shallow waters (<50 cm deep) and were rarely found above a depth of 150 cm. At a larger scale, however, Torgersen and Close (2004) found that larval abundance increased with water depth, likely because reaches containing large numbers of deep pools were structurally complex and more likely to protect larvae from scouring and other forms of flow-induced stress. In addition to possible differences due to scale, other discrepancies may be related to larval size (e.g., with larger larvae being found in deeper waters; see Sect. 3.2.3) or species. Taverny et al. (2012), for example, found maximal occurrence of sea lamprey larvae in the Gironde-Dordogne River basin at depths >2 m, whereas *Lampetra* larvae generally occurred at much shallower depths. There may also be seasonal effects; Potter et al. (1986) found that pouched lamprey larval density was greater in shallower waters in the summer, but was greater in deeper waters in the winter. These authors explained this anomaly by suggesting that the geomorphology of this stream (which lacked a flood plain and was instead contained within a steep-sided U-shaped gutter) resulted in desirable substrate being deposited in deeper water in the winter when water levels and flow rates are high. Notably though, the water depth in the winter (2–71 cm) was still relatively shallow.

Furthermore, although larvae are most frequently captured in shallow ("wadeable") waters, they have also been found in relatively deep water. Sea lamprey ammocoetes have been documented in deepwater habitats in tributaries of the Great Lakes and in proximity to river mouths (Hansen and Hayne 1962; Wagner and Stauffer 1962; Lee and Weise 1989; Bergstedt and Genovese 1994). In Lake Superior, for example, it is thought that periodic floods scour the lower portions of the tributaries and flush sea lamprey larvae into the lake (Fodale et al. 2003). Although the majority of larvae located in lentic environments are likely due to downstream drift, Vancouver lamprey *Entosphenus macrostomus* (and occasionally other species) have been observed spawning in these environments (R. J. Beamish 1982; Russell et al. 1987; see Chap. 6). Use of deepwater sampling equipment such as suction dredges (e.g., Beamish and Youson 1987; Taverny et al. 2012) and deepwater electrofishers (e.g., Bergstedt and Genovese 1994; Jolley et al. 2012) are increasingly detecting larval and metamorphosing lampreys in deep water in large river systems as well. Metamorphosing North American river lamprey *Lampetra ayresii* are frequently recovered during dredging operations in the Fraser River, British Columbia (Beamish and Youson 1987), and, as noted above, sea lamprey larvae have been captured in the Gironde-Dordogne River basin in France at depths >2 m (Taverny et al. 2012). Recent studies of occupancy and habitat use by Pacific lamprey and *Lampetra* spp. in deepwater areas of the mainstem Willamette and Columbia rivers of the Pacific Northwest, found larval lampreys were widespread in a variety of habitats in depths up to 16 m (Silver et al. 2008; Jolley et al. 2012, 2013). Larvae were of a variety of sizes, suggesting multiple age classes and the ability of ammocoetes to disperse considerable distances. Other anecdotal observations exist regarding larval Pacific lamprey occurrence in large river mainstem habitats, mainly at hydropower facilities or in downstream juvenile bypass reaches (Moursund et al. 2003; Columbia River Inter-Tribal Fish Commission 2008), impinged on juvenile bypass screens, or through observation during dewatering events (Hammond 1979; Moursund et al. 2003; Dauble et al. 2006; Columbia River Inter-Tribal Fish Commission 2008). Occurrences of larvae at hydropower facilities are generally thought to be associated with their downstream movement (see Sect. 3.5). References to other species occurring in deepwater or lacustrine habitats are scarce but examples may include the silver lamprey *Ichthyomyzon unicuspis* (Cochran and Lyons 2004) and Miller Lake lamprey *Entosphenus minimus* (Lorion et al. 2000).

As the collecting effectiveness of backpack electrofishing gear significantly declines as water depth increases (Steeves et al. 2003), estimates of larval populations in deepwater and lentic areas have been made using deepwater electroshockers equipped with a pump to move emerging larvae to the surface for collection (Bergstedt and Genovese 1994). For lampreys of conservation concern, a deepwater electroshocker was developed by Mueller et al. (2012) to reduce handling of larvae while determining their presence-absence with an optical camera in habitats up to 8 m deep. A remote seabed classification device has been used to identify potential larval sea lamprey habitat in a deepwater lentic area of Batchawana Bay, Ontario, which was then sampled with a deepwater electrofisher (Fodale et al. 2003). The authors found that, in this lentic environment, the presence of larvae was significantly related to substrate type, distance from the stream mouth, and slope of the lake bottom (Fodale et al. 2003). Ammocoetes were not found at depths greater than 15 m, however, and this absence was not explained by either substrate particle size distribution or thermal acclimation (Lee and Weise 1989). Lee and Weise (1989) therefore suggested that gross lentic habitat selection revolves around the nearshore distribution of food particles and the interdiction of the thermocline. Preliminary data collected on Great Lakes larval sea lamprey inhabiting three lentic areas indicate that growth and transformation rates of larvae in lentic areas are comparable to stream resident larvae (Nicholas S. Johnson, U.S. Geological Survey, Hammond Bay Biological Station, Millersburg, MI, personal communication, 2014). Given the potential importance of deepwater and lacustrine larval rearing habitat in some systems, the dredging of large rivers and river mouths for navigation may represent a significant but underappreciated loss of larval lamprey habitat for species of conservation concern (see Chap. 8) whereas in the invasive sea lamprey, these areas may contribute substantially to the production of parasitic juveniles (Fodale et al. 2003). The relative importance of these deepwater habitats should be studied further.

3.2.2.3 Riparian Canopy

The importance of riparian canopy as an indicator of larval lamprey abundance may also vary depending on the spatial scale examined (Almeida and Quintella 2002; Torgersen and Close 2004). At smaller spatial scales, larval abundance appears to increase with the presence of riparian cover. Removal of riparian vegetation is thought to have contributed to the declines observed in some lamprey species (e.g., northern brook lamprey; Fortin et al. 2007). This may be due to a loss of shade, since evidence suggests that ammocoetes are photophobic (Potter and Rogers 1972). Although Malmqvist (1980) did not find a significant relationship between amount of shade and abundance of European brook lamprey, Potter et al. (1986) found significant relationships between the density of larval pouched lamprey and the degree of low-angle shading (positive) and light intensity (negative) in at least two of their seasonal models. Where burrowable habitat is found, often partially shaded by trees, diatoms may also form an incrustation on the interface between the silt and the water, probably contributing to the stability of larval microenvironments (Hardisty 1979). At larger spatial scales, Neeson et al. (2012a) found the amount of preferred sea lamprey habitat to be positively associated with the amount of forest in the riparian corridor. A negative correlation is expected between the amount of preferred larval substrate habitat and the sediment transport rate (Neeson et al. 2012a), and empirical studies describe the negative correlation between forested landscapes and sediment transport rates (Milliman et al. 1987). However, Torgersen and Close (2004) found that larval Pacific lamprey abundance was positively associated with an open riparian canopy. They observed exceptionally high larval density (>100 larvae/m^2) in the most exposed sites. Qualitative observations by Kan (1975) also indicated a negative association between abundance of this species and a closed riparian canopy, and suggested that this effect might be related to decreased primary productivity. Autumnal thinning of the riparian canopy was concluded to be the cause of increased primary algal productivity observed by Sutton and Bowen (1994), which coincided with a September peak in diet ash-free dry mass, and in assimilation efficiency for both ash-free dry mass and amino acids for northern brook lamprey in three oligotrophic Great Lakes streams. However, Arctic lamprey feeding on fallen leaf material had greater increases in mass than those on a diet of algae (Shirakawa et al. 2009), and the relative importance of such nutrient input from the canopy is not known.

3.2.2.4 Water Chemistry

Relatively few studies have found that water chemistry (e.g., conductivity, pH) is important in limiting larval lamprey distribution (Hardisty and Potter 1971a) although, as pointed out by these authors, this does not imply that such factors are not important, but only that they likely do not reach limiting values within the type of habitats where ammocoetes generally occur (i.e., where other factors are favorable). More recently, Goodwin et al. (2008) found that European river lamprey and European brook lamprey ammocoete abundance at a regional scale (i.e., across Northern Ireland), was associated with pH (Goodwin et al. 2008); sites with pH > 8.16 yielded more ammocoetes (9.5 per site) compared to those with lower pH (2.6 ammocoetes per site). These authors caution, however, that this relationship may be partly the result of differences in climate, bedrock type, land use, and watershed capacity, which in turn may influence pH. Nevertheless, water chemistry has been observed to affect larval growth. Young et al. (1990a) found that streams with higher conductivity (i.e., hardwater streams) were associated with larger sea lamprey larvae at age 2+ and found that conductivity was correlated with total phosphorus and alkalinity. Hardwater streams generally have greater productivity than softwater streams, and presumably provide a greater amount of food to larval lampreys (see Sect. 3.3). Interestingly, water chemistry differences among streams or sets of streams (i.e., in the elemental composition of the water) may provide stream- or watershed-specific statolith signatures that allow stream of origin to be determined in Great Lakes sea or other lampreys (see Sect. 3.2.4).

3.2.2.5 Thermal Requirements

On a global scale, temperature is the environmental variable that best explains lamprey distribution (Ferreira et al. 2013). Lampreys are generally found north and south of the 20° isotherm, with average lethal temperatures around 28 °C (Potter 1980a). In their study evaluating the influence of 11 macrohabitat variables on the distribution of European river and brook lampreys in Portugal, Ferreira et al. (2013) found that lampreys were found in areas where the average maximum temperature of the warmest month did not exceed 30 °C. Morman et al. (1980) reported that high water temperatures may be responsible for the absence of lamprey ammocoetes from the lower sections of Lake Ontario streams during the late summer.

Temperature is not usually identified as an important factor affecting lamprey distribution at small spatial scales, but likely also has some localized effects. Where sea lamprey larvae are present in Great Lakes tributaries characterized by high summer temperatures, they are often limited to areas of groundwater inflow (Morman et al. 1980). Conversely, ammocoetes in cooler streams have been noted to avoid habitats influenced by cold springs and seeps (Applegate 1950).

These findings correspond with experimental studies on the temperature preferenda of lampreys. In a laboratory experiment, the preferred thermal niche of sea lamprey larvae was 20.8 °C, with maximum scope of activity occurring at approximately 19 °C (Holmes and Lin 1994). Rodríguez-Muñoz et al. (2003) assessed the influence of thermal regime on the development, survival rates, and early growth of embryos of sea lamprey incubated at five constant temperatures (7, 11, 15, 19 and 23 °C). Survival from fertilization to hatching was 61, 89, 91 and 89 % at 11, 15, 19 and 23 °C, decreasing to 58, 70 and 70 % from hatching to burrowing at 15, 19 and 23 °C, respectively. The authors also observed body length at the burrowing stage was longest for embryos incubated at 19 °C, but body mass increased in the interval 15–23 °C. Meeuwig et al. (2005) assessed the influence of thermal regime on development and survival rates of Pacific lamprey and western brook lamprey incubated at four temperatures (10, 14, 18 and 22 °C). Survival was greatest at 10, 14, and 18 °C, while survival at 22 °C was significantly lower than at other temperatures. An increased incidence of developmental abnormalities was also observed at 22 °C. The incipient lethal temperature of pouched lamprey is 28.3 °C, which almost certainly accounts for the restriction of this species to the southernmost rivers in Western Australia (Macey and Potter 1978).

3.2.2.6 Oxygen Requirements

Ammocoetes are sensitive to low oxygen tensions and unable to survive in very low concentrations (Potter et al. 1970). However, the rate of oxygen consumption, and, thus the oxygen requirements of ammocoetes of the mountain brook lamprey *Ichthyomyzon greeleyi* is lower than the values given by Winberg (1956) for several teleost fishes of similar weight (Hill and Potter 1970). Ammocoetes can tolerate, for at least 4 days, oxygen tensions as low as 7–10 mmHg at 5 °C, 12–16 mmHg at 15.5 °C, and 13–21 mmHg at 22.5 °C (Potter et al. 1970). The very low oxygen consumption of ammocoetes may well be a major factor in enabling the animals to colonize the silt banks in slow-flowing areas where oxygen tensions must often be low (Hill and Potter 1970). In contrast, metamorphosing lampreys are generally found in water with higher dissolved oxygen content (Richards and Beamish 1981; see Sect. 3.2.3), consistent with their higher rate of oxygen consumption (see Chap. 4). Interestingly, oxygen levels in the streambed have been found to be significantly increased by the burrowing and feeding activities of ammocoetes (Shirakawa et al. 2013).

3.2.2.7 Proximity to Spawning Habitat

As demonstrated above, larval abundance is directly linked to environmental variables, but the spatial context of biological factors, such as the spawning distribution of adults, also plays an important role in larval distribution (Torgersen and Close 2004). The distribution of sea lamprey ammocoetes along the river is strongly associated with the spawning areas, with larval density being inversely related to the distance downstream from the spawning areas (Morman et al. 1980; Almeida and Quintella 2002; Quintella et al. 2003). Dawson and Jones (2009) studied four Great Lakes streams, and found that streams with higher sea lamprey survival-to-age-1 had distributions of spawning and larval habitats that were most favorable to ammocoete production (i.e., the largest amount of spawning habitat in the upper reaches and the largest amount of preferred larval habitat in the lower reaches). Distribution of ammocoetes of migratory species (e.g., European river lamprey and sea lamprey) is also related to adult access to spawning habitats from their feeding grounds, with distance from a large water body (e.g., sea, estuary, or lake) and presence of potential migration barriers influencing ammocoete abundance (Goodwin et al. 2008; Ferreira et al. 2013).

Furthermore, given that adult lampreys during the migratory season increase their upstream movements and are attracted to a pheromone cue released by larvae in the system (Yun et al. 2011; Meckley et al. 2012; see Chap. 5), Neeson et al. (2011, 2012b) suggest that there will be feedback loops between the number and distribution of spawners and the number and distribution of ammocoetes. These feedback loops will be influenced by the river's network structure (i.e., its branching pattern), since the downstream propagation of pheromone will be affected by the river's discharge and the number and size of confluent tributaries. In addition, each larval cohort will in turn contribute to the river's "pheromonal landscape," thus creating interannual feedback between adult migration and larval habitation. In streams where trapping has proven effective, catch rates of adults are often low or variable in years following removal of the larval population with lampricide treatments in

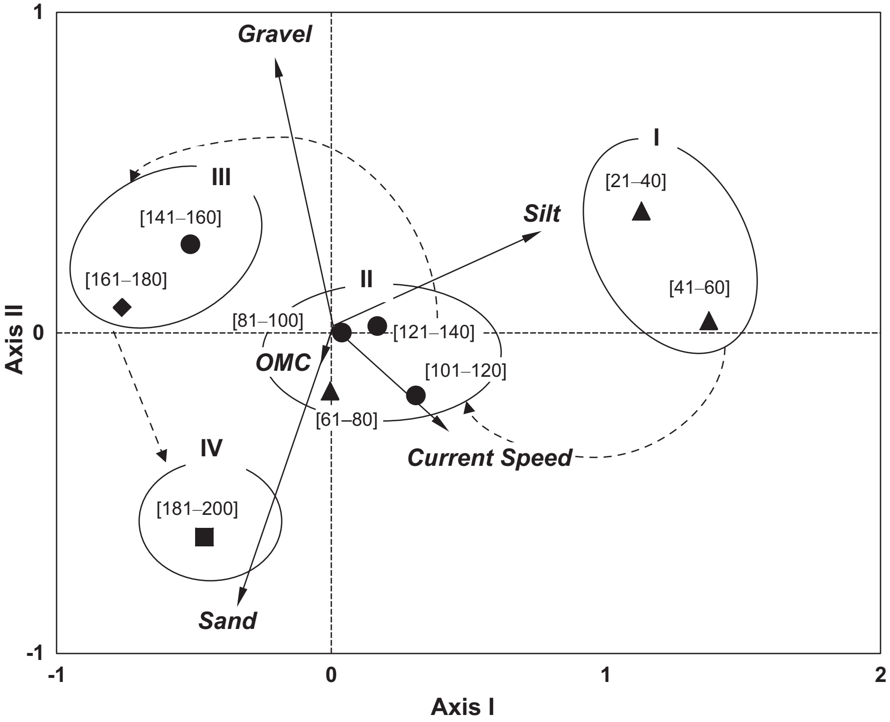

Fig. 3.1 Sea lamprey ammocoete length-class distribution according to sediment particle size, organic matter content (OMC) and velocity (current speed). Detrended Canonical Correspondence Analysis ordination diagram, with symbols corresponding to the nine length classes (from 20–40 mm to 180–200 mm), and *arrows* representing the environmental variables. The *roman numerals* identify the groups with similar preferences. The *dash arrows* represent the colonization sequence of the different sediment type. Age classes are also represented (▲, 1st year class;●, 2nd year class; ♦, 3rd year class; ■, 3rd and 4th year class). (This figure was originally published in Almeida and Quintella (2002) and reproduced with permission of John Wiley & Sons, Inc.)

the Great Lakes basin (Moore and Schleen 1980). Thus, there is evidence that lampricide treatments in the Great Lakes basin alter the feedback between adults and larvae and affects subsequent patterns of larval habitation, regardless of the small- and large-scale environmental factors discussed in previous sections.

3.2.3 Habitat Preferences Related to Larval Size and Metamorphosis

The relative importance of habitat variables can change with ammocoete size (Young et al. 1990a; Almeida and Quintella 2002; Sugiyama and Goto 2002). Several studies, for example, have demonstrated that larger larvae appear to show preference toward larger particle sizes. In the anadromous sea lamprey, smaller

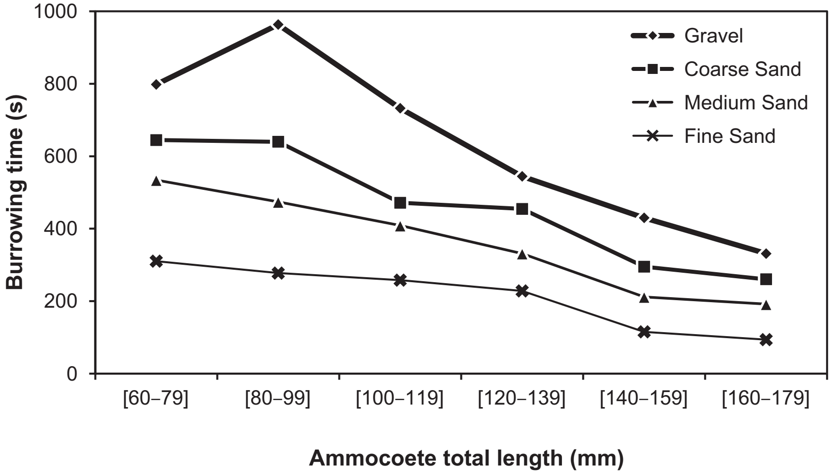

Fig. 3.2 Burrowing performances of larval sea lamprey according to their length class and substrate grain size (Gravel: 2.0–0.39 mm; Coarse Sand: 1.0–1.99 mm; Medium Sand: 0.5–0.99 mm; Fine Sand: 0.25–0.49 mm). (Redrawn from data of Quintella et al. (2007))

ammocoetes (20–60 mm total length) preferred silty-sand substrates (i.e., sediments with a comparatively higher percentage of sand), but also with a relatively large portion of silt (Almeida and Quintella 2002; Fig. 3.1). Medium-size ammocoetes (60–140 mm) were mainly found in gravel-silty-sand substrate, where gravel and silt seem to have an identical contribution to the composition of this more heterogeneous sediment. Larger ammocoetes (140–200 mm) preferred coarse-grained sediments (gravelly-sand and sand; Almeida and Quintella 2002). In the landlocked sea lamprey, Sullivan (2003) likewise showed that as larvae grow, their preference shifts toward larger particle sizes, although even large larvae (> 120 mm) are rarely found in coarse substrates such as gravel, cobble, or rubble (Jones 2007). Lampreys going through the process of metamorphosis have also been observed in coarser substrates (see below).

Differences in habitat preference with body size may be related to burrowing abilities. In a laboratory experiment, smaller sea lamprey ammocoetes had lower burrowing performance than larger individuals across all substrate types tested (i.e., gravel, coarse sand, medium sand, and fine sand), but the differences were greater in coarser substrates (Quintella et al. 2007; Fig. 3.2). Additionally, coarser sediment particles increased the time spent on burrowing regardless of larval size, which is likely related to fatigue (Quintella et al. 2007). These authors suggested that smaller ammocoetes are usually associated with fine-grained sediments, because these softer sediments allow younger larvae, with a reduced swimming capacity, to propel the head and branchial region below the surface (Quintella et al. 2007). Larger ammocoetes, on the contrary, may colonize a wider range of sediment types because their burrowing capacities are considerably higher (Quintella et al. 2007). Since the selection of the burrowing sediment is a size-dependent characteristic, the differences observed in the preferences for distinct sediment types within the same age group probably resulted from a reorganization of the ammocoete distribution pattern at the end of each annual growing season. This behavior could be a strategy developed by this species to avoid high densities in the areas colonized by younger individuals, and therefore reduce intraspecific competition for space and food (Almeida and Quintella 2002).

A similar preference by smaller larvae for smaller substrate particle sizes (and a narrower range of preferred particle size) has been identified in other lamprey species. Small (≤50 mm total length) Far Eastern brook lamprey larvae preferentially selected substrate in the 0.125–1 mm diameter range, whereas larger larvae (>50 mm) selected all three substrate size classes (<0.125 mm, 0.125–1 mm, and 1–2 mm diameter) equally (Sugiyama and Goto 2002). In the least brook lamprey, small ammocoetes (<50 mm) had a stronger preference (54.7%) for fine sand compared to large ammocoetes (100–150 mm; 49.7%), and a moderate number of large ammocoetes (17.7%) also selected coarse sand habitat (Smith et al. 2011; see Sect. 3.2.1.1). However, not all studies are in consensus regarding different habitat preferences of ammocoetes of different length classes. Optimal particle size and abundance for American brook lamprey did not change with larval length (Beamish and Lowartz 1996), and Goodwin et al. (2008) similarly found no relationship between particle size and ammocoete length in the Ballinderry River in Northern Ireland.

In the study by Sugiyama and Goto (2002), large Far Eastern brook lamprey larvae also showed a greater preference for deeper substrate and occupied a wider range of water depths (0–38 cm) than the small larvae (0–24 cm). In an extensively sampled river in northern Wisconsin, no difference was detected in density of larger sea lamprey larvae (>51 mm TL) between deep (>0.8 m) and shallow (<0.8 m) water; however, small larval sea lamprey (<51 mm TL) showed a greater preference for shallower water (Treble unpublished data). Earlier studies also suggested that larger sea lamprey ammocoetes are found more commonly in deep water (Wagner and Stauffer 1962; Manion and McLain 1971; Manion and Smith 1978). These results suggest that larvae change habitats as they grow, and size segregation among different habitats has also been found in pouched lamprey ammocoetes in New Zealand streams (Kelso and Todd 1993), and with sea lamprey in Portuguese rivers (Almeida and Quintella 2002).

Spatial segregation may be even more pronounced between larvae and transformers. It has been observed in several different species that as larvae approach metamorphosis, there is a tendency for some to move to coarser substrates (Potter 1970). Richards and Beamish (1981), for example, reported that metamorphosing Pacific lamprey typically occurred in coarser substrate with better oxygenated water than did ammocoetes, and Kelso and Todd (1993) similarly found metamorphosing pouched lamprey in downstream reaches where substrate was coarser and flows were higher. Potter and Brown (1975) suggested that European river lamprey move into faster-flowing areas with more oxygenated sediments sometime during metamorphosis, whereas the non-migratory non-parasitic European brook lamprey may remain in silted areas typical of the larvae until just prior to spawning. Differences in the ecology of these two species are likely related to differences in their oxygen requirements during and after metamorphosis (see Sect. 3.2.2.6; see Chap. 4). Other studies likewise report transformers in nursery habitat alongside ammocoetes of varying year classes (Potter et al. 1980; Quintella et al. 2003). Not all brook lampreys, however, remain in the ammocoete beds during metamorphosis. Although Beamish and Medland (1988a) reported that "it was not unusual" to find adult and ammocoete mountain brook lamprey in the same areas, as metamorphosis progressed, this species tended to shift to coarser substrates and higher water flows.

Differences in whether or not ammocoetes and transformers are spatially segregated may be related to other features of the habitat. Streams with a high gradient, for example, may show more downstream movement of larvae, especially during periods of flooding, so that age and size of larvae increases with distance from the spawning grounds. Streams with a lower profile may show less movement and less sorting by age and size (Hardisty 1986). Kelso and Todd (1993) suggested that downstream movement of pouched lamprey with age is significant in New Zealand streams since stream gradients are high and flooding is frequent.

During the initial stages of metamorphosis, transformers are more sedentary in comparison to ammocoetes (Quintella et al. 2005). Later on, juveniles burrow less frequently and are found hiding between pebbles, under aquatic vegetation, rocks and other structures (Almeida unpublished data).

3.2.4 Macroenvironmental Statolith Signature

The elemental composition of the habitat in which lampreys are found is reflected in their statoliths. Statoliths are structures in lampreys that are analogous to otoliths in teleost fishes, and the analysis of statolith microchemistry could possibly be used as a means of providing gross population structure of sea lamprey in the Great Lakes (Brothers and Thresher 2004). Previous Great Lakes otolith microchemistry studies have successfully discriminated among local spawning locations in yellow perch *Perca flavescens* (Brazner et al. 2004; Ludsin et al. 2006). The elemental composition of larval sea lamprey statoliths was found to reflect the ambient elemental concentrations of the river systems from which the lampreys originated (Brothers and Thresher 2004). These authors indicated that strontium (Sr) and rubidium (Rb) differences alone were sufficient to correctly assign most larval sea lamprey to their natal rivers, and almost perfectly distinguished between specimens from the St. Marys River (connecting lakes Superior and Huron) and those from the drainages of Michigan's Lower Peninsula, with Sr and Rb differences likely due to the regional differences in the geochemistry of the Canadian Shield and the Michigan basin. Hand et al. (2008) quantified elemental concentration in larval sea lamprey statoliths, and were able to discriminate among larvae from 13 streams located in lakes Michigan, Huron, and Superior with 82 % classification accuracy. However, several streams carried a common signature, and the ability to discriminate among lakes (when all streams within a lake were grouped into a single category) was only about 60 %. This demonstrates that stream-specific signatures differ within each of these systems, and that local geology, watershed runoff, and pollutant sources may overwhelm regional, basin-wide geology (Hand et al. 2008).

Statolith elemental signatures within river systems are relatively stable over time and are affected only slightly by year-class variability (Brothers and Thresher 2004). However, it appears that statolith elemental signatures may not be stable during the course of the lamprey life cycle. Recent research has found that in newly metamorphosed sea lamprey, the portion of the statolith deposited during the larval stage was enriched in rubidium (Rb), which suggests a chemical reworking of statoliths during metamorphosis (Lochet et al. 2013). Since discriminating among sea lamprey from different streams mostly relies on premetamorphic levels of Rb, strategies for the use of statoliths to identify the natal origin of juvenile and adult sea lamprey should take into account the chemical changes associated with metamorphosis (Lochet et al. 2013).

3.3 Feeding

Ammocoetes feed by trapping small, water-borne particles in mucus within the pharynx (Mallatt 1981), and larval habitats provide a regular supply of the suspended organic matter upon which larval lampreys feed (Sutton and Bowen 1994; Yap and Bowen 2003). Allowing for the effect of other environmental variables, an increase in the amount of organic material often—but not always—corresponds to an increase in larval density (see Sect. 3.2.1.3). Habitat type selected by larval northern brook lamprey had relatively minor consequences for organic matter and amino acids in the diet, but had major consequences for assimilation efficiency for both nutrients, with highest efficiencies occurring in depositional areas where larvae aggregated at low densities (Yap and Bowen 2003). Whereas most suspension feeders meet their food requirement by moving dilute suspensions rapidly across their feeding structures, ammocoetes meet nutrient needs by slowly processing concentrated suspensions (Mallatt 1983). A slow rate of water flow through the pharynx, necessitated by the high resistance of the substrate inhabited and the design of the pharyngeal pump, confines ammocoetes to environments where food suspensions are concentrated (Mallatt 1983). Since the burrowing habit that limits flow rate is necessary for protecting lampreys from predation during the larval stage (Morman et al. 1980), the requirement for concentrated suspensions seems basic to the animal's biology (Mallatt 1983).

The larval lamprey diet consists of a mixture of algae (primarily diatoms), organic detritus, and bacteria (Sutton and Bowen 1994), with the detrital fraction serving as the primary food source (Moore and Beamish 1973; Moore and Potter 1976a, b; Sutton and Bowen 1994; Mundahl et al. 2005). Sutton and Bowen (2009) found that diets of larval northern brook lamprey were dominated by detritus, which ranged from 94 to 99 % of the organic fraction of the gut contents. The remainder of the contents in the digestive tract was composed of algae and bacteria, which in sum contributed less than 6 % of the total diet ash-free dry mass (Sutton and Bowen 2009). Similar observations of organic detritus-dominated diets have been reported for sea lamprey and American brook lamprey during the summer months (Sutton and Bowen 1994; Mundahl et al. 2005). Specific physiological attributes, such as efficient digestion and assimilation and a low metabolic rate, have been identified as adaptations that allow larval lampreys to effectively use this food source (Moore and Beamish 1973; Moore and Mallatt 1980; Sutton and Bowen 1994; Yap and Bowen 2003; Mundahl et al. 2005). Shirakawa et al. (2009) experimentally found positive growth of sub-yearling Arctic lamprey ammocoetes given a diet of fallen leaves and negative growth of those given algae, although comparison to wild ammocoetes suggested a varied diet that may contain leaves and algae. In contrast, another experimental study indicated that larval Pacific lamprey grew more when given diets of algae or salmon carcass analogs and had negative growth when given diets of leaves (Jolley unpublished data). In this latter study, the presence of the unique stable isotope signatures in each of the food items confirmed consumption. Bacteria and organic substances dissolved in water are also likely significant as a food source for larval lampreys (Moore and Potter 1976b). Analysis of sea lamprey larvae gut contents found that microalgae belonging to the class Bacillariophyceae were the major constituents of the algal portion of the diet of ammocoetes (Quintella 2000). Among the diatoms found, the genera *Melosira* and *Navicula* were the two most important algal food items, occurring in more than 95 % of the observed gut contents, and corresponding to 86 % of the total identified microalgae. The genera *Cyclotella*, *Cymbella*, *Nytzschia*, *Cocconeis*, *Bacillaria*, *Synedra* and *Rhizosolenia* were also classified as preferred algal food items (Fig. 3.3). During the spring and summer periods, as expected, the diversity of microalgae present in the analyzed gut contents was much higher than during autumn and winter (Fig. 3.3). The diversity of algal food items was low throughout the year mainly due to the almost absolute dominance of the genera *Melosira* and *Navicula.*

In British populations of European brook lamprey, Moore and Potter (1976b) found that feeding rate was most intense in early spring (as water temperatures rose from 5 to 12 °C), which was about two months before the spring algal bloom. Rates remained relatively constant throughout the summer, and declined in October, although temperatures (10 °C) were still similar to those observed in spring. Maximal rates of feeding in the spring and summer are, not surprisingly, consistent with high summer growth rates (see Sect. 3.7.2).

No consistent pattern of change in the size of ingested material with length of larvae has been observed. Composition of gut contents among larval individuals of landlocked sea lamprey, anadromous sea lamprey, and American brook lamprey for a given season and river did not change greatly, irrespective of body length (Moore and Beamish 1973). Further, the authors found no consistent pattern of change in size of ingested algae with length of larvae. However, by the end of the larval stage, lampreys must have accumulated sufficiently large lipid reserves to act as an energy source during the subsequent long non-trophic period of metamorphosis (Moore and Potter 1976b), as no lamprey species has been found to feed during the metamorphic period (Hardisty and Potter 1971a; see Chap. 4).

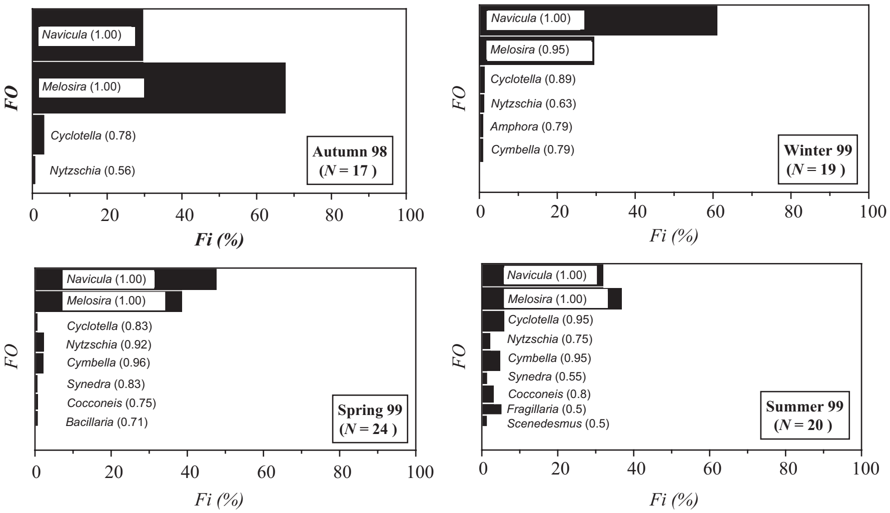

Fig. 3.3 Seasonal evaluation of the microalgal food items found in the diet of sea lamprey larvae in the River Mondego, Portugal, showing numerical frequency (F_i) and frequency of occurrence (*FO*) of the preferential food organisms. In each of the graphics, the width of the bars is proportional to the *FO* indicated between brackets. (Figure adapted from Quintella 2000)

3.4 Lamprey Demographics

3.4.1 Density

As with the effect of various environmental factors on larval distribution and abundance, larval density will depend on the spatial scale at which it is measured. Malmqvist (1983) reviewed several previous studies, and reported that maximum densities in optimal habitats (i.e., on a fine scale) can number hundreds to thousands of individuals per m^2 (e.g., up to 126, 113, and 2,000 larvae/m^2 in northern brook, European brook, and European river lampreys, respectively; Churchill 1945; Malmqvist 1980; Tuunainen et al. 1980). Nursall and Buchwald (1972) reported as many as 284 Arctic lamprey burrows per m^2, and more recent studies in other species also show high maximum densities (e.g., as many as 104 pouched lamprey larvae and more than 100 Pacific lamprey larvae/m^2; Kelso and Todd 1993; Torgersen and Close 2004). Presumably, there is a negative relationship between larval size and density; the 40–2,000 European river lamprey reported per square meter were for young-of-the-year larvae (8–36 mm) in spawning areas (Tuunainen et al. 1980).

Mean densities over larger areas of suitable habitat will be much lower. The earlier studies reviewed by Malmqvist (1983) show average densities to range from < 1 to about 20 larvae/m^2 (e.g., Hansen and Hayne 1962; Kainua and Valtonen 1980; Malmqvist 1980), and more recent studies show similar ranges over this scale. Beamish and Youson (1987) estimated larval North American river lamprey densities in the Fraser River, British Columbia, to range from 2.8 to 64.3/m^2, with an average of 26–28 larvae/m^2. Mundahl et al. (2006) examined densities and age structures of American brook lamprey larvae in several streams in southeastern Minnesota, where they found that mean densities of lamprey larvae varied from 0.33 to 5.78 larvae/m^2 in the best habitats available. During a survey to characterize microhabitat preferences of European brook and river lampreys in two Portuguese watersheds, Almeida et al. (2011) found a mean (± standard deviation, SD) density of 3.97 ± 4.41 larvae/m^2 ranging from 0.44 to 24.50 larvae/m^2. In a study of nine river basins in the Galicia region of northwest Spain during the summer period between 2007 and 2009, the density of sea lamprey ammocoetes captured with electrofishing was on average 4.9 larvae/m^2, with a mean value per river basin ranging from 0.7 to 13.4 larvae/m^2 (Gradín 2010). In Northern Ireland, Goodwin et al. (2008) found the density of European river and brook lamprey ammocoetes to range from 0.1 to 2.4/m^2 (average 0.79/m^2). In the Gironde-Dordogne River basin in France, Taverny et al. (2012) recovered as many as 9 and 19 sea and *Lampetra* larvae per square meter (averages 3.4 and 7 larvae/m^2, respectively).

In the Laurentian Great Lakes, the Great Lakes Fishery Commission and its agents have successfully reduced sea lamprey populations by approximately 90 % from peak levels (Marsden and Siefkes in press). A moderate to high density of larval sea lamprey in the Great Lakes is now considered to be >5/m^2 (Steeves et al. 2003). Slade et al. (2003) estimated mean larval catch in 15-m^2 plots of Type I habitat from 214 infested stream reaches in 1996–1998 and calculated mean density to be 1.16 larvae/m^2. In 51 stream reaches in the Lake Superior and Michigan basins, mean density in Type I habitat ranged from 0.01 to 8.45 larvae/m^2 (Lake Superior) and 0.04–10.4 larvae/m^2 (Lake Michigan). Using data from 26 Great Lakes tributaries surveyed between 1991 and 1995, Slade et al. (2003) estimated that sea lamprey density in Type II habitat was approximately 10 % of that in Type I habitats. However, these authors suggested that more recent data estimated density in Type II habitat to be 27.5 % that of Type I habitat; this latter value is similar to the relative densities observed by Zerrenner and Marsden (2005) in Type I and II habitats. In Lewis Creek, Vermont, in the Lake Champlain basin (which has been subject to lampricide treatments since 1990), Zerrenner and Marsden (2005) estimated mean sea lamprey densities in 1999 and 2000 to be 5.02–6.96/m^2 and 1.93–3.30/m^2 in Type I and Type II habitats, respectively. These numbers included larvae and transformers, with transformers making up 2.4–5.8 % of the total number.

Based on the above studies, it is becoming clear that natural densities of lampreys are often much lower than those used in laboratory and in-stream studies, which have shown negative effects of larval density on growth rates and survival (see Sects. 3.6.1 and 3.7.2). Many of these studies use experimental densities that are more in line with maximum observed densities and even the “low-density” treatments are often high relative to naturally observed densities.

3.4.2 Abundance

Over moderate to large scales, the abundance of spawning-run lampreys is more readily measured than that of the stream-resident stages, but counts of downstream-migrating juveniles are now being made as well (e.g., as they pass through dams, salmon smolt traps, or other counting structures; Fish Passage Center 2013) and abundance estimates for even the cryptic larval and metamorphosing stages are also emerging.

The earliest known attempt to estimate total larval abundance within an entire stream system was made by Hansen and Hayne (1962). In the Ogontz River, a small tributary to Lake Michigan, they estimated the total larval lamprey population in a 15-km reach at 136,800. In Ogontz Bay, an estimated 30,100 sea lamprey and 2,900 American brook lamprey larvae were present. These estimates were made in 1959 and 1958, respectively, and Hansen and Hayne (1962) felt that these numbers were not substantially affected by an electromechanical barrier first operated in 1958. For more recent estimates, we used the data provided in Table 3 of Slade et al. (2003) to calculate the total abundance of sea lamprey larvae (age 1+) in 24 and 27 stream reaches in the Lake Superior and Lake Michigan basins, respectively (but note that infested length in this table should be in m, not km; Jeffrey W. Slade, U.S. Fish and Wildlife Service, Ludington, MI, personal communication, 2014). In the Lake Superior basin, total estimated abundance ranged from 136 in a 7.6-km infested reach of the Black Sturgeon River to 311,032 in a 66-km reach of the Goulais River. In the Lake Michigan basin, estimated total abundance ranged from 18 in Arthur Bay (where the infested reach was only 0.16 km long) to almost 1.4 million in a 14.6-km infested reach in the Platte River. Total abundance from these 24 Lake Superior and 27 Lake Michigan stream reaches totaled almost 800,000 and over 2.2 million larvae, respectively. Total larval abundance in a 9.4-km infested reach of Lewis Creek, Vermont, was estimated at 30,089–116,762 between 1990 and 2000 (Zerrenner and Marsden 2005). The streams in these recent estimates, of course, have been subject to periodic lampricide treatments. In a portion of the Black Sturgeon River currently not exposed to lampricide application (i.e., above a barrier), Sea Lamprey Control Centre personnel in 2006 estimated that the total abundance of *Ichthyomyzon* ammocoetes (presumably northern brook lamprey since newly metamorphosed individuals of this species were also captured during sampling) to be more than 14.7 million (Mike Steeves, Fisheries and Oceans Canada, Sea Lamprey Control Centre, Sault Ste. Marie, ON, personal communication, 2014).

Abundance estimates have also been made for metamorphosing lampreys. In the case of the Great Lakes sea lamprey, sea lamprey control efforts aim to kill the larvae before they metamorphose; control agents, therefore, attempt to predict in advance (rather than measure after the fact) the production of transformers in Great Lakes tributaries (Marsden and Siefkes in press). Slade et al. (2003) estimated the potential production of metamorphosed sea lamprey from 57 Lake Superior and 58 Lake Michigan tributaries at 0–82,497 (average 4,318) and 0–103,027 (average

3,566), respectively. In the Black Sturgeon River study mentioned above, it was predicted that 115,066 northern brook lamprey would metamorphose that year (Treble unpublished data).

Counts of downstream-migrating juveniles are available for some species. Beamish and Youson (1987), for example, calculated that as many as 6.5 million juvenile North American river lamprey left the Fraser River in British Columbia in 1979. Beamish and Levings (1991) estimated that, per year, 19,000–176,000 Pacific lamprey juveniles migrated out of one Fraser River tributary, the Nicola River, in 1984–1985 and 1987–1988. For more recent time periods, counts of juvenile lamprey (Pacific lamprey and/or western brook lamprey) as they pass through the mainstem hydrosystem in the Columbia River basin are recorded and are available at the Fish Passage Center (Columbia Basin Fishery Agencies and Tribes 2014).

The above studies are a valuable start to permitting a more thorough appreciation for total lamprey numbers in river systems but, particularly in species other than sea lamprey in the Great Lakes, there is still a need for standardized measurements to be made over time. Detection probability models are currently being used to determine occurrence of Pacific lamprey in the Columbia River basin, which may provide a baseline for comparison with future studies (Jolley et al. 2012; Dunham et al. 2013). In many species of conservation concern, there is evidence of population declines (mostly from the number of upstream migrants or harvest rates; see Chap. 8), but temporal trends in larval and metamorphosing stages are, in general, still poorly documented.

3.4.3 Sex Ratios

A small but variable excess of males has long been observed in spawning-phase lampreys (e.g., Dean and Sumner 1898; Young and Cole 1900; Wigley 1959; Zanandrea 1961). Skewed larval sex ratios have also been reported, and there is some evidence to suggest that sex ratios may be related to larval density. As sea lamprey numbers in the upper Great Lakes were drastically reduced following the initiation of sea lamprey control, the proportion of males correspondingly declined and a preponderance of female larvae (and adults) was soon observed (Smith 1971; Purvis 1979; Torblaa and Westman 1980). Sex ratio variations were also observed among least brook lamprey populations in Maryland, Delaware, Kentucky, Tennessee, and Alabama (which have not been subjected to lampricide treatment), and differences were related to larval density; the proportion of males increased significantly with relative density (Docker and Beamish 1994). In this study, larval sex ratio was not significantly related to water hardness, pH, annual thermal units, or latitude. It has thus been suggested that sex determination in larval lampreys is density dependent (Purvis 1979; Docker and Beamish 1994), occurring during a prolonged period (1–3 years) of sexual indeterminacy (see Docker et al. in press). Beamish (1993) also presented evidence for the existence of environmental sex determination in the southern brook lamprey. He noted that when conditions for larval growth were favorable, increased occurrence of males was positively correlated with larval density. He found that under poor growth conditions, higher densities were associated with fewer males. Torblaa and Westman (1980) found highly variable sex ratios of larval sea lamprey present in Great Lakes streams with divergent physical and chemical characteristics, which lends credibility to the view that environmental factors may play an important role in sexual differentiation of the ammocoete. However, approximately equal proportions of male and female larvae in other species (i.e., European river and brook lampreys) led Hardisty (1960) to rule out an environmental effect on sex differentiation. In a more recent study examining sea lamprey sex ratios in the Great Lakes, Wicks et al. (1998) were likewise unable to detect an effect of larval density on sex ratio, although this may be because larval densities in Great Lakes streams now remain low due to the control program (Jones et al. 2003). In an experimental study, Docker (1992) also found no significant relationship between rearing density and sea lamprey sex ratio but, in this case, it appears that all experimental densities were high (between 57 and 470 larvae/m^2) compared to natural densities (see Sect. 3.4.1).

The possible adaptive significance of environmental sex determination in lamprey could be compensation for changes in density to favor an equilibrium population. However, only experimental studies at more natural densities can verify a causal relationship between density and sex ratio, and further experimental and field studies may shed some light on density-related differences between the sexes (Docker and Beamish 1994).

Other possible explanations for unequal sex ratios in larval lampreys (i.e., other than environmental sex determination) include sex-specific differences in mortality during the larval stage or differential rates of metamorphosis. In the least brook lamprey, however, sex ratio variations were not likely the result of differential mortality between the sexes since sex ratios varied among streams from the time of gonadal differentiation, and remained relatively constant thereafter (Docker and Beamish 1994). Furthermore, among sea lamprey larvae maintained at various densities for over 3 years, there was no evidence of sex-specific mortality (Docker 1992). There is also no evidence that lampricides applied to Great Lakes streams are selectively toxic to male lamprey (Purvis 1979). There is evidence of sex-specific differences in age at metamorphosis (i.e., that females metamorphose at an older age than males, particularly in non-parasitic species; Purvis 1970; Docker and Beamish 1994; Docker 2009; see Chap. 4) but, since the sex ratio variations observed in the least brook lamprey were established at the time of gonadal differentiation, Docker and Beamish (1994) asserted that differential recruitment to the adult stock was not responsible for the differences in larval sex ratios.

The demographic effects of skewed larval sex ratios (e.g., on overall rates of recruitment and mortality) are unknown, and will probably vary greatly between resident and anadromous species (see Sect. 3.10).

3.5 Movement

Data show that the ammocoete life stage is not entirely at the mercy of the environment. Although dispersal is largely determined by changes in current velocity or water levels, with floods and spring thaw events regarded as a major factor in their redistribution (Hardisty and Potter 1971a), the possibility that ammocoetes may actively seek out more favorable areas for colonization is supported by numerous studies. For example, multiple studies suggest high drift or movement rates soon after sea lamprey larval emergence. The initial migration from the spawning site appears to be a result of a mass emergence from the nest substrate caused by sudden changes in the larvae at the critical stage of yolk absorption (Applegate 1950). Manion and McLain (1971) suggested that age-0 sea lamprey larvae initially remained close to spawning areas and by age 1 had only moved a few hundred meters; they reported a more widespread distribution of larvae by age 2. A more recent study of this species by Derosier et al. (2007), based both on field observations and genetic data (i.e., which allowed the researchers to use distance separating full sibling larvae as a proxy of dispersal distance), does not support this previous observation. According to these authors, age-0 larvae did not cluster near the spawning nests, but dispersed widely soon after emergence, and were equally likely to be found in habitats greater than 150 m from the nest as within 50 m. Genetic data showed that age-0 siblings were found up to 0.9 km from each other within 3 months of emergence (Derosier et al. 2007). Age-1 larvae showed even greater dispersal after a single year; larvae were frequently found greater than 1 km downstream (Derosier et al. 2007). Kelso and Todd (1993), based on the downstream distribution of age-0 pouched lamprey larvae, likewise suggested a more rapid downstream colonization in this species. In addition, age-0 Pacific and western brook lampreys (<30 mm TL) were locally abundant in tributary mouth depositional areas of the Columbia River and likely originated some distance upstream (Jolley unpublished data).

Various biotic and abiotic factors have been found to affect the movement of larval sea lamprey. Larval movement was observed to occur significantly more often at higher densities and significantly less often at temperatures below 18.5 °C in the laboratory (Derosier et al. 2007). Relatively high movement rates were observed during warmer temperatures, with 20–30 % of larvae emerging from the sediment and drifting during a single night (Derosier et al. 2007). Derosier et al. (2007) hypothesized that the risk of movement for sea lamprey larvae into less suitable habitats in the fall (when temperatures below 18.5 °C are more likely to occur) outweighs the benefits of seeking habitats with lower densities.

Although earlier authors have suggested that larval movement is largely passive (e.g., Applegate 1950), Potter (1980a) countered this argument, citing the tagging studies of Smith and McLain (1962) and Manion (1969) that showed that sea lamprey larvae may occasionally move a short distance upstream. More recently, Quintella et al. (2005), monitoring sea lamprey ammocoetes marked with passive integrated transponders (PIT) tags, similarly observed a considerable proportion of short movements in an upstream direction. As expected, however, observations during laboratory experiments revealed that ammocoetes spent most of the time motionless and, when active, downstream movements were more frequent and longer compared to upstream movements (Quintella et al. 2005).

Furthermore, although ammocoetes spend most of their time burrowed, they are adept at performing and recovering from vigorous anaerobic exercise. Such attributes could be important when these animals are vigorously swimming or burrowing as they evade predators or forage (Wilkie et al. 2001). Laboratory experiments conducted by Sutphin and Hueth (2010) to measure the swimming performance of Pacific lamprey ammocoetes suggest relatively high swimming capacities of larval lampreys. According to these authors, ammocoetes are able to swim considerable periods of time at a prolonged-sustained level, ranging from 43.0 min when exposed to a low velocity of 0.1 m/s, to 0.4 min when exposed to 0.5 m/s water velocity. The burst swimming speeds of larval Pacific lamprey tended to increase with size of the individuals tested, ranging from 0.3 to 0.8 m/s (Sutphin and Hueth 2010).

As reviewed by Potter (1980a), the downstream movement of larval lampreys occurs mainly at night; this is evident in many species. Abundant nighttime catches of larval Pacific lamprey in drift nets were noted in the Deschutes River in the Columbia River basin (Gadomski and Barfoot 1998), and White and Harvey (2003) found larval drift in this species to occur almost exclusively at night. For European river lamprey larvae in the main channel of the Derwent River in England, nighttime catches were eight times higher than daytime catches; for transformers, nighttime catches were 24 times higher (Bracken and Lucas 2013). Ammocoetes are, in general, more active at night (Almeida et al. 2005), and nocturnal downstream movement likely makes them less vulnerable to predation (Naesje et al. 1986; Harvey 1991). More recent studies also support previous observations that downstream movement is highly seasonal. For example, peak catches of European river lamprey larvae and transformers in the Derwent River occurred in mid-winter and December–April, respectively, and may be coupled with higher winter flows (Bracken and Lucas 2013; see Sect. 3.9.1). White and Harvey (2003) found larger Pacific lamprey ammocoetes to drift almost exclusively during higher flows in spring, and smaller (presumably newly hatched) larvae drifted during the summer.

In several different species, studies have revealed that as larvae approach metamorphosis, they have a tendency to move further downstream into coarser substrates where the water velocity and dissolved oxygen content is higher (see Sect. 3.2.3). In Arctic lamprey, larger (presumably older) individuals have been found in the downstream reaches, closer to river mouths (Heard 1966; Nursall and Buchwald 1972; Bradford et al. 2008). Likewise, as sea lamprey larvae increase in size, movement towards the mouth of streams and lentic areas has been noted (Quintella et al. 2003; Jones 2007), although the rate of movement and the habitats occupied during this migration are unknown (Jones 2007). Kelso and Todd (1993) found that the size of pouched lamprey larvae in two New Zealand streams was greatest at downstream sites, the range in size was greatest downstream, and transformers were typically found in the downstream reaches. Although very small (presumably age-0) Pacific lamprey ammocoetes have also been found close to or in the mouths of rivers that meet the Columbia River mainstem, the results suggests that these habitats are primarily inhabitated by larger larvae.

3.6 Mortality

Mortality during the larval life stage is an important demographic parameter about which we presently have very limited information (Jones et al. 2009). Sea lamprey mortality is thought to be high in the egg phase and immediately following hatching when ammocoetes disperse from nest sites to suitable larval habitats (Potter 1980a). Available evidence suggests that ammocoetes older than age-0 experience relatively low and uniform mortality throughout the remainder of the larval stage; their propensity to burrow in sediments presumably allows them to avoid predators (Potter 1980a). Metamorphosis, however, may represent a second critical stage in lamprey development (Hardisty and Potter 1971a).

3.6.1 Mortality Factors in Different Life Stages

Available estimates of egg viability suggest reasonably high (but variable) survival in the absence of predation. When sampled shortly before hatch (at approximately 8–13 days after fertilization), 0–90 % (average 43.4 %) and 57.8–100 % (average 84.4 %) of the eggs in sea and Pacific lamprey nests, respectively, were found to be viable (Bergstedt et al. 2003; Ward et al. 2012). Under optimal laboratory conditions (i.e., at 18.4 °C), Piavis (1961) found 78 % survival to the burrowing stage (17–33 days after fertilization). However, lamprey eggs appear to be preyed upon by a number of fish species, including speckled dace *Rhinichthys osculus* (Brumo 2006) and hornyhead chub *Nocomis biguttatus* (Cochran 2009). Eggs dislodged from the nest seem to be particularly vulnerable. Using an experimental hatching system, Smith and Marsden (2009) found that a high proportion (85 %) of sea lamprey eggs was washed out of the nest, and predation rates on eggs outside the nest were high. Brumo (2006), however, found that egg predation did not have a significant effect on the relative survival of Pacific lamprey ammocoete cohorts. Large parasitic lampreys have high fecundity (averaging approximately 45,000–79,000 and 98,000–238,000 eggs per female for landlocked sea and Pacific lampreys, respectively; see Docker et al. in press) and highly variable recruitment (Jones et al. 2003), leading to the potential for offspring to exceed the capacity of early rearing environments to support them (Derosier et al. 2007). Fecundity in small, non-parasitic lamprey species, however, rarely exceeds 2,000 eggs per female (Docker et al. in press); the effect of egg predation on these species is unknown.

As mentioned above, mortality throughout the remainder of the larval stage is thought to be relatively low and uniform. Actual larval survival rates are highly uncertain, but some estimates are available. In the pouched lamprey, Kelso and Todd (1993) calculated annual larval survival rates to be approximately 47 % for age 0 and 1 larvae and 77 % for age 1 and 2 larvae. Weise and Pajos (1998) estimated annual survival of one age class of sea lamprey larvae to be 61 % (see below). A recent study, in which sea lamprey larvae > 60 mm total length were tagged, released into six Great Lakes tributaries following lampricide treatment, and later recaptured, provided survival rate estimates of 56.8–57.6 % (Johnson et al. 2014). These estimates are somewhat higher than the values (39.5–51.8 %) used in sea lamprey population model simulations (Jones et al. 2009; Irwin et al. 2012), but are generally lower than those (52–96 %) reported by Morman (1987) from cage studies in which predators would have been excluded.

Larval lampreys are eaten by a variety of fishes, amphibians, reptiles, birds, and mammals, and predation on lampreys is known in both marine and freshwater habitats (Cochran 2009). However, predation is thought to be a more important source of mortality in migrating (including downstream-migrating juveniles, see below) and spawning lampreys than in larval lampreys (Cochran 2009). Teleost predators of larval lampreys include species of minnows (Cyprinidae), sticklebacks (Gasterosteidae), eels (Anguillidae), sculpins (Cottidae), walleye and perch (Percidae), salmon and trout (Salmonidae), burbot (Lotidae), pike (Esocidae), and bullheads or catfishes (Ictaluridae) (Hardisty 1961a, b; Heard 1966; Manion 1968; Tuunainen et al. 1980; Maitland 2003; Nakamoto and Harvey 2003; Cochran 2009). Birds known to eat larval lampreys include herons (Ardeidae), gulls (*Larus* spp.), mergansers (*Mergus* spp.), cormorants (Phalacrocoracidae), and terns (e.g., Forster's tern *Sterna forsteri*) (Poe et al. 1991; Maitland 2003; Antolos et al. 2005; Cochran 2009).

The burrowing habits of larval lampreys appear to protect them from predation. According to a laboratory experiment performed by Smith et al. (2012), the availability of fine sand habitat may influence the predation risk of ammocoetes, since survival from predation was found to be highest in fine sand and lower in other substrates (see Sect. 3.2.1.1).

The substrate largely protects larval lampreys from predators, but their burrowing habit does make them vulnerable to large-scale anthropogenic disturbances of the sediment, particularly dredging (e.g., for mining or channel maintenance for flood control and navigation; see Chap. 8). Not only does dredging remove desirable substrate (see Sect. 3.2.1.1), it likely also results in the removal of the ammocoetes themselves. Unlike more mobile fishes that might quickly move from the site of a disturbance, ammocoetes often emerge from the sediment long after operations cease and they are not salvaged. Although poorly studied, these losses may be substantial (e.g., O'Connor 2004, 2006). Channelization also reduces habitat heterogeneity, eliminating or reducing the flow refugia important to larval lampreys (see Sect. 3.2.1).

Larval mortality due to disease is not well-studied (see Chap. 8). Research has largely focused on the impact of potential lamprey pathogens on human health or their potential transmission to commercially-important fishes. One recent study (Kurath et al. 2013), however, showed that Pacific lamprey ammocoetes exposed to common fish rhabdovirus pathogens—infectious hematopoietic necrosis virus (IHNV) and viral haemorrhagic septicaemia virus (VHSV)—showed no evidence of viral infection, replication, or persistence.

Larval density in the stream bed appears to be an important factor determining survival to metamorphosis (Manion and Smith 1978; Malmqvist 1983). Morman (1987) placed sea lamprey in cages in five Michigan streams at two densities (25 and 75 larvae/m^2), and monitored growth for 4½ years. Total mortality of larvae from ages 1 to 5 in the low and high density cages ranged from 4 to 8 % and 32 to 48 %, respectively. Weise and Pajos (1998) measured growth and density using length-frequency data between year classes of sea lamprey during recolonization of a Great Lakes tributary following a lampricide treatment in August 1989. They identified intraspecific competition, found no significant change in density of the 1990 year class during the study, and measured annual mortality of the 1991 year-class (interpreted as intraspecific mortality) as 39 %.

Survival of ammocoetes is also related to temperature, which is reflected in their geographical distribution (see Sect. 3.2.2.5). Van de Wetering and Ewing (1999) found lethal temperatures for larval Pacific lamprey beginning at 28 °C, which is similar to that found in earlier studies for other species: Potter and Beamish (1975) recorded incipient lethal temperatures ranging from 28 to 30.5 °C for northern brook, sea, European brook, and American brook lampreys; and Macey and Potter (1978) determined the incipient lethal temperature of pouched lamprey to be 28.3 °C. Meeuwig et al. (2005), however, reported decreasing survival of Pacific lamprey and western brook lamprey larvae as temperatures reached as little as 22 °C. Acclimation (i.e., to higher temperatures) appears to have little effect on incipient lethal temperature in lampreys. In teleosts, a rise of 3 °C in acclimation temperature generally results in a 1 °C increase in incipient lethal temperature; however, this trend was not observed in larval lampreys (Macey and Potter 1978). In fact, incipient lethal temperature in pouched lamprey acclimated at 5 and 25 °C was 27.3 and 28.2 °C, respectively (Macey and Potter 1978). This small (0.9 °C) rise over a 20 °C range in acclimation temperature is typical of other larval lampreys (Potter and Beamish 1975), and may be related to the low metabolic rate of ammocoetes (Hill and Potter 1970; Potter and Rogers 1972).

Mortality rates are thought to increase again at metamorphosis. Extensive morphological and physiological changes are occurring during this non-trophic period, including dramatic changes to the respiratory system (see Chap. 4) that are assumed to produce a "partial asphyxiation" (Hardisty and Potter 1971a). In addition, dams and other engineering works may represent significant sources of mortality in those species that undergo downstream migration following metamorphosis (see Chap. 8). Lampreys appear to swim lower in the water column than fishes with swim bladders and may thus pass beneath turbine bypass screens designed for juvenile salmonids (Long 1968; Moursund et al. 2003). In addition, those lampreys that encounter salmonid bypass screens may become impinged, leading to elevated mortality rates (Hammond 1979; Moursund et al. 2003; Dauble et al. 2006; Columbia River Inter-Tribal Fish Commission 2008). However, juvenile lampreys that pass through dam turbines may survive relatively better than other fishes. A recent study found no mortality or injury to juvenile Pacific lamprey exposed to a rapid decrease in pressure similar to what would occur during turbine passage; mortality or injury would be expected in 97.5 % of juvenile Chinook salmon *Oncorhynchus* *tshawytscha* similarly exposed (Colotelo et al. 2012). Nevertheless, lampreys that survive passage through dams may become disorientated and suffer increased predation rates. Predatory fishes have been observed to congregate downstream of turbine outflows (Lucas and Baras 2001).

3.6.2 Mortality Ascribed to Pollution and Water Quality

Pollution can affect survival of lampreys. Occassional mortalities have been ascribed to pollution, and significant levels of pollution can eliminate whole populations of lampreys from rivers. Sea lamprey and European river lamprey disappeared from the polluted Thames and Clyde rivers in the United Kingdom (see Chap. 8) and, in Portugal, industrial pollution is thought to be mainly responsible for the extirpation of sea lamprey in the Ave River basin (Quintella 2006). According to Almeida et al. (2008), industrial pollution was also the primary factor responsible for the extremely low density of sea lamprey larvae found in the lower reaches of River Cávado in Portugal. Embryos and larvae using toxic sediments are likely more at risk than are juvenile and adult lampreys migrating through polluted waters (see Chap. 8); given that the larvae remain burrowed in river sediments for years, they may be particularly at risk. Pacific lamprey ammocoetes in the Trinity River, California, contained mercury concentrations (legacy mining contaminants) 12–25 times higher than freshwater mussels from the same site, and were well above concentrations considered to be detrimental in other fishes (Bettaso and Goodman 2010). Pacific lamprey larvae were found to be particularly sensitive to pentachlorophenol, one of the pollutants found in the Portland Superfund area of the Willamette River (Andersen et al. 2010). Morman et al. (1980) observed that streams affected by domestic, industrial, or agricultural pollution usually have no larvae or only small, discrete populations. However, Young et al. (1996) found that peaks in abundance of larval sea lamprey in the St. Marys River in 1971 and 1983 were both before and after reported declines in sediment contamination which could have influenced larval populations.

Few studies are available that concern the water quality requirements of lampreys (Maitland 2003). In comparison with the information on teleost fishes, for example, very little is known about the effects on lampreys of acid water and its associated environmental changes. Those studies available, however, suggest there is cause for concern. According to Myllynen et al. (1997), hatching success of European river lamprey and the survival of newly hatched larvae are clearly reduced by the prevailing water quality of the river. It appears that high iron concentration especially, together with acidic pH, reduces the hatchability of the eggs and increases the mortality of newly hatched larvae (Myllynen et al. 1997). These authors also observed that changes in water quality affected European river lamprey populations in Finnish rivers, as larval populations diminished in areas that otherwise should have been suitable for larval growth.

3.7 Duration of Larval Life and Growth Rates

3.7.1 Duration of Larval Life

The duration of the larval period in the life cycle of lampreys has been found to vary among species and within species (Potter 1980a; Youson 2003; Table 3.2). In general, non-parasitic species appear to persist longer in the larval phase and attain greater lengths at metamorphosis than parasitic species, at least when comparing "paired" (i.e., closely-related) parasitic and non-parasitic lampreys (Potter 1980b; Docker 2009). For example, average duration of the larval period in the European river lamprey in the River Teme has been estimated to be 4¼ years, whereas average length of larval life in the European brook lamprey is approximately 6¼ years (Potter 1980a). However, some earlier studies (Knowles 1941; Hardisty 1944) suggest a much shorter larval phase in the latter species (see Table 3.2). Furthermore, this trend is less apparent when comparing across taxa, and considerable variation in age at metamorphosis has been observed among parasitic species. Some species (e.g., pouched lamprey, European river lamprey, and short-headed lamprey *Mordacia mordax*) initiate metamorphosis at relatively young ages (3¼–4¼ years; Potter 1980a) whereas duration of the larval period for the anadromous sea lamprey was estimated at 6–8 years in Canadian rivers (Beamish and Potter 1975) and at approximately 5 years for British populations (Hardisty 1979). The age at metamorphosis of Pacific lamprey has been estimated at 4–8 years, with the majority of transformers being ages 5–7 (Russell 1986; Beamish and Northcote 1989).

For sea lamprey in the Great Lakes watershed, larvae generally range between 2 and 7 years of age at the time they enter metamorphosis (Potter 1980a; Morkert et al. 1998), although metamorphosis in as few as 2 years is unusual. The Chippewa River in Michigan, where many sea lamprey were found to undergo metamorphosis as early as age 2, is a highly productive stream (Morkert et al. 1998). In the Big Garlic River in Michigan, which is a relatively cold, unproductive stream, a known-age population of ammocoetes were not yet undergoing metamorphosis by age 6 (Dawson unpublished data). Higher productivity associated with higher water temperatures may enhance feeding efficiency and growth, resulting in an earlier age-at-metamorphosis (Morman 1987). Relative to more northerly situated river basins, anadromous sea lamprey ammocoetes from the Portuguese River Mondego presented a shorter larval stage duration of 4 years (Quintella et al. 2003; Fig. 3.4). The relationship between age-at-metamorphosis and ammocoete growth rate is discussed further below (Sect. 3.7.2); size at metamorphosis is discussed in Sect. 3.8.1.

3.7.2 Growth Rate of Ammocoetes

The growth rate of ammocoetes is correlated with factors important to the duration of larval life (such as water temperatures) and can vary considerably between geographic regions with different climatic regimes (Potter 1980a). Landlocked sea

Table 3.2 Summary of past research on the determination of lamprey larval stage duration. The methods listed are those used to determine age/growth

Species	Larval stage (years)	Method	Author
Geotria australis, pouched lamprey	4.25	Length–frequency	Potter and Hilliard (1986)
Geotria australis	3.5	Length–frequency	Todd and Kelso (1993)
Ichthyomyzon gagei, southern brook lamprey	3.25–4.25	Length–frequency	F. W. H. Beamish (1982)
Ichthyomyzon greeleyi, mountain brook lamprey	5.2–6.2	Length–frequency	Beamish and Austin (1985)
Ichthyomyzon greeleyi	5.25–6.25	Length–frequency	Potter and Bailey (1972)
Lampetra aepyptera, least brook lamprey	4–5	Length–frequency/statolith	Docker and Beamish (1994)
Lampetra fluviatilis, European river lamprey	4.5	Length–frequency	Hardisty and Huggins (1970)
Lampetra planeri, European brook lamprey	2–3	Length–frequency	Knowles (1941)
Lampetra planeri	3.5–4	Length–frequency	Hardisty (1944)
Lampetra planeri	6.25	Length–frequency	Hardisty (1961b)
Lethenteron camtschaticum, Arctic lamprey	4	Length–frequency/statolith	Kucheryavyi et al. (2007)
Mordacia mordax, short-headed lamprey	3.5	Length–frequency	Potter (1970)
Petromyzon marinus, sea lamprey	3.4–3.9	Length–frequency	Applegate (1950)
Petromyzon marinus	5	Length–frequency	Hardisty (1969)
Petromyzon marinus	6	Length–frequency	Lowe et al. (1973)
Petromyzon marinus	6–8	Length–frequency	Beamish and Potter (1975)
Petromyzon marinus	5	Length–frequency	Hardisty (1979)
Petromyzon marinus	5	Cage	Morman (1987)
Petromyzon marinus	2	Length–frequency/statolith	Morkert et al. (1998)
Petromyzon marinus	3–4	Statolith	Griffiths et al. (2001)
Petromyzon marinus	4	Length–frequency/statolith	Quintella et al. (2003)

lamprey in the lower Great Lakes (lakes Erie and Ontario) are known to achieve larger sizes more quickly than sea lamprey in the upper lakes (lakes Superior, Michigan, and Huron; Potter 1980a; Hansen et al. 2003; Slade et al. 2003; Hansen and Jones 2009). More favorable climatic conditions are likely to induce higher growth rates. The majority (96 %) of known-age sea lamprey larvae in a warm, high alkalinity Lake Huron tributary (Ogemaw Creek) achieved lengths of 120 mm or more by late summer at age 5, and some ammocoetes were observed undergoing metamorphosis. However, none of the known-age larvae in a cold, low alkalinity Lake Superior tributary (Big Garlic River) achieved a length of 120 mm by late summer at age 6 (Fig. 3.5). Quintella et al. (2003) used length-frequency analyses and statolith readings to measure growth and larval stage duration of the sea lam-

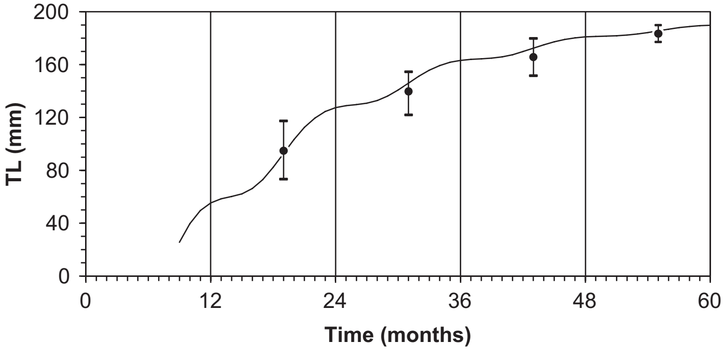

Fig. 3.4 Graphic expression of the seasonal von Bertalanffy growth formula estimated for sea lamprey ammocoetes in the River Mondego, Portugal. Also represented is the mean total length (mm ± SD) of lamprey (●) for each age group assigned with statoliths readings. (This figure was originally published in Quintella et al. (2003) and reproduced with permission of John Wiley & Sons, Inc.)

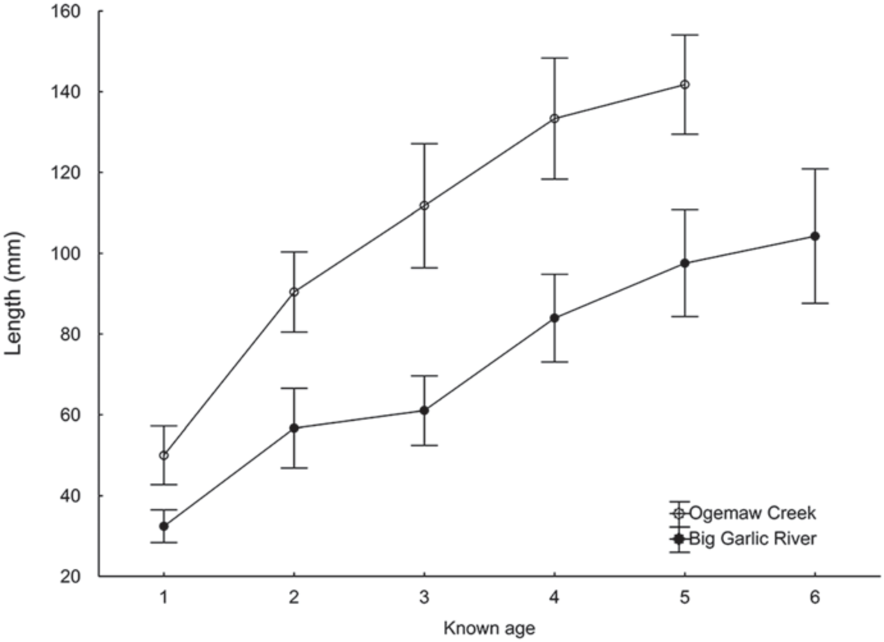

Fig. 3.5 Length at known age for natural populations of sea lamprey in two Michigan streams. Ogemaw Creek is a warm, high alkalinity tributary of Lake Huron, while the Big Garlic River is a cold, low alkalinity tributary of Lake Superior (Dawson unpublished data)

prey in the River Mondego in Portugal. The theoretical growth model based on length-frequency distribution of sea lamprey larvae from this system, confirmed by the number of annuli identified on statoliths, suggested approximately 4 years of larval life (Fig. 3.4). The seasonal von Bertalanffy growth formula, calculated using the length-frequency distribution of the sea lamprey ammocoetes sampled in River Mondego on a monthly basis and during a 3-year period, displayed a marked seasonal pattern of growth throughout the year with a relatively short period of slow growth (± 1.2 months), apparently taking place between January and February, the cooler period of the year (Fig. 3.4). On average, ammocoetes attained 36.7 % of the theoretical maximum length (TL_∞) in the first year (i.e., 72 mm), 68.6 % at the end of the second year (i.e., 136 mm), 84.4 % at the end of the third year (i.e., 168 mm), and 92.3 % of the TL_∞ at the end of the fourth year (i.e., 183 mm; Fig. 3.4). In the Quintella et al. (2003) study, the ages assigned from the number of annuli were consistent with ages derived from the theoretical growth model (Fig. 3.4).

Hansen et al. (2003) found that sea lamprey growth varied significantly among Great Lakes streams and years. This observation is consistent with other studies that indicate variability in larval growth likely derives from watershed characteristics, which define the productivity of each stream and contribute to the variation in growth among streams (Manion and Smith 1978; Purvis 1979; Potter 1980a; Holmes 1990; Young et al. 1990a; Morkert et al. 1998; Rodríguez-Muñoz et al. 2001). Within streams, annual environmental characteristics, such as temperature and precipitation, contribute to variability in growth (Manion and McLain 1971; Young et al. 1990b). Lamprey feed slowly but efficiently on organic detritus in streams, accumulating most of their energy during summer when temperatures are warm and food quality is high (Sutton and Bowen 1994; Yap and Bowen 2003; see Sect. 3.3). This is consistent with previous observations by Lowe et al. (1973) that increases in length of larval sea lamprey in Shelter Valley Creek, a small tributary to Lake Ontario, were almost entirely restricted to the warmest months.

Lowe et al. (1973) also observed that further increases in length did not take place during the final year of larval life. This so-called “arrested growth phase” or “rest period” prior to metamorphosis is not due to environmental conditions, but rather suggests that metabolism prior to metamorphosis is focused more on lipidogenesis than somatic growth (O’Boyle and Beamish 1977; Potter 1980a; Bird and Potter 1981; Treble 2006; see Chap. 4). It is not known, however, whether all lamprey larvae undergo a pre-metamorphic arrested growth phase. Such information is critical for predicting rates of metamorphosis and potential recruitment of sea lamprey to the Great Lakes based on the size structure of larval populations (Slade et al. 2003).

Laboratory studies have shown negative effects of larval density on growth rates in lampreys, both in single species (Mallatt 1983; Malmqvist 1983; Murdoch et al. 1992) and multispecies (Murdoch et al. 1991) experiments. Growth of sea lamprey ammocoetes was observed to decrease significantly with increasing density (Murdoch et al. 1992). Over an 8-month period, the authors recorded changes in length (mean ± standard error) of 17.3 ± 3.0, 4.3 ± 4.5, and -1.4 ± 1.0 mm at larval densities of approximately 34, 172, and 345 per m^2, respectively. Rodríguez-Muñoz et al. (2003) assessed the role of population density and waterborne-mediated interference on the growth rate of sea lamprey larvae in two laboratory experiments. The effects of these factors were evaluated by comparing growth of larvae reared at three different densities (27, 75, and 128 individuals/m^2) or in preconditioned water (i.e., water taken from aquaria containing sea lamprey larvae at the same three densities). The authors found that water conditioning had a negative but weaker effect on growth than larval density, with larvae reared in water preconditioned at the two higher densities having shown a lower mass increase than those growing in water preconditioned at the lowest density. These results suggest that chemical or biological agents released into the surrounding water by conspecifics may influence growth in larval sea lamprey (Rodríguez-Muñoz et al. 2003).

The effect of density on larval growth rate has also been measured in situ through the use of cages (Malmqvist 1983; Morman 1987; Zerrenner 2004). Morman (1987) observed in his long-term cage experiments that sea lamprey ammocoete lengths were significantly greater in the low-density cages (25 larvae/m^2) by the end of the study than in the high density cages (75 larvae/m^2). He also found that some larvae had entered metamorphosis in the low-density cages (presumably as the result of attaining a larger size), while no metamorphosing animals were observed in the high density cages. Zerrenner (2004), however, found growth of sea lamprey larvae held in circular cages (0.16 m^2) in streams for a period of 1 year was not significantly affected by density (25, 50, 100, 150, and 200/m^2).

The experimental densities used in the above studies are generally much higher than average larval densities observed in nature (see Sect. 3.4.1). Nevertheless, comparisons within and among streams have also suggested that larval density influences growth rate at natural densities (Manion and Smith 1978; Morman 1987; Jones et al. 2003). Overall, most evidence supports a general reduction in growth rate of larvae with increasing density.

Negative growth must be experienced by lampreys during the non-trophic metamorphic period, although reductions in weight are often relatively modest (especially compared to reductions observed during the non-trophic upstream spawning migration of some species; see Chap. 5) and changes in length are often complicated by morphological changes associated with metamorphosis (e.g., elongation of the snout and development of the oral disc in parasitic species; Hardisty and Potter 1971b). In metamorphosing landlocked sea lamprey observed between October and early March, Wigley (1959) observed that weight decreased by about 11 % but that length increased by 5 %. Over a similar time period in metamorphosing European river lamprey, Hardisty (1970) observed that weight decreased by about 8 % but length stayed the same. In non-parasitic species, completion of metamorphosis overlaps with gonadal maturation, further complicating comparisons (Hardisty et al. 1970; Hardisty and Potter 1971b). Earlier studies (e.g., in northern brook lamprey; Leach 1940) showed overall reductions in length and weight between transformation and sexual maturity, but Beamish and Medland (1988a) showed that neither length nor weight of mountain brook lamprey males or females changed significantly between metamorphic stages 1 and 7. In the latter study, condition factor increased significantly between stages 1 and 2, and did not change significantly after stage 2. Only at sexual maturity (stage 8) in females did weight change significantly, but it also increased. Beamish and Medland (1988a) concluded that lipid reserves used during the 3.3–4.7 months required to complete metamorphosis

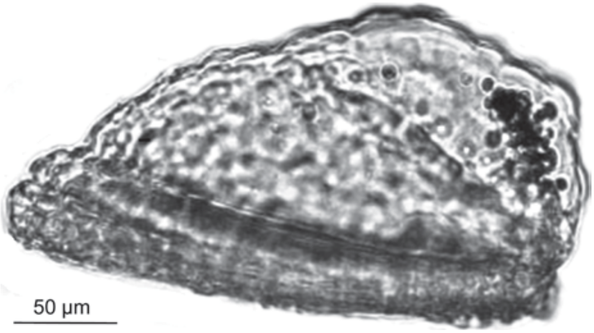

Fig. 3.6 Photograph of a statolith from a larval sea lamprey. (Photo: Nuno Andrade)

were replaced by water so that total length and body weight did not change. More research is required to determine the energetic costs of metamorphosis.

3.7.3 *Reliable Aging Methods Required to Estimate Duration of Larval Life and Growth*

Analyses that require age-composition data, such as growth and duration of the larval life stage, have been generally avoided due to the unreliability of age-assessment methods for larval lampreys. For a review of past research on larval stage duration, see Sect. 3.7.1 and Table 3.2. Historically, sea lamprey ammocoetes have been assigned ages using visual assessment of length-frequency distributions (Hardisty and Potter 1971a; Beamish and Medland 1988b). Determining age based on length-frequency distributions is subjective because of heterogeneity in larval growth rates within and across streams, and the resulting overlap in lengths between age classes introduces uncertainty into the estimates of population age composition (Potter 1980a). The great individual variability in growth rates of ammocoetes and the consequent wide scatter of lengths within the same age class have frequently made it difficult to identify with certainty the individuals belonging to the older age groups in the length-frequency distribution (Hardisty and Potter 1971a; Hardisty 1979). Even the age at transformation of a re-established population of ammocoetes (e.g., after lampricide treatment) is difficult to determine if residual larvae are also present in the stream (Purvis 1979). Only a small percentage of a year class may transform during the year metamorphosis begins, and it is often impossible to separate these animals from the small residual population when the length frequencies of the two groups overlap (Purvis 1979).

Statoliths, the only calcareous structure in lampreys, have been used as an alternative technique to age ammocoetes (e.g., Volk 1986; Beamish and Medland 1988b; Hollett 1998). Statoliths display alternating narrow opaque bands, which represent prolonged slow growth during winter, with the translucent band deposited during rapid growth periods associated with increased temperatures and feeding (Beamish and Medland 1988b; Barker et al. 1997; Fig. 3.6). When determining age using statoliths, each opaque band or annulus is counted as representing 1 year

(Volk 1986). Most studies provided similar age estimates when comparing ages determined from statoliths and length-frequency distribution (Volk 1986; Beamish and Medland 1988b; Docker and Beamish 1994; Barker et al. 1997; Morkert et al. 1998; Griffiths et al. 2001; Quintella et al. 2003). Meeuwig and Bayer (2005) did report some modal separation for western brook lamprey from Washington, but more year classes were observed by aging statoliths than were apparent from the length-frequency histogram. However, the reliability of the use of statoliths to accurately assess the age of ammocoetes is not consensual among lamprey researchers.

To use statoliths as a method of assessing age of larval sea lamprey, the structures must be validated so that the banding pattern can be repeatedly visualized by a reader and represents the true age of the ammocoete over multiple years in contrasting streams (Jones 2007). Most studies using statoliths to estimate larval lamprey population age composition measure the precision (the deviation of each age assignment from the mean age assigned by readers) as an assessment of error and not the accuracy (deviation of age assignment from the true age; Dawson et al. 2009). Recently, Dawson et al. (2009) established known-age populations of sea lamprey in two contrasting Great Lakes streams and assessed the precision and accuracy of statolith aging over multiple years. The authors found that the precision average percent error (APE) ranged from 12.6 to 19.7%, and was smaller than the accuracy APE (bias) that ranged from 24.3 to 36.2 %. These results indicate a lack of accuracy in age assessments using statoliths (Fig. 3.7). Accurate estimates of age composition are better obtained by combining length-frequency information with a small sample of bias-corrected statolith annuli counts in a statistical model of growth of lamprey ammocoetes (Dawson et al. 2009). However, the bias in annuli counts by readers is variable by stream and by age. Additional research combining length-frequency information with statolith size data from the population did not improve estimates of age composition (Dawson unpublished data). Thus, the use of statoliths as a tool to reliably age lampreys is in question.

3.8 Onset of Metamorphosis

The microphagous period of the larval life stage and the parasitic juvenile stage (or, in the case of non-parasitic species, the non-trophic adult period) are separated in all lampreys by a non-feeding period (the duration of which varies within and among species) and a radical transformation (Potter et al. 1980). The transformation of larval lampreys represents one of the few “true” vertebrate metamorphoses, as most organ systems undergo some sort of reorganization to facilitate the impending change in lifestyle (see Chap. 4). In some ways, however, lamprey metamorphosis in anadromous species is similar to the smolting period of salmonids, in which juvenile animals prepare for life in a marine environment after hatching and rearing in fresh water, by developing silvery coloration, large eyes, and the ability to osmoregulate in a marine environment (Potter and Huggins 1973).

The precise onset of metamorphosis is difficult to detect in larval lampreys because many internal changes may be occurring before it is externally apparent. As a

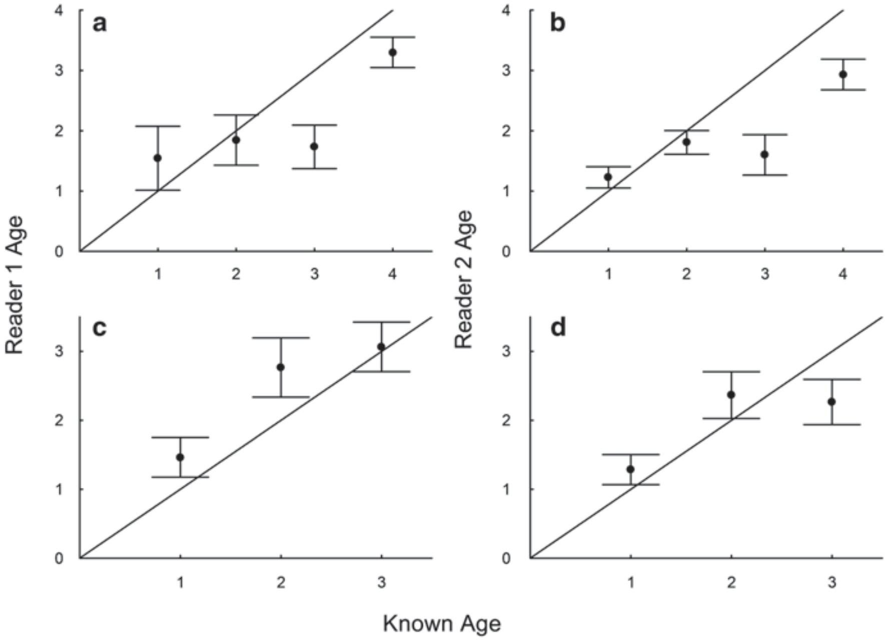

Fig. 3.7 Age bias plots constructed from sea lamprey statoliths evaluated from two "known-age" populations that were aged by two readers. Panels (**a**) and (**b**) compare the average age coded by each reader to the true age when evaluating the slow-growing Big Garlic River population. Panels (**c**) and (**d**) compare the average age coded by each reader to the true age when evaluating the fast-growing Ogemaw Creek population. *Error bars* indicate 95 % confidence intervals surrounding the average age assigned by each reader. This figure was originally published in Dawson et al. (2009) and reproduced with permission of Taylor & Francis Ltd. (http://www.tandf.co.uk/journals)

result, older studies of lamprey metamorphosis may not have recognized the earliest stages and thus there is a great deal of variability in the estimated duration of the metamorphic period for some species (Potter 1980b). However, two components are required before lampreys can enter into metamorphosis: a suitable water temperature regime prior to the onset of metamorphosis and sufficient size/lipid reserves to provide enough energy to support all of the developmental changes that occur while the animal ceases to feed (Youson et al. 1993). The process of metamorphosis is described in detail in Manzon et al. (see Chap. 4), but aspects relevant to the ecology of the stream-resident stage of the lamprey life cycle are discussed below.

3.8.1 Size of Metamorphosing Lampreys

Metamorphosis generally occurs at lengths ranging from approximately 90 to 170 mm (Potter 1980a; Docker 2009; see Chap. 4). However, there is considerable variability in ammocoete length and weight at the time of metamorphosis between different lamprey species, as well as within a single species. Temperature and stream productivity influence growth rates of larval populations (see Sect. 3.7.2), adding inter- and intra-annual variation in lamprey size at metamorphosis (Holmes 1990; Young et al. 1990a). Population density (both conspecifics and heterospecifics) influences the size at which larval lampreys initiate metamorphosis as competition for available food resources may negatively influence larval growth rate (Murdoch et al. 1992; Rodríguez-Muńoz et al. 2003). This is evident in the Great Lakes basin, where transforming lamprey that are residuals from a lampricide treatment (and thus are at lower density) are routinely observed to be larger than those observed during the lampricide treatment a year or two prior (Purvis 1980). Further, the landlocked variety of sea lamprey found in the Great Lakes enters metamorphosis at a larger size than the anadromous form from which it is derived (Potter et al. 1978).

As mentioned above (Sect. 3.7.2), an arrested growth phase, whereby there is an increase in weight and lipid content—but not length—has been observed in some lamprey species prior to metamorphosis. Consequently, lampreys preparing for metamorphosis are presumably "fatter" for a given length than are other larvae. A condition factor criterion (combined with length and weight criteria) has thus been used to identify presumptive metamorphosing sea lamprey larvae (Holmes and Youson 1994, 1997, 1998; see Chap. 4). However, condition factor has performed well in predicting metamorphosis in close proximity to the event (Youson 2003), but not many months in advance of its onset (Treble et al. 2008). Using a mark-recapture technique, Treble et al. (2008) determined that the factors most likely to predict onset of metamorphosis of larval Great Lakes sea lamprey in eight streams were weight, age, larval density, stream temperature, and geographic location.

A general trend across the lamprey genera suggests that parasitic species metamorphose at a smaller length and/or weight than closely-related non-parasitic species (Vladykov and Kott 1979; Docker 2009; see Chap. 4). This may be related to the fact that while parasitic species feed for a few months to several years after metamorphosis before their gonads ripen, non-parasitic lampreys become sexually mature shortly after metamorphosis, without any further intake of food. Although not as fecund as parasitic species, this would still represent a significant increase in energy requirements (see Sect. 3.7.1). However, the ability to distinguish between species of ammocoetes from the same genus is often difficult and thus usually limits comparisons to allopatric populations (Docker 2009), where paired parasitic and non-parasitic species may be subject to different environmental conditions. Furthermore, the trend observed between paired species should not necessarily be taken to mean that parasitic species in general metamorphose at a smaller size than non-parasitic species. As with age at metamorphosis (see Sect. 3.7.1), considerable variation in size at metamorphosis has been observed among parasitic species. Pouched lamprey, for example, metamorphose at a relatively small size (c. 90 mm; Potter 1980b), whereas anadromous and landlocked sea lamprey metamorphose at much larger sizes (c. 130 and 140 mm, respectively; see Chap. 4). Likewise, even within a population, there can be differences among individuals in size at metamorphosis; in the non-parasitic species at least, there is evidence that females metamorphose at a larger size than males (see Docker 2009).

3.8.2 Seasonal Incidence and Duration of Metamorphosis

A generally accepted fact is that the onset of metamorphosis is highly synchronous in a given species within a particular river system (within 3–4 weeks), despite the variability observed inter-annually (Potter 1980a). This is related to latitude, as well as local environmental conditions (Potter et al. 1978; Youson et al. 1993; see Chap. 4). In both Northern and Southern hemispheres, transformation begins during the spring or summer months, when water temperatures are the most favorable, and is generally completed by winter or early the following spring (e.g., Richards and Beamish 1981; Potter et al. 1982; Potter and Hilliard 1986; Holmes and Lin 1994; Quintella et al. 2003; McGree et al. 2008). Beamish and Medland (1988a) compared timing of metamorphosis in six Northern Hemisphere lamprey species, and observed that those occurring at lower latitudes tend to enter metamorphosis later than those at higher latitudes (Beamish and Medland 1988a). Southern brook lamprey, for example, were found to enter metamorphosis as late as early September (Beamish and Thomas 1984), whereas more northerly species such as Arctic lamprey, Pacific lamprey, and European river lamprey generally initiate metamorphosis in July (Beamish and Medland 1988a; Youson et al. 1993; Kucheryavyi et al. 2007; McGree et al. 2008). There is also variability in the timing of metamorphosis between conspecifics at the latitudinal extremes of their ranges. Tennessee populations of American brook lamprey start metamorphosis around mid-August (Seagel and Nagel 1982), whereas populations of the same species in the more northerly Great Lakes basin are found to start metamorphosis as early as late June (Holmes et al. 1999). For sea lamprey, initiation of metamorphosis typically occurs in midsummer (August/September) in Portugal (Quintella et al. 2003), and early to mid-July at more northerly latitudes (Potter 1980b; Youson et al. 1993). However, there do appear to be exceptions to this pattern. For example, the Mexican lamprey *Tetrapleurodon spadiceus* and Mexican brook lamprey *T. geminis* enter metamorphosis in April (Cochran et al. 1996), and the precocious or Australian brook lamprey *Mordacia praecox* initiates metamorphosis in October or November, the equivalent of spring in the Northern Hemisphere (Potter 1970); all three species occur at low latitudes (20° N, 20° N, and 35–44° S, respectively).

Lamprey metamorphosis generally lasts 3–4 months, but can be variable among species. Comparisons among studies, however, may be complicated by differences in defining the exact point of completion of metamorphosis. Although metamorphosis was initially divided into five (Manion and Stauffer 1970) and later seven (Bird and Potter 1979; Youson and Potter 1979) stages based on the sequential changes of five key morphological features (see Chap. 4), some studies report instead when initiation of downstream migration and commencement of parasitic feeding occurs; these ecological transitions may occur sometime after the morphological completion of metamorphosis (see Sect. 3.9). Furthermore, they are not applicable to non-parasitic species. The duration of the metamorphic phase does not appear to be related to latitude, temperature, or whether the animal follows a parasitic or non-parasitic life history. Duration of metamorphosis may be as short as 3–3.5 months in

Siberian brook lamprey *Lethenteron kessleri* (Poltorykhina 1971), European river lamprey (Bird and Potter 1979), and anadromous sea lamprey (Reis-Santos et al. 2008), or as long as 7–8.2 months in European brook lamprey (Bird and Potter 1979) and 9 months in North American river lamprey (Beamish and Youson 1987).

3.9 Downstream Migration

After metamorphosis is complete, some species (e.g., European brook lamprey) remain burrowed in the substrate until ready to spawn, whereas others (e.g., sea lamprey, European river lamprey, short-headed lamprey) burrow less often, instead preferring to hide under logs and rocks during the day (generally in areas with appreciable water flow) and moving at night (Potter 1970; Potter and Huggins 1973). In Pacific lamprey in the Fraser River, British Columbia, 99 % of all downstream migrants were captured at night (Beamish and Levings 1991). The downstream migration of newly metamorphosed lampreys applies almost exclusively to parasitic species migrating to feeding grounds, although presumably a small number of brook lampreys migrate downstream to colonize new tributaries in landlocked populations. Anadromous parasitic lampreys migrate to the marine environment, although several species that are typically anadromous also appear to exist as freshwater-resident populations or individuals. The best known example, of course, is the Great Lakes sea lamprey, but other examples include populations of Arctic and European river lampreys that feed in other large lakes (e.g., Heard 1966; Nursall and Buchwald 1972; Adams et al. 2008; see Docker and Potter in press). Although poorly studied, these and other freshwater-resident parasitic lampreys undergo more limited downstream migrations than most anadromous lampreys. This, presumably, is particularly true of those species that feed predominantly in river rather than lake systems (e.g., chestnut lamprey *Ichthyomyzon castaneus*, Ohio lamprey *Ichthyomyzon bdellium*, Carpathian lamprey *Eudontomyzon danfordi*; Renaud 2011). The following sections, therefore, deal only with anadromous species and the well-studied Great Lakes sea lamprey.

3.9.1 Environmental Triggers and Timing of Downstream Migration

Unlike the onset of metamorphosis, which is highly synchronized within a population, the timing of downstream migration can be quite variable (Potter et al. 1982), and evidence suggests that it is triggered by environmental cues. The most significant environmental trigger appears to be increases in river flow resulting from freshet events (Bird et al. 1994; Quintella et al. 2005; Columbia River Inter-Tribal Fish Commission 2011). Downstream migration of European river lamprey juveniles in Germany shows a peak in the spring (Thiel and Salewski 2003). In a

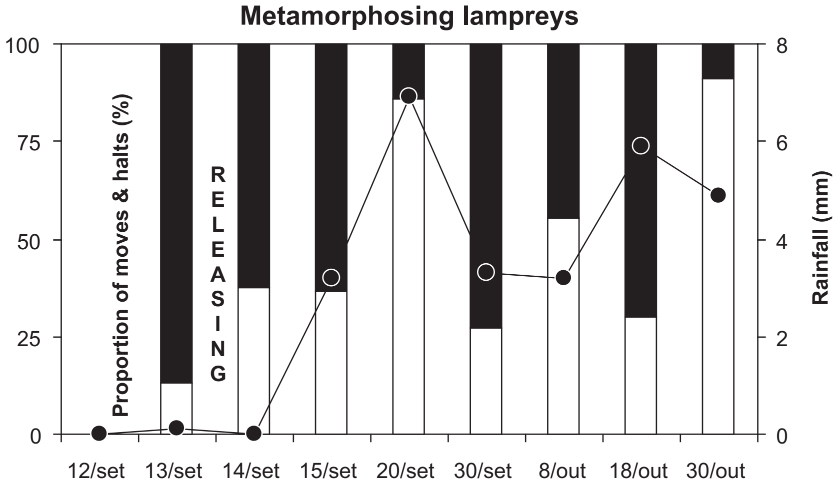

Fig. 3.8 Relationship between the rainfall (-●-) observed in a tributary of River Mondego, Portugal, and the proportion of moves (□) and halts (■) for metamorphosing sea lamprey. Dates (day/month) are given on the horizontal axis (*set* = Sept; *out* = Oct). (This figure was originally published in Quintella et al. (2005) and reproduced with permission of John Wiley & Sons, Inc.)

tributary of the River Mondego, Portugal, a significant increase in the proportion of downstream movements of transformers followed rainfall episodes (Quintella et al. 2005; Fig. 3.8). Downstream movement of juvenile North American river (Beamish and Youson 1987) and Pacific (Beamish and Levings 1991) lampreys likewise appears to coincide with increased discharge. Beamish and Youson (1987), in fact, suggested that the prolonged period of metamorphosis observed in the North American river lamprey (see Sect. 3.8.2) may have evolved in response to the pattern of discharge in the Fraser River (i.e., that this species delays completion of metamorphosis until flow increases in the spring). In Pacific lamprey in the Fraser River, downstream migration started in late September, with the largest number of migrants captured in mid-March to mid-May (Beamish and Levings 1991). Counts of juvenile lamprey (presumably mostly Pacific lamprey) as they pass through the mainstem dams and upriver salmon smolt traps in the Columbia River basin likewise show spring peaks of migration that coincide with periods of increased flow (Columbia Basin Fishery Agencies and Tribes 2014). There may be other peaks in winter as large pulses of juvenile lamprey have been observed in salmon smolt traps on the Umatilla River, a Columbia River tributary (Mary L. Moser, Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle WA, personal communication, 2014).

Although increases in stream discharge appear to be the primary trigger for the initiation of downstream migration, water temperature is also an important cue (Potter and Huggins 1973). The downstream migration of newly-transformed juvenile sea lamprey is monitored annually on the St. Marys River, which connects Lake Superior and Lake Huron. As water levels on this river are controlled, temperature is the primary cue for downstream migrants, with the timing of the peak of the run varying from year to year, but generally occurring after water temperatures fall below 8 °C in any given year (Treble unpublished data). Applegate (1950) observed that downstream migration of metamorphosed Great Lakes sea lamprey peaked in the fall (around November) and again in spring (around April). Those that enter the lakes in the fall can start the parasitic feeding phase 3–7 months earlier than the spring outmigrants, which overwinter in the stream substrate without feeding (Swink 1995). A recent study by Swink and Johnson (2014), however, found no significant differences in survival or growth over the entire feeding phase (i.e., between downstream migration and spawning) in fall versus spring migrants (see Chap. 4).

3.9.2 Salinity Tolerance

Because all lamprey species spend the majority of their life as ammocoetes burrowed in the sediments of freshwater streams, the ability to tolerate brackish and salt water is a critical developmental phase in the life cycle of anadromous species. The process of marine osmoregulation consists of swallowing sea water, uptake of water and ions across the gut wall, and excretion of excess ions through the gills and opisthonephros (kidney) (Bartels and Potter 2004). Some of the developmental characteristics that allow this include the opening of the foregut and development of numerous lateral folds, as well as the presence of numerous mitochondrial-rich cells (also known as chloride cells) containing Na^+/K^+-ATPase transporting enzyme in the gill filaments (Potter and Huggins 1973; Richards and Beamish 1981; Reis-Santos et al. 2008).

Osmoregulatory efficiency correlates well with the expression of branchial Na^+/K^+-ATPase and chloride cell proliferation, which all increase during metamorphosis (Bartels and Potter 2004; Reis-Santos et al. 2008). Several studies have demonstrated that larval lampreys are generally unable to osmoregulate in water with salinities higher than 10 practical salinity units (psu) or ‰ (e.g., Hardisty 1956; Beamish et al. 1978; Morris 1980; Reis-Santos et al. 2008), which corresponds to c. 28 % full strength sea water. Pacific lamprey larvae have been found to tolerate salinities up to 10 psu for 14 days, although Pacific and western brook lamprey larvae have been observed in tidally influenced areas experiencing up to 15 psu (Gregory S. Silver, U.S. Fish and Wildlife Service, Vancouver, WA, personal communication, 2014). Salinity tolerance (in anadromous species at least, see below) develops during metamorphosis. In anadromous sea lamprey, early transformers (stages 3–5) were already capable of tolerating transfer to water salinity of 25 psu or 70 % full strength sea water, although these early transformers did not survive at full strength sea water and, even at 25 psu, they were inactive during the first two days (Reis-Santos et al. 2008). All later staged transformers (stage 6) in this study survived in full strength sea water. In Pacific lamprey, Richards and Beamish (1981) reported that individuals in stage 5 of metamorphosis were able to survive salinities > 13.4 psu

(>38 % full strength sea water), and those in stage 6 survived a direct transfer to 30 psu (85 % sea water). Thus, it appears that the ability to acclimate to full strength sea water is developed around metamorphic stage 6 (see Chap. 4), which coincides with the formation of the foregut in these two species (Richards and Beamish 1981; Reis-Santos et al. 2008). Once metamorphosis is complete (i.e., at stage 7), survival rates are high with either acclimated (Potter et al. 1980; Beamish et al.1978; Clarke and Beamish 1988; Reis-Santos et al. 2008) or direct (Potter and Beamish 1977) transfer to full strength sea water. Similar results were observed in young adults of European river and pouched lampreys (Potter and Huggins 1973; Potter et al. 1980).

Freshwater-resident populations of normally anadromous species (see Docker and Potter in press) likely retain some ability to osmoregulate in salt water. Youson and Freeman (1979) demonstrated that feeding adults of the landlocked sea lamprey still contained well developed chloride cells in their gills. Tolerance to salt water, however, appears to be related to body size; only when landlocked sea lamprey juveniles reached almost 280 mm in length did they survive direct transfer to full seawater for periods of approximately 2 weeks (Mathers and Beamish 1974). Non-parasitic lampreys, which remain in fresh water throughout their lives, appear to be less tolerant of salinity than parasitic (and certainly anadromous) species (e.g., European brook versus European river lamprey; Hardisty 1956). However, some non-parasitic lampreys (those that are, presumably, recently derived from anadromous parasitic ancestors) still retain well developed chloride cells in their gills (e.g., American brook lamprey; Bartels et al. 2011) and may be capable of limited osmoregulation in sea water. This might enable transformers of these species, if swept downstream into estuaries, to survive and swim back into rivers. As discussed above (Sects. 3.2.3 and 3.5), metamorphosed individuals typically occur in the downstream reaches of rivers; in streams where high flow events are frequent, they may be vulnerable to being swept out of the stream altogether.

3.10 Potential Compensatory Effects of Sea Lamprey Control

Compensatory mechanisms refer to processes that increase birth rates or decrease death rates when population density decreases. Thus, there is concern that the successes achieved in sea lamprey control in the Great Lakes may, in part, be counteracted by compensatory mechanisms (Jones et al. 2003). For example, increased growth as the result of lampricide-induced decreases in density could, in turn, result in higher survival or earlier age at metamorphosis. The consequences to the sea lamprey control program of the former are clear, and shortening the duration of the larval period would necessitate more frequent lampricide applications per stream. However, there is little evidence of a strong, repeatable influence of density-dependent compensatory mechanisms in Great Lakes sea lamprey populations. Some studies have suggested accelerated growth and time to metamorphosis as a result of lower densities following lampricide application (e.g., Purvis 1979; Weise and Pajos 1998; Morkert et al. 1998). Purvis (1979), for example, noted that metamorphosing lamprey were consistently larger (longer) in post-treatment populations than in pre-treatment populations in the same stream, suggesting that growth rates were accelerated following treatment. However, since there is no age-composition data on these larvae, it is impossible to determine whether the increased size is indicative of size- or age-dependent differences in treatment mortality or potential changes in the duration of the larval stage (Jones et al. 2003). In the Lake Champlain basin, Zerrenner and Marsden (2006) reported that transformation occurred at a smaller size (131 mm vs. 143 mm) and at a younger age (100 % age 4 vs. 100 % age 5; larvae were aged using statoliths) in a tributary following lampricide treatment (albeit where densities were still high) relative to a tributary that had never been chemically treated. These authors suggested that this may be due to selection for early transformation in larvae due to exposure to lampricide treatments.

Other studies, however, do not suggest compensatory effects. Jones et al. (2003) compared the average sizes reached by successive sea lamprey cohorts following treatment of a stream with lampricide to evaluate whether lower density would lead to mean lengths of ammocoetes in the first cohort being greater than in later cohorts. These authors found that lengths of age-0 and age-1 ammocoetes were not consistently greater in the first year following treatment. Griffiths et al. (2001) similarly found that the daily growth of larvae in lampricide-treated streams was similar to that in populations that were never exposed to lampricides. Johnson et al. (2014), who monitored tagged sea lamprey larvae released into six Great Lakes tributaries following lampricide treatment, found that survival and size at metamorphosis of these residual larvae were very similar to those of untreated populations. These results suggest that other factors that vary from year to year in the natural environment, such as weather and timing of hatching, may be at least as important as ammocoete density in controlling cohort mean lengths (Jones et al. 2003).

A large shift in sex ratios of both adult and larval Great Lakes sea lamprey was observed in all three of the upper Great Lakes and a Lake Champlain stream (Zerrenner and Marsden 2005) after the implementation of sea lamprey control (Purvis 1979; Heinrich et al. 1980). This shift is presumably a demographic response of the lamprey populations to reductions in their overall abundance (Jones et al. 2003; see Sect. 3.4.3). Prior to control, adult lamprey populations in all three lakes were predominantly (54–70 %) male (Smith 1971). After the control program had successfully reduced the lamprey populations in these lakes to far below their pre-treatment levels (e.g., estimated reductions of 76–92 % in Lake Superior; Smith and Tibbles 1980), sex ratios shifted sharply to a predominance of females (with males comprising only 21–44 %; Purvis 1979). The most pronounced shifts in sex ratios of sea lamprey larvae and transformers have been toward an increased proportion of females occurring predominantly in high-density streams supporting disproportionate numbers of males during original treatments (Torblaa and Westman 1980). Sex compositions in streams where relatively low densities of larvae existed during original treatments remained remarkably stable since the advent of chemical control (Torblaa and Westman 1980). If the supply of eggs (number of females) is correlated with the production of larvae and the supply of males does not limit recruitment, then a shift from a preponderance of males to a preponderance of females should, all else being equal, tend to compensate for a reduction in overall numbers of adults (Jones et al. 2003). Whether this is indeed the case, however, will depend on the mating system of sea lamprey (see Chap. 6).

3.11 Conclusions

Remarkable similarities exist across lamprey species with respect to the larval stage of their life cycle and the process of metamorphosis; thus, ecological requirements of this group are also similar. Habitat variables corresponding to larval lamprey abundance are different depending on the spatial scale examined and the size of the ammocoete. On the river-basin scale, the existence of suitable conditions for ammocoete colonization is dependent on stream gradients, which will, in turn, determine the overall velocity of the current and, consequently, the type of substrate particles that are deposited (Hardisty and Potter 1971a). Recent studies have also indicated that the spatial context of biological factors, such as the spawning distribution of adults, also plays an important role in larval distribution. Evidence exists that freshet events, larval density, and temperature can affect movement of larval lampreys, with movements occurring primarily in a downstream direction, as evidenced by tagging studies and the accumulation of larger larvae in lentic areas near the mouths of streams (Jones 2007). Nevertheless, it is misleading to regard ammocoetes as entirely at the mercy of their environment in terms of dispersal or foraging, as they are capable of moving short distances in the upstream direction against slow currents (Quintella et al. 2005). Environmental characteristics such as temperature, precipitation, and water chemistry contribute to variability of larval growth within streams (Manion and McLain 1971; Young et al. 1990b), as do other factors such as larval density (Mallatt 1983; Malmqvist 1983; Murdoch et al. 1992). Estimation of the growth rate and duration of the larval stage of lampreys is complicated by the unreliability of age-assessment methods for larval lampreys.

All species of lampreys go through a true vertebrate metamorphosis to change from the larval to the adult form (Youson 2003; see Chap. 4). The start of metamorphosis is highly synchronous (within 3 to 4 weeks) within a population and is related, in large part, to the latitude of the population in question, as well as by local environmental conditions (Potter et al. 1978; Youson et al. 1993). There is evidence that the synchronous nature of the downstream migration of anadromous species is triggered by environmental cues, namely increases in river flow resulting from heavy rain and/or spring thaw events (Bird et al. 1994; Quintella et al. 2005). Unlike the timing of metamorphosis, the duration of the metamorphic phase does not appear to be related to latitude, temperature, or whether the animal follows a parasitic or non-parasitic life history, with the duration of metamorphosis recorded as occurring in as little as 3 months and as long as 9 months in different species. Considerable variability also exists in ammocoete length, weight, and age at the onset of metamorphosis, both between and within species. Large lipid reserves are required to undergo the process of metamorphosis, although the temporal pattern of lipid deposition varies between ammocoetes of different species (Bird and Potter 1981). It is following metamorphosis that the ecology (and hence physiology) of species with different adult life history types diverge; in anadromous species, it appears that the ability to acclimate to full strength sea water develops around metamorphic stage 6 (see Chap. 4). Evidence exists of environmental sex determination in lampreys (Docker and Beamish 1994). A large shift in sex ratios of both adult and larval Great Lakes sea lamprey was observed in all three of the upper Great Lakes after the implementation of the sea lamprey control program during the 1960s (Purvis 1979; Heinrich et al. 1980), which likely resulted from a demographic response of the lamprey populations to reductions in their overall abundance (Jones et al. 2003). Understanding the ecology of larval and metamorphosing lampreys has been critical for control of the invasive sea lamprey in the Great Lakes, and is becoming increasingly more important for the management of many threatened and endangered lamprey species worldwide.

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