Life History and Abundance of Young Adult *Lampetra 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 *Lampetra ayresi* begins in July but is not completed until approximately April of the following year when the oesophagus 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 oesophagus, some metamorphosing *L. ayresi* congregate just upstream of the salt water that moved into the river from the ocean. Soon after the oesophagus opens, lampreys are able to osmoregulate 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 *Lampetra ayresi* commence en juillet mais ne se termine qu'en avril de l'année suivante quand l'oesophage s'ouvre. La période prolongée de métamorphose est différente des autres espèces de lamproie et peut s'être développée en réaction au régime de débit du fleuve Fraser. Avant l'ouverture de l'oesophage, certaines *L. ayresi* en métamorphose se réunissent juste en amont des eaux salées qui pénètrent dans l'embouchure du fleuve. Peu après l'ouverture de l'oesophage, on observe une capacité d'osmorégulation en eau salée; de mai à juillet, les lamproies gagnent le détroit de Georgie. 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 lamproies 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-juin; 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 migrateurs dévalants menée en 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 Georgie, 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 cause de mortalité chez le hareng et le saumon.

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Lampetra ayresi, the river lamprey, is an anadromous parasitic lamprey that occurs on the west coast of central North America (Vladykov and Follett 1958; Beamish and Williams 1976; R. J. Beamish 1980; Bond et al. 1983). They enter salt water from May to July where they live near the surface and feed voraciously on herring and salmon (R. J. Beamish 1980). During the brief trophic period, river lamprey increase in size from an average of 12 cm and 2 g to 25 cm and 20 g. They continue to feed until about mid-September after which they are seldom found in salt water. In this study, one upstream-migrating adult female (24 cm, 32 g) was captured about 160 km from the mouth of the Fraser River in early August 1983, indicating that some adults reenter fresh water as early as July.

In Canada, Hart (1973) reported that river lamprey occurred in the Fraser River, the Skeena River, and in Skidegate Lake (Fig. 1). R. J. Beamish (1980) reported *L. ayresi* from Morrison Creek and the Quinsam River (Fig. 1). A reexamination of the specimens from Skidegate Lake and Morrison Creek

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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 Withler 1986.) 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 (Withler 1955) which had been examined by Vladykov 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 235 000 km^2, approximately one quarter of the area of the Province of British Columbia (Ages and Woollard 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.

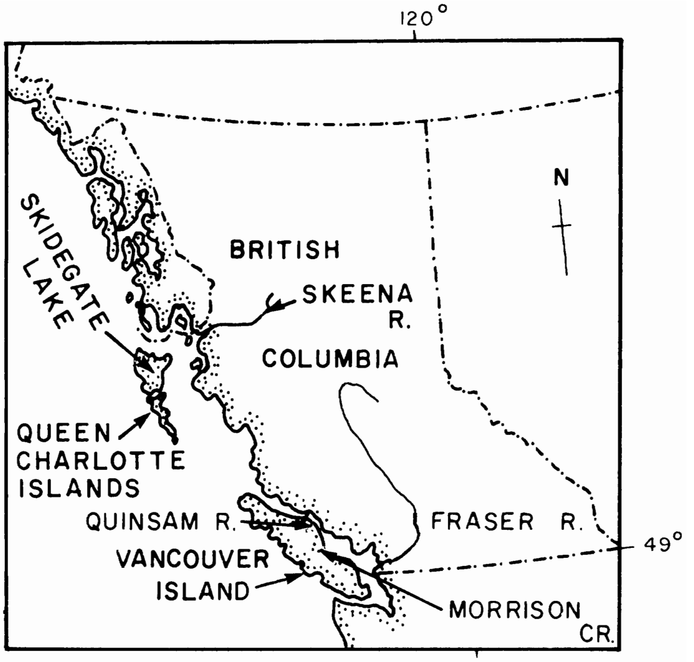

FIG. 1. Location of *L. ayresi* in British Columbia, Canada.

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* (e.g. Tutty and Morrison 1976). The dredging and monitoring techniques, described by Tutty 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 1982.

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 50 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. (1974) 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 d in salt water after each experiment. Over the period March 18 to June 25, 14 acclimation 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 either haematoxylin and eosin or periodic acid – Schiff, haemalum, and orange G.

Abundance

Downstream-migrating young adult lampreys were collected under contract as part of a salmon migration study in 1978 and

TABLE 1. Results of experimental acclimation of *L. ayresi* from fresh water to salt water, 1982.

Date started	Date ended	Salinity change per day (‰)	Number of lamprey: Start	Dead	Live	% survival
March 18	March 20	10	26	25	1	3.8
March 22	April 4	2	25	15	10	40.0
April 8	April 10	10	25	23	2	8.0
April 17	May 1	2	25	11	14	56.0
May 2	May 4	10	6	4	2	33.3
May 6	May 8	10	11	10	1	9.1
May 12	May 14	10	24	13	11	45.8
May 18	May 20	10	8	4	4	50.0
May 24	May 26	10	10	4	6	60.0
May 24	June 6	2	196	17	179	91.3
June 10	June 12	10	7	0	7	100.0
June 14	June 16	10	97	10	87	89.7
June 19	July 2	2	91	23	68	74.7
June 25	June 27	10	96	17	79	82.3

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 stretched mesh 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 1978 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 downstream 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 Inland Waters Directorate, Water Survey of Canada (1983).

An estimate of the percent of young adults that survived passage through the dredge at Annacis 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 Sookachoff 1975a, 1975b; Tutty 1976). A total of 713 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 bottom at the dredge site.

Ammocoetes collected by Northcote et al. (1976) were identified by comparing them with ammocoetes of similar sizes known to be *L. ayresi*. The ammocoetes 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 downstream migration and raised to spawning adults.

Results

Metamorphosis

Some of the ammocoetes 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 branchiopores, while oval in shape, still retained some interconnecting grooves that were characteristic of ammocoetes. Teeth were round, white, and without cusps. The infraoral laminae and the lingual laminae were present but no cusps or serrations were evident. By mid-January 1983 there was little or no change in the stage of metamorphosis. Cornified 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. Lampreys 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* ammocoetes 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 branchiopores were oval and the longitudinal groove was barely detectable in four lampreys and was absent in the more highly developed specimen. The oral disc was round in four specimens and cirrhi were present in the buccal 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 lampreys collected from the Fraser River 140−160 km from the mouth in mid-January and mid-February 1985 was similar to the lampreys that initiated metamorphosis in the laboratory and were examined in January and February 1983 and 1984. The lampreys in the 1985 sample had silver irises and bodies. The cornified tips of some cusps were visible but the infraoral 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-

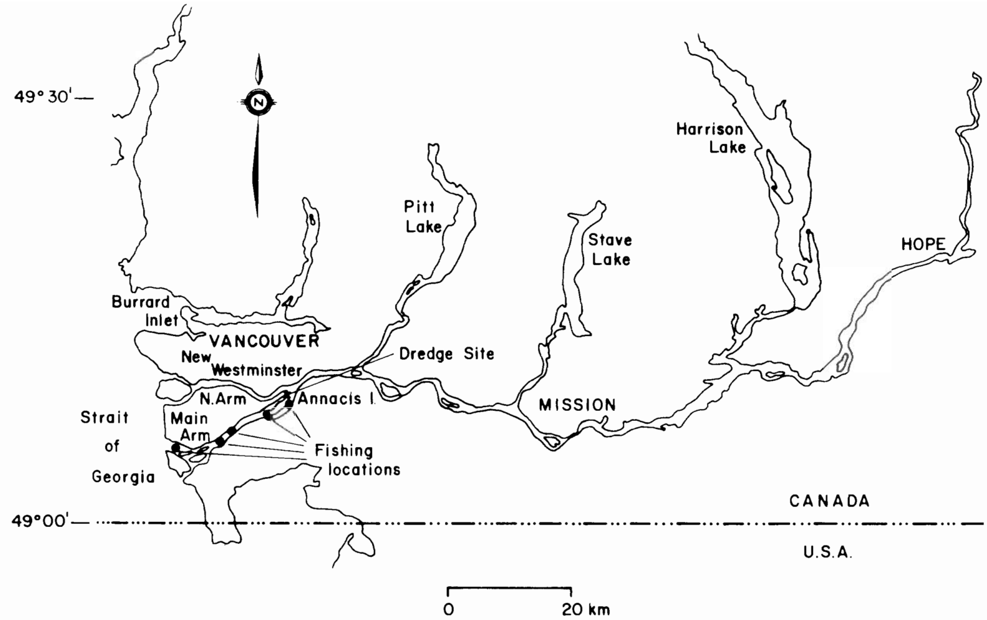

FIG. 2. Lower Fraser River showing fishing locations and the portion of the river below the city of Hope.

February 1983. The lampreys from the March 18 and 22 samples (8–12 cm) had silver irises and bodies and the tips of the cusps 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. ayresi* 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 increases 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 fresh water 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. ayresi* were observed under rocks in a freshwater holding tank. They were immediately provided with live herring. Within days, these lamprey 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 14.6 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

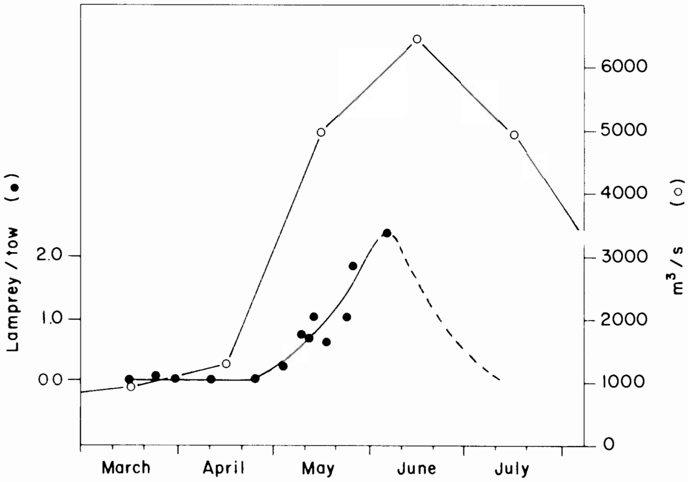

FIG. 3. Catches of young adult *L. ayresi* migrating to sea in 1979 and hydrograph for Fraser River at Hope for 1979 showing discharge volume (Inland Waters Directorate, Water Survey of Canada 1983).

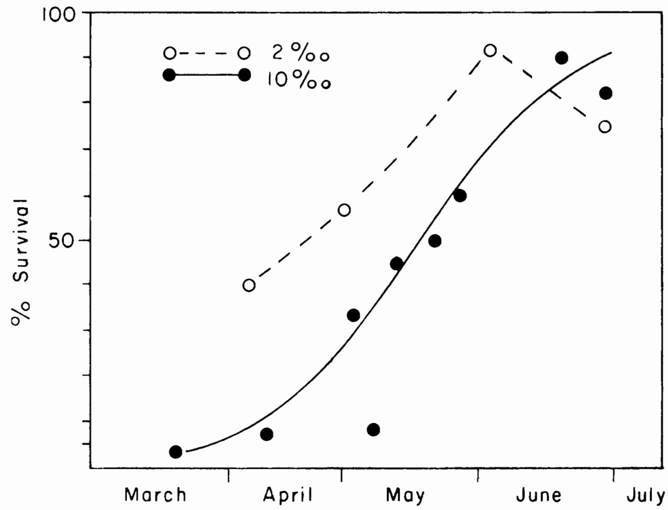

FIG. 4. Percentage of *L. ayresi* that acclimated to salt water from March to June. When salinity was increased 2‰/d, the date when 30‰ was reached was used to graph percent survival. When the salinity was increased 10‰/d, the last date of the experiment was used because of the short duration of the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

TABLE 2. Catches of *L. ayresi* in the Fraser River, downstream of the upstream end of Annacis Island, 1979.

Date	Number of tows	Catch	Catch/tow	SD
March 16	24	0	0	—
March 24	12	1[a]	0.08	—
March 28, 29, 30	60	2[a]	0.03	0.18
April 10, 11, 12	60	1	0.02	—
April 24, 25, 26	60	4	0.06	0.35
May 3–4[b]	44	13	0.30	0.70
May 9	24	18	0.75	1.03
May 10	24	17	0.71	1.08
May 11	36	37	1.03	1.08
May 16–17[b]	46	29	1.63	0.61
May 22, 23	48	49	1.02	1.23
May 24	36	66	1.83	1.50
June 5	12	28	2.33	2.93

[a]Species not identified, possibly *L. tridentata*.
[b]Day/night sets.

counts and body proportions of these specimens with other *L. ayresi* 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 in specimens collected from January 19 to June 29 over a 3-yr period. Included were young adult *L. ayresi* recently captured in the field, 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. That is, 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 (Peek 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 360-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 archinephric 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 mitotic 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 these 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

TABLE 3. Survival of *L. ayresi* in freshwater, 1979.

Date	Holding tanks (control)			Experiment		
	n	Dead	% mortality[a]	*n*	Dead	% survival[b]
March 17	1165	0	0			
20	1048	20	1.7			
29	1003	13	1.2			
April 5	990	11	1.0			
May 24	870	8	0.8			
June 3	666	1	0.1			
14				98	0	100.0
15						
16	466	26	4.7	89	9	90.8
17						
18				80	9	81.6
19	440	22	4.1			
20	318	24	7.5	71	9	72.4
21	294	30	10.2	61	10	62.2
22	264	30	11.4	44	17	44.9
23	234	38	16.2	34	10	34.7
24	196	41	20.9	22	8	22.4
25	115	29	18.7	14	8	14.3
26	30	3	10.0	13	1	13.3
27	27	2	7.1	12	1	12.2
28						
29				9	3	9.2
30	25	8	32.0			
July 1	17	1	5.9	7	2	7.1
2						
3	16	3	18.8	5	2	5.1
4						
5	13	1	7.7	3	2	3.1
6						
7						
8						
9	12	1	8.3	2	1	2.0
10	11	1	9.1	1	1.	1.0
11						
12						
13	10	1	10.0			
14	8	2	20.0			

[a]Mortality is expressed as a percentage of fish in the tank that died relative to the total number on that date. A survival percentage was not estimated because fish were continually being removed for experiments.

[b]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 (Ages and Woollard 1976) and extends to the downstream end of Annacis Island (Fig. 2). Farther downstream (6–7 km), salinity concentrations on the bottom can range from 15 to 24‰ at this time of year (Ages 1979). Recent unpublished information (A. Ages, pers. comm.) 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 (Ages 1979).

In 1979, midwater sampling for downstream-migrating lampreys started on March 16 (Table 2). A few unidentified lamprey were caught near the estuary on March 24 and 30 and in the river in mid-April. *Lampetra ayresi* 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. Maitland 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. ayresi*. If this is correct, then the area under the catch per tow curve in Fig. 4 indicates a total catch of approximately 82 lamprey for

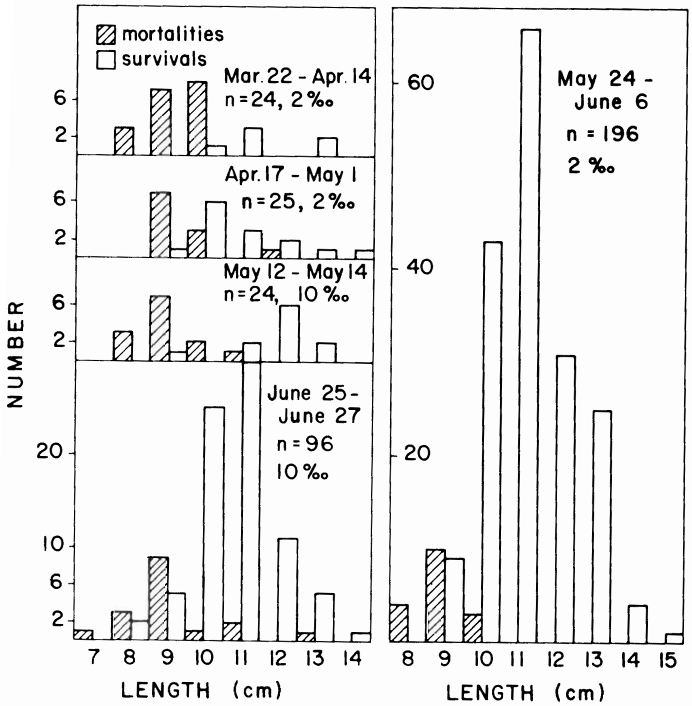

FIG. 5. Length frequency of lamprey in the freshwater to saltwater acclimation experiments.

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, 7165 m^3 would be sampled. For the period April 28 to July 10, one tow would fish 5.3×10^5 m^3 and would produce 82 lamprey. Using the average discharge rates for March through to July 1979 (Inland Waters Directorate, Water Survey of Canada 1983), it can be estimated by summing the volume of discharge passing New Westminster and of all tributaries downstream that 4.21×10^{10} m^3 of water left the Fraser River from April 28 to July 10. Dividing this discharge by 5.3×10^5 and multiplying by 82 indicates that approximately 6.5×10^6 *L. ayresi* went to sea, assuming that the distribution of lampreys between the north arm of the Fraser River and the main arm 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 (Beak 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 the 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 96 day sets and 28 lampreys from the 84 night sets (Beak 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. Beamish (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 swift current during maximum discharge (1.6 m/s average during May and June, Ages and Woollard 1976) and the extreme turbidity of about 80 ntu (a wide variation in turbidity occurs but an average of about 80 ntu occurred in June 1979, J. Servizi, pers. comm.) probably results in an almost passive movement downstream and little net avoidance.

The estimate assumes that maximum numbers of migrants occurred about June 5 and then declined normally. In 1978, preliminary tests of the sampling gear by Beak Consultants Ltd. (V. Pullen, pers. comm.) caught lamprey in approximately the same numbers (Table 4) 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 adult *L. ayresi* 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 lampreys. A total of 15 550 lampreys were captured from March 15 to April 6 when dredging stopped (Table 5). 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 nearest 50 lampreys and about one third of the catch was checked to determine species. A few metamorphosed *Lampetra tridentata* and a few *L. ayresi* 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 insertion into the dredge and a total of 189 of the 713 were captured. If the recovery percentage of 26.5% is representative of the survival from the dredging operation and lampreys were not being recruited to the area, then 58 700 young adults lampreys were in the 11 250-m^2 area being dredged, or a density of 5.2/m^2.

A second test of lamprey survival was conducted in 1982 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 lamprey were used and 37 recovered, resulting in a survival rate of 3.7% (Joe Arsenault, 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 Tutty and Morrison (1976) corroborate this observation.

Abundance of *L. ayresi* 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 reexamination of 146 of these lampreys from this study showed that all specimens were *L. ayresi* and not *Lampetra richardsoni*. The *L. ayresi* ammoceotes ranged in length from 8 to 93 mm, with an average length of 22.5 mm, and approximately 80% ranged from 8 to 27 mm. When compared with measurements of *L. ayresi* that were hatched and reared in the laboratory (Table 6) for 1 yr (mean size 38.0 mm), most of the lamprey from the benthos samples were judged to

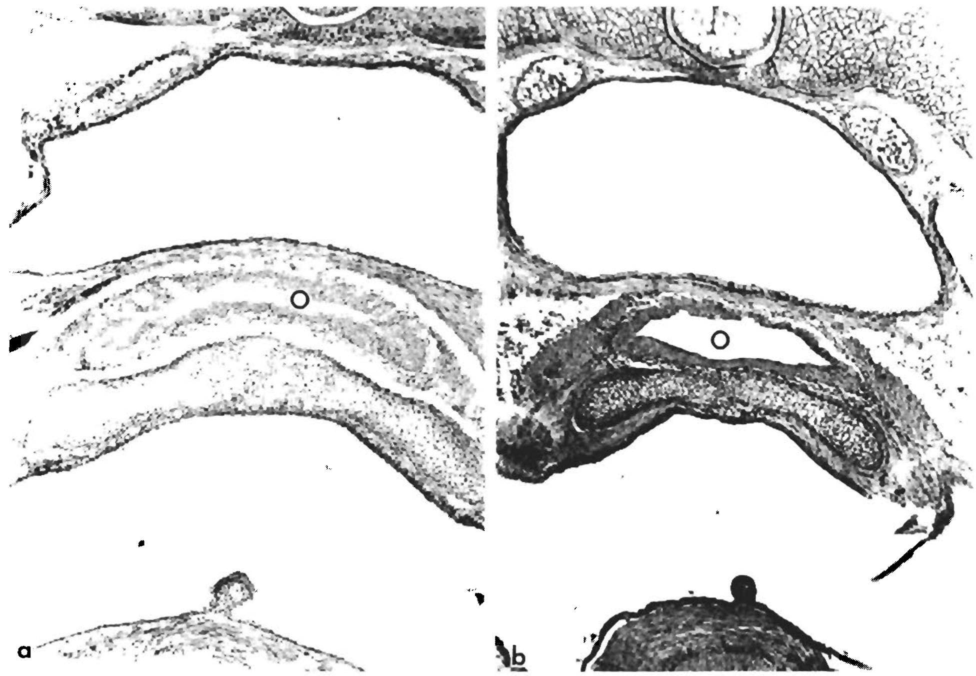

FIG. 6. Transverse sections of the most anterior region of the oesophagus (O) of *L. ayresi*. Showing (a) no lumen, March 18, and (b) lumen present, April 22. Magnification 63×.

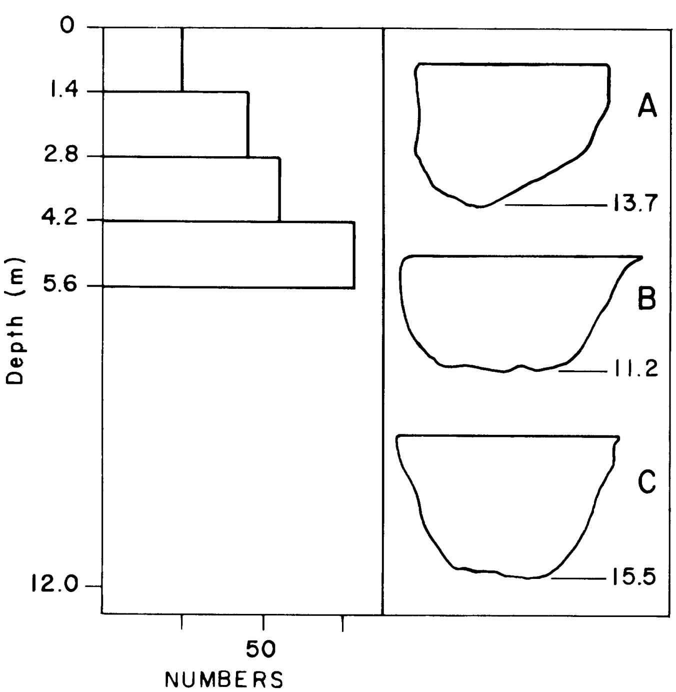

FIG. 7. Average number of *L. ayresi* per tow and depth and cross-section profile of major sampling areas with maximum depth in waters. A, Annieville Channel; B, St. Mungo Bend; C, Deas Island.

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 28.4 in 1973. This produces an average estimate of 27 lampreys/m^2 along the 130 km of river bottom.

TABLE 4. Catches of *L. ayresi* during net trials in 1978. Catches on June 5, 1979, are included for comparison.

Date	No. of tows	Catch	Catch/tow (SD)
June 6	10	19	1.9 (2.81)
June 7	10	23	2.3 (1.89)
June 8	10	18	1.8 (1.55)
June 9	10	20	2.0 (1.56)
June 5, 1979	12	28	2.33 (2.93)

Discussion

The stages of metamorphosis have been described for four other parasitic lamprey that enter salt water to feed. *Lampetra fluviatilis*, which is closely related to *L. ayresi* (Vladykov and Follett 1958), begins metamorphosis in mid-July (Hardisty et al. 1970) and becomes a downstream migrant as early as October (Bird and Potter 1979; 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 (Morris 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 anadromous sea lamprey, *Petromyzon marinus*, and the Pacific lamprey, *L. tridentata*, also begins in July (Beamish and Potter 1975; Potter et al. 1978; Youson and Potter 1979; Richards 1980). Metamorphosis is completed

TABLE 5. Number of metamorphosing *L. ayresi* that survived passage through the dredge and settling pond, 1982.

Date[a]	Number
March 15–16	1 200
17	1 850
18	850
19	700
22	1 150
23–24	1 850
25	500
26–27	1 250
28	700
29	400
30	950
March 31 – April 2	2 100
April 4–6	2 050
Total	15 550

[a]On March 20 and 21 there was no dredging.

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 1980). Both species are known to migrate into the ocean in the fall and spring (Mansuetti 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 (Applegate 1950).

In the Southern Hemisphere, *Geotria australis* begins metamorphosis 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 6 mo 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. ayresi* that began metamorphosis 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 fall migration of young adult *L. ayresi* into salt water occurred. However, the laboratory studies and histology showed a closed oesophagus and it was unlikely that any *L. ayresi* 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. ayresi* only from May to September (R. J. Beamish 1980; R. J. Beamish, unpubl. data). Therefore, it is probable that *L. ayresi* enter salt water only from May to about July. If future studies indicate a fall migration, this will undoubtedly show that it is confined to a few individuals. Thus, *L. ayresi* 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 delay in the complete development of the oesophagus. This portion of the alimentary canal develops from a dorsal ridge of tissue in the pharynx (Youson 1981), and it is not until the oesophageal 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 oesophagus has been reported to be essential to saltwater osmoregulation in the Pacific lamprey *L. tridentata* (Richards and Beamish 1981). As in other lamprey species (Hardisty et al. 1970; Youson 1981), the final portion of the oesophagus to open in *L. ayresi* is the most anterior section. The delay of 9–10 mo to complete the opening may be unique to *L. ayresi*.

It has been shown from examination of metamorphosing *P. marinus* (Ooi and Youson 1977) that the adult kidney develops more rapidly than many other organs. This is due to the concomitant regression of the larval kidney (Ooi and Youson 1979) and the demands for both freshwater osmoregulation (i.e. production of large volumes of a dilute urine) and for the prevention of proteinuria. Despite this rapid development in the kidneys of both landlocked and anadromous *P. marinus*, young adults have some difficulty osmoregulating in seawater (Mathers and Beamish 1974; Youson 1982a, 1982b). The dilation and convolution of the ventral kidney tubules and the dilated lumen of the archinephric duct which were typical of saltwater-acclimating *L. ayresi* 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 osmotic stress and may be a partial explanation for the death of many *L. ayresi* in the acclimation experiments.

The epithelium of the gills of ammocoetes undergoes a transformation during metamorphosis during which time chloride cells develop (Peek and Youson 1979a). These cells play a prominent role in saltwater osmoregulation in juveniles of anadromous *P. marinus* (Peek and Youson 1979b; F. W. H. Beamish 1980). Chloride cells were observed in all juvenile *L. ayresi*, and therefore the gills were presumed to be functioning as a site for the excretion of monovalent 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* (Langille and Youson 1984) 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. ayresi* awaits further study with the electron microscope.

It is known that *Lampetra japonica*, *L. fluviatilis*, *P. marinus*, *L. tridentata*, and *G. australis* initiated downstream migrations in response to increasing river discharges that occurred both in the fall and in the spring (Gritsenko 1968; Potter and Huggins 1973; Potter and Beamish 1977; R. J. Beamish 1980; Richards and Beamish 1981; Potter et al. 1980). In the Fraser River, discharge declines steadily from fall to winter and increases dramatically in the spring, reaching maximum flows in June. The delay in completion of metamorphosis coincident with declining discharges in the fall, the completion of metamorphosis 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 the migration during maximum river discharges are strong evidence that the pattern of metamorphosis in *L. ayresi* in the Fraser River has evolved in response to the discharge pattern of

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

	Number			Number			Number	
Length[a]	Benthos[b]	Reared[c]	Length	Benthos	Reared	Length	Benthos	Reared
8	2	0	21	4	0	34	0	0
9	4	0	22	7	0	35	0	0
10	2	0	23	7	1	36	3	0
11	10	0	24	3	2	37	0	1
12	10	0	25	7	0	38	1	0
13	10	0	26	3	0	39	1	1
14	7	0	27	5	1	40	3	2
15	3	0	28	2	1	41	2	1
16	7	0	29	2	2	42	0	2
17	10	0	30	1	1	43	3	2
18	6	0	31	1	1	44	0	0
19	3	0	32	2	1	45	0	2
20	7	0	33	1	0	46	1	1

[a]Lengths of six fish from benthos samples and three from the reared samples were larger than 46 mm.
[b]Combined for 1972 and 1973.
[c]Measured 1 yr after hatching.

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

Station	Number[a]	Number/m^2, 1972	Number[b]	Number/m^2, 1973
7	3	5.7	3	2.8
8	4	7.6	11	10.4
9	10	18.9	28	26.5
10	1	3.8	10	9.5
11	17	64.3	55	52.0
12	10	18.9	33	31.2
13	19	35.9	38	35.9
14	26	49.1	34	34.0
Average		25.5		28.4

[a]Number of lamprey from 10 samples except stations 10 and 11 (5 samples).
[b]Number of lamprey from 20 samples.

the river.

The migrations of *L. japonica*, *L. fluvialitis*, and *G. australis* have been reported to occur only at night (Gritsenko 1968; Potter and Huggins 1973; Potter et al. 1980). In this study, *L. ayresi* migrated during the day and during the night. It is probable that the velocity and turbitity 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. ayresi* 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. ayresi* 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. ayresi* 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. tridentata* (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. ayresi* might remain in brackish water or not go to sea. It is also possible that forms or subspecies of *L. ayresi* 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 (Mathers and Beamish 1974) and *G. australis* (Potter et al. 1980); however, it was not observed for the anadromous sea lamprey (Potter and Beamish 1977) or reported for the anadromous *L. tridentata* (Richards 1980; R. J. Beamish 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 oesophagus is open, downstream migration into the sea begins and the young adults enter the Strait of Georgia for the next 2 mo. The laboratory studies clearly indicated that most *L. ayresi* 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. Beamish 1980). This prolonged period of metamorphosis, during which it is unlikely that any feeding occurs, should deplete lipid reserves (Beamish et al. 1979; Youson 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 6.5×10^6 young adult *L. ayresi* entering the Strait of Georgia in 1979 compares well with the estimate of 0.67×10^6 to 6.2×10^6 lampreys in the Strait of Georgia in 1976 (Beamish and Williams 1976). The 1976 estimate was made by attempting to purse 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 at 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 22% 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 two other indicators of abundance to determine whether *L. ayresi* should be considered to be abundant.

The estimated number entering the Strait of Georgia in 1976 was approximately 100 times larger than the estimated 58 700 metamorphosing *L. ayresi* in the 11 250-m^2 area dredged in 1982. This estimate of abundance was considered conservative because a conservative survival rate was used. Survival rates for salmonids passing through dredging and monitoring operations range from 1.2 to 26% (Dutta and Sookachoff 1975a, 1979b; 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 apply rates from other studies on other species directly to lamprey. Because *L. ayresi* are known to be abundant throughout the lower 150 km of the Fraser River and dredge operators have reported a number of areas of lamprey abundance near 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 5–7 million lampreys does not appear to be too large.

Another estimate of relative abundance was made by comparing the relative densities of ammocoetes in the 130 km of river from Hope to Annacis Island. The average density of 27 age 1 and age 2 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 density 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 ammocoetes and the average age at metamorphosis were not known. However, the average density can be compared with densities reported for other parasitic species.

In the Ogerutz 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 lamprey/m^2 (Hansen and Hayne 1962). Over larger areas they found densities of 1.1–3.6 larvae/m^2 for *P. marinus* and *Lampetra lamottei* combined. Densities of landlocked sea lampreys in "typical" untreated streams in Ontario and Michigan range from 3 to about 12–15 lampreys/m^2 for all age classes (J. Weise and B. Mormon, pers. comm.). In a Swedish stream, Malmqvist (1983) found an average density for *Lampetra planeri* to be 3.6 larvae/m^2. Higher mean densities of 6–21 lampreys/m^2 were reported for *L. fluviatilis* in three Finnish rivers (Kainua and Valtonen 1980). Thus, by comparison, the densities in the Fraser River appear to be high and clearly indicate that *L. ayresi* is abundant. Considering that the estimates produced using the Northcote et al. (1976) study were similar for 1972 and 1973 and that the distributions within the river appeared rather uniform, one must conclude that the abundance of *L. ayresi* 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. ayresi* feeds by removing chunks of muscle and tissue (Roos et al. 1973; Beamish and Williams 1976; R. J. Beamish 1980); thus it is probable that hosts do not survive attacks. In such cases, *L. ayresi* is a predator rather than a parasite. The closely related species (Hubbs and Potter 1971) *L. japonica* is known to cause scarring to 60% of the herring catch in the White Sea and 40% of the smelt (*Osmerus mordax*) in the Gulf of Amur (Nikol'skii 1956, Manteifel, cited in Holcik 1986). Marks resulting from attachments of *L. japonica* have been reported on 20 and 60% of pink salmon (*Oncorhynchus gorbuscha*) in the Gulf of Amur in some years (Birman 1950; Gritsenko 1968; Holcik 1986).

Beamish and Williams (1976), analyzing the gut contents of *L. ayresi* 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. ayresi* are actively feeding in the Strait of Georgia in August, with some feeding continuing in September (R. J. Beamish 1980), then it can be estimated that a lamprey feeds for about 10 wk. Using the 1979 estimate of 6.5×10^6 lampreys feeding for 10 wk on a diet of 86% herring at a rate of 0.8 fish per lamprey per day (R. J. Beamish 1980) and assuming most feeding occurs on age 2 herring of average length of 16.1 cm and weight of 54 g, then approximately 19 600 Mt of herring could be killed by *L. ayresi*. 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 ayresi also feeds on salmon in the surface waters (R. J. Beamish 1980), and all five species of salmon (*Oncorhynchus*) found in British Columbia occur in the surface waters of the Strait of Georgia for all or part of the time that *L. ayresi* are feeding (Godfrey 1968; Healey 1978, 1980; Levings and Kotyk 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. Beamish 1980) and it is possible that more than 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. Beamish 1980), and 51×10^6 salmon could have been attacked by the *L. ayresi* population in 1979. This number of attacks represents between 8 and 13% of the average number of all salmon (300×10^6 to 500×10^6, Healey 1980) that enter the Strait of Georgia and 78% of the combined average number (48.3×10^6) 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 their marine phase. However, they indicate that *L. ayresi* can be an important source of direct or indirect mortality to salmon and herring.

The four estimates of abundance of *L. ayresi* 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). Lamprey have seldom been studied in British Columbia and they are nocturnal except during spawning; therefore their existence in most streams and rivers (R. J. Beamish, unpubl. data) is usually not known. Only recently have feeding adults been reported from the Strait of Georgia and this may indicate a recent increase in abundance.

The stomach analysis studies, the laboratory feeding studies, and the rapid growth of *L. ayresi* in the ocean (R. J. Beamish 1980) show that *L. ayresi* is an important predator of salmon and herring. If it has always been abundant in the Fraser River, then the average 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.

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