

## **Bill Beamish's Contributions to Lamprey Research and Recent Advances in the Field**

This paper is based on an oral presentation given at a symposium honouring Bill Beamish and his contributions to fisheries science at the Canadian Conference for Fisheries Research, in Windsor, Ontario on January 7, 2005

Margaret F. Docker  
Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON,  
N9B 3P4, Canada

Current Address:  
Department of Zoology, University of Manitoba, Winnipeg, MB, R3T 2N2, Canada  
(e-mail: [dockerm@cc.umanitoba.ca](mailto:dockerm@cc.umanitoba.ca))

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**Synopsis**

Since his first lamprey paper in 1972, Bill Beamish has published more than 50 papers on numerous aspects of lamprey biology, reporting on several native lamprey species as well as the Great Lakes sea lamprey. Bill and his colleagues have contributed to our knowledge of the basic biology of larval lampreys (e.g., abundance, habitat, feeding, growth, and gonadogenesis), helped refine techniques to determine age in larvae (using statoliths, structures analogous to the teleost otolith), and studied the process of metamorphosis and the feeding and bioenergetics of juvenile (parasitic) lampreys. Current research continues to build on Bill's contributions, and also makes many advances in novel directions. This exciting current research includes: the use of high-resolution ultrasound to study gonadogenesis and evaluate sex ratio in live larval lampreys; the elucidation of some of the exogenous and endogenous triggers of metamorphosis; examination of the neuroendocrine control of reproduction and the role of unconventional sex steroids in lampreys; the discovery of migratory and sex pheromones and their potential use in sea lamprey control; the use of molecular markers to study lamprey mating systems and phylogeny; and the renewed interest in the conservation of native lampreys.

## **Introduction**

Since his first lamprey paper in 1972, Bill Beamish has published more than 50 papers on numerous aspects of lamprey biology, reporting on several native lamprey species as well as the Great Lakes sea lamprey. Current research continues to build on Bill's contributions, but also makes advances in areas of research that probably were not even anticipated in 1972. This paper reviews Bill's contributions to lamprey research, and describes some of the recent advances in the field; in some cases, these recent advances include some of Bill's contributions (e.g., Griffiths et al. 2001; Lowartz et al. 2003, 2004). Although there were dozens of recent and exciting lamprey studies to choose from, only 12 topics are presented here. These 12 topics were chosen to represent research dealing with both the exotic sea lamprey in the Great Lakes and the other "native" lamprey species found in temperate regions worldwide, and to include research from a range of fields (e.g., ecology, physiology, phylogeny). As much as possible, these topics were also chosen to highlight the use of modern techniques to address many of the long-standing questions regarding lamprey biology. Approximately half of the chosen topics build on Bill's contributions and half make advances in entirely novel directions. This paper will start with an introduction to basic lamprey biology and a brief review of the lamprey life cycle, and will provide an overview of Bill's contributions to our knowledge of lamprey biology. Some of Bill's contributions will be described in greater detail in the following two sections, where they are particularly relevant to some of the recent advances in lamprey research. These recent advances involve: a) research into the ecology and physiology of sea lampreys, where the nine topics presented are organized by the stages of the sea lamprey life cycle; and b) research focusing predominantly on phylogenetic relationships among lamprey species and populations (three topics).

### *Background – Basic Lamprey Biology:*

Lampreys are extant representatives of the ancient vertebrate group Agnatha and are one of the oldest groups of living fishes in the fossil record, approximately 300 million years old (Janvier & Lund 1983). They superficially resemble eels, but they are radically different in terms of their evolutionary history, anatomy, and physiology. Most notably, instead of hinged jaws, they have an oral disc that they use to attach to the side of a fish. Teeth on this disc and on their tongue are used to rasp a hole into the fish where they feed on their host's tissue, blood, or other body fluids. Lampreys also lack a bony skeleton, scales, and paired fins. There are approximately 38 extant species of lampreys, found in the temperate regions of both Northern and Southern hemispheres. Although the best known species is likely the landlocked sea lamprey, *Petromyzon marinus*, which is an exotic pest in the Great Lakes and is thus the subject of considerable study and extensive control measures, most lamprey species worldwide are of conservation concern (Renaud 1997).

All lampreys spend the first years of life as blind larvae known as ammocoetes that burrow in the silt bottoms of rivers and streams and feed by filtering microscopic plant and animal material and detritus (Sutton et al. 1994; Mundahl et al. 2005) through the oral hood. At metamorphosis, these larvae undergo a dramatic transformation (Youson 1980), providing the adult with the necessary features for parasitic feeding or spawning (e.g., teeth and oral

disc, functional eyes). Following metamorphosis in parasitic species, the juveniles generally migrate downstream and feed either in freshwater lakes (e.g., the landlocked sea lamprey) or, in the case of anadromous species, the ocean. They then undergo final sexual maturation, and migrate back upstream to spawn and die in fresh water.

Approximately half of all lamprey species, however, are nonparasitic (Potter & Gill 2003). Following metamorphosis, they bypass the migration and feeding phases, and immediately begin sexual maturation. These nonparasitic species spawn and die within 6–9 months of metamorphosis, and are referred to as “brook” lampreys because they remain in their natal stream throughout their life.

*Brief Overview of Bill Beamish’s Contributions to Lamprey Research:*

Bill Beamish has published more than 50 papers on numerous aspects of lamprey biology. In addition to his contributions regarding lamprey sex determination, the use of statoliths to age lampreys, and the bioenergetics of metamorphosis and the parasitic feeding phase (which are described in greater detail below, where recent advances continue to build on these contributions), Bill and his colleagues have added to our knowledge of many other aspects of lamprey biology. For example:

- a. Larval Stage – Many of Beamish’s papers deal with the larval stage of the life cycle, such as larval habitat (Beamish & Jebbink 1994; Beamish & Lowartz 1996), abundance (Beamish & Jebbink 1994), feeding (Moore et al. 1973), growth (Beamish & Austin 1985; Murdoch et al. 1991, 1992; Griffiths et al. 2001), and temperature requirements (Potter & Beamish 1975).
- b. Metamorphosis – He and his colleagues have also studied the blood morphology and behaviour of sea lampreys during metamorphosis (Beamish & Potter 1972; Potter & Beamish 1978), environmental and endogenous triggers for metamorphosis (Youson et al. 1993; Holmes et al. 1994), and metamorphosis of the southern (Beamish & Thomas 1984) and mountain (Beamish & Medland 1988a) brook lampreys.
- c. Feeding (Parasitic) Phase – He has also published papers that deal with oxygen consumption (Beamish 1973), swimming performance (Beamish 1974), and feeding and osmoregulation (Mathers & Beamish 1974; Beamish et al. 1978; Beamish 1980a, b; Richards & Beamish 1981) in lampreys.
- d. Maturation and Reproduction – Bill and his colleagues have also studied the physiology of upstream migrants (Potter & Beamish 1978; Beamish et al. 1979), the bioenergetics of reproduction (Beamish 1979), adult sex ratio (Potter et al. 1974; Beamish & Potter 1975), and egg size and fecundity (Beamish & Potter 1975; Beamish 1980b; Beamish 1982; Docker & Beamish 1991; Beamish et al. 1994).

Although much of Bill Beamish’s work deals with the landlocked sea lamprey, several of the papers listed above also deal with the anadromous sea lamprey (e.g., Beamish & Potter 1975; Potter & Beamish 1977; Beamish 1980b), the chestnut lamprey, *Ichthyomyzon castaneus* (Beamish & Thomas 1983), and the Pacific lamprey, *Lampetra tridentata* (Russell et al. 1987). Bill has also contributed greatly to our knowledge of several nonparasitic lamprey species: the southern brook lamprey, *Ichthyomyzon gagei* (e.g., Beamish 1982; Beamish & Legrow 1983), mountain brook lamprey, *Ichthyomyzon*

*greeleyi* (e.g., Beamish & Austin 1985), least brook lamprey, *Lampetra aepyptera* (Docker & Beamish 1991, 1994), and American brook lamprey, *Lampetra appendix* (Beamish & Lowartz 1996).

Although Bill's published research on lampreys is the focus of this review, his contributions to lamprey research go well beyond his publications. Bill has been very generous with his time and ideas, and has even shared his hard-earned collection sites and contacts with novices and senior biologists alike, in order to help others working on lampreys. In addition, he has contributed greatly through his work with the Great Lakes Fishery Commission and, in particular, his emphasis on the importance of basic research to the sea lamprey program.

## **Recent Advances in the Ecology and Physiology of Sea Lampreys**

This section deals primarily with recent research on the biology of the landlocked sea lamprey in the Great Lakes. Given the interest in understanding and controlling this exotic predator (see Christie & Goddard 2003), funding for such research from the Great Lakes Fishery Commission has been considerable. Many recent advances have been made, and some of the most exciting advances relate to developing control strategies that may be used as alternatives to lampricide treatment (Twohey et al. 2003a, Docker et al. 2003). Many of these advances, however, deal with general lamprey biology and physiology, and the findings are not necessarily exclusive to the sea lamprey. The findings are organized by the stage of the lamprey life cycle to which they pertain: the larval stage, metamorphosis, the feeding (parasitic) phase, and sexual maturation and reproduction.

### **Larval Stage**

#### **1. Sex Differentiation and Determination in Lampreys**

##### *Previous Studies:*

Other investigators, most notably the late Martin Hardisty, have shown that lampreys are characterized by a prolonged period of sexual indeterminacy and by a certain degree of intersexuality (Hardisty 1965a, b). For example, sex differentiation in sea lampreys is generally not complete until larvae are approximately 90 mm in length or 2–3 years of age, and even after that point, it is not uncommon for the occasional oocyte to be observed in the gonad of presumptive males (Hardisty 1965b). It has been suggested that sex is labile during this period of sexual indeterminacy and subject to environmental influence (Hardisty 1954, 1961a). In particular, density-dependent sex determination has been suggested since a shift in sex ratio, from a predominance of males to excess of females, was observed in larval and adult lampreys in the upper Great Lakes following the initiation of sea lamprey control (Purvis 1979; Heinrich et al. 1980).

##### *Beamish's Contributions:*

#### **A. Density-Dependent Sex Determination**

Beamish (1993) and Docker & Beamish (1994) demonstrated the same phenomenon, a relationship between larval abundance and sex ratio, in two brook lamprey species (the southern and least brook lampreys, respectively) that have not been subjected to treatment with the lampricide 3-trifluoromethyl-4-nitrophenol (TFM). For both species, the proportion of males was positively correlated with density, although in the southern brook lamprey, this relationship was observed only when conditions for larval growth were favourable; under poor growth conditions, higher densities were associated with fewer males (Beamish 1993). These results further suggested that sex determination was density-dependent, and not just the result of TFM treatment (i.e. differential mortality between the sexes or chemical feminization).

### B. Sex Reversal

Recent work by Bill Beamish and colleagues, however, showed that the period of sexual indeterminacy in lampreys was even longer than previously thought and that intersexual or otherwise abnormal gonads were more prevalent (Barker et al. 1998; Wicks et al. 1998; Barker & Beamish 2000). Such abnormalities (e.g., atretic oocytes or an unusual number of germ cells) were observed in anadromous as well as landlocked sea lampreys and consequently were not just the result of lampricide treatments. Barker & Beamish (2000) suggested that these atypical gonads were in transition from one sex to another. Lowartz & Beamish (2000) therefore developed a gonadal biopsy technique to study the possibility of sex reversal in lampreys. Whereas the identification of sex using conventional histology kills the ammocoetes, gonadal biopsy techniques (which involve making an incision and removing a small portion of the gonad for histological analysis) are non-lethal and allow the gonad to be monitored over time. Using this technique, Lowartz & Beamish (2000) demonstrated actual sex reversal in some larvae following primary differentiation, which had not been previously shown. However, sex did not appear to change once the lampreys entered the juvenile period (Beamish & Barker 2002).

### *Recent Advances:*

#### A. Compensatory Mechanisms in Great Lakes Sea Lampreys

Compensatory mechanisms refer to processes that increase birth rates or decrease death rates when population density decreases. For example, if the production of ammocoetes is correlated with the number of females (i.e. the supply of eggs) and the supply of males does not limit recruitment, then a shift in sex ratio to a preponderance of females could compensate for overall declines in adult abundance. Compensatory mechanisms might therefore reduce the effectiveness of alternative control strategies such as the release of sterilized males and adult trapping (see Jones et al. 2003). A review of the historical evidence, however, showed that density-related changes in sex ratio were evident only when sea lamprey control was first initiated in each of the Great Lakes (Jones et al. 2003). Further shifts in sex ratio were not observed within the range of sea lamprey abundance levels observed since the implementation of control measures. Wicks et al. (1998), for example, were unable to demonstrate a relationship between larval density and sex ratio in Great Lakes sea lamprey populations in 1995 and 1996.

Recent studies have also examined potential compensatory changes in larval growth rates

and age at metamorphosis since previous work suggested accelerated growth and time to metamorphosis as a result of lower densities following lampricide application (e.g., Purvis 1979; Weise & Pajos 1998; Morkert et al. 1998). These studies, however, found no evidence of a strong, repeatable influence of density-dependent compensatory mechanisms on sea lamprey populations (Griffiths et al. 2001; Jones et al. 2003).

#### B. Non-Invasive Technique to Determine Sex in Larval Lampreys

The gonadal biopsy technique developed by Lowartz & Beamish (2000) was an important advance in studying sexual differentiation and sex reversal in lampreys but such surgical methods are still time-consuming and invasive, and manipulation of the gonad during surgery may influence its subsequent development. In other fish species (e.g., Siamese fighting fish, *Betta splendens*), mechanical manipulation of ovarian tissue induced sex inversion (Becker et al. 1975). A high-resolution ultrasound technique therefore was developed recently to non-invasively determine sex in live larval lampreys (Maeva et al. 2004). Conventional low-frequency ultrasound (3.5 to 15 MHz) has been used to determine sex and stage of maturity in several commercially important fish species, but has been unreliable and difficult for identification of sex in immature fish (e.g., Martin-Robichaud & Rommens 2001; Moghim et al. 2002). Acoustic microscopy, however, uses a focusing lens to concentrate high-frequency ultrasound (15–100 MHz), and in larval sea lampreys, can generate high-resolution cross-sectional images showing such internal body structures as the gonad, intestine, kidneys, cardinal veins, notochord, and musculature in approximately 30 seconds per animal. Using this technique, females could be identified by the presence of a relatively large (1–1.5 mm diameter) ovary, which was considerably less reflective to the acoustic signals than the surrounding kidney tissue. Although males could sometimes be recognized by the appearance of a small (0.2–0.3 mm) testis with slightly stronger reflective properties than the kidney, identification of sex merely by the presence or absence of an ovary was reliable in 100% of all larvae greater than 110 mm in length. This acoustic method is faster than histological sex determination, and the non-invasive nature of the technique will be important for experimental studies that need to monitor the gonad over time or that require live larvae of known sex (e.g., to examine sex-specific differences in endocrine profiles or other physiological parameters). Subsequent acoustic studies will be needed to determine if this technique is also capable of detecting the gonadal abnormalities that were reported by Barker et al. (1998), Wicks et al. (1998), and Barker & Beamish (2000).

## **2. Use of Statoliths**

Statoliths are the small calcareous bodies in the inner ears of lampreys and are analogous to the teleost otolith. They serve as a permanent record of the environment experienced by the lamprey since they grow incrementally throughout the life of the ammocoete and incorporate trace elements from the surrounding water as they grow (Volk 1986).

#### *Beamish's Contributions:*

#### Using Statoliths to Determine Age of Larval Lampreys

Although Carlstrom (1963) described the pattern of internal banding in lamprey statoliths and Volk (1986) reported a positive correlation between the number of bands and total length for larval sea lampreys, these statolith bands were validated as year marks by Beamish and colleagues (Medland & Beamish 1987; Beamish & Medland 1988b). Medland & Beamish (1991) also studied the effect of temperature, photoperiod, and ontogeny on lamprey statolith banding-patterns. This validation was important to provide a direct method of ageing larval lampreys, independent of their size (see Jebbink & Beamish 1995). However, Barker et al. (1997) reported that statoliths from larval and metamorphosing sea lampreys from some streams were either absent or did not have typical bands. This variability in statoliths appeared to be related to ambient calcium ion concentration, especially during periods of rapid larval growth.

*Recent Advances:*

Using Elemental Composition of Statoliths to Identify Stream Origins of Sea Lampreys

Since sea lampreys do not home to their natal streams (Bergstedt & Seelye 1995), it is difficult to determine which tributaries contribute most parasitic- and spawning-stage sea lampreys to the population. The relative contribution of each tributary currently can only be determined using tagging studies or by assuming that the number of parasitic- and spawning-stage lampreys produced by a stream is correlated with larval abundance or the number of metamorphosing lampreys that emerge from each tributary. Tagging studies, however, are labour-intensive and yield low tag returns, and estimates based on the abundance of ammocoetes or metamorphosing lampreys assumes that survival rates to the parasitic and adult life stages are equal across all tributaries. However, an alternative means to identify stream of origin in parasitic- and spawning-phase sea lampreys using natural tags, trace elements incorporated into sea lamprey statoliths during larval stream residence, appears promising<sup>1</sup>. Edward Brothers (EFS Consultants, Ithaca, NY) found that elemental composition patterns established in ammocoetes persisted into adults<sup>1</sup>. Furthermore, ammocoetes from the St. Marys River, a major spawning area for lampreys in Lake Huron, were distinguishable from three Lake Huron tributaries in Michigan's lower peninsula<sup>1</sup>. This was predominantly due to differences in strontium levels, reflecting regional differences in the geochemistry of the Canadian Shield and the Michigan basin, and demonstrates that statolith analysis can at least provide a means of assessing gross population structure of sea lampreys in the Great Lakes (Brothers & Thresher 2004). In addition, ammocoetes from two sites within the St. Marys River could be distinguished; those from a polluted site showed anthropogenically elevated levels of iron, manganese, lead, and nickel relative to a "clean" site (Brothers & Thresher 2004).

Studies by S.A. Ludsin, J.E. Marsden, and B.J. Fryer are currently attempting to use statolith elemental signatures to distinguish among lampreys from different tributaries within a region, i.e. to determine if statolith analysis can reliably determine specific stream

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<sup>1</sup> Brothers, E.B. 2003. Elemental composition of statoliths of sea lamprey (*Petromyzon marinus*). Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI. Available from the Internet URL [http://www.glfsc.org/pubs\\_out/annualreports.php](http://www.glfsc.org/pubs_out/annualreports.php)

of origin within a region. In a pilot investigation in Lake Champlain, statolith microelemental analysis was performed on 2–5 larvae from each of eight sea lamprey spawning tributaries. Due largely to differences in concentrations of zinc and rubidium among rivers, they were able to correctly classify 25 of the 26 individuals (S.A. Ludsin, Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI, unpublished data). In an ongoing project, Ludsin et al. (unpublished data) are attempting to: a) determine whether statolith elemental signatures similarly differ among ammocoetes produced in different Lake Huron streams; b) use these elemental signatures to identify origins of parasites and spawners in Lake Huron; and c) develop relationships to predict statolith elemental chemistry from water chemistry, which eventually could help eliminate the need to sample larvae annually to develop stream-specific signatures.

### 3. Larval Dispersal

#### *Previous Studies:*

Little is known about the early life history of sea lamprey ammocoetes, in particular, the dispersal of age-0 ammocoetes from nests into suitable larval rearing habitat.

#### *Recent Advances:*

As with the previously described advances that use modern techniques (i.e. acoustic microscopy and microelemental analysis of statoliths), the dispersal of larval sea lampreys has been investigated recently using genetic (microsatellite) markers (Derosier 2001). When a relatively small number of adult lampreys (fewer than 40) were introduced to streams above barriers (so that all lampreys present were the result of deliberate introductions), it was possible to assign parentage to the resulting larvae. Larvae of common parentage (i.e. from the same reproductive event and inferentially from the same nest) were distributed over more than 900 m of stream habitat within two months of emergence (Derosier 2001) and over as much as 5 km after a year<sup>2</sup>. These results show that age-0 larvae are capable of extensive movements and can access most downstream habitats over the course of a single year, implying that the proximity of spawning and larval rearing habitats is not a critical prerequisite for the successful recruitment of sea lampreys<sup>2</sup>.

### Metamorphosis

#### 4. Energetics of Metamorphosis

##### *Beamish's Contributions:*

Some of Bill Beamish's first published papers on lampreys (Lowe et al. 1973; O'Boyle &

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<sup>2</sup> Scribner, K.T. & M.L. Jones. 2002. Genetic assignment of larval parentage as a means of assessing mechanisms underlying adult reproductive success and larval dispersal. Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI. Available from the Internet URL [http://www.glfsc.org/pubs\\_out/annualreports.php](http://www.glfsc.org/pubs_out/annualreports.php)

Beamish 1977) showed that lipid accumulation in sea lampreys prior to metamorphosis and lipid depletion during metamorphosis are key metabolic events in this developmental process. Subsequent studies by Beamish and colleagues identified condition factor (i.e. weight relative to length) as an important predictor of metamorphosis (Youson et al. 1993; Holmes et al. 1994). These studies suggested that larvae in landlocked populations of sea lamprey that are at least 120 mm long, weigh 3 g, and have a condition factor of 1.5 or greater in the fall can be predicted to metamorphose the following summer.

*Recent Advances:*

There has recently been heightened interest in lipid metabolism during metamorphosis. Much has been learned about the patterns of lipid accumulation and depletion in metamorphosing lampreys (e.g., Kao et al. 1997a, b) and the hormones involved in regulating lipid metabolism (see Youson 2003). One area currently being pursued is whether there is a cue from the fat-containing tissues indicating when larvae have sufficient energy reserves for metamorphosis. In mammals and other higher vertebrates, such a signal to the brain and other target tissues comes from a hormone called leptin, which is a 16kDa protein secreted by white adipose tissue. Leptin appears to have the property of a “lipostat”; its effect is to reduce the desire to feed and it signals the animal’s nutritional status to several other physiological systems (Friedman & Halaas 1998; Hossner 1998).

Leptin-immunoreactive proteins have recently been identified in the blood and fat-containing tissues of sea lampreys (Yaghoubian et al. 2001). In particular, a 16kDa protein found in the nephric fold, which is the primary site of fat deposition in sea lampreys, may represent a leptin-like molecule which signals metabolic readiness for metamorphosis in sea lampreys (Yaghoubian et al. 2001). Attempts to clone the lamprey version of leptin, however, have been unsuccessful to date, perhaps because the leptin-like hormone in lampreys has a very different structure from that of higher vertebrates. Current efforts are now directed at finding a leptin receptor<sup>3</sup>.

## **Parasitic Feeding Phase**

### **5. Lamprey Feeding Models**

*Beamish’s Contributions:*

Another one of Bill Beamish’s first published papers on lampreys (Farmer & Beamish 1973) examined the incidence of sea lamprey attack on different freshwater teleosts according to species and size. This and subsequent laboratory (Farmer et al. 1975, 1977; Beamish et al. 1979) and modelling (Lett et al. 1977) studies provided a foundation for much of the later research on the parasitic feeding phase of lampreys. Since parasitic-phase sea lampreys are difficult to study in the wild, much of this recent work uses feeding

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<sup>3</sup> Youson, J.H. & M.F. Filosa. 2003. Regulation and manipulation of metamorphosis in sea lampreys: the relevance of a sea lamprey obesity factor and brook lamprey life history. Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI. Available from the Internet URL [http://www.glf.org/pubs\\_out/annualreports.php](http://www.glf.org/pubs_out/annualreports.php)

models to estimate the damage caused by sea lampreys to host populations in the Great Lakes.

*Recent Advances:*

Many of the lamprey feeding models (e.g., Cochran & Kitchell 1986, 1989) have been derived largely from the experimental work of Farmer and colleagues (Farmer & Beamish 1973; Farmer et al. 1975, 1977). However, recent additional research includes laboratory (e.g., Swink 2003; Cochran et al. 2003a) and field (Bergstedt & Swink 1995; Bergstedt et al. 2003) studies that have generated further empirical data on the parasitic feeding phase of sea lampreys, and subsequent studies that use these data to refine the feeding models.

Examples of recent refinements to the lamprey bioenergetics models include the following:

- a. Cochran et al. (1999) refined the previous models by Cochran & Kitchell (1986, 1989). Cochran & Kitchell (1986, 1989) quantified energy intake and growth by a sea lamprey as a function of lamprey size, host size, interval between feedings, and duration of the feeding attachment. These previous models, however, were applicable only to lampreys feeding at 10°C and were tested against a small number of lampreys. Cochran et al. (1999) tested the model over a greater range of temperatures (0 to 21°C), with a larger sample size (N = 272 versus N = 14), and over a greater range of lamprey sizes (2 to 365 g versus 5 to 11 g). The model predictions of instantaneous growth were highly correlated with observed growth except for late in the year, when predicted growth was generally much higher than observed growth. This suggested that large overwintering lampreys may reduce their feeding rates while attached to hosts or that there are seasonal or size-related shifts in the fate of consumed energy.
- b. Cochran et al. (2003) tested the hypothesis generated by Cochran et al. (1999) that a seasonal or size-related increase in wet energy density of sea lamprey tissue contributed to the tendency of that model to overestimate growth in large sea lampreys late in the year. They demonstrated that wet energy density of parasitic-phase sea lampreys did indeed increase with wet body mass, due to a decrease in water content and an increase in energy density of dry tissue in these larger lampreys. When this relationship between wet energy density and wet body mass was incorporated into the previous sea lamprey feeding model, it improved its ability to predict instantaneous growth.
- c. Madenjian et al. (2003) used the ontogenetic changes in energy density documented by Cochran et al. (2003a) and the thermal regimes generated by Bergstedt et al. (2003) to refine the individual-based model of MacKay (1992). MacKay (1992) in turn improved the lamprey feeding model of Kitchell & Breck (1980) by including size-based interactions between individual sea lampreys and individual lake trout. Madenjian et al. (2003) used their individual-based model to examine seasonal patterns in blood consumption and lamprey-induced mortality, and to test whether strain composition (i.e. Marquette or Seneca strains) was an important factor affecting the total number of lamprey-induced lake trout deaths. The modelling results indicated that the rate of blood consumption and rate of mortality should peak in late October, which is consistent with previous field results (Bergstedt & Swink 1995). The results also indicated, however, that the total number of lake trout deaths was unaffected by strain composition, which is inconsistent with the findings of Schneider et al. (1996).

## **Maturation and Reproduction**

### **6. Migratory Pheromone**

#### *Previous Studies:*

As mentioned previously, it has been shown that sea lampreys in Lake Huron do not home to their natal streams (Bergstedt & Seelye 1995); instead, migratory adults appear to locate spawning streams using a pheromone released by stream-resident larvae. The attractiveness of larvae to migratory adults was noted by Moore & Schleen (1980), who observed that Lake Superior streams routinely experienced large decreases in the number of spawning adults captured the year after their larval populations were reduced by lampricide treatment. The existence of a lamprey migratory pheromone was first suggested by Teeter (1980).

#### *Recent Advances:*

Considerable and rapid progress on the origins, identity, and function of a migratory pheromone has been made by Peter Sorensen and colleagues at the University of Minnesota and the Hammond Bay Biological Station in Michigan. They demonstrated that:

- a. Chemical compounds released by larval sea lampreys attracted migratory adult sea lampreys of both sexes at low, biologically relevant concentrations (Bjerselius et al. 2000; Vrieze & Sorensen 2001).
- b. Adult lampreys with occluded olfactory systems were not attracted to larval stream water (Vrieze & Sorensen 2001).
- c. In addition to guiding lampreys into spawning streams, the migratory pheromone appears to influence adult migration once they are within the river. Migratory adult sea lampreys exposed to larval odour swam upstream at nearly twice the rate of those exposed to control water, and the response to larval odour was particularly strong at night when adult migration peaks (Li 1994; Bjerselius et al. 2000).
- d. The migratory pheromone consists of at least two unique bile acids, petromyzonol sulfate, PS, and its apparent precursor, allocholic acid, ACA (Li et al. 1995). Although parasitic and spawning-phase adults do not produce identifiable bile acids, large quantities of PS and ACA were found in larval gall bladders (Polkinghorne et al. 2001). Larvae released these bile acids primarily through their feces (Polkinghorne et al. 2001).
- e. PS and ACA were released by recently-fed larvae, but starved larvae released very little bile acid (Polkinghorne et al. 2001), suggesting that pheromone release rates should peak in the spring when adult migration commences.
- f. The adult sea lamprey olfactory system was acutely and specifically sensitive to PS and ACA at very low concentrations (Li & Sorensen 1997; Sorensen & Caprio 1998), and this sensitivity appeared to peak at the onset of their spawning migration (Sorensen et al. 1995).
- g. Larval odour likely contains attractive components in addition to PS and ACA since adult lampreys preferred larval holding water to water containing PS and ACA, even

when the concentration of these bile acids exceeded that found in the holding water (Vrieze & Sorensen 2001). Fine and Sorensen (2005) suggested that ACA is not important to the migratory pheromone, but recent unpublished studies suggest that at least one other component that may resemble PS is (see Sorensen et al. 2003).

- h. Other species of European and North American lampreys (including species native to the Great Lakes) also produce PS and ACA, and migratory sea lampreys were attracted to the odours of these heterospecific larvae (Fine et al. 2004). This is consistent with reports of adult sea lampreys entering Great Lake streams that lack larval sea lampreys but which have populations of native lamprey larvae; this could in fact explain how the sea lamprey first became established in the Great Lakes.
- i. If the migratory pheromone could be isolated from larvae in quantity or synthesized at a reasonable cost, it could be used for sea lamprey control. Possible control applications include addition of the pheromone to traps (to increase their efficiency at capturing migrating adults) or to certain streams (i.e. those that are blocked, have inferior habitat, or are more easily treated with lampricide). Using the migratory pheromone to attract sea lampreys to such streams could perhaps be accomplished at low cost by stocking larval native lampreys in these streams (Sorensen & Vrieze 2003).

## 7. Endocrine Control of Reproduction

### *Previous Studies:*

Within the past 20 years, substantial progress has been made in understanding the cascade of endocrine events that controls reproduction in lampreys. Identification of two molecular forms of gonadotropin-releasing hormone, lamprey GnRH-I and GnRH-III (Sherwood et al. 1986; Sower et al. 1993), provided evidence for brain control of reproduction in lampreys through the hypothalamus-pituitary-gonadal (HPG) axis. GnRH is released from the hypothalamus in response to external and internal cues; GnRH then acts on the pituitary, where gonadotropins are released; and gonadotrophins in turn influence steroidogenesis and gametogenesis in the gonad.

### *Recent Advances:*

#### Gonadotropin-Releasing (Hypothalamic) Hormones:

Much research has subsequently been performed on the hypothalamic (i.e. neuroendocrine) components of the HPG axis (see Sower 2003). Recently, the complementary DNAs (cDNA) of lamprey GnRH-I and -III have been identified (Suzuki et al. 2000; Silver et al. 2001; Silver et al. 2004), and their functions have been investigated. MacIntyre et al. (1997), for example, suggested that GnRH-III is the major form regulating final maturation in lampreys. Whereas GnRH-I levels remain relatively low in female sea lampreys during final maturation, GnRH-III is present in higher concentrations and undergoes significant increases during this period. Previous studies<sup>4</sup> suggested that GnRH-I influences

<sup>4</sup> Sower, S.A. & L.H. Hanson. 1992. Vertebrate sex determination/differentiation workshop. Great Lakes Fishery Commission Publication, Ann Arbor, MI.

spawning behaviour.

Recent advances have also been made in the use of GnRH analogs for male lamprey sterilization, for use by control agencies in the Sterile-Male-Release Technique (SMRT). Application of SMRT to sea lamprey control began in the 1970s, pioneered by Lee Hanson at Hammond Bay Biological Station. Sterilization has been used successfully to control numerous insect pests; since this method becomes increasingly effective as population numbers decline, it is used most effectively when integrated with a pesticide control program. Bisazir is an effective sterilant currently used in the sea lamprey SMRT (Hanson & Manion 1980), but it is extremely hazardous to humans. It can be used only in a special sterilization facility at Hammond Bay Biological Station, and all male lampreys must be shipped there for sterilization (see Twohey et al. 2003b). GnRH analogs (e.g., Sower et al. 1995) therefore offer promising alternatives to bisazir because they are non-toxic to humans and other non-target organisms, easily degraded, easy to administer, and relatively easy and inexpensive to synthesize. Furthermore, as expected given the different functions of the two molecular forms of lamprey GnRH, current data suggest that analogs to GnRH-III would sterilize lampreys without affecting their spawning behaviour (see Sower 2003). In addition, some GnRH-I analogs may be capable of enhancing spawning behaviour in sterile males (Young et al. 2004).

#### Pituitary Hormones:

Compared to the neuroendocrine component of the lamprey HPG axis, the other components are less well understood. Until recently, the only pituitary hormone that had been structurally identified in the lamprey was arginine vasotocin (Lane et al. 1988). Since 1995, several additional pituitary hormones have been identified (e.g., Heinig et al. 1995; Suzuki et al. 1995; Takahashi et al. 1995; Kawauchi et al. 2002), but a gonadotropic hormone (GTH) has yet to be identified (see Sower 2003). Evidence from physiological (e.g., hypophysectomy and substitution therapy with pituitary extracts of mammalian GTHs; Sower & Larsen 1991) and immunocytochemical (e.g., Nozaki et al. 1999) studies, however, strongly support the presence of a GTH-like molecule in lampreys. A lamprey GTH is also implied from the presence of two high affinity binding sites for lamprey GnRH-I and -III in the pituitary of adult female sea lampreys, and from the fact that these hypothalamic hormones differentially regulate lamprey pituitary function (Materne et al. 1997; Sower 1998). The search for a GTH-like molecule in lampreys continues (see Sower 2003).<sup>5</sup>

#### Gonadal Steroids:

The structure and function of gonadal steroids in lampreys is not well known, although there have been several recent advances. In particular, there is growing evidence that lampreys produce gonadal steroids that are different from those of other vertebrates by possessing an additional hydroxyl group at the C15 position. The use of these unconventional steroids by lampreys was previously suggested (Kime & Rafter 1981;

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<sup>5</sup> Note added in press: A GTH $\beta$ -like protein has been identified by cDNA cloning in sea lamprey (Sower, S.A., S. Moriyama, M. Kasahara, A. Takahashi, M. Nozaki, K. Uchida, J.M. Dahlstrom & H. Kawauchi. 2006. Identification of sea lamprey GTH $\beta$ -like cDNA and its evolutionary implications. *General and Comparative Endocrinology* 148: 22-32).

Kime & Callard 1982), but has been confirmed recently: 15 $\alpha$ -hydroxytestosterone (15 $\alpha$ -T) and 15 $\alpha$ -hydroxyprogesterone (15 $\alpha$ -P) were produced *in vitro* in sea and river lamprey testes (Bryan et al. 2003, 2004; Lowartz et al. 2003; Golla et al. 2000) and 15 $\alpha$ -hydroxyestrogens were produced in ovarian tissue (Lowartz et al. 2003).

Furthermore, radioimmunoassays have been developed to detect 15 $\alpha$ -T and 15 $\alpha$ -P (Bryan et al. 2003, 2004, respectively) and were used to demonstrate that: a) both steroids are present in the plasma of sea lampreys (i.e. *in vivo*); b) both 15 $\alpha$ -T and 15 $\alpha$ -P rise dramatically in response to injections of GnRH (Young et al. 2004; Bryan et al. 2004); and c) 15 $\alpha$ -T levels increase prior to ovulation and spermiation; although levels remain high in spermiated males, levels fall in ovulated females (Bryan et al. 2003). These *in vivo* observations lend support to the hypothesis that lampreys use these steroids as reproductive hormones. It is possible that 15-hydroxylated steroids evolved as functional hormones in lampreys as a response to parasitism (so that the parasitic lamprey would be less susceptible to the influence of the reproductive hormones in its host's blood) or are simply a primitive form of steroid hormone.

## 8. Sex Pheromones

### *Previous Studies:*

That sea lampreys may use sex pheromones to attract mates was first suggested almost 70 years ago when Fontaine (1938) reported that French fishermen routinely caught large numbers of mature female lampreys in traps baited with sexually mature male lampreys. Laboratory tests later suggested that both male and female sea lampreys, after reaching a certain stage of sexual maturation, release pheromones that signal their sex and reproductive state and attract members of the opposite sex (Teeter 1980; Lisowski et al. 1986).

### *Recent Advances:*

The identify of and exact response to these sex pheromones has been studied in detail in recent years by Weiming Li and colleagues at Michigan State University and John Teeter at Monell Chemical Senses Center in Philadelphia. They demonstrated that:

- a. The odourant from spermiating males was highly stimulatory to the olfactory organ of mature females (Bjerselius et al. 1996).
- b. Females showed a dramatic increase in swimming and searching behaviours when exposed to male odourant (Li et al. 2002). Since male lampreys often arrive on the spawning grounds before the females and initiate nest construction at sites with a unidirectional flow of water, this increased searching behaviour and upstream movement in ovulatory females likely attracts them to the spawning nests.
- c. The level of sexual maturation was critical for both the release of and response to the pheromone. Washings from spermiating males were 1000-10,000 times more potent in stimulating the olfactory sensory epithelia of females than washings from pre-spermiating males (Li 1994; Bjerselius et al. 1996). Behavioural studies showed that only mature females were attracted to odour from mature males; sexually immature

- females were not attracted to washing from either pre-spermiating or spermiating males (Li et al. 2002).
- d. Males sterilized by injection with bisazir released the sex pheromone and attracted ovulating females (Siefkes et al. 2003a).
  - e. The sex pheromone released by spermiating males, which was identified and named 3-keto petromyzonol sulfate, 3kPZS by Li et al. (2002), is very similar in structure to the bile acid petromyzonol sulfate that functions as a migratory pheromone (see above). 3kPZS has been purified and was found to be highly stimulatory to the olfactory organs of adult females (Li et al. 2002; Siefkes & Li 2004).
  - f. Another possible component of the male pheromone is 3-keto allocholic acid, 3kACA, which is released in amounts of approximately 4% of 3kPZS (Yun et al. 2003). Although its exact role has yet to be determined, preliminary studies suggest that this bile acid may serve to augment the action of 3kPZS at very low concentrations (see Li et al. 2003a).
  - g. Although evidence suggests that bile acids may function as sex pheromones in salmonids as well (e.g., Vermeirssen & Scott 2001; Zhang et al. 2001), all sex pheromones identified to date in teleosts are sex hormones (see Li et al. 2003b). Since bile acids can be produced in relatively large quantities (considering the size of the liver), bile acid pheromones may permit signalling over a longer distance in rapidly flowing water than a sex steroid pheromone could (Li et al. 2003a).
  - h. Although most pheromones in fish are released through the urinary tract, the release of 3kPZS and 3kACA took place exclusively through the gills (Siefkes et al. 2003b). Since adult lampreys do not have bile ducts or gall bladders (Youson 1985), the bile acids are probably transported via the bloodstream to the kidney and gills. A gill-based release is potentially very efficient, however, since the hepatic veins carry blood directly to the heart and all the blood from the heart goes through the gills (Li et al. 2003a).
  - i. Sexually mature females also release a pheromone that attracts male lampreys (Teeter 1980). The structure of this compound has not yet been identified, but it appears to be associated with the ovarian fluid (J.H. Teeter, Monell Chemical Senses Center, Philadelphia, PA, unpublished data). The female pheromone, however, does not appear to increase swimming activity in males (M.J. Siefkes & W. Li, Michigan State University, East Lansing, MI, unpublished data), suggesting that its main function is to keep males in the vicinity (see Li et al. 2003b).
  - j. Possible applications to sea lamprey control include luring ovulatory females into traps (e.g., Johnson et al. 2005) or unsuitable spawning areas, particularly if a synthetic male sex pheromone could be produced at reasonable cost. Similarly, if it is possible to enhance biosynthesis and release of the pheromone in sterile male sea lampreys, sterile males could be made more attractive to females than their fertile counterparts (Li et al. 2003b).

## 9. Sea Lamprey Mating Systems and Reproductive Success

### *Previous Studies:*

Sea lamprey reproductive behaviour is not fully understood. Manion & Hanson (1980)

concluded that sea lampreys are generally monogamous spawners, but suggested that the proportion of individuals that are monogamous may vary, perhaps as the result of skewed sex ratios. Furthermore, O'Connor (2001) found that not all of the adult sea lampreys entering a stream spawn and suggested that nesting success may decline with increases in population size. However, it is still unclear what factors affect successful nest construction and spawning.

*Recent Advances:*

Sea lamprey mating systems therefore have been investigated recently using genetic markers, in conjunction with the above study of larval dispersal<sup>2</sup>. Microsatellite markers were used to assign parentage to sea lamprey ammocoetes, in order to determine the number of offspring produced by each male and female stocked in streams above barriers. It was found that most adults contributed to reproduction; an average of 80.6% of the adults produced at least one offspring. However, there was wide variation in reproductive success among the adults, and the most successful males and females in each stream typically mated with each other. There was also evidence of polygyny and polyandry; most males and females mated with more than a single individual, and matings with three or more individuals were common.

## **Recent Advances in the Phylogeny and Phylogeography of Lampreys**

There have been several recent studies on the morphology (e.g., Collin & Potter 2000; Yamazaki et al. 2001), distribution (e.g., Tumilson & Tumilson 1999; Holčik & Delić 2000; Sotnikov & Solov'ev 2002), larval habitat (e.g., Sugiyama & Goto 2002), feeding (e.g., Cochran et al. 2003b; Yap & Bowen 2003; Mundahl et al. 2005), and spawning behaviour (Yamazaki & Goto 2000; Takayama 2002) of some of the other lamprey species found in the temperate regions of both Northern and Southern hemispheres. In addition, since most lamprey species worldwide are of conservation concern (Renaud 1997), many recent studies are of specific conservation interest (e.g., Beamish et al. 2001; Close et al. 2001; Moser et al. 2002a, b; Mesa et al. 2003; Mejía *et al.* 2004). Several of these studies build on Bill Beamish's contributions, and almost half of them cite one or more of his papers. Nevertheless, this review, which attempts to highlight the use of modern techniques to address many of the long-standing questions regarding lamprey biology, will focus predominantly on recent phylogenetic studies examining relationships among lamprey species and phylogeographic studies examining population structure in some of these species. The relationship between lampreys and other vertebrates is also of considerable evolutionary interest and continues to be disputed (e.g., Rasmussen et al. 1998; Mallatt & Sullivan 1998; Kuraku et al. 1999), but this review will deal only with phylogenetic studies examining relationships within the Petromyzontiformes.

### **10. Phylogeny of Lampreys**

*Previous Studies:*

Species identification and determination of generic status in lampreys has largely been based on adult dentition, as well as on other morphological characteristics such as differences in body proportions and number of trunk myomeres (Hubbs & Potter 1971). Compared to bony vertebrates, however, lampreys are difficult to classify since they lack the scales, gill rakers, vertebrae, and other bony structures typically used in fish taxonomy. There is still considerable disagreement therefore regarding the appropriate classification of several species of Northern Hemisphere lampreys (e.g., Hubbs & Potter 1971; Vladykov & Kott 1979a; Bailey 1980).

*Recent Advances:*

A. Phylogeny of Living Parasitic Lampreys Based on Morphological Data

Gill et al. (2003) determined the relationship among the 18 extant species of parasitic lampreys using a cladistic analysis of 32 morphological, anatomical, and karyological data (and a composite agnathan fossil as an outgroup). Although their results support the retention of each of the two Southern Hemisphere genera (*Geotria* and *Mordacia*) as distinct families and all the Northern Hemisphere lampreys as a third family (Hubbs & Potter 1971), within the Northern Hemisphere lampreys, they:

- a. Supported the retention of *Ichthyomyzon* and *Petromyzon* as separate genera, but suggest that they should be grouped together as either a subfamily or tribe. However, they refuted the view of Vladykov & Kott (1979a) and Bailey (1980) that *Caspiomyzon* should be grouped with *Ichthyomyzon* and *Petromyzon*.
- b. Concluded that *Entosphenus* is monophyletic and sufficiently unique to be considered a separate genus. This is consistent with classification proposed by Vladykov & Kott (1979a), but contrasts with that of Hubbs & Potter (1971) who classified *Entosphenus* as a subgenus of *Lampetra*.
- c. Found the final group of Northern Hemisphere lampreys to be formed by *Lethenteron* and *Lampetra*, which were also given subgeneric status by Hubbs & Potter (1971), and the Eurasian genus *Eudontomyzon*. Support for monophyly was weak, however, and *Lampetra* was more closely related to *Eudontomyzon* than to *Lethenteron*, which is inconsistent with the placement of *Lampetra* and *Lethenteron* into a single genus.

These results therefore support retention of genus status for each of the seven Northern Hemisphere taxa, which is consistent with the nomenclature of Renaud (1997). Gill et al. (2003), however, point out that attainment of greater resolution and greater support will require the use of other types of characters (e.g., molecular data), since they have already used the vast majority of morphological characters present in lampreys.

B. Molecular Phylogeny of Lampreys

Docker et al. (1999) used mitochondrial DNA sequence to examine relationships within the genus *Lampetra* (comprising the subgenera *Entosphenus*, *Lampetra*, and *Lethenteron*), and, in a follow-up study to Gill et al. (2003), N.J. Lang, K.J. Roe, R.L. Mayden, F. Chapleau, H.S. Gill, I.C. Potter, and C.B. Renaud constructed a phylogeny using mtDNA sequence from almost all lamprey species worldwide (N.J. Lang, Saint Louis University, St. Louis, MO, unpublished data). Both studies showed that molecular phylogenies including nonparasitic species were not concordant with the morphological tree of Gill et al. (2003) that was based only on parasitic species. Although most nonparasitic species

were genetically indistinguishable from their parasitic counterpart (“paired” or “satellite” species, see below), inclusion of the so-called relict species (nonparasitic lampreys that occur at or near the extreme southern limits of distribution of the Northern Hemisphere lampreys; Hubbs & Potter 1971) altered the tree topologies. For example, *Entosphenus* was no longer monophyletic when the Kern brook lamprey (*Lampetra* (*E.*) *hubbsi*) was included, and support for distinct *Lampetra* and *Lethenteron* genera was weakened with inclusion of the Po brook lamprey (*Lampetra* (*Le.*) *zanandreae*) (Docker et al. 1999; see Fig. 1 this paper).

Yamazaki et al. (2003) also showed that classification based on morphology alone can be misleading. Two populations of lampreys previously described as *Lampetra* (*Lethenteron*) *reissneri* from northern Japan and from southern Japan and Korea (*L. sp. N.* and *L. sp. S.*, respectively) were shown to be genetically distinct from each other and from other Eurasian *Lethenteron* species (*L. japonicum*, *L. kessleri*, and *L. reissneri* from Russia). In particular, *L. sp. S.* was so divergent from other *Lethenteron* (Yamazaki & Goto 1998) that Yamazaki et al. (2003) suggested that it may not even belong within the *Lampetra* group (i.e. *Entosphenus*, *Lampetra*, and *Lethenteron*). Reconstruction of the phylogenetic relationship among all lamprey species for which cytochrome *b* sequence data are available (Fig. 1) agrees with Yamazaki et al. (2003) in suggesting that *L. sp. S.* is phylogenetically distinct from other *Lethenteron* species, but indicates that *L. sp. S.* does belong within the *Lampetra* “complex.” These data suggest that *L. sp. S.* may be a sister group to *Entosphenus* (Fig. 1). The phylogeny currently being estimated for almost all lamprey species worldwide using complete cytochrome *b* sequence (N.J. Lang, Saint Louis University, St. Louis, MO, unpublished data) will better elucidate the taxonomic relationship between *L. sp. S.* and other lamprey species.

## **11. Relationship between Paired and Satellite Species:**

### *Previous Studies, Including Beamish’s Contributions:*

In most lamprey genera, groups of two or more species exist in which the larvae are morphologically similar but the adults differ in terms of feeding or migratory type; the terms “paired” and “satellite” species were coined by Zanandrea (1959) and Vladykov & Kott (1979b), respectively. Most lamprey taxonomies recognize adult feeding type as a species-specific characteristic (see Salewski 2003). However, some lamprey populations appear to be polymorphic for feeding type (e.g., Manion & Purvis 1971; Beamish 1987) and some authors (e.g., McPhail & Lindsey 1970; Savvaitova & Maksimov 1979) consider paired or satellite species to be races of a single species.

The ability to distinguish between larvae of paired species is generally poor, although subtle differences in pigmentation have been reported in some paired species (e.g., Vladykov & Kott 1980; Richards et al. 1982; Lanteigne 1988). Some studies (e.g., Hardisty 1961b; Beamish & Thomas 1983) also suggest that the differences between paired species in adult fecundity are already evident in the ammocoete as differences in oocyte number.

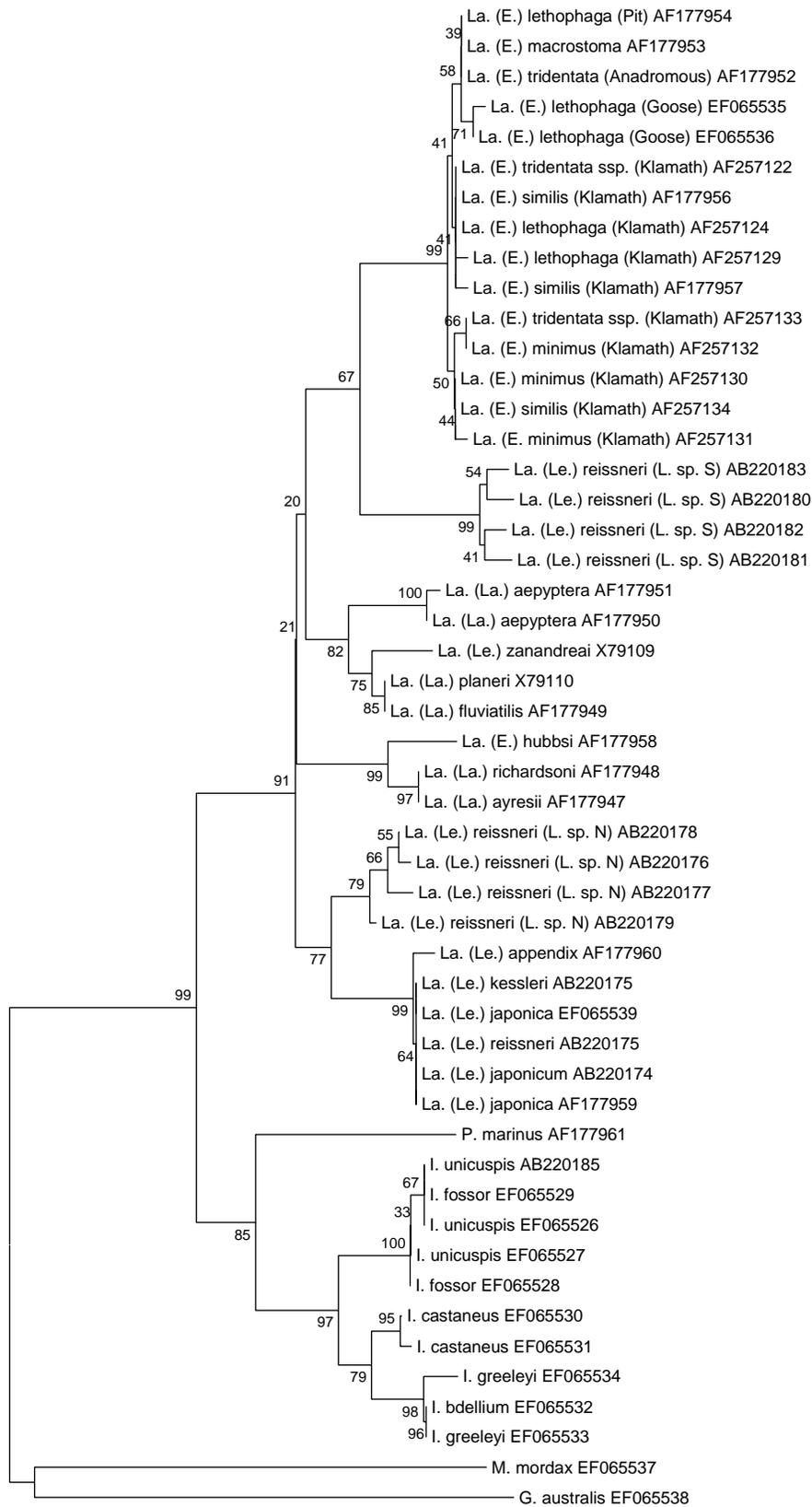


Fig. 1. Phylogeny of lampreys inferred from 267 bp of mitochondrial cytochrome *b* sequence using Kimura's (1980) two-parameter distance model and the neighbor-joining algorithm; numbers at nodes are bootstrap values for 1000 replications. *Lampetra* subgenera are abbreviated La (*Lampetra*), Le (*Lethenteron*), and E (*Entosphenus*). Sequence data were obtained from the following sources: AF177947–AF177976 (Docker et al. 1999); AF25120–AF257134 (Lorion et al. 2000); AB220174–AB220185 (Yamazaki et al. 2006); EF065526–EF065539 (this paper). Tree topology was the same when *L. zanandreae* and *L. planeri* sequences were omitted and 384 bp were compared in the remaining species.

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### *Recent Advances:*

#### A. Morphological Differences Between Larvae of Paired Species

Recent studies have failed to find diagnostic morphological differences between larvae of such paired species as the European river and brook lampreys, *Lampetra fluviatilis* and *L. planeri*<sup>6</sup>, and the silver and northern brook lampreys, *Ichthyomyzon unicuspis* and *I. fossor* (Neave 2004). Neave (2004) used traditional morphological methods (using linear distances) and geometric morphometrics, qualitative and quantitative analyses of pigmentation, and analysis of oocyte number in histological cross-sections in an attempt to identify silver and northern brook lamprey ammocoetes. He compared ammocoetes from known northern brook lamprey streams (based on historical adult capture records) to those from mixed northern brook lamprey/silver lamprey streams since allopatric populations of silver lampreys have not been found in the Great Lakes basin. Only analysis of oocyte numbers appeared promising as a means of distinguishing between the two species. There were 13–42 oocytes per cross-section in the known northern brook lamprey populations and 15–93 per section in the mixed population, suggesting that the individuals with the most oocytes per section in the mixed population were silver lampreys. Given the lack of known silver lamprey ammocoetes, however, the degree of overlap between species (and therefore the diagnostic nature of this character) could not be determined.

#### B. Genetic Differences Between Paired Species

Molecular phylogenetic studies (e.g., Schreiber & Engelhorn 1998; Docker et al. 1999; Lorion et al. 2000) have similarly failed to find species-specific genetic differences between most sympatric paired and satellite species (see Fig. 1). The only diagnostic differences reported to date are between the anadromous Pacific lamprey and the freshwater-resident Klamath River lamprey, *Lampetra similis*, which both spawn in the lower Klamath River basin (Lorion et al. 2000). Although Docker et al. (1999) and Lorion et al. (2000) compared only short fragments of the mitochondrial genome, a more recent study compared over 10,000 bp of mtDNA sequence from parasitic silver lampreys and nonparasitic northern brook lampreys in Great Lakes tributaries and still found no

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<sup>6</sup> Gardiner, R. 2003. Identifying lamprey. A field key for sea, river and brook lamprey. Conserving Natura 2000 Rivers Conservation Techniques Series No. 4. English Nature, Peterborough, UK. Available from the Internet URL [http://www.english-nature.org.uk/lifeinukrivers/publications/lamprey\\_key.pdf](http://www.english-nature.org.uk/lifeinukrivers/publications/lamprey_key.pdf).

diagnostic genetic differences between species<sup>7</sup>. Two mitochondrial lineages were observed, but these lineages did not correspond with species; both species were found within both lineages (Fig. 1). This suggests that the two species are polyphyletic, and are due to independent and parallel evolution within each lineage. This also suggests that, where they are sympatric, the two species either diverged very recently (within the past 4000-5000 years; Brown et al. 1979) or have not diverged and continue to experience gene flow.

Using higher-resolution microsatellite markers, Filcek et al. (2005) found near-fixed differences between northern brook and silver lampreys. Although not diagnostic, these differences permitted the two species to be distinguished with a high degree of accuracy and suggested barriers to gene flow. However, Filcek et al. (2005) compared northern brook and silver lampreys from tributaries to Lake Superior and Lake Michigan, respectively. In a follow-up study that used these microsatellite markers in sympatric populations of silver and northern brook lampreys (e.g., from the same Lake Huron tributaries), there was no significant genetic differentiation between the species<sup>8</sup>. Rather than being distinct species, therefore, the nonparasitic northern brook and parasitic silver lampreys appear comparable to the different feeding types found in other fish species. For example, benthic and limnetic forms of smelt, whitefish, and sticklebacks exist (Taylor and Bentzen 1993; Pigeon et al. 1997; Taylor 1999), and these different trophic types are identified by same Latin binomial.

## 12. Phylogeography of Lampreys

### *Previous Studies:*

Most lamprey species are of conservation concern (e.g., Renaud 1997; Close et al. 2001), and many are also of phylogeographic interest (Moyle 1976). Past connections of different basins and sub-basins can be inferred from the genetic relatedness of the lamprey species found there now, and such relationships among populations has control and conservation implications.

### *Recent Advances:*

#### A. Sea Lampreys in Lake Ontario

For example, although sea lampreys are presently considered by U.S. and Canadian government agencies to be an invasive species within the entire Great Lakes watershed, there has been considerable debate on this issue (see Waldman et al. 2004). Since sea lampreys had not been noted in Lake Ontario until 1835, 12 years after completion of the eastern section of the Erie Canal, some investigators (e.g., Mandrak & Crossman 1992) concluded that sea lampreys entered Lake Ontario via this route. However, other authors

<sup>7</sup> Mandrak, N.E., M.F. Docker & D.D. Heath. 2004. Native *Ichthyomyzon* lampreys of the Great Lakes: development of genetic markers and a morphological key to ammocoetes. Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI.

<sup>8</sup> Docker, M.F., N.E. Mandrak, D.D. Heath & K.T. Scribner. 2005. Genetic markers to distinguish and quantify the level of gene flow between northern brook and silver lampreys. Great Lakes Fishery Commission Project Completion Report, Ann Arbor, MI.

(e.g., Radforth 1944; Lawrie 1970; Bailey & Smith 1981) argued that sea lampreys are indigenous to Lake Ontario. Previous genetic analyses were equally conflicted: Brussard et al. (1981) suggested that sea lampreys were native to Lake Ontario but a follow-up study with an expanded data set concluded that they were probably invasive (Wright et al. 1985). Recent mtDNA analysis, however, indicates that sea lampreys are indigenous to Lake Ontario (Waldman et al. 2004). Pronounced differences in the frequency of control region haplotypes between sea lampreys from the Atlantic coast and Lake Ontario support the idea of post-Pleistocene natural colonization. If sea lampreys are indeed native to Lake Ontario, sea lamprey control policies might need re-evaluation.

### B. Population Structure in Other Species

Although there are generally no diagnostic genetic differences between paired or satellite species (see above), fixed intraspecific differences have been observed between different populations within species. Phylogeographic studies using mtDNA sequence data have demonstrated that:

- a. There are fixed differences in the control region between sea lampreys from North American and Spanish rivers (Rodríguez-Muñoz et al. 2004). These results indicate that there is no gene flow between North American and European sea lampreys, and suggest that their designation as a single species should receive additional study.
- b. The freshwater-resident Upper Klamath Lake lamprey in Oregon (currently considered an undescribed subspecies of the Pacific lamprey, *L. tridentata*) is genetically distinct from anadromous *L. tridentata* (Lorion et al. 2000). The Upper Klamath Lake lamprey and anadromous Pacific lamprey could be distinguished at several fixed sequence differences, indicating that the Upper Klamath Lake lamprey is not a recently landlocked population of *L. tridentata* (Fig. 1).
- c. The Pit-Klamath brook lamprey, *Lampetra lethophaga*, in the Pit River basin in northeastern California and southern Oregon (including Goose Lake) is genetically distinct from populations of this species found in the Klamath basin (M.F. Docker and S.B. Reid, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, unpublished data; see Fig. 1). This suggests that nonparasitism has evolved independently in the two basins, and may refute the hypothesis of a past headwater connection between the Klamath and Pit River basins that was based largely on the presence of this species in both basins (Moyle 1976).

These genetic results suggest that species designations should be re-evaluated in many lampreys. Some paired species, despite pronounced differences in adult morphology, appear not to be genetically distinct and may represent a single species, whereas several lamprey populations, despite the lack of clear morphological differences among them, show pronounced genetic differences (e.g., Yamazaki et al. 2003). Decisions regarding species designations cannot be based entirely on genetic results, but these new data will be very valuable in addressing these long-standing issues.

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