Chapter 6
Reproductive Ecology of Lampreys

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Abstract Lampreys typically spawn in riffle habitats during the spring. Spawning activity and diel (i.e., during daylight and at night) behavioral patterns are initiated when spring water temperatures increase to levels that coincide with optimal embryologic development. Nests are constructed in gravel substrate using the oral disc to move stones and the tail to fan sediment out of the nest. Spawning habitat used by individual species is generally a function of adult size, where small-bodied species construct nests in shallower water with slower flow and smaller gravel than large-bodied species. The mating system of lampreys is primarily polygynandrous (i.e., where multiple males mate with multiple females). Lamprey species with adult total length less than 30 cm generally spawn communally, where a nest may contain 20 or more individuals of both sexes. Lamprey species with adult sizes greater than 35 cm generally spawn in groups of two to four. Operational sex ratios of lampreys are highly variable across species, populations, and time, but are generally male biased. The act of spawning typically starts with the male attaching with his oral disc to the back of the female's head; the male and female then entwine and simultaneously release gametes. However, alternative mating behaviors (e.g., release of gametes without paired courtship and sneaker males) have been observed. Future research should determine how multiple modalities of communication among lampreys (including mating pheromones) are integrated to inform species recognition and mate choice. Such research could inform both sea lamprey control strategies and provide insight into possible evolution of reproductive isolation mechanisms between paired lamprey species in sympatry.

Keywords Agnatha · Behavior · Heterospecific matings · Mate choice · Mating system · Pheromones · Sex ratio · Spawning habitat · Sympatric speciation

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6.1 Introduction

Biologists have long been fascinated by the reproductive behavior of lampreys and it is from their unique and signature nesting behavior (where the oral disc is used to move rocks) that lampreys (order Petromyzontiformes, “stone sucker”) derive their name. In the late nineteenth century, naturalists reported unexpectedly discovering lampreys spawning in shallow riffle areas of clear headwater streams (Young and Cole 1900 and references therein). They watched with intrigue for hours and sometimes days as groups of lampreys remained vigorously entwined in what was taken as a romantic effort to contribute to the next generation during their terminal life stage. The allure of observing and characterizing lamprey reproduction has not diminished in the twenty-first century and is further motivated by the ecological, cultural, and economic importance of lamprey species around the world (see Chap. 1). An enhanced understanding of the reproductive ecology of lampreys is needed, both for the more than 20 lamprey species that are threatened or endangered in at least part of their range (Renaud 1997; see Chap. 8) and for control of the invasive sea lamprey in the Laurentian and other Great Lakes (see Marsden and Siefkes in press). Furthermore, as representatives of an ancient vertebrate lineage (Janvier 2010), lampreys provide a unique insight into vertebrate mating systems and sensory modalities.

The lampreys, one of the two surviving groups of agnathan (jawless) vertebrates, currently consist of at least 41 recognized species (see Chaps. 2 and 8). They exhibit an antitropical distribution (Renaud 2011); the four Southern Hemisphere species are placed in families Geotriidae (one species) and Mordaciidae (three species), and the remaining 37–40 Northern Hemisphere species are placed in Petromyzontidae (see Chap. 2). All lampreys pass through a prolonged filter-feeding larval stage (see Chap. 3). Following a dramatic metamorphosis (see Chap. 4), 18 species are parasitic, feeding on the blood or tissue of actinopterygian fishes or other vertebrates in marine or freshwater systems (see Renaud and Cochran in press). Some of the anadromous species (e.g., sea lamprey *Petromyzon marinus*, Pacific lamprey *Entosphenus tridentatus*, and pouched lamprey *Geotria australis*) can reach total lengths (TL) in excess of 60–80 cm (see Docker and Potter in press) and can migrate several 100 km to headwater streams to spawn (see Chap. 5); lampreys that are parasitic in fresh water are smaller at maturity (20–30 cm). The remaining 23–26 species are non-parasitic “brook” lampreys; they bypass the adult feeding phase (thus maturing at lengths of approximately 11–14 cm) and remain within their natal streams (see Docker 2009). Most parasitic lamprey species are “paired” with one or more non-parasitic species; these paired species are morphologically and genetically similar and generally overlap in their distribution (Docker 2009; Docker and Potter in press). Paired lamprey species are examples of possible sympatric speciation through assortative mating (Beamish and Neville 1992; Salewski 2003).

The lamprey spawning stage, although the shortest life stage, is most commonly documented due to its relatively high accessibility for observation compared to the larval and parasitic stage. Lampreys spawn during daylight and at night, typically in large groups, and are not easily disturbed. However, accounts of lamprey reproductive ecology, although extensive and informative, are scattered in the literature and commonalities or differences among species are infrequently summarized. Furthermore, many studies may be inaccessible to English-speaking readers (e.g., are in Russian and German), are often in the older literature, and generally provide descriptions of the spawning behavior of a single species. Two insightful reviews by Hardisty and Potter (1971) and Malmqvist (1986) amalgamated studies describing lamprey reproduction, but there have been few recent efforts to synthesize new discoveries concerning lamprey mating systems, spawning site selection, reproductive behavior, and communication modalities (Jang and Lucas 2005).

This chapter therefore provides an updated synthesis of the reproductive ecology of lampreys. In many cases, information from the older papers referred to above has been taken from the species accounts provided in *The Freshwater Fishes of Europe*, Volume 1, Part 1, Petromyzontiformes (e.g., Holčík 1986a, b, c; Hardisty 1986a, b, c); interested readers are referred to the references therein. Topics will be presented chronologically, beginning with the migration to the spawning grounds and concluding with senescence. Discussions will be focused on those species that have been most intensively studied; hypotheses will be proposed to explain commonalities and differences among species and existing knowledge gaps will be highlighted.

6.2 Migration and Environmental Control of Spawning Behavior

6.2.1 Migration to Spawning Habitat

Lamprey upstream migration has been reviewed in this volume (Chap. 5), but highlights will be briefly reiterated here to provide background for discussions of reproductive ecology. In nearly all cases, lampreys have been observed spawning in streams (but see Sect. 6.3.2). Parasitic lamprey species, which may be displaced over hundreds of kilometers by host fishes, must first locate streams that are suitable for reproduction. Migration has been studied extensively in sea lamprey which—unlike salmonids—do not home to their natal streams (Bergstedt and Seelye 1995; Waldman et al. 2008). Instead, adult sea lamprey use their olfactory system to locate streams containing migratory pheromones excreted by conspecific larvae (Sorensen et al. 2005; Meckley et al. 2012). In the Great Lakes ecosystem, although some sea lamprey migrate into streams without significant larval populations (as evidenced by the rapid re-infestation of streams recently treated with lampricide), adults are more likely to enter streams that contain large numbers of larvae (Moore and Schleen 1980), presumably because larvae emit bile acids that are highly attractive to sexually immature migratory-phase adults (Sorensen et al. 2005). Once a suitable stream is located, migration into specific tributaries continues to be directed by larval odor (Wagner et al. 2006). Recent genetic evidence suggests that Pacific lamprey likewise do not home to their natal streams (Goodman et al. 2008; Spice et al. 2012), and it appears that migratory pheromones emitted by larvae are conserved among lamprey species (Jellyman et al. 2002; Fine et al. 2004; Gaudron and Lucas 2006; Robinson et al. 2009; Yun et al. 2011).

The duration of the pre-spawning migration is highly variable among and within lamprey species (see Chap. 5). For example, sea lamprey migration occurs over a period of 2–3 months (Applegate 1950), while pouched lamprey migration occurs over 15–16 months (Potter et al. 1983). The reasons for such differences in the duration of migration remain unknown; they are not explained solely by differential migration distance, as sea lamprey and pouched lamprey migrate over similar distances. European river lamprey *Lampetra fluviatilis* have distinct autumn and spring spawning runs (Maitland et al. 1994) and have been found in estuaries (i.e., at the beginning of the upstream migration) between July and April (Abou-Seedo and Potter 1979). Pre-spawning migrations of non-parasitic species have also been documented in populations of the Far Eastern brook lamprey *Lethenteron reissneri* (Takayama 2002) and European brook lamprey *Lampetra planeri* (Hardisty 1961a; McIntyre 1969), but such migrations—which only need to be sufficient to correct for downstream larval drift—are typically less than 20 km and confined to their natal watershed (Hardisty 1944; Malmqvist 1980; Takayama 2002).

Natural barriers such as waterfalls and man-made barriers such as dams often limit access to spawning areas and are serious impediments to lamprey restoration efforts (Renaud 1997; Close et al. 2002; see Chap. 8), but are advantageous for the control of invasive sea lamprey in the Great Lakes (Lavis et al. 2003; Marsden and Siefkes in press).

6.2.2 Environmental Control of Adult Lamprey Behavior

The most critical environmental factor influencing the timing of the spawning migration, nest construction, and spawning itself is water temperature (Hardisty and Potter 1971), although pheromones may also play a significant role (see Sect. 6.6.1). Upstream migration is most intense during periods when water temperature and stream flow increase in the spring (Hardisty and Potter 1971; Robinson and Bayer 2005; Binder and McDonald 2010; see Chap. 5). Sexually immature adults begin to migrate at night when water temperatures are generally 2–6 °C below the temperatures at which spawning occurs (see below). Arrival at the spawning grounds coincides with the occurrence of water temperatures appropriate for spawning, the onset of diel behavioral patterns (i.e., showing activity during the day and night; Binder and McDonald 2008a), and the final stages of sexual maturation (Docker et al. in press). Temperature regulation of migration and spawning behavior probably developed in response to the strict thermal requirements for embryonic development (Clemens et al. 2010). Sea lamprey development, for example, occurs at temperatures between 15 and 25 °C (Piavis 1961; McCauley 1963); Pacific lamprey and western brook lamprey *Lampetra richardsoni* development is optimal between 10 and 18 °C (Meeuwig et al. 2005).

Northern Hemisphere lampreys generally spawn during the spring at temperatures ranging from 6 to 26 °C (Table 6.1). Given the importance of elevated water temperature in initiating spawning activity, spawning generally occurs later at higher (i.e., more northerly) latitudes than at lower latitudes. Lampreys occupying higher latitudes generally spawn between April and June: for example, Heard (1966) found ripe and spent Arctic lamprey *Lethenteron camtschaticum* in the Naknek River, Alaska (at approximately 58°40′N) in June; Pletcher (1963) observed western brook and Pacific lampreys spawning in the Salmon River, British Columbia (50°29′N), from April to June; and spawning chestnut lamprey *Ichthyomyzon castaneus* were observed in the Rat River, Manitoba (49°35′N) in mid-June. Sea lamprey in the upper Great Lakes generally spawn in June (although the spawning season may extend from May until September; Manion and Hanson 1980); in the anadromous sea lamprey in Connecticut and Maine, spawning occurs in late May to late June (Gardner et al. 2012). American brook lamprey *Lethenteron appendix* in the upper Great Lakes and Quebec spawn in late April to mid-May (Morman 1979; Mundahl and Sagan 2005), but have been observed spawning as early as March (Cochran et al. 2012). Lampreys occurring at southern latitudes generally spawn at similar temperatures but earlier in the spring or, in some cases, in the winter. Southern brook lamprey *Ichthyomyzon gagei* in Alabama (at approximately 32°30′N) were observed spawning in mid-April to early May (Beamish 1982), and populations of American brook lamprey at the southern edge of this species' range (L'Eau Frais Creek in Arkansas; 34°06′N) spawn in early March (Tumlison and Tumlison 1999). Even more dramatically, two lamprey species found at approximately 20° N (the Mexican lamprey and Mexican brook lamprey, *Tetrapleurodon spadiceus* and *T. geminis*, respectively) reproduce from November to January (Hardisty and Potter 1971).

Spawning seasons may also not be as coordinated and condensed at lower latitudes, presumably because water temperatures are suitable for embryonic development for several months, whereas temperatures at higher latitudes may only be suitable for a few weeks during the late spring. Cochran et al. (1996) postulated that the spawning period of the two Mexican species may exceed 6 months. Similarly, Renaud (1982) documented Macedonia brook lamprey *Eudontomyzon hellenicus* with developed secondary sex characteristics (see Sect. 6.5) in both January and May in Kefalárion Brook (at approximately 37°36′N), and suggested that this represents two distinct spawning periods. Ahmadi et al. (2011) reported Caspian lamprey *Caspiomyzon wagneri* in the final stages of maturity in both the fall and spring (at 34°44–50′N).

Spawning has not been described in any of the four Southern Hemisphere species (see Sect. 6.4.3.1), although the spawning period has been inferred from museum collections of advanced spawning-run adults and the appearance of the young-of-the-year larvae. In this manner, Potter (1970) inferred that short-headed lamprey *Mordacia mordax* spawn in the Moruya River in New South Wales (35°55′S) in the late austral winter or early spring (i.e., August to November) and Maskell (1929), Potter et al. (1983), and Potter and Hilliard (1986) likewise estimated that pouched lamprey spawn over a period of several months during the austral spring and winter.

Table 6.1 List of 22 Northern Hemisphere lamprey species, their adult feeding type (P = parasitic, NP = non-parasitic), migratory type (A = anadromous, F = freshwater), most prevalent mating system, other species that have been observed in the same nest (Heterospecific with), temperature at which spawning occurs, and number of adults observed on a nest (mean and/or range). In the reference column, "inferred" means that mating system was categorized by the authors based on references listed for that species

Species	Feeding type	Migratory type	Mating system	Heterospecific with	Temperature (°C)	Number on nest	Reference
Ichthyomyzon							
Silver lamprey *I. unicuspis*	P	F	Polygynandry				Inferred
				Sea, northern brook, American brook	13–23	2.2 (1–10)	Morman (1979)
					18.2	1–15	Cochran and Lyons (2004)
Northern brook lamprey *I. fossor*	NP	F	Polygynandry				Inferred
				Silver, sea	13–23	6.7 (3–13)	Morman (1979)
Chestnut lamprey *I. castaneus*	P	F	Polygynandry				Inferred
				Southern brook			Cochran et al. (2008)
				Sea, American brook	16–22	1.3 (1–4)	Morman (1979)
					17	c.50	Case (1970)
Southern brook lamprey *I. gagei*	NP	F	Polygynandry				Inferred
				Chestnut			Cochran et al. (2008)
					15–22		Cochran and Gripentrog (1992)
					14–24		Beamish (1982)
						Up to 20	Dendy and Scott (1953)
Mountain brook lamprey *I. greeleyi*	NP	F	Polygynandry	Ohio			Cooper (1983)
					18.8	5–9	Raney (1939)

Table 6.1 (continued)

Species	Feeding type	Migratory type	Mating system	Heterospecific with	Temperature (°C)	Number on nest	Reference
Petromyzon							
Sea lamprey *P. marinus*	P	A, F	Monogamy, polygyny				Inferred
			Lentic spawning (still-water enclosure in river)				Scott (1957)
				Chestnut, silver, American brook, northern brook	11–26	2.4 (1–10)	Morman (1979); Cochran et al. (2008)
					10–26	2–6	Applegate (1950); Beamish and Potter (1975); Manion and Hanson (1980); Gardner et al. (2012)
Caspiomyzon							
Caspian lamprey *C. wagneri*	P	A	–	–	15–23	–	Nazari and Abdoli (2010); Holčík (1986a)
Eudontomyzon							
Ukrainian brook lamprey *E. mariae*	NP	F	–	–	8–13.5	–	Holčík and Delić (2000)
					11–12		Abakumov (1960)
Tetrapleurodon							
Mexican lamprey *T. spadiceus*	P	F	–	–	16.2–22.5	–	Alvarez del Villar (1966)

Table 6.1 (continued)

Species	Feeding type	Migratory type	Mating system	Heterospecific with	Temperature (°C)	Number on nest	Reference
Mexican brook lamprey *T. geminis*	NP	F	–	–	16.2–22.5	–	Alvarez del Villar (1966)
Entosphenus							
Pacific lamprey *E. tridentatus*	P	A, F	Monogamy, polygyny				Inferred
				Western brook			Brumo (2006)
					10.1–17.3	1–3	Stone (2006)
					10–15		Robinson and Bayer (2005)
			Lentic spawning (c. 1 %)			2	Russell et al. (1987)
Vancouver lamprey *E. macrostomus*	P	F	Lentic spawning	–	–	–	Beamish (1987)
Miller Lake lamprey *E. minimus*	P	F	Polygyny				Inferred
				–	12	5	Lorion et al. (2000)
			Lentic spawning				Kan and Bond (1981)
Lethenteron							
Arctic lamprey *L. camtschaticum*	P	A, F	Polygynandry				Inferred
				Anadromous, “praecox,” and non-parasitic morphs (possibly Far Eastern brook lamprey)		6–44	Savvaitova and Maksimov (1979); Kucheryavyi et al. (2007a)
					12–15	5–8	Heard (1966)

Table 6.1 (continued)

Species	Feeding type	Migratory type	Mating system	Heterospecific with	Temperature (°C)	Number on nest	Reference
Siberian brook lamprey *L. kessleri*	NP	F	Polygynandry				Inferred
					8.7–13	Up to 6–8	Holčík (1986b)
Far Eastern brook lamprey *L. reissneri*	NP	F	Polygynandry	Possibly Arctic lamprey			Savvaitova and Maksimov (1979); Kucheryavyi et al. (2007a)
					6.0–12.2	13	Takayama (2002)
Alaskan brook lamprey *L. alaskense*	NP	F	Polygynandry	–	–	–	Vladykov and Kott (1978)
American brook lamprey *L. appendix*	NP	F	Polygynandry	Sea, chestnut, silver			Renaud (2011)
			Lentic spawning		7–21	2.6 (1–9)	Morman (1979)
					9–16	4.2 (2–14)	Mundahl and Sagan (2005)
						Up to 20	Gage (1928)
Lampetra							
European river lamprey *L. fluviatilis*	P	A, F	Polygynandry				Inferred
			Lentic spawning	European brook			Huggins and Thompson (1970); Hardisty (1986a, c); Lasne et al. (2010)
					11		Hagelin and Steffner (1958)
					8	12–16	Jang and Lucas (2005)

Table 6.1 (continued)

Species	Feeding type	Migratory type	Mating system	Heterospecific with	Temperature (°C)	Number on nest	Reference
European brook lamprey *L. planeri*	NP	F	Polygynandry				Malmqvist (1983); Hardisty (1986b)
				European river			Huggins and Thompson (1970); Hardisty (1986a, c); Lasne et al. (2010)
					10		Hardisty (1961a)
					12.3	3	McIntyre (1969)
					8.6–17.7	2 (1–13)	Rooney et al. (2013)
Western brook lamprey *L. richardsoni*	NP	F	Polygynandry				Inferred
				Pacific			Brumo (2006)
					9.4–16.0	2–12	Stone (2006)
					10.6–11.1		Schultz (1930)
			Lentic spawning (still-water tanks)				Russell et al. (1987)
Least brook lamprey *L. aepyptera*	NP	F	–	–	10		Trautman (1957)
						10–12	Brigham (1973)

Water temperature trends have large impacts on nesting and spawning activity. For a particular population of lamprey at higher latitudes, spawning seasons are shortest when water temperatures are warm and stable and longest when water temperatures are low and unstable, resulting in sporadic spawning activity (Hardisty and Potter 1971). Spawning is most vigorous at high and stable water temperatures (Case 1970), but spawning activity can decrease or completely cease with sudden drops in water temperatures of even 1 or 2 °C. Reductions in mating behavior are especially prevalent early in the spawning season and when water temperatures drop during the day (Applegate 1950; Hardisty 1961a).

6.3 Spawning Habitat and Nest Construction

6.3.1 Size-Assorted Spawning Habitat

Spawning accounts in either Geotriidae or Mordaciidae have yet to be published (Renaud 2011). Therefore, descriptions of spawning habitat and behavior herein are limited to the family Petromyzontidae. In nearly all accounts, lampreys spawn in riffle habitats (i.e., shallow areas with fast, turbulent water running over rocks) located in streams. Streams with gradients between 2 and 6 m/km often contain productive spawning riffles and larval beds (Baxter 1954). Lamprey nests are most commonly observed at the head of shallow riffles at transition areas between run (i.e., a deep area with fast water and little or no turbulence) and riffle. Lamprey species have been reported to spawn at a variety of depths and water velocities, as long as there is unidirectional flow and gravel substrate (Schleen et al. 2003; but see Sect. 6.3.2). Although larval lampreys are found in fine sediment (see Chap. 3), spawning lampreys either avoid a substrate of fine particles (< 2 mm diameter; Gardner et al. 2012) or the nest-building activities themselves reduce the amount of silt (see Sect. 6.3.3.1). Smaller lampreys are known to use vacant nests constructed by larger-bodied species (Morman 1979), and European river and brook lampreys have been reported using nests constructed several months earlier by sympatric salmonids (Nika and Virbickas 2010).

Lamprey species of different adult size often spawn in specific microhabitats within riffles, where small-bodied species spawn on smaller gravel substrate, in shallower water, with slower velocity (Table 6.2). Small lampreys are likely restricted to spawning on smaller substrate because they are unable to move larger stones (Cochran and Lyons 2004) or navigate in high water velocities. Therefore, size-assorted spawning habitat preferences may function as an ecological barrier to hybridization of paired species (Beamish and Neville 1992; but see Sect. 6.4.3.5). In the Great Lakes basin, landlocked sea lamprey (mean adult size 35 cm TL, range 11–60 cm) construct nests in gravel substrate 0.9–5.1 cm in diameter, in water 10–170 cm deep, with velocities of 50–150 cm/s (Applegate 1950). Silver lamprey *Ichthyomyzon unicuspis* (mean adult size 28 cm, range 9–39 cm), a parasitic freshwater species that is sympatric with sea lamprey in the Great Lakes region, construct

Table 6.2 Adult length, spawning habitat, and nest size of 16 Northern Hemisphere lamprey species

Species	Adult size (cm)	Habitat			Nest size		Reference
		Water depth (cm)	Substrate diameter (cm)	Velocity (cm/s)	Width (cm)	Depth below substrate (cm)	
Ichthyomyzon							
Silver lamprey *I. unicuspis*	9–39	60	0.4–3	–	30	11	Morman (1979); Manion and Hanson (1980); Cochran and Lyons (2004)
Chestnut lamprey *I. castaneus*	9–36	38	1	–	60	5	Case (1970)
Southern brook lamprey *I. gagei*	9–13	15	–	35	–	–	Beamish (1982)
Mountain brook lamprey *I. greeleyi*	11–17	10–20	–	–	20–25	5	Raney (1939); Beamish and Medland (1988)
Petromyzon							
Sea lamprey (landlocked) *P. marinus*	11–60	13–170	0.9–5.1	50–150	45	20	Applegate (1950); Manion and Hanson (1980)
Sea lamprey (anadromous) *P. marinus*	60–90	40–60	1–5	100–200	40–225	20–40	Hardisty (1986b); Gardner et al. (2012); Sousa et al. (2012)
Entosphenus							
Miller Lake lamprey *E. minimus*	12–14	30	–	–	10	3	Lorion et al. (2000)
Pacific lamprey *E. tridentatus*	10–80	28	2.7	20	–	7	Beamish (1980); Stone (2006)
Lethenteron							
Arctic lamprey *L. camtschaticum*	11–63	10–30	3–5	60–80	20–50	5–10	Holčík (1986b); Kucheryavyi et al. (2007a)
Far Eastern brook lamprey *L. reissneri*	11–20	22	–	20	–	–	Takayama (2002)
American brook lamprey *L. appendix*	10–22	31	1–2	14	16	4	Manion and Hanson (1980); Mundahl and Sagan (2005)

Table 6.2 (continued)

Species	Adult size (cm)	Habitat			Nest size		Reference
		Water depth (cm)	Substrate diameter (cm)	Velocity (cm/s)	Width (cm)	Depth below substrate (cm)	
Lampetra							
European river lamprey *L. fluviatilis*	9–49	20–150	–	–	105	7	Jang and Lucas (2005); Nika and Virbickas (2010)
European brook lamprey *L. planeri*	9–17	10	0.2–1.9	70	28	4	Hardisty (1961a); McIntyre (1969); Nika and Virbickas (2010)
Western brook lamprey *L. richardsoni*	8–15	20	1.5	12	–	3	Stone (2006)
Least brook lamprey *L. aepyptera*	8–18	–	–	100	20	–	Brigham (1973)
Eudontomyzon							
Ukrainian brook lamprey *E. mariae*	12–22	20–30	–	10–15	5–10	–	Holčík and Renaud (1986)

nests in gravel substrate 0.4–3.0 cm in diameter (Manion and Hanson 1980), in water 47–68 cm deep (Cochran and Lyons 2004). American brook lamprey (mean adult size 16 cm, range 10–22 cm), which is broadly sympatric with sea and silver lampreys in the Great Lakes region, but is non-parasitic, constructs nests in gravel substrate 1.0–2.0 cm in diameter (Manion and Hanson 1980), in water 15–55 cm deep, at velocities 5–21 cm/s (Mundahl and Sagan 2005).

A similar relationship between lamprey body size and spawning habitat is observed in Europe and western North America. European river lamprey (mean adult size 30 cm, range 9–49 cm) construct nests in gravel 1.6–6.4 cm in diameter, in water 11–40 cm deep, at velocities 20–90 cm/s, whereas European brook lamprey (mean adult size 13 cm, range 9–17 cm) construct nests in gravel 0.8–3.2 cm in diameter, in water 8–33 cm deep, at velocities around 15–75 cm/s (Nika and Virbickas 2010; Rooney et al. 2013). Pacific lamprey (mean adult size 40 cm, range 10–80 cm) construct nests in gravel 2.7 cm in diameter, in water 28 cm deep, at velocities around 20 cm/s, whereas western brook lamprey (mean adult size 12 cm, range 8–15 cm) construct nests in gravel 1.5 cm in diameter, in water 20 cm deep, at velocities around 12 cm/s (Stone 2006).

Note, however, that heterospecific spawning associations involving both large- and small-bodied lampreys are not uncommon (Table 6.1, Sect. 6.4.3.3).

6.3.2 Alternative Spawning Habitats

Although spawning in riffle habitats is most common, alternative spawning habitats have been reported. Cochran and Gripentrog (1992) provided detailed accounts of chestnut lamprey, northern brook lamprey *Ichthyomyzon fossor*, and southern brook lamprey spawning beneath cover (e.g., boulders, woody debris and, at one site, vegetation). In these species, nesting beneath cover was most likely to occur in larger rivers, where swift currents may reduce accessibility to riffle habitats or where cover may have allowed spawning despite the faster-flowing conditions. Lampreys nesting beneath cover may also experience reduced predation, although this hypothesis has not been directly tested (Cochran and Gripentrog 1992). Gunckel et al. (2009), defining cover as any structure under which an adult lamprey could hide, found that 86 % of western brook lamprey nests were associated with a variety of cover types (predominantly large cobble substrates, but to a lesser extent, wood and vegetation), but found that only 43 % of Pacific lamprey nests—presumably because of their larger size—were associated with cover. Rooney et al. (2013) also reported a small number of European brook lamprey spawning among woody debris in the River Liffey, Ireland, but it appears that spawning beneath vegetation or woody debris is rare in lampreys. Holčík (1986a) reported that Caspian lamprey only rarely makes nests in areas with submerged vegetation, and some species (e.g., European brook lamprey, sea lamprey) show a preference for sunlit areas when spawning is in progress (Hardisty 1986a, b).

Lampreys have been observed spawning in depths greater than 5 m. Silver lamprey and sea lamprey spawn at depths greater than 5 m in the connecting channels of the Great Lakes (Lamsa et al. 1980; Morse et al. 2003). Cochran and Lyons (2004) postulated that silver lamprey may spawn in swifter deeper water than other *Ichthyomyzon* species do, and observed silver lamprey spawning at deeper depths (>1 m) when present with sea lamprey. Caspian lamprey eggs have been found at depths ranging from 3.5 to 19 m (see Holčík 1986a), suggesting that the adults may spawn at depths greater than 5 m. Use of deepwater sampling equipment such as suction dredges (e.g., Beamish and Youson 1987; Taverny et al. 2012) and deepwater electrofishers (e.g., Jolley et al. 2012) are increasingly detecting larval lampreys of various species (anadromous sea lamprey, Pacific lamprey, and North American river lamprey *Lampetra ayresii*) in deep water in large river systems (see Chap. 3). It is not known, however, to what extent the presence of larvae in these habitats is the result of deepwater spawning or downstream movement of larvae from smaller tributaries.

Spawning in lakes (lentic spawning)—or at least spawning in the absence of a unidirectional current—has been reported in Vancouver lamprey *Entosphenus macrostomus*, Miller Lake lamprey *Entosphenus minimus*, and Pacific, western brook, American brook, and landlocked sea lampreys (Table 6.1). This type of spawning in Pacific, sea, and western brook lampreys is a rare deviation from their typical stream riffle spawning habitat. For example, although Russell et al. (1987) observed anadromous Pacific lamprey spawning in shallow water in two regions of the Babine Lake system in British Columbia, the frequency of lentic to lotic spawning (i.e., spawning in flowing water) in this system was low. Likewise, a sea lamprey pair was reported to have successfully spawned in a no-flow enclosure of a small river (Scott 1957), but this is considered rare, and most occurrences of sea lamprey larvae in lentic habitats are thought to be the result of downstream movement (e.g., during periodic floods) from the lower portions of rivers (Fodale et al. 2003). In contrast, Vancouver lamprey primarily spawn on shallow gravel bars in nearshore lake habitat, although some spawning also likely occurs in streams (Beamish 1987). Lentic spawning in Vancouver and Miller Lake lampreys may have developed as a reproductive adaptation after becoming landlocked (Russell et al. 1987). This observation is relevant to management of landlocked sea lamprey in the Great Lakes, where chemical control effectively kills larvae in streams, but lentic treatments of larvae are much less effective and more costly (Schleen et al. 2003). If lentic spawning is a genetically-linked trait, highly effective chemical control of sea lamprey larvae in streams with less effective treatments in lentic environments may favor selection of lentic spawning in landlocked sea lamprey (Russell et al. 1987).

6.3.3 Nest Construction, Size, and Function

6.3.3.1 Nest Construction

Lampreys construct nests using their oral disc to move stones and their tail to fan small gravel and silt out of the nest site. Nest construction of landlocked sea lamprey has been described in detail and will be used to highlight typical behaviors. Male sea lamprey have been observed initiating nest construction up to 8 weeks

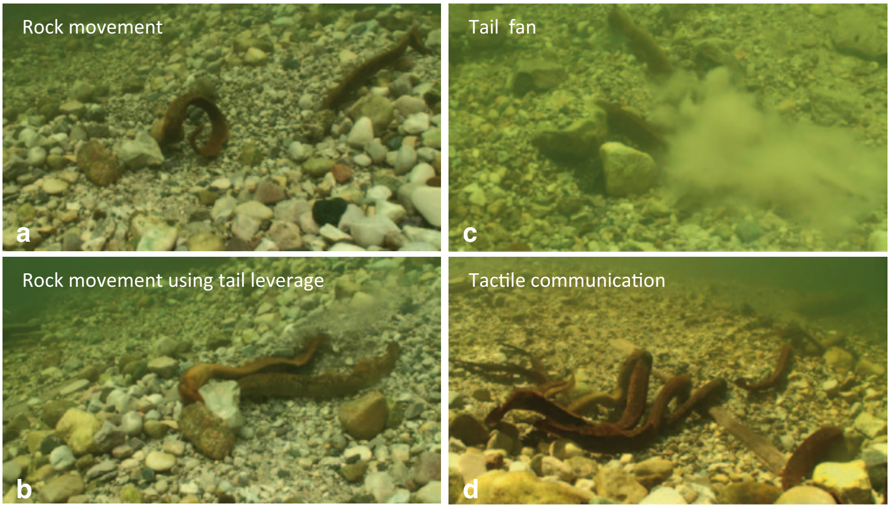

Fig. 6.1 Typical lamprey nesting behaviors. Photos are of sea lamprey spawning in the Cheboygan River, MI. **a** Rock movement by male. **b** Movement of large rock by leveraging tail against substrate. **c** Female cleaning sediment from the nest using rapid tail movements. **d** Tactile communication between male and female with oral discs. (Photos: Cory O Brant)

prior to spawning (Applegate 1950). Nest construction occurs day and night when water temperatures are suitable for mating (Table 6.1). Early in the spawning season, individual male sea lamprey construct several small nests and reside in one until joined by a female (Applegate 1950; Manion and Hanson 1980). Males vigorously defend nests from other males by attaching to intruding males and violently twisting and shaking as the current pushes them downstream of the nest (Applegate 1950; Manion and Hanson 1980). The victor, whether it was the male that established the nest or the intruder, quickly returns to the nest and awaits the arrival of a female. Male to male aggression has also been reported in European brook lamprey (Malmqvist 1983; Hardisty 1986a), European river lamprey (Hagelin and Steffner 1958), American brook lamprey (Young and Cole 1900), and in Siberian brook lamprey *Lethenteron kessleri* (Holčík 1986b), but not in Arctic lamprey (Heard 1966), Pacific lamprey (Brumo 2006; Stone 2006), or silver, chestnut, and northern brook lampreys (Manion and Hanson 1980).

Males and females participate in collaborative nest construction and rearrangement prior to and during spawning (e.g., Savvaitova and Maksimov 1979; Manion and Hanson 1980; Holčík 1986a, b, c; Sousa et al. 2012). Using the oral disc, lampreys latch onto stones and move them downstream using the assistance of the current, although sometimes stones are moved upstream and side stream (Fig. 6.1a). Large rocks are dragged from the nest by arching the back and leveraging the tail against the bottom to dislodge them (Fig. 6.1b). A few large stones typically remain at the upstream rim of the nest and are used as oral disc attachment points during nest cleaning and mating. Lampreys clear nests of silt by latching to a large rock in the upstream portion of the nest and vigorously fanning their tail laterally

(Fig. 6.1c). Rapid tail fanning stirs up sediment that is carried out of the nest by the current.

Deviations from typical lamprey nesting behavior have been reported. In European river lamprey, males arrive at the spawning riffles first, but females initiate nest construction (Jang and Lucas 2005). Female nest construction in European river lamprey is likely related to their generally promiscuous mating system (Jang and Lucas 2005), and potentially when there is a preponderance of females (see Sect. 6.4.2). Northern brook lamprey orient their body vertically, rather than horizontally as do most lampreys (Scott and Crossman 1973).

6.3.3.2 Nest Size

Nest size is generally a function of the body size of the species involved and the number of spawning adults present. For example, Great Lakes lamprey species excavate smaller nests with decreasing species size (Table 6.2). Landlocked sea lamprey nests are constructed to an average of 45 cm wide, 40 cm long, and 20 cm deep (Applegate 1950); silver lamprey nests are constructed to an average of 30 cm wide and 11 cm deep (Manion and Hanson 1980); and American brook lamprey nests are constructed to an average of 16 cm wide, 16 cm long, and 4 cm deep (Mundahl and Sagan 2005). The trend is also consistent in Europe where river lamprey nests average 105 cm wide, 129 cm long, and 7 cm deep; and average nest size for the much smaller European brook lamprey is 28 cm wide, 29 cm long, and 4 cm deep (Nika and Virbickas 2010). On both sides of the Atlantic, nests of the large anadromous sea lamprey may exceed 100–200 cm along their longest diameter (Hardisty 1986b; Gardner et al. 2012; Sousa et al. 2012). In the Coura River in Portugal, for example, where spawning sea lamprey averaged 882 mm total length, maximum nest length ranged from 80 to 225 cm (average 149 cm) and nest depth varied between 20 and 40 cm (average 28 cm; Sousa et al. 2012). Within a species, nest diameter and depth increases with the number of lamprey occupying the nest (Mundahl and Sagan 2005), and Rooney et al. (2013) reported the occurrence of "super redds," where smaller adjacent nests had merged into a single larger structure more than 40 cm wide.

6.3.3.3 Utility of Nest Physical Characteristics

The physical characteristics of the nest facilitate spawning behavior and embryo survival. A large rock located at the upstream rim of the nest (an "anchor") is central to nest cleaning and egg deposition in the nest. Without an anchor, the vigorous act of spawning will dislodge the pair, causing eggs to be scattered outside of the nest. The physical design of the nest produces upwelling of the water current, which increases oxygenation and reduces siltation (White 1990). Embryos retained in the nest have high survival rates (90 % in sea lamprey, Manion 1968; Manion and Hanson 1980), likely due to reduced predation by fishes and crustaceans, increased oxygenation, and minimal silt accumulation. However, Smith and Marsden (2009) estimated that

85 % of sea lamprey eggs are not deposited within the nest. Eggs dislodge from nests stochastically and embryo survival outside the nest is nearly zero percent under most conditions, primarily due to predation and increased siltation (Smith and Marsden 2009). However, when stream flow is low, eggs that do not remain in the nest settle into gravel outside the nests and are thus better protected, resulting in higher production of embryos than during high stream flows (Smith and Marsden 2009).

6.4 Mating Systems, Sex Ratios, and the Spawning Act

6.4.1 Mating Systems

The reproductive behaviors of 16 lamprey species have been described in the literature sufficiently to allow a mating system to be assigned (Table 6.1 and references therein). However, mating system plasticity has been documented in most species. Polygynandry, defined here as multiple males mating with multiple females, is the most prevalent mating system in lampreys.

In species where mean adult size is less than 30 cm TL, communal spawning of multiple males and females is common. Spawning aggregations of over 20 individuals have been observed in American brook lamprey (Young and Cole 1900), European brook lamprey (Lasne et al. 2010), southern brook lamprey (Cochran et al. 2008), and Far Eastern brook lamprey (Takayama 2002). Small parasitic species such as silver, chestnut, Arctic, and European river lampreys are also polygynandrous communal spawners (Case 1970; Morman 1979; Savvaitova and Maksimov 1979; Jang and Lucas 2005; Kucheryavyi et al. 2007a), with up to 50 chestnut lamprey (Case 1970) and 44 Arctic lamprey (Savvaitova and Maksimov 1979) having been observed spawning in a single nest. Kucheryavyi et al. (2007a), however, also observed spawning in pairs in Arctic lamprey. In the European river lamprey, males are promiscuous and are found in multiple nests across a large area, while females remain in single nests (Jang and Lucas 2005).

Pacific and sea lampreys, which are greater than 35 cm in length as adults, have been described as monogamous tending toward polygyny, with generally fewer than five individuals per nest (Applegate 1950; Brumo 2006; Stone 2006; Gardner et al. 2012). However, large-bodied parasitic lamprey species show greater variation in mating systems than non-parasitic and small parasitic species. For example, the sea lamprey mating system can change through the spawning season from monogamy to polygyny (Applegate 1950). A genetic analysis of embryos produced by a known population of spawning sea lamprey showed that female sea lamprey may visit multiple nests and that males and females mate with several different partners (Gilmore 2004). If indeed this occurs widely in sea lamprey, the mating system of this species could also be described as polygynandrous. However, it appears that individual male sea lamprey most commonly defend nests from other males and females visit multiple nests, and polygynandry is common only in small-bodied species that spawn communally.

Communal spawning in lamprey species with adult sizes less than 30 cm TL may be an adaptation to increase embryo survival through increased egg retention in nests. In non-parasitic and small parasitic species, a communal group of males and females can construct larger nests than an individual male of the same species. Several Siberian brook lamprey together have been observed pushing away heavier stones during nest construction (see Holčík 1986b). In contrast, individual male sea and Pacific lampreys can construct sufficiently large nests on their own. Presumably larger nests would retain more eggs than smaller nests and embryo survival is positively correlated to egg retention in a nest (Smith and Marsden 2009). Conversely, communal spawning may also increase the probability of eggs being displaced from the nest by repeated spawning events and nest construction. However, McIntyre (1969) observed male European brook lamprey covering spawned eggs with gravel after each copulation event; such nest rearrangement might aid in egg retention. The hypothesis that communal spawning is an adaptation to increase egg retention in nests has not been experimentally evaluated.

6.4.2 Operational Sex Ratio

Operational sex ratios of spawning lampreys (i.e., the number of sexually competing males that are ready to mate relative to the number of sexually competing females that are ready to mate) vary across species, across populations of the same species, and through time within a population. A generally small, but variable, excess of males is present among most spawning adult lampreys (Hardisty 1954, 1961b; Hardisty and Potter 1971; Beamish 1982; Takayama 2002; Nazari and Abdoli 2010), particularly in non-parasitic species (Purvis 1970; Mundahl and Sagan 2005). However, exceptions do occur. Mundahl and Sagan (2005) report an overall sex ratio of 1:1 (male to female) in spawning American brook lamprey, but noted variability among streams, where one stream had more males and another more females. Other studies documented American brook lamprey sex ratios as high as 1:5 (Seagle and Nagel 1982). The sex ratio of adult Caspian lamprey was recently reported as 1:1 (Nazari and Abdoli 2010; Ahmadi et al. 2011), but has been reported as high as 3:1 (Ghasempouri 1993). A nearly equal number of European river lamprey males and females were observed over an entire mating season (Jang and Lucas 2005).

In several species, males are generally first to arrive at the spawning grounds (e.g., in American brook lamprey, Young and Cole 1900; sea lamprey, Applegate 1950; and southern brook lamprey, Beamish 1982), and the proportion of females thus tends to increase over the course of the spawning season (Applegate 1950). A similar shift toward a greater proportion of females later in the spawning season was reported in a population of European brook lamprey (Hardisty 1961a), although Pletcher (1963) reported the opposite for western brook lamprey in British Columbia. Jang and Lucas (2005) provide a systematic account of changes in operational sex ratio in a population of European river lamprey. During nest construction, females outnumbered males 1:3.5. Sex ratio then shifted to a preponderance of males (1:0.4) in spawning aggregations, and back again to a preponderance of females in post-spawning aggregations (1:3.7). Shifts in operational sex ratio through the season could be attributed to sex differences in timing of maturation, longevity, or chemical signaling (Pletcher 1963; Jang and Lucas 2005), but this has yet to be investigated in detail.

At the population level, annual changes in adult lamprey sex ratios have been correlated with relative abundance. Hardisty (1961b) found a significant correlation between annual variability in adult sex ratios (1:1.2–1:3.4) and adult relative abundance in an isolated population of European brook lamprey. Similar changes in sex ratios have been observed in adult landlocked sea lamprey after chemical control of larval populations; an excess of males was observed when sea lamprey abundance was high but shifted to female-biased sex ratios following initiation of control measures (Applegate 1950; Wigley 1959; Torblaa and Westman 1980). Evidence for density-dependent sex determination in lampreys is discussed in Chap. 3 and Docker et al. (in press).

Operational sex ratios can influence nesting behavior and mating systems in lampreys. For example, although males often arrive first at the spawning grounds and initiate nest construction, female sea lamprey are also known to initiate nest construction when they are numerically dominant late in the season (Applegate 1950). Furthermore, mating system plasticity has been documented in most species and is often correlated to operational sex ratio. For example, the sea lamprey mating system can change from monogamy early in the mating season to polygyny late in the season (see Sect. 6.4.1), and mating system differences observed in European river lamprey may be related to differences in sex ratio or size of mating groups (Hagelin and Steffner 1958; Hagelin 1959; Jang and Lucas 2005).

6.4.3 The Spawning Act

6.4.3.1 General Spawning Description

Spawning has not been reported for any of the four Southern Hemisphere lamprey species. Glova (1995) and Jellyman et al. (2002) attempted to observe spawning in pouched lamprey by keeping adults in tanks for a year or more and either radio-tagging and releasing them just before sexual maturation for observation in a natural setting (Jellyman et al. 2002) or providing them in the laboratory with conditions thought suitable for spawning (Glova 1995); in neither case was spawning observed. Anecdotal reports that pouched lamprey are capable of moving tennis ball-sized stones with their oral discs (Renaud 2011) implies that spawning has been observed, presumably by Māori fishermen, for whom lampreys have historically had great value as a food source. Although speculative, it is conceivable that recent biologists have not observed spawning in Geotriidae or Mordaciidae because the spawning habitat or mating behavior of these lampreys is considerably different than what has been characterized for the family Petromyzontidae.

Within Petromyzontidae, described spawning behaviors are generally analogous among species. Hardisty and Potter (1971) reviewed mating behaviors in lampreys (see Table 6.1 for additional references). A thorough description of European river lamprey spawning behavior has been provided by Hagelin and Steffner (1958) and Hagelin (1959). Applegate (1950) provided a useful description of sea lamprey spawning behavior. Pletcher (1963) described spawning behavior in western brook and Pacific lampreys; Brumo (2006) and Stone (2006) provide brief accounts of Pacific lamprey spawning. Species not listed in Table 6.1 have little or no information in the literature concerning spawning behavior. Common spawning behaviors will be highlighted here with a brief discussion and illustrations (Fig. 6.2). As far as the present authors can ascertain, all descriptions of lamprey spawning have had their origin from daytime observations.

Lampreys aggregated on a nest actively engage in courtship and nest maintenance behaviors when not copulating. Little is known about when spermiation and ovulation occur relative to the time active spawning begins. Copulations occur every few minutes during active spawning, but respites of over an hour can occur. Studies of European river lamprey indicate that copulation in this species is initiated by the female. In what has been described as courting behavior to signal readiness to males, female European river lamprey swim in circles over males occupied with nest building (Hagelin 1959 and references therein). Then, immediately prior to mating, the female will attach to a large rock at the upstream rim of the nest. A receptive male responds by gliding his head along the female's body from tail to head and, sometimes only briefly (for <1 s), attaches to the female's head. Mating occurs, however, when male gliding is followed by firm attachment to the female's head. As the male attaches, he wraps his tail around the female, sliding and squeezing his tail in a posterior direction stopping at a few centimeters anterior of the female's urogenital region. The female responds to the male's tail wrapping and sliding by violently vibrating. The male vibrates together with the female, and with backs arched, gametes are simultaneously released. Fertilization occurs externally, with the male's genital papilla directing sperm toward the eggs. About 5 s pass from the male glide to gamete release. The number of eggs released per mating event has been reported to range from 10 to 50 in European brook lamprey (McIntyre 1969; Malmqvist 1983) and from 20 to 40 in landlocked sea lamprey (Applegate 1950). Eggs are highly adhesive and readily attach to stones and sand on the downstream rim of the nest. After gamete release, the pair unwinds and continues nest construction and maintenance. Occasionally after mating, the male and female will lay still side-by-side in the nest for several minutes. In the laboratory, females are typically spent after 1–3 days of active mating (Hagelin and Steffner 1958), but males may spawn for up to a week. Little empirical evidence is available to determine how long individuals actively spawn in the wild. Observations of European river lamprey suggest that individual lamprey only remain on spawning riffles for a few days (Jang and Lucas 2005).

6.4.3.2 Alternative Spawning Behaviors

Multiple lampreys can be involved in the act of spawning at the same time. Five chestnut lamprey have been observed attached to each other while spawning (Case

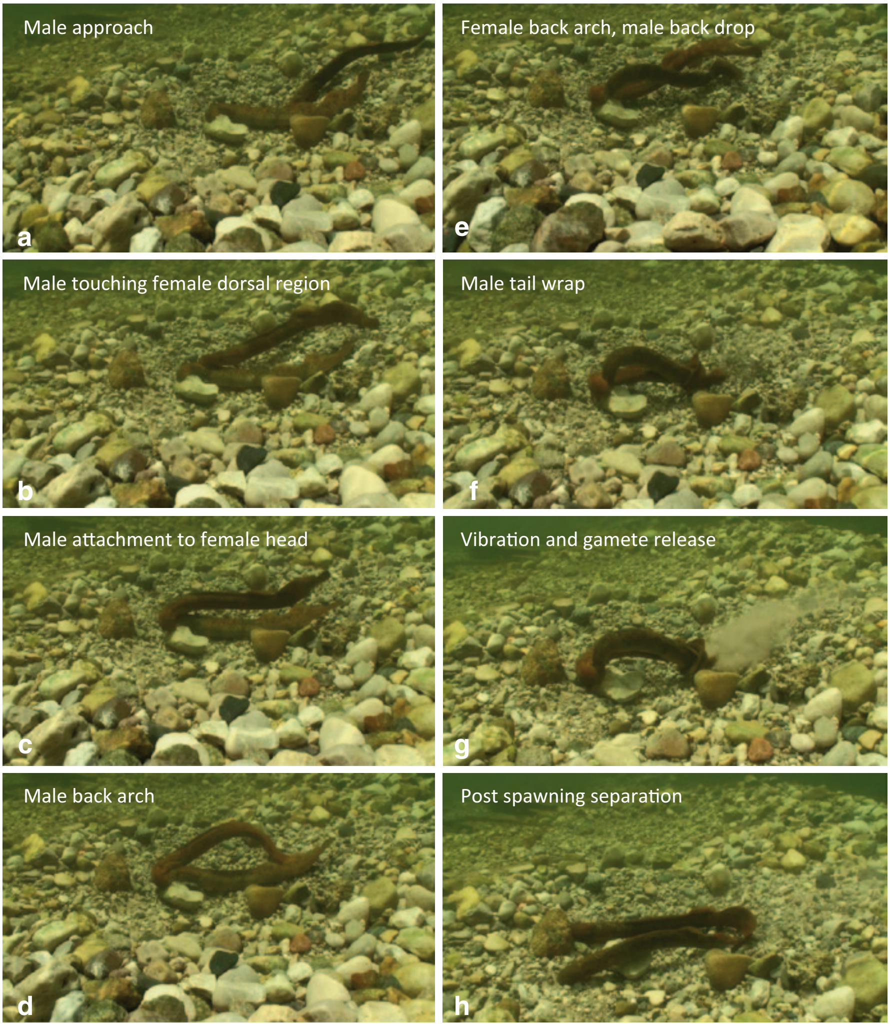

Fig. 6.2 Typical succession of behaviors during lamprey reproduction. Photos are of sea lamprey spawning in the Cheboygan River, MI. **a** Female attached to large rock at upstream end of the nest; male approaches the female from downstream. **b** Swimming along the female's back from posterior to anterior, the male touches the female dorsal region with its oral disc. **c** The male firmly attaches to the female's head with oral disc. **d** Immediately after the male attaches to the female's head, the male arches its back. **e** The female then arches its back allowing the male to slide its tail underneath the female's tail. **f** The male's tail tightly coils around the female between the dorsal fins, aligning their urogenital papillae. **g** Male and female vibrate violently stirring up sediment while releasing gametes. **h** Male and female release from each other after spawning. (Photos: Cory O Brant)

1970). Malmqvist (1983) reported several European brook lamprey coiled around a single female. Huggins and Thompson (1970) report two male European river lamprey mating with one female. Stone (2006) reported four male western brook lamprey coiled around two females.

An alternative reproductive behavior has been observed in European and American brook lampreys, where "satellite" males attempt to gain fertilizations by approaching the urogenital area of a mating pair and presumably attempting to fertilize the eggs as they are extruded by another male (Malmqvist 1983; Cochran et al. 2008). Recently, Hume et al. (2013a) demonstrated satellite (or "sneak male") mating tactics in anadromous and freshwater-resident European river lamprey and in European brook lamprey, observing this behavior both within and between species or morphs. In no case, however, has fertilization success of satellite males been determined.

Scott and Crossman (1973) noted an exception to the tail coil spawning behavior in northern brook lamprey, where males did not wrap around the female, but vibrated vigorously next to each other during spawning.

6.4.3.3 Heterospecific Mating Associations

Heterospecific mating associations are commonly observed between paired species and among two or more "unpaired" species that occur in sympatry (Table 6.1). Huggins and Thompson (1970) described heterospecific spawning of European brook and river lampreys, but did not report interspecific copulation attempts. Lasne et al. (2010) similarly documented that 54 % of the nests they observed contained both European brook and river lampreys (the remaining nests contained only European river lamprey), but—contrary to Huggins and Thompson (1970)—did note interspecific copulation attempts in the mixed nests. They observed a male brook lamprey attempting to mate with a female river lamprey and another brook and two river lamprey males trying to mate with a single river lamprey female, but were unable to determine whether any successful fertilization occurred (see Sect. 6.4.3.5). Heterospecific spawning associations have also been documented in lamprey species in the Great Lakes, where the paired silver and northern brook lampreys, and chestnut, American brook, and sea lampreys have been observed spawning in various combinations on the same nest (Morman 1979; Manion and Hanson 1980). Cochran et al. (2008) observed the paired chestnut and southern brook lampreys spawning in the same nests in Wisconsin, and documented a southern brook lamprey male attempting to mate with a female chestnut lamprey (although no quivering or release of gametes was observed). "Unpaired" Pacific and western brook lampreys have also been documented in the same nests (Brumo 2006).

Two hypotheses, with potentially different fitness consequences, have been developed to explain the origins of heterospecific spawning associations. The first suggests that lampreys may find the increased nest size of larger heterospecifics attractive (Morman 1979), and their association with larger nests may thus provide fitness benefits through increased embryo survival and reduced predation risk to themselves (Cochran et al. 2008). This hypothesis seems reasonable considering the earlier postulations about the origin of communal mating in small-bodied lampreys (see Sect. 6.4.1). An alternative hypothesis is that lampreys are attracted to hetrospecifics, not the physical nest structure, through conserved pheromones (Cochran et al. 2008; Buchinger et al. 2013). Pheromones of anadromous species may be released in larger amounts compared to non-anadromous species because their body size is larger and they signal (migrate) over longer distances. However, pheromonal attraction of lampreys to heterospecific nests may reduce fitness through wasted mating effort, interference with mating behavior, and increased predation risk due to enhanced conspicuousness.

6.4.3.4 Fertilization of Eggs

Lamprey gametes are generally viable for much longer than those of other fishes. In the laboratory, sea lamprey eggs could be fertilized for up to 3 h, although fertilization success rate declined significantly after 40 min (from 85–95 % at 0–40 min to 32 % after 3 h; Ciereszko et al. 2000). Arctic and sea lamprey sperm are viable in fresh water for several minutes (Kobayashi 1993; Ciereszko et al. 2000). Assuming all lamprey gametes have similar viabilities, the ecological consequence is that during communal and heterospecific spawning associations, males could fertilize eggs up to a few hours after deposition. Satellite males (Sect. 6.4.3.2) may also have an increased opportunity to fertilize eggs in the rear of the nest. Once eggs are fertilized, a fast block occurs at the plasma membrane level and then the perivitelline space acts as a permanent block to polyspermy (Arctic lamprey, Kobayashi and Yamamoto 1994).

6.4.3.5 Potential for Hybridization of Paired Species

Despite the occurrence of mixed-species spawning associations and even mating attempts between heterospecifics (see Sect. 6.4.3.3), natural hybrids of paired species have not been documented in nature (Beamish and Neville 1992; Yamazaki and Goto 1998). It is generally thought that size-assortative homogamy reduces the probability of paired species cross-fertilizing (Hagelin 1959; Malmqvist 1983). In North American river lamprey and western brook lamprey, for example, fertilization success is low when males and females differ in length by more than 20 % due to misalignment of the urogenital regions (Beamish and Neville 1992). However, some fertilizations can occur even when size differences exceed 30 % (Beamish and Neville 1992) and many lamprey species pairs differ in length by less than 20–30 %, particularly paired species with freshwater-resident or "praecox" (i.e., small anadromous) parasitic forms (Docker 2009). Kucheryavyi et al. (2007b), for example, found considerable overlap in size and no evidence of assortative mating among three life history types of Arctic lamprey in the Utkholok River, Russia. Furthermore, "satellite" male behavior (Sect. 6.4.3.2), external fertilization, and extended gamete viability (Sect. 6.4.3.4) also increase the probability of genetic mixing between paired species, especially those that have viable hybrid offspring, such as northern brook and silver lampreys (Piavis et al. 1970), European river and brook lampreys (Enequist 1937; Hume et al. 2013b), and North American river and western brook lampreys (Beamish and Neville 1992). Therefore, although size differences may have been an important factor allowing the sympatric speciation of non-parasitic species from parasitic species (Salewski 2003), additional barriers to hybridization such as spawning habitat differences (Sect. 6.3.1) and sensory cues (Sect. 6.6) may also have been needed to maintain reproductive isolation of paired species (Beamish and Neville 1992; Docker 2009).

Although hybrids have not been demonstrated to date, it is important to note that hybrids may be difficult to detect (certainly as larvae, when the species themselves are often indistinguishable; see Docker 2009). The taxonomic status of paired species could be challenged if successful hybridization is documented in the wild. Reclassification of paired species—where, instead of being considered separate species, they are considered different ecotypes of the same species (Enequist 1937)—could have profound impacts on conservation of rare or endangered lampreys (Docker 2009; Docker et al. 2012).

6.5 Secondary Sexual Characteristics

6.5.1 Male

The general secondary sexual characteristics for male and female lampreys have been previously reviewed (Vladykov 1949; Smith et al. 1968) and will be briefly highlighted with special emphasis on newly described structures and functions of previously described structures. During sexual maturation, male lampreys develop an elongated urogenital papilla (Hardisty and Potter 1971; Kott et al. 1988). The papilla is not used to internally fertilize eggs, but to direct milt towards eggs released by females (Kucheryavyi et al. 2007a). Mature males develop swollen cloacal lips, a straight or downwardly bent tail to aid in nest construction, and a heightened, serrated and vascularized second dorsal fin generally about 1 week before spawning. Mature male European river, European brook, and sea lampreys develop glandular cells in gill epithelial tissue when spermiated (Pickering and Morris 1977; Siefkes et al. 2003). Glandular cells of mature males likely function as transporters of mating pheromone from the blood into the riverine environment during respiration (Siefkes et al. 2003; see Sect. 6.6.1).

During sexual maturation of pouched lamprey and Chilean lamprey *Mordacia lapicida*, a highly pronounced gular pouch develops (Hardisty and Potter 1971). The gular pouch of these two Southern Hemisphere parasitic lamprey species has been described as a fibrous muscle with extensive vascularization resembling mammalian erectile tissue (Hardisty and Potter 1971; Potter and Welsch 1997). In the other parasitic Southern Hemisphere species, the short-headed lamprey, mature males may have some loose skin in the gular region (Renaud 2011). The gular pouch is also present in sexually immature and mature male parasitic lampreys in the Northern Hemisphere (including sea and Caspian lampreys; chestnut lamprey, silver lamprey, and Ohio lamprey *Ichthyomyzon bdellium*; Pacific and Miller Lake lampreys and Klamath lamprey *Entosphenus similis*), but in a much reduced state (Monette and Renaud

2005). The gular pouch of pre-spawning Pacific and sea lampreys contains lipids, which Monette and Renaud (2005) postulated could serve as an energy resource to support the protracted spawning migration of these anadromous species. The gular pouch is unlikely to aid in stone movement because male sea lamprey can move larger rocks than similarly-sized male pouched lamprey and yet have a smaller gular pouch. Where described, the gular pouch of mature males is larger than that of mature females and thus may also be involved in courtship (Monette and Renaud 2005).

A characteristic unique to mature male sea lamprey is a rope-like tissue that extends along the dorsal surface from approximately the posterior gill slit to the beginning of the anterior dorsal fin (Hardisty and Potter 1971). Unexpectedly, the rope was discovered to consist of a thermogenic adipose tissue that produces heat when in the presence of an ovulated female, but not when in the presence of other males (Chung-Davidson et al. 2013a). This is the first discovered thermogenic secondary sexual characteristic and the only example of a thermogenic fat outside the mammalian clade. Sea lamprey mate in generally the same manner as other Northern Hemisphere lampreys, so perhaps the rope tissue helps maintain reproductive isolation. Additional experiments are needed to determine if females can detect the heat produced in the rope and how heat production influences mate selection and mating behavior.

6.5.2 Female

Upon sexual maturation, female lampreys also develop an elongated urogenital papilla, but it is much reduced compared to that of a mature male conspecific. The female urogenital papilla helps direct eggs into the nest (Kucheryavyi et al. 2007a). Mature females also develop a keel behind the cloaca and upward bent tail (Applegate 1950; McIntyre 1969; Kott et al. 1988; Kucheryavyi et al. 2007a). The upward bent tail likely aids in nest cleaning or may be involved with expressing the eggs. In Arctic lamprey, the keel behind the cloaca is thought to be important for nest cleaning, mixing of eggs and sperm, and as a male tail “brake” helping to align male and female urogenital papillae (Kucheryavyi et al. 2007a). Similarly, a swelling at the anterior base of the posterior dorsal fin in mature female European river lamprey also appears to help align urogenital papillae during mating (Hagelin 1959). Females of the above mentioned Northern Hemisphere parasitic lamprey species (Sect. 6.5.1) have a gular pouch of reduced size relative to males of their own species (Monette and Renaud 2005).

6.6 Sensory Modalities that Facilitate Mating

Sensory modalities known to play roles in lamprey reproduction include olfaction, tactile sensation, and electroreception. Chemical communication is important for reproduction as adult lampreys have well-developed olfactory organs and exceptionally large olfactory bulbs relative to the brain (Kleerekoper 1972). In sea lamprey, this anatomically dominant system is highly sensitive to compounds that direct spawning migrations into streams with established larval populations (Teeter 1980; Bjerselius et al. 2000; Sorensen et al. 2005; see Chap. 5) and to spawning grounds populated with spermiated males (Li et al. 2002; Siefkes et al. 2005; Johnson et al. 2009). The function of mating pheromones in sea lamprey reproduction has been reviewed (Li et al. 2007; Johnson and Li 2010), and will be briefly highlighted here. Additionally, other sensory modalities suspected to play a part in lamprey reproduction will be discussed.

6.6.1 Pheromones

6.6.1.1 Sea Lamprey Mating Pheromones

Upon spermiation, male sea lamprey release a mating pheromone that is highly attractive to ovulated females, luring them to nests. In natural populations, it is not known how far ovulated females need to travel to locate spermiated males or how long it takes for a female to locate a nest. A component of the mating pheromone released by males has been identified as 7α,12α,24-trihydroxy-3-one-5α-cholan-24-sulfate (3kPZS; Li et al. 2002; Yun et al. 2003) and shown to be highly attractive to ovulated female sea lamprey at in-stream concentrations ranging from 10^{-11} M to 10^{-13} M (Siefkes et al. 2005; Johnson et al. 2009). Only spermiated male sea lamprey release 3kPZS and only ovulated female sea lamprey are attracted to 3kPZS (Siefkes et al. 2005). Males release 3kPZS through their gills, likely through the profuse glandular cells with secretory papillae (Siefkes et al. 2003). Female olfactory sense is critical for locating spermiated males (Johnson 2005; Johnson et al. 2006). Ovulated females likely locate sources of 3kPZS by integrating tactile information concerning flow direction and olfactory information concerning pheromone concentration through a mechanism termed odor-conditioned rheotaxis (Johnson et al. 2012a). The male mating pheromone consists of multiple components that induce attraction to the nest, retention on the nest, rock movements, and tail fanning (Johnson et al. 2012b). 3,12-diketo-4,6-petromyzonene-24-sulfate (DKPES) is a minor component of the mating pheromone that, when mixed with 3kPZS at specific ratios, attracts more ovulated females than 3kPZS alone (Li et al. 2013). Additional components, however, remain unidentified; experiments directly comparing mixtures of 3kPZS and DKPES and water conditioned by spermiating males showed the latter to still be more attractive to females (Li et al. 2013).

The sea lamprey male mating pheromone also contains components that function as stimulatory and inhibitory priming pheromones. Sexually immature males and females exposed to washings of mature males or to synthesized 3kPZS mature faster than those exposed to water containing no pheromone (Chung-Davidson et al. 2013b). Further investigation revealed that immature sea lamprey exposed to 3kPZS exhibit increases in circulatory 15α-hydroxyprogresterone concentrations and forebrain gene expressions (Chung-Davidson et al. 2013b). However, exposure of immature males to 7α,12α-dihydroxy-5α-cholan-3-one-24-oic acid (3kACA), which is released by mature males (Yun et al. 2003), inhibits steroidogenesis (Chung-Davidson et al. 2013c). Because 3kACA is released by mature males at a rate about 10 times less than 3kPZS, the inhibitory impacts of 3kACA likely only occur when males are at close proximity; for example, when competing for nest sites. Taken together, increases in spring water temperature and the presence of male mating pheromones are likely important triggers that synchronize maturation of early and late arriving migrants to enable spawning during the 2–3 week period.

The sea lamprey has become a model for how pheromones may be used in the control of invasive vertebrates (Li et al. 2007) because it is an ecologically and economically damaging pest in the Laurentian Great Lakes and Lake Champlain (Smith and Tibbles 1980; Marsden and Siefkes in press). Pheromone-baited traps show promise for increasing the capture of female sea lamprey (Johnson et al. 2009; Luehring et al. 2011), and disruption of pheromone communication through antagonists or application of high concentrations of 3kPZS may also be effective in reducing mating success (Johnson et al. 2009). When 3kPZS alone was applied to existing traps in the Great Lakes basin, trap efficiencies significantly increased (Johnson et al. 2013).

6.6.1.2 Mating Pheromones in Other Lamprey Species

Mating pheromones have been hypothesized to be used by European river, pouched, silver, and Pacific lampreys. Jang and Lucas (2005) reported that the majority of a population of European river lamprey in an 80 km segment of river spawned at a single site, indicating possible coordination of reproduction through mating pheromones released by mature adults. In this case, migratory pheromones released by larvae (Fine et al. 2004; Sorensen et al. 2005; see Chap. 5) would not likely coordinate reproduction, as larvae would be present downstream of spawning areas. The presence of glandular cells in mature male European river lamprey suggests that bile acid pheromones may be released across the gills to coordinate reproduction (Pickering and Morris 1977). Radio-tagged pouched lamprey all entered the same tributary immediately prior to the putative mating season, supporting the hypothesis that chemical cues may coordinate spawning site selection (Jellyman et al. 2002). Pacific lamprey have high olfactory sensitivity to the sea lamprey mating pheromone 3kPZS (Robinson et al. 2009), but no behavioral tests have been conducted to evaluate if females are attracted to synthesized 3kPZS. Given the protracted spawning migration of Pacific and pouched lamprey (see Sect. 6.2.1), it is possible that the newly arrived migratory cohort may be exposed to mating pheromones from the spawning adult cohort. Therefore, upon arrival to fresh water, Pacific and pouched lampreys may use mating pheromones released by the upstream spawning cohort while still in the migratory stage as an honest indicator of tributaries containing spawning habitat (Robinson et al. 2009). Silver lamprey appear to use 3kPZS as a migratory pheromone, but not as a mating pheromone as observed in sea lamprey (see Sect. 6.6.1.1). Female preference for 3kPZS in a migratory context may be a bias leading to male signaling with 3kPZS, where male sea lamprey may have evolved to take advantage of an existing preference of females (Buchinger et al. 2013).

Questions remain concerning species specificity, production, and release of lamprey mating pheromones. As discussed above, spermiated male sea lamprey actively release mating pheromones at high rates (Sect. 6.6.1.1). Sea lamprey defend nests from other males, and therefore the male obtains direct benefit from attracting mates. A different ecology is true of communal spawners, where multiple males compete for mating opportunities in a nest. Perhaps communally spawning males, if they release mating pheromones, share fitness benefits with other males in the nest. Investigations of pheromone communication in satellite males (see Sect. 6.4.3.2) would be interesting because pheromone production may be suppressed to help them remain cryptic. Mating pheromones in general are expected to be species specific because reproductive isolation often provides significant fitness benefits (Wyatt 2003). Yamazaki and Goto (2000), for example, suggested that pheromones may prevent interbreeding in two undescribed *Lethenteron* species (*L.* sp. N and *L.* sp. S) where they occur sympatrically. Although spawning seasons and sizes at maturity overlap, heterospecific nesting assemblages have not been observed. Species specific mating pheromones may be another factor facilitating reproductive isolation within heterospecific spawning associations (Sect. 6.4.3.3), but this has not yet been investigated.

Pheromones have the potential to benefit restoration efforts in lamprey species (Robinson et al. 2009) whose populations are in decline (Renaud 1997; see Chap. 8). Migratory pheromones could direct migratory-phase adults into streams from which they had been extirpated or into specific tributaries with high quality spawning and larval rearing habitat. Mating pheromones could be used to direct spawning-phase adults to specific high quality spawning riffles. Both pheromones could be effective at low concentrations (i.e., 10^{-12} M), meaning that once identified, implementation of pheromone-based restoration techniques could be cost-effective. Additionally, advances in pheromone quantification in stream water could allow for non-invasive, rapid population assessment (Li et al. 2011; Stewart et al. 2011; Xi et al. 2011).

6.6.2 Additional Sensory Modalities used During Reproduction

6.6.2.1 Tactile

Tactile communication is important once lampreys are aggregated on nests and engaged in mating behavior (Fig. 6.1d, 6.2). Lampreys probe with their oral disc during nest construction to locate rocks to be moved. Lampreys likely use tactile cues to determine if the physical characteristics of the nest are suitable for spawning. Hagelin and Steffner (1958) reported that when mating, European river lamprey males glide their oral discs along the side of females immediately prior to attachment to the head. Reighard (1903) hypothesized that such tactile cues in American brook lamprey may determine sex when multiple lamprey are in the nest. For example, when a male attaches to a receptive female, the female will remain attached to a rock, triggering the male to wrap his tail around her. In contrast, if the male attaches to another male, the second male will typically detach from the rock and drift around the nest. In sea lamprey, the increased heat generation in female presence and frequent contact with the female urogenital pore indicates that the male rope tissue may be involved in tactile communication on the spawning nest (Chung-Davidson et al. 2013a).

6.6.2.2 Electroreception

Adult lampreys respond to weak, low frequency electrical fields (Bodznick and Northcutt 1981), but limited knowledge is available concerning the function of electroreception during mating. Chung-Davidson et al. (2008) provided evidence that sea lamprey use electroreception to locate conspecifics or that electroreception may be used to regulate sexual behavior along with tactile cues. However, additional research is needed to determine the extent to which electroreception influences mate choice and reproductive behavior in lampreys.

6.6.2.3 Vision

There is no evidence that vision is used by adult lampreys to direct spawning migrations, locate mates, or to facilitate spawning behavior. Experimentally blinded sea lamprey migrated upstream at the same rate as lamprey that were not blinded, and both groups showed the same nocturnal activity patterns (Binder and McDonald 2007). The switch from migration only at night to becoming active during both day and night (i.e., showing diel behavior) has been shown in part to be mediated by the dermal photophores rather than the eyes (Binder and McDonald 2008a, b). Although all light-associated behaviors are mediated by the eyes in mammals, such "extraocular" photoreceptors are not uncommon among lower vertebrates (Foster and Hankins 2002). In sea lamprey, the reduction in light avoidance behavior in spawning-phase lamprey is the result of reduced dermal photosensitivity in response to elevated stream temperatures (Binder and McDonald 2008a, b).

There is anecdotal evidence to suggest that vision is also not used to locate mates or during reproduction. Applegate (1950) noted the degeneration of the eyes of spawning sea lamprey and suggested that vision was not important to them for mating. Further, lampreys can be readily approached and observed during the day without sign of being disturbed.

6.6.3 Acoustic

Acoustic signals produced by fishes have been widely implicated to facilitate species recognition and influence mate choice (Verzijden et al. 2010). Mating decisions are often based on the collective information from multiple modalities (Johnstone 1996). Although lampreys have been shown to use chemical and tactile communication, acoustic signals could also serve an important role. To date, no studies have evaluated the role of acoustic cues in lamprey reproduction. Future research should investigate whether lampreys produce sound during mating and whether those sounds influence mate choice and mating behaviors.

6.7 Senescence

All lampreys die after spawning (i.e., they are semelparous). A few exceptions have been reported in the literature, that is, of possible repeat spawning in Pacific lamprey (Michael 1980, 1984) and survival of European river lamprey until the following year (at which time they may participate in the spawning migration but be unable to breed; see Hardisty 1986c), but it is questionable whether this is possible (Hardisty 1986c). Although survival can be extended if spawning is delayed or prevented (e.g., at low temperatures; Larsen 1980), survival after spawning seems highly unlikely given the severe atrophy of the intestine, degeneration of the liver and eyes, the inability of anadromous species to osmoregulate in salt water after spawning, and the depletion in lipids (Hardisty and Potter 1971; Larsen 1980). Caspian lamprey females have been reported to die immediately after releasing their eggs, while males were documented to survive until spermiation ceased (see Holčík 1986a). Pletcher (1963) observed that female western brook lamprey usually died within a week of spawning (with males living for 1–2 months). Female sea and European river lamprey that deposit all their eggs early in the season may survive up to a week and continue to participate in spawning behaviors (Applegate 1950; Hagelin and Steffner 1958). Post-spawn lampreys are believed to move downstream (Jang and Lucas 2005) and seek refuge under cover until death occurs (Hagelin 1959). The odor of dead sea lamprey is repulsive to migratory-phase conspecifics (Wagner et al. 2011), and may cue to newly arrived migrants that the spawning season has ended or there is considerable risk of mortality upstream.

6.8 Conclusion

As the terminal life stage of an unusual primitive fish, reproduction of lampreys has fascinated biologists for centuries. Much has been revealed concerning the reproductive ecology of lampreys such as spawning preferences, mating systems, and behavior. Critical knowledge gaps still exist, however. Spawning has never been reported for any of the four Southern Hemisphere lamprey species, perhaps because their reproductive ecology differs substantially from that of the well-studied Northern Hemisphere species. Furthermore, how multiple modalities of communication among lampreys (including mating pheromones) are integrated to inform species recognition and mate choice remains poorly understood. This is especially interesting for ecologists in light of heterospecific mating associations and the apparent sympatric speciation of paired species. For conservationists and fisheries managers, an enhanced understanding of the reproductive ecology of lampreys is needed, both for the more than 20 lamprey species that are threatened or endangered in at least part of their range and for control of invasive sea lamprey in the Laurentian and other Great Lakes.

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