Life History and Abundance of Young Adult *Lamproptera ayresi*

in the Fraser River and Their Possible Impact on Salmon
and Herring Stocks in the Strait of Georgia

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Metamorphosis in *Lamproptera ayresi* begins in July but is not completed until approximately April of the following year when the osphragous opens. The prolonged period of metamorphosis differs from that of other lamprey species and may have evolved in response to the pattern of discharge of the Fraser River. Prior to the opening of the osphragous, some metamorphosing *L. ayresi* congregate just upstream of the salt water that moved into the river from the ocean. Soon after the osphragous opens, lampreys are able to tolerate and forage in salt water and enter the Strait of Georgia from May to July. Maximum numbers go to sea in early June, correlated with the maximum discharge from the Fraser River. Laboratory studies indicated that there was a relatively short period during which it was possible for the lampreys to go to sea. The mortality of *L. ayresi* held in fresh water in the laboratory greatly increased after mid-June, with few surviving beyond mid-July. These mortalities indicate that most *L. ayresi* must go to sea. In the laboratory a small number grew and reproduced normally in fresh water. A population estimate of the number of downstream migrants in 1979 indicated that *L. ayresi* were very abundant in the Fraser River. Three additional estimates of density and abundance were used to corroborate this observation. Even though *L. ayresi* feed for only about 10 wk in the Strait of Georgia, they are an important source of direct or indirect mortality to herring and young salmon. If *L. ayresi* was uncommon in British Columbia in the past, as previously described, then this present level of predation is an important new source of mortality to herring and salmon.

La métamorphose de *Lamproptera ayresi* commence en juillet mais ne se termine qu'en avril de l'année suivante quand l'osphragos s'ouvre. La période prolongée de métamorphose est différente des autres espèces de lamproyes et peut s'être développée en relation avec le régime de débit du fleuve Fraser. Avant l'ouverture de l'osphragos, certaines *L. ayresi* en métamorphose se rassemblent juste en amont des eaux salées qui pénètrent dans l'embranchure du fleuve. Peu après l'ouverture de l'osphragos, on observe une capacité d'osphragos en eau salée. De mai à juillet, les lampreys gagnent le détroit de Georgia. La plupart se dirigent vers l'océan au début de juin, ce qui correspond au débit maximum du fleuve Fraser. Des études en laboratoire révèlent que les lampreys disposent de peu de temps pour se rendre en mer. La mortalité de *L. ayresi* gardée en eau douce en laboratoire a fortement augmenté après la mi-juillet; peu d'individus ont survécu après la mi-juillet. Ces mortalités indiquent que la plupart des *L. ayresi* doivent se rendre en mer. On a observé une croissance et une reproduction normales en eau douce chez un petit nombre gardé en laboratoire. Une estimation du nombre de migrant des débuts de 1979 indique que *L. ayresi* était très abondante dans le fleuve Fraser. Trois estimations supplémentaires de la densité et de l'abondance ont été utilisées pour corroborer cette observation. Quoique *L. ayresi* ne se nourrisse que pendant 10 sem dans le détroit de Georgia, elle cause une importante mortalité directe ou indirecte du hareng et du jeune saumon. Si *L. ayresi* n'était pas commune en Colombie-Britannique par le passé, comme on l'a mentionné, le niveau actuel de prédation constitue une importante nouvelle source de mortalité dans le hareng et le saumon.

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showed that they were not *L. ayresi*. (The taxonomy of the former will be discussed in a future report; the Morrison Creek variety is discussed in Beamish and Whitehead 1966.) The identification of the Quinsam River specimen as *L. ayresi* is also in doubt. It was not possible to reexamine the single specimen reported from the Skeena River (Wither 1955) which had been examined by Vladikov and Follett (1958) and considered to be *L. ayresi*. Because only one specimen has been reported, the species is probably not abundant in the Skeena River.

*Lampetra ayresi* is abundant in the Fraser River, the major salmon-producing river in Canada. It drains 2,53,000 km², approximately one-fifth of the area of the Province of British Columbia (Ages and Woodland 1976). At Hope (160 km east of the mouth) the river flows into an alluvial valley where it widens. At low discharges during the winter, the tidal influence extends as far as Chilliwack, 97 km from the mouth.

This article describes the biology of *L. ayresi* in the Fraser River following the onset of metamorphosis until entry into salt water. This part of the life cycle of river lamprey differs from that of other species and provides insight into the variability of lampreys in general. The abundance and effects of this lamprey on commercially important fishes are also discussed.

### Materials and Methods

**Metamorphosis**

The term young adult is used to describe *L. ayresi* that have metamorphosed to the stage of having a well-developed eye, a silver-colored body, and prominent teeth. During the period 1975–83, dredging operations in the Fraser River frequently produced young adult *L. ayresi* (Tary and Morrison 1976). The dredging and monitoring techniques, described by Tary and Morrison (1976), resulted in bottom sediment and debris being sucked up and pumped through approximately 1.5 km of 61-cm discharge pipe into a large settling pond on shore. The settling pond drained through large screens with 3-mm-square wire mesh. All fish were collected on these screens and lampreys were either preserved in 5% formalin, kept alive, or released. Most dredge samples used in this study were collected in 1977.

It has not been possible to collect *L. ayresi* during early metamorphosis from the Fraser River because of the difficulty of collecting in the river in the high-water period in the summer and fall. The earliest sample was obtained in mid-January 1985, when 13 metamorphosing lampreys were collected from dredging operations, 22 km upstream from the mouth of the river. In mid-February 1985, three metamorphosing lampreys were collected about 120 km from the mouth of the river using electroshockers. In 1982, metamorphosing *L. ayresi* were obtained from dredging operations beginning March 17. A sample of 30 individuals from a catch of 825 was preserved on March 18 and a similar sample was obtained from a catch of 1150 lampreys on March 22. Smaller samples, from the live lampreys held in the laboratory, were preserved at regular intervals after March 22. Metamorphosing river lampreys also have been obtained from ammocoetes reared in the laboratory. Ammocoetes were held at the Pacific Biological Station in sandy substrate, in flowing dechlorinated fresh water of ambient temperature. Procedures for rearing lampreys were similar to those of Hanson et al. (1954) and have been described in Richards et al. (1982). Small samples were obtained in 1982, 1983, and 1985; however, it was not possible to compare the staging of metamorphosis in the laboratory with that in the river.

**Osmoregulation in Salt Water and Fresh Water**

The ability of young adult lampreys to acclimate to the salinity in the Strait of Georgia (30%) was examined for varying sample sizes. Young adult *L. ayresi* (n = 1175) were brought into the laboratory from the Fraser River dredging site on March 17, 1982, and held in fresh water. Samples of lampreys were tested for the ability to survive in salt water and later to survive in fresh water. Controls for these experiments changed from holding specimens in fresh water to holding them in salt water, as the ability to osmoregulate in fresh water changed. All lampreys were held a minimum of 3 days in salt water after each experiment. Over the period March 18 to June 25, 14 aclimination experiments from fresh water to salt water were carried out (Table 1). In 4 experiments, saltwater concentration was increased by 2%/d, and in 10, the daily change was 10%/d. Samples of specimens from these experiments were preserved in either 5% formalin or in Bouin's fluid for 24 h and then stored in 70% ethyl alcohol.

The ability to remain in fresh water was also examined. One sample of 100 lampreys was held in flowing dechlorinated fresh water of ambient temperature without treatment for disease. Freshly killed herring were supplied for food. In addition, all mortalities in the tanks used to supply young adult lampreys for the saltwater acclimation studies were noted.

Portions of the entire bodies of animals that had been preserved in either formalin or Bouin's fluid were embedded in paraffin and serial sectioned at 10 μm to determine when the oesophagus was open. Sections were stained with zinhydroxyxyl and eosin or periodic acid – Schiff, haematoxylin, and orange G.

**Abundance**

Downstream-migrating young adult lampreys were collected under contract as part of a salmon migration study in 1978 and 1979.
1979, and procedures are described in Beak Consultants Ltd. (1981). A modified midwater trawl, 9.1 m long with an opening of 2.8 × 2.8 m, was mounted on the bow of a self-propelled scow. The net had 3.8-cm mesh stretched at the mouth that gradually narrowed to 0.6-cm stretched mesh at the codend. The net was held open at the mouth by a steel frame and was protected from debris by a 10-cm-square mesh trash rack mounted in front of the net. Each haul was 10 min long and the velocity at the net mouth was maintained at approximately 1.5 m/s, as measured by a Price current meter, by adjusting the speed of the scow. Two depth strata of 0–2.8 and 2.8–5.6 m were sampled. In 1979 the river was sampled from June 6 to 9 and in 1979 from April 24 to June 5. Sampling sites were approximately 3–15 km from the river mouth.

An estimate of the abundance of young adult L. ayresi entering salt water was made by determining the volume of water sampled by the midwater trawl in a tow, dividing this into the estimated river discharge for the period of down-stream migration, and then multiplying this number by the average catch per tow. The total discharge of the Fraser River during the period of migration into salt water was estimated using discharge rates supplied by Island Waters Directorate, Water Survey of Canada (1983).

An estimate of the percent of young adults that survived passage through the dredge of Macmillan Island in the Fraser River (Fig. 2) was made using a procedure that was devised to estimate salmon mortality (Conlin and Tutty 1979; Dutta and Sookackoef 1979a, 1979b; Tutty 1976). A total of 711 young adults were captured from the dredge effluent and kept alive in a small pond. On March 24 they were immersed in a 0.5 g/140 L solution of bismark brown-Y dye for 30 min and then inserted into the dredge so they could not escape out of the intake, but would have to pass through the dredge pipes and out into the settling pond. The total survival percentage was used to estimate the abundance of young adults in the river basins at the dredge site.

Ammonocetes collected by Northcote et al. (1976) were identified by comparing them with ammonocetes of similar sizes known to be L. ayresi. The ammonocetes that were known to be L. ayresi came from eggs that were fertilized in the laboratory from L. ayresi collected in the Fraser River during their down-stream migration and raised to spawning adults.

Results

Metamorphosis

Some of the ammonocetes collected in the spring of 1982 commenced metamorphosis late in July 1982. By mid-August, 34 individuals were metamorphosing. A sample of five of these individuals preserved on October 1, 1982, were silver in color with a well-developed silver iris. The oral disc was round and the branchiopods, while oval in shape, still retained some interconnecting grooves that were characteristic of ammonocetes. Teeth were round, white, and without cusps. The inframarginal laminae and the lingual laminae were present but no cusp or serrations were evident. By mid-January 1983 there was little or no change in the stage of metamorphosis. Cor- nified tips on teeth were visible in two individuals from a sample of five preserved on February 21, 1983, but unfortunately, no more specimens were preserved from this sample. Lamprays from a sample that started metamorphosis in the laboratory in July 1983 were similar to the 1982–83 sample when examined in January 1984. In 1985, five of the L. ayresi ammonocetes held in the laboratory commenced metamorphosis, probably in July. At the end of August they had well-developed eyes. One individual had a silver iris and body, and the bodies of the other four remained a dark yellow–brown. The branchiopods were oval and the longitudinal groove was barely detectable in four lamprays and was absent in the more highly developed specimen. The oral disc was round in four specimens and cirths were present in the bucal cavity as small, branched papillae-like projections. Teeth were not present, but the laminae were visible as enlarged white projections.

The stage of metamorphosis of lamprays collected from the Fraser River 140–160 km from the mouth in mid-January and mid-February 1985 was similar to the lamprays that initiated metamorphosis in the laboratory and were examined in January and February 1983 and 1984. The lamprays in the 1985 sample had silver irises and bodies. The cornified tips of some cusps were visible but the inframarginal laminae and lingual laminae had no cusps or serrations.

Individuals of the March 18 and 22, 1982, samples, which had been collected from the river, were a little more developed than those observed metamorphosing in the laboratory and sampled on October 1, 1982, mid-January 1983, and mid-
February 1983. The lampreys from the March 18 and 22 samples (8–12 cm) had silver irises and bodies and the tips of the cups on the teeth were prominent. The laboratory and field samples indicated relatively little or very slow development from October until mid-March. From mid-March until the end of April there was an enlargement of the oral disc, enhancement of the silver coloration of iris and body, and a sharpening of teeth. The first confirmed *L. advena* to migrate out of the river in 1979 was captured in late April (Fig. 3, Table 2).

**Freshwater and Saltwater Survival**

One half of the lampreys that were subjected to 10‰/d increase in salinity acclimated to Strait of Georgia salt water by mid-May, and the maximum percentage that acclimated occurred in early June (Fig. 4). In the experiments that received increases of 2‰/d, one half of the fish acclimated to Strait of Georgia salt water by late April and the maximum percentage occurred in late May and early June (Fig. 4). By the end of June in both experiments, there was a decrease in the percentage that acclimated to salt water. Fish that remained in freshwater during the acclimation experiments showed very little mortality from March 17 until mid-June (Table 3).

In five of the experiments the mean lengths of dead and surviving lamprey were compared. These five experiments were selected because the number of dead and live fish was large enough to allow statistical comparisons. Fish that survived in all of these experiments were significantly larger (t-test, $P < 0.001$) than those that died (Fig. 5). In particular, lamprey smaller than 10 cm did not acclimate as well as those larger than 10 cm.

The 179 lampreys that were acclimated to salt water at a rate of 2‰/d from May 24 to June 6 were held and fed in salt water. During the first 7 wk in salt water there were 28 mortalities, 19 in the first week and 9 in the next 6 wk. Mortalities continued at an average rate of one to two per week. The occurrence of deaths in the first few days in full-strength Strait of Georgia salt water was common in all experiments. Mortalities that occurred immediately after the termination of an experiment probably were related to the experiment. The deaths that followed this initial mortality were at a relatively constant rate and appeared to be related to disease, absence of feeding, and other culture related problems. Because these additional mortalities were not included in calculating the percentage survival (Table 1), it is probable that acclimation occurred over a longer period than indicated by Fig. 4.

Mortality in fresh water increased in mid-June in both the holding tanks and in the experiment to study survival in fresh water. In the freshwater holding tanks, mortality continued from mid-June into mid-July when the observations were terminated (Table 3). Similarly, mortalities in the freshwater holding experiment continued from mid-June until July 15 when all animals were dead. In this experiment some feeding occurred on herring but the amount of feeding was much less than in salt water. Some of the lampreys that died in fresh water had been attacked by other lampreys; however, the number attacked was small and the wounds were small.

Observations on freshwater mortalities stopped in mid-July but on August 7, 1982, five *L. advena* were observed under rocks in a freshwater holding tank. They were immediately provided with live herring. Within days, these lampreys started feeding. Lamprey preferred freshly caught live herring but would feed on freshly killed herring and even on frozen herring. Feeding behavior was identical to that observed in salt water (R. J. Beamish 1980). No length or weight measurements were made at this time because of the possibility of inducing fungus infections. One lamprey died on August 12 and one on August 24. These two lampreys had a mean length of 10 cm and a mean weight of 1.0 g. By mid-October the three remaining fish averaged 23.7 cm and weighed 18 g. One male (23.2 cm, 20.6 g) was preserved for future study and the remaining two continued to feed in fresh water until October 29, 1982. At that time, both animals started losing their countershading and both spawned in the tank in May 1983. The male was 19.1 cm and 14.0 g and the female was 17.7 cm and 12.4 g. The average shrinkage in length from October 21, 1982, until May 30, 1983, was 23.2%. A comparison of tooth

counts and body proportions of these specimens with other L. ayest from the Fraser River did not indicate any differences.

**Histology**

Histological observations were made of several body regions from the oral cavity to the cloaca of specimens collected from January 19 to June 29 over a 3-year period. Included were young adult L. ayest recently captured in the river, those that had been kept in fresh water in the laboratory (up to 6 mo) since the beginning of metamorphosis, and those used in the saltwater acclimation studies. Particular attention was paid to the degree of development and changes in those organs which were known to be involved in osmoregulation, namely the oesophagus, intestine, gills, and kidneys. The intestine, gills, and kidneys were considered to have reached the adult state of development in all of the samples. Thus, the intestine had numerous longitudinal folds (Youson and Connelly 1978), the kidneys had a well-developed renal corpuscle and tubules filled most of the nephric fold (Ooi and Youson 1977), and the gill epithelium possessed chloride cells (Peck and Youson 1979a). The oesophagus, however, did not attain its adult form until the end of March. This was considered attained when the lumen of the oesophagus was patent throughout its length. Although a lumen was present throughout much of the length of the oesophagus even by January 19, the most anterior 240- to 500-μm section, which leads directly from the oral cavity, had no lumen (Fig. 6). Early March samples in fresh water showed a similar pattern, but by mid-March the length of the "closed" anterior oesophagus was reduced to a 55- to 95-μm region. A similar region of closed anterior oesophagus was apparent in both March 23 and April 23 samples. However, a larger animal with cornified dentition, sacrificed on April 22, had a completely patent lumen (Fig. 6). No other freshwater samples were examined until June 8 at which time the oesophageal lumen was consistently found to be open throughout its length.

The acclimation experiments resulted in some alteration to the morphology of both the kidneys and the oesophagus. In animals that had reached at least 20% salinity, the kidney tubules in the ventral region appeared dilated and highly convoluted. The lumen of the archicoroid duct was also highly dilated. In early March, some samples of animals in 24-28% salt water that died in the experiments had alternating open and closed sections in the anterior region of the oesophagus. In addition, some animals not used in any experiments and preserved between March 4 and 17 had both completely opened and completely closed anterior oesophageal lumina. Based on the small numbers of longitudinal folds in the mucosal layer and the numerous ciliated figures in the mucosal epithelium, the oesophagus in each animal studied in the March period was considered to be immature. It was completely open in all samples from specimens that acclimated to salt water in April but it was not until April 27 that it could be considered well-developed, i.e. with numerous, prominent longitudinal folds. May samples included those animals that had survived acclimation to 20% and those that had recently died in this environment. All those individuals had a completely open, well-developed oesophagus. Distribution, Migration, and Abundance

The young adults that were obtained in dredge material in mid-March 1979 were in an area opposite to the upstream

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**Fig. 4.** Percentage of L. ayest that acclimated to salt water from March to June. When salinity was increased 2%/d, the date when 30% was reached was used to graph parent survival. When the salinity was increased 10%/d, the last date of the experiment was used because of the short duration of the experiment.

**Fig. 3.** Catches of young adult L. ayest migrating to sea in 1973 and hydrograph for Fraser River at Hope for 1979 showing discharge volume (Inland Waters Directorate, Water Survey of Canada 1983).
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*Mortality is expressed as a percentage of fish in the tank that died relative to the total number on that day. A survival percentage was not estimated because fish were continually being removed for experiments.

*Survival is expressed as a percentage of fish remaining relative to original sample number.

portion of Annacis Island (Fig. 2). The upper limit of the salt "wedge" that penetrates into the Fraser River occurs in the winter at low discharge (Aages and Wooltart 1976) and extends to the downstream end of Annacis Island (Fig. 2). Further downstream (67 km), salinity concentrations on the bottom can range from 15 to 24%. At this time of year (Aages 1979), recent unpublished information (A. Aages, pers. commun.) indicates that the salt water may reach the upstream end of the Island in March where for about 1 wk concentrations of 10-15% may occur for about 1 h/d. As discharge increases in the spring, the salinity wedge does not extend as far into the river. At average discharges, salt water extends up the river as far as approximately 10 km downstream of Annacis Island (Aages 1979).

In 1979, midwater sampling for downstream-migrating lampreys started on March 16 (Table 2). A few unidentified lampreys were caught near the estuary on March 24 and 30 and in the river in mid-April. *Lampetra ayreii* were first identified in the catch at the end of April. Average catches per tow increased steadily and the largest average catch per tow was on June 5, the last day of sampling (Table 2). Because numbers per tow increased steadily from the end of April (Fig. 3), it is possible that the number migrating to sea reached a maximum early in June and then declined. It is probable that the rate of decline would be similar to the rate of increase, and if the catch per tow curve is normal, then by approximately July 10, downstream migration would have ended. Maidland et al. (1984) showed that the numbers of downstream-migrating *Lampetra fluviatilis* were normally distributed over the period of migration; thus, it is probable that the distribution is also normal for *L. ayreii* if this is correct, then the area under the catch per tow curve in Fig. 4 indicates a total catch of approximately 82 lampreys for Can. J. Fish. Aquat. Sci., Vol. 44, 1987.
the volume that would be sampled by the net if fished from April 28 to July 10. During one 10-min tow and a current of 1.5
m/s, 7160 m³ would be sampled. For the period April 28 to July 10, one tow would fish 5.7 × 10⁵ m³ and would produce 82 lampreys. Using the average discharge rates for March through to July 1979 (Inland Waters Directorate, Water Survey of Canada 1981), it can be estimated by summation the volume of discharge passing New Westminster and of all tributaries downstream that 4.2 × 10⁷ m³ of water left the Fraser River from April 28 to July 10. Dividing this discharge by 5.7 × 10⁵ and multiplying by 82 indicates that approximately 6.5 × 10⁶ i.e., 82% went to sea, assuming that the distribution of lampreys between the north branch of the Fraser River and the main branch of the river (Fig. 2) is proportional to the discharge in the two arms.

The population estimate assumes that the average catch per tow in the depths sampled is similar to the depths not sampled. This appears to be a conservative assumption because larger catches may occur with depth (Fig. 7). (The depth of the three areas sampled ranged from 11.2 to 13.0 m during the sampling period (Boak Consultants Ltd. 1981). The maximum depth used in Fig. 7 is an average of the depths observed during maximum discharge.)

Another conservative assumption was that catches during the day would be representative of the night catches. Day and night sets were made on May 3—4 and 17—18. The total catch was 13 lampreys from the 46 day sets and 28 lampreys from the 84 night sets (Boak Consultants Ltd. 1981). Although only two days were studied, there was a significantly larger catch (t-test, P < 0.05) during the night catches reported in R. J. Beaumier (1980) were incorrect.

The velocity of the river in the sampling area was affected by the tide. Catches of lamprey during both the day and night sets appeared to be largest during periods of reduced velocities; however, because sampling was not continuous over a 24-h period, catches at flood and ebb tides could not be compared statistically. It was assumed that the nets adequately sampled the population of downstream migrants. The twist current during maximum discharge (6.6 m/s average during May and June, Ages and Woodland 1976) and the extreme turbidity of about 80 mg/l in a wide variation in turbidity occurs but an average of about 80 m/l occurred in June 1979. J. Servijs, pers. comm. probably results in an almost passive movement downstream and little net avoidance.

The estimate assumes that maximum numbers of migrants occurred in June 5 and then declined normally. In 1978, preliminary tests of the sampling gear by Boak Consultants Ltd. (Y. Pullet, pers. comm.) caught lamprey in approximately the same numbers (Table 3) at almost the same time that peak catches occurred in 1979. This corroborates the conclusion that the main period of downstream migration into salt water occurs early in June.

Abundance at Dredge Site

The area that was being dredged adjacent to the upstream end of Annacis Island in 1982, which contained young adults, L. ammocoetes was approximately 75 × 150 m. The bottom consisted of fine wood fibre over fine sand. A rocky area immediately downstream of this location had no lamprey. A total of 15,250 lampreys were captured from March 15 to April 6 when dredging stopped (Table 3). Because of large catches, the need to count salmon, and the time required to keep debris off the collecting screens, abundance was estimated to the nears 50 lampreys and about one third of the catch was judged to determine species. A few estuarine-adapted Lamproptera triangularis and a few L. ammocoetes were captured, but they were less than 1% of the total catch.

The lampreys that were marked with bismark brown-Y turned a yellowish brown color and were easily recognized. The first marked lamprey was recovered 30 min after injection into the dredge and a total of 189 of the 713 were captured. If the recovery percentage was 26.5% it is representative of the survival from the dredging operation and lampreys were not being recaptured to the area, then 8800 young adults lampreys were in the 11.25 m² area being dredged, or a density of 5.2 m². A second test of lamprey survival was conducted in 1987 with the same dredge but at a different site. However, because a booster pump was used in the dredge this time, the survival rates are not directly comparable. In this second test, 1000 lampreys were used and 73 recovered, resulting in a survival rate of 7.3% (J. Arscelli, pers. comm.). No additional estimates could be made because no other sites were sampled. However, dredge operators have reported that many other sites exist and the observations of Tuttly and Morrison (1976) corroborate this observation.

Abundance of L. ammocoetes

Ammocoetes were collected during a study of the benthos of the Fraser River downstream of the city of Hope (Northcote et al. 1976). A recannulation of 146 of these lamprey from this study showed that all scapomiscus were L. ammocoetes and not Lamproptera richardsonii. The L. ammocoetes were tagged in length from 8 to 93 mm, with an average length of 22.5 mm, and approximately 80% ranged from 5 to 27 mm. When compared with measurements of L. ammocoetes that were caught and tagged in the laboratory (Table 6) for 1 yr (mean size 38.0 mm), most of the lamprey from the benthos samples were judged to

be in their first year of growth or age 0.

Stations 1–6 in the benthos study were in an area that received salt water on bottom at some time throughout the year. Only the stations upstream of the salt water could be considered to be suitable lamprey habitat. These stations were evenly spaced throughout the 130-km distance from the upstream end of Annacis Island to Hope (Table 7). The average number of lampreys per square metre at these sites was 25.5 in 1972 and

![Image](image-url)

**Fig. 6.** Transverse sections of the most anterior region of the oesophagus (O) of *L. ayresi*. Showing (a) no lumen. March 18, and (b) lumen present. April 22. Magnification 63x.

![Image](image-url)

**Fig. 7.** Average number of *L. ayresi* per tow and depth and cross-section profile of major sampling areas with maximum depth in water: A. Annerville Channel; B. St. Mungo Bend; C. Dear Island.

<table>
<thead>
<tr>
<th>Date</th>
<th>No. of tows</th>
<th>Catch</th>
<th>Catch/low (STD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 6</td>
<td>10</td>
<td>19</td>
<td>1.9 (2.81)</td>
</tr>
<tr>
<td>June 7</td>
<td>10</td>
<td>23</td>
<td>2.3 (1.89)</td>
</tr>
<tr>
<td>June 8</td>
<td>10</td>
<td>18</td>
<td>1.8 (1.55)</td>
</tr>
<tr>
<td>June 9</td>
<td>10</td>
<td>20</td>
<td>2.0 (1.56)</td>
</tr>
<tr>
<td>June 5, 1979</td>
<td>12</td>
<td>28</td>
<td>2.33 (2.93)</td>
</tr>
</tbody>
</table>

28.4 in 1973. This produces an average estimate of 27 lampreys/m² along the 130 km of river bottom.

**Discussion**

The stages of metamorphosis have been described for four other parasitic lamprey that enter salt water to feed. *Lampea fluviatilis*, which is closely related to *L. ayresi* (Vladychkov and Flekett, 1958), begins metamorphosis in mid-July (Hardisty et al., 1970) and becomes a downstream migrant as early as October (Bird and Potter, 1976; Potter et al., 1982). Other migrants enter the estuary in October, November, and December (Weissenberg, 1925, 1927; Bahr, 1952), yet it appears that the largest downstream migration occurs in the spring (Potter and Huggins, 1973). The timing of the opening of the oesophagus is variable, as some have an open oesophagus in October and have been acclimated to 100% seawater (Morriss, 1972), while others do not have an open oesophagus until early spring (Hardisty et al., 1970). Thus the opening of the oesophagus and the downstream migration occurs over a period of approximately 6 mo for this species.

Metamorphosis of the anomalous sea lamprey, *Petromyzon marinus*, and the Pacific lamprey, *L. tridentatus*, also begins in July (Beamish and Potter, 1975; Potter et al., 1978; Youson and Potter, 1979; Richards, 1980). Metamorphosis is completed.

quickly between late September and early November when the juvenile adults readily acclimate to full-strength seawater and will commence feeding in the laboratory (Youson and Potter 1979; Richards 1986). Both species are known to migrate into the ocean in the fall and spring (Manuetti 1962; Beamish and Potter 1975; Potter and Beamish 1977; Potter et al. 1978; R. J. Beamish 1980), indicating that there is variability in the time they enter salt water. A similar pattern of metamorphosis, downstream migration, and onset of feeding is found in the landlocked sea lamprey (Aplodinotus 1950).

In the Southern Hemisphere, Geotria australis begins meta-
morphosis in late January (corresponding to mid July and early August in the Northern Hemisphere) and reaches the stage prior to the downstream migrant in May and June (Potter et al. 1980). Downstream migration occurs in July and August about 60 miles after the onset of metamorphosis. If there is no appreciable discharge, the migration can be delayed until November; Potter et al. (1980) indicated that during late July and early August, 90% of the animals survived a gradual acclimation to full-strength seawater.

Metamorphosis was found to be delayed over the winter and was completed when discharge rates in the Fraser River were increasing in the spring. Histological examination, acclimation experiments, and the location of young adults in the river confirmed that L. acris was the major metamorphos that in the midsummer were unable to osmoregulate in salt water until the next spring.

There were no midwater trawl samples collected from July until March; therefore, it was not possible to determine if a full migration of young adult L. acris into salt water occurred. However, the laboratory studies and histology showed a closed osmophagus and it was unlikely that any L. acris were capable of surviving in the Strait of Georgia at that time. In addition, fishing operations in the Strait of Georgia using small mesh nets have caught L. acris only from May to September (R. J. Beamish 1980; R. J. Beamish, unpubl. data). Therefore, it is probable that L. acris enter salt water only from May to about July. If they do, it is likely a full migration, this will undoubtedly show that it is confined to a few individuals. Thus, L. acris takes approximately 9 mo to complete metamorphosis and then goes to sea over the next 3 mo. In extreme cases, it may be 12 mo from the onset of metamorphosis until entry into the sea.

The prolonged period of metamorphosis is caused by a dryst in the complete development of the osmophagus. This portion of the alimentary canal develops from a dorsal ridge of endoderm in the pharynx (Youson 1981), and it is not until the osmophagous lumen is patent throughout its length that water can be swallowed to permit saltwater osmoregulation (F. W. H. Beamish 1980). The timing of the opening of the osmophagus has been reported to be essential to saltwater osmoregulation in the Pacific lamprey L. tridentata (Richards and Beyersmith 1981). As in other lamprey species (Hardisty et al. 1970; Youson 1981), the final portion of the osmophagus to open in L. acris is the most anterior section. The delay of 9-10 mo to complete the opening may be unique to L. acris.

It has been shown from examination of metamorphosing P. marinus (Oos and Youson 1977) that the adult kidney develops more rapidly than many other organs. This is due to the con-

constant regression of the larval kidney (Oos and Youson 1970) and the demands for both freshwater osmoregulation (i.e. production of large volumes of a dilute urine) and for the pre-
vvention of proteinuria. Despite this rapid development in the kidney of both landlocked and anadromous P. marinus; young adults have some difficulty in osmoregulating in seawater (Mathers and Beamish 1974; Youson 1982a, 1983a). The di-

lation and convolution of the ventral kidney tubules and the dilated lumen of the ileohepatic duct which were typical of saltwater-acclimated L. acris in the present study were also previously noted in juvenile anadromous P. marinus under similar conditions (Youson 1982b). It is believed that these features reflect osmoregulatory stress and may be a partial explanation for the death of many L. acris in the acclimation experiments.

The epithelium of the gills of ammocoetes undergoes a trans-
formation during metamorphosis when which time chloride cells develop (Peck and Youson 1979a). These cells play a prominent role in saltwater osmoregulation in juveniles of ana-
dromous P. marinus (Peck and Youson 1979b; F. W. H. Beamish 1980). Chloride cells were observed in all juvenile L. acris, and therefore the gills were presumed to be func-
tioning as a site for the excretion of solvovolent ions during saltwater acclimation. Cells of similar morphology were also present in the anterior intestine of both L. fluviatilis (Pickering and Morris 1973) and P. marinus (Lamille and Youson 1983) and are responsible for ion absorption. Definitive documentation of the presence of chloride cells that are capable of ion transport in gills and the anterior intestine of L. acris awaits further study with the electron microscope.

It is known that Lampetra japonica, L. fluviatilis, P. marinus, L. tridentata, and G. australis exhibited downstream mi-
greations in response to increasing river discharges that occurred both in the fall and in the spring (Gebenkov 1968; Pottet and Huggins 1973; Potter and Beamish 1977; R. J. Beamish 1980; Richards and Beamish 1961; Potter et al. 1980). In the Fraser River, discharge declines slowly from fall to winter and in-
creases dramatically in the spring, reaching maximum flows in June. The delay in completion of metamorphosis coincident with decreasing discharges in the fall is completed by meta-

morphosis as discharge increases in the spring, the increasing ability to osmoregulate in salt water in the laboratory during this period of increasing discharge and the occurrence of migration during maximum river discharges are strong evi-
dence that the pattern of metamorphosis in L. acris in the Fraser River has evolved in response to the discharge pattern of

The migrations of *L. japonica*, *L. flavilatris*, and *G. australis* have been reported to occur only at night (Grimes 1968; Potter and Huggins 1973; Potter et al. 1980). In this study, *L. australis* migrated during the day and during the night. It is probable that the velocity and turbidity of the river directly contributed to the continuous 24-h migration.

Metamorphosing lampreys collected in March and held in fresh water in the laboratory survived with a minimum number of mortalities until mid-June. In mid-June, mortalities increased dramatically and few lampreys survived in fresh water past mid-July. Early to mid-June was also the period in which the maximum proportion of *L. australis* could be acclimated to salt water. After this period, the percentage that could acclimate successfully declined. Apparently, physiological changes not only may stimulate the animal to migrate to sea and enable it to osmoregulate in salt water, but also to alter its ability to osmoregulate in fresh water. These changes occurred quickly in *L. australis* and affected all but a small number of individuals. Again, the abruptness and uniformity in behavior distinguishes this species from the reported behavior of other anadromous parasitic lampreys.

A small number of *L. australis* were able to remain in fresh water, feed, grow, and reach maturity. While the difficulty of maintaining anadromous parasitic lamprey in fresh water has been reported for *P. marinus* (Potter and Beamish 1977) and *L. tridentatus* (R. J. Beamish 1980), this is the first report of an anadromous lamprey being maintained in fresh water for its entire postmetamorphic period. It demonstrates that under conditions similar to those in the laboratory, a very small percentage of the population of *L. australis* might remain in brackish water or not go to sea. It is also possible that forms or sub-species of *L. australis* that cannot be identified by the conventional methods used in this study might exist in the Fraser River.

R. J. Beamish (1980) reported that the mean size of lampreys caught in the river on June 5, 1979, was 0.8 cm smaller than the mean size of samples collected earlier. Because smaller lamprey did not acclimate to salt water as well as larger lamprey in the laboratory experiments, the smaller lamprey in the river may be the last to move into salt water. It is possible that these smaller lamprey that were less able to acclimate to salt water were better able to cope with the demands of freshwater osmoregulation. A relationship between size and the ability to osmoregulate in salt water was reported for the landlocked sea lamprey (Matthers and Beamish 1974) and *G. australis* (Potter

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**Table 6. Comparison of lengths (mm) of *L. australis* ammocoetes collected in the benthos study of Northcote et al. (1976) with *L. australis* ammocoetes hatched and reared in the laboratory.**

<table>
<thead>
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<th>Number</th>
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<th>Beethos</th>
<th>Rearred</th>
<th>Length</th>
<th>Beethos</th>
<th>Rearred</th>
<th>Length</th>
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</tbody>
</table>

Lengths of six fish from benthos samples and three from the rearred samples were larger than 46 mm.


* Measured 1 yr after hatching.

**Table 7. Density of *L. australis* ammocoetes in the benthos of the Fraser River downstream of Hope (calculated from Northcote et al. 1976).**

<table>
<thead>
<tr>
<th>Station</th>
<th>Number</th>
<th>Number/m², 1972</th>
<th>Number</th>
<th>Number/m², 1973</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>3</td>
<td>5.7</td>
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<td>26</td>
<td>49.1</td>
<td>34</td>
<td>34.0</td>
</tr>
</tbody>
</table>

**Average**

25.1

28.4

* Number of lamprey from 10 samples except stations 10 and 11 (5 samples).

* Number of lamprey from 20 samples.
et al. 1980); however, it was not observed for the anadromous sea lamprey (Potter and Bearson 1977) or reported for the anadromous L. tridentata (Richards 1980; R. J. Bearson 1980). It is possible that a few individuals could remain in the river for the entire adult period if prevented from going to sea. However, if the stimulus to migrate into salt water is independent of the ability to remain in fresh water, it is possible that the few individuals that could remain in fresh water will still go to sea.

Once the oocyte is open, downstream migration into the sea begins and the young adults enter the Strait of Georgia for the next 2 ms. The laboratory studies clearly indicated that most L. aceris could not survive in fresh water beyond mid- 

June and must enter the sea or die. When the river lamprey enters the sea, it begins feeding immediately (R. J. Bearson 1980). This prolonged period of metamorphosis, during which it is unlikely that any feeding occurs, should deplete lipid reserves (Bearson et al. 1979; Yvon et al. 1979) and the immediate feeding undoubtedly is necessary to restore these depleted lipid reserves. Deaths in fresh water probably were a result of depleted lipid reserves and they could be exacerbated by increasing temperatures.

Abundance

The estimate of 6.5 x 10^6 young adult L. aceris entering the Strait of Georgia in 1979 compares well with the estimate of 0.67 x 10^6 to 6.2 x 10^6 lampreys in the Strait of Georgia in 1976 (Bearson and Williams 1976). The 1976 estimate was made by attempting to pursue seine throughout the strait. The large area, the difficulty with fishing in some locations, and the difficulty associated with estimating the area fished made this a less accurate survey than the Fraser River survey. The upper limit of the abundance range was similar to the Fraser River estimate.

The 1979 estimate assumed that the migration rate observed up to June 5 would decline at a similar rate. It was also assumed that the distribution of lampreys below the depths sampled would decline normally. Both these assumptions appeared reasonable because it was unlikely that the lamprey distribution in the water column would be abruptly truncated. There was evidence for continued migration during the day and night and it was unlikely that significant net avoidance occurred. However, it appeared that more lampreys migrated downstream as night, and because sampling was done during the day, the estimate of abundance could be conservative. Catches also appeared to be better when river velocities were reduced because of tides. It is difficult to assess the relative importance of this observation because sampling was initiated 1 h after the change of tides and not throughout a tidal cycle. The north arm of the Fraser River was not sampled and it is possible that the migration here was not proportional to the discharge. However, the north arm accounts for only 25% of the total discharge. It is apparent that each assumption should be tested before the error associated with it can be determined. However, testing these assumptions is difficult and expensive. Instead, the population was compared with other indicators of abundance to determine whether L. aceris should be considered to be abundant.

The estimated number entering the Strait of Georgia in 1976 was approximately 100 times larger than the estimated 500 metamorphosing L. aceris in the 11 250-m^2 sea dredged in 1992. This estimate of abundance was considered conservative because a conservative survival rate was used. Survival rates for salmonids passing through dredging and monitoring oper- ations range from 1.2 to 26% (Dutta and Sookachoff 1975a, 1990b; Tutty 1976). It appears that survival rates vary depending on the species, the type of dredge, the material being dredged, and the use of settling ponds. Because of the magnitude of the variation in survival rates, it was not advisable to compare the estimates from the other studies directly with the estimates for the lamprey. Because L. aceris are known to be abundant throughout the lower 150 km of the Fraser River and dredge operators have reported it in stretches of the Fraser River away from the mouth of the Fraser River, it is probable that there may be many sites similar to the one studied. Thus, the estimate of approximately 5 x 10^6 young lampreys does not appear to be excessive.

Another estimate of relative abundance was made by comparing the relative densities of anemone roosts in the 130 km of river from Hope to Anacortes Island. The average density of 27 lampreys/m^2 would have to be adjusted to include older age groups and a correction factor applied for young lampreys that avoided capture. Thus, the average den- sity of 27 lampreys/m^2 must be considered to be a conservative estimate. It is not possible to calculate a total population size or to predict the number of young adults that might exist in the river because the percentage of substrate suitable to lampreys was not determined, and the natural mortality of anemone roosts and the average age at metamorphosis were not known. How- ever, the average density can be compared with densities re- ported for other parasitic species.

In the Opequon River that flows into Lake Michigan, the portion of the stream with the highest density of all age groups of the landlocked sea lamprey (P. marinus) contained 4.0 lampreys/m^2 (Hansen and Hayne 1962). Over larger areas they found densities of 1.1–3.6 larvæ/m^2 for P. marinus and Lampetra lacerata combined. Densities of landlocked sea lampreys in "typical" untrammled streams in Ontario and Michigan range from 3 to above 12–15 lampreys/m^2 for all age classes (Barker and Henderson 1979). However, in the Lampeter estuarine stream, Malmut (1983) found an average density for Lampetra planeri to be 3.5 larvæ/m^2. Higher mean densities of 6–21 lampreys/m^2 were reported for L. fluviatilis in three Finnish rivers (Kainan and Vatohnen 1980). Thus, by comparison, the densities in the Fraser River appear to be high and clearly indicate that L. aceris is abundant. Considering that the esti- mates produced using the Northcote et al. (1976) study were similar for 1973 and 1973 and that the distributions within the river appeared rather uniform, one must conclude that the abun- dance of L. aceris in the Fraser River is astonishingly high.

There is very little information about the feeding habits of any of the anadromous parasitic lampreys while in the ocean. It is known that L. aceris feeds by removing chunks of muscle and tissue (Roos et al. 1973; Bearson and Williams 1976; R. J. Bearson 1980); thus it is probable that hosts do not survive attacks. In such cases, L. aceris is a predator rather than a parasite. The closely related species (Hubbs and Potter 1971) L. japonica is known to cause scarring and 40% of the herring caught in the White Sea and 40% of the smelt (Osmerus mordax) in the Gulf of Amsel (Nikol'ski 1956, Mantefiel, cited in Holcik 1986). Macks resulting from attachements of L. japonica have been reported on 20 and 60% of pink salmon (Oncor- hyus gorbuscha) in the Gulf of Amsel in some years (Birman 1950; Grigor'ev 1960; Holcik 1960). Bearson and Williams (1976), analyzing the gut contents of L. aceris feeding in the Strait of Georgia, concluded that an average of 0.8 fish were attacked by each lamprey per day. This was very similar to the average of 1.3 fish per lamprey per

day killed in laboratory experiments. If maximum migration occurs in early June and L. alexis are actively feeding in the Strait of Georgia in August, with some feeding continuing in September, as has been shown (Beadle et al., 1980), then it can be estimated that a lamprey feed for about 10 wk. Using the 1979 estimate of 6.5 x 10^7 lampreys feeding for 10 wk on a diet of 86% herring at a rate of 0.8 fish per lamprey per day (R. J. Beadles 1980) and assuming most feeding occurs on age 2 herring of average length of 16.1 cm and weight of 54 g, then approximately 10,000,000 herring could be killed by L. alexis. This estimate assumes that only one lamprey feeds on one herring. If multiple attacks occur, the estimated number of herring killed will be smaller.

_Lampetra axelrodi_ also feeds on salmon in the surface waters (R. J. Beadles 1980), and all five species of salmon (Oncorhynchus) are found in the surface waters of the Strait of Georgia for all or part of the time that _L. axelrodi_ are feeding (Godfrey 1966; Healey 1978, 1980; Leving and Koyt 1983). During this time, salmon range in average size from 12 to 24 cm. Depending on size, the salmon may be killed or wounded by a lamprey attack (R. J. Beadles 1980) and it is possible the same one lamprey will feed on a single salmon. However, if the assumptions made for herring can be applied to salmon, then the diet of lamprey is 14% salmon (R. J. Beadles 1980), and 51 x 10^7 salmon could have been attacked by the _L. axelrodi_ population in 1979. This number of attacks represents between 8 and 11% of the average number of all salmon (300 x 10^6 to 500 x 10^6) (Healey 1940) that enter the Strait of Georgia and 78% of the combined average number (48.3 x 10^7) of juvenile Chinook salmon (O. tshawytscha) and coho salmon (O. kisutch) that leave the Fraser River annually. These estimates are very approximate and exaggerate the effects on herring and salmon because they are not adjusted for lamprey mortality during that marine phase. However, they indicate that _L. axelrodi_ can be an important source of direct or indirect mortality to herring and salmon.

The four estimates of abundance of _L. axelrodi_ indicate that this species is very abundant in the alluvial valley portion of the Fraser River and is not uncommon as previously suggested (Carl et al. 1959). Lampreys have seldom been studied in British Columbia and they are nocturnal except during spawning; therefore their existence in most streams and rivers (R. J. Beadles, unpubl. data) is usually not known. Only recently have feeding audi tats been reported from the Fraser River and this may indicate a recent increase in abundance.

The stomach analysis studies, the laboratory feeding studies, and the rapid growth of _L. axelrodi_ in the ocean (R. J. Beadles 1980) show that _L. axelrodi_ is an important predator of salmon and herring. If it has always been abundant in the Fraser River, then the effect on salmon and herring populations probably has not changed. However, if there has been a substantial increase in abundance in recent years, then this is an important new source of mortality.

Acknowledgments

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