Adult biology of the river lamprey (Lampetra ayresi) and the Pacific lamprey (Lampetra tridentate) from the Pacific coast of Canada

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Adult Biology of the River Lamprey (*Lampetra ayresi*) and the Pacific Lamprey (*Lampetra tridentata*) from the Pacific Coast of Canada

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River lamprey (*Lampetra ayresi*) metamorphose in late July with downstream migration occurring in the following year from May to July. Once adults enter salt water they begin to feed immediately by consuming chunks of flesh primarily from herring and young salmon. From June until September they increase in size by an estimated 11–14 cm and 12–18 g. In 1975, 667 000 lamprey were estimated to be in the Strait of Georgia resulting in the deaths of 60 000-000 juvenile fish. Between September and late winter river lamprey return to freshwater. Spawning occurs in the spring, from April to June and adults die after spawning. The length of adult life from the onset of metamorphosis until death following spawning is 2 yr. Pacific lamprey (*Lampetra tridentata*) begin metamorphosis in July and the known period of entry into salt water is from December until June. Feeding can commence in freshwater or salt water by mid-October. Pacific lamprey move into water deeper than 20–70 m and are present in all major fishing grounds off Canada's west coast. A relatively high incidence of lamprey attacks has been observed on sockeye and pink salmon that are aggregating in preparation to return to freshwater. The smallest mature or maturing pacific lamprey found in this study measured 16 cm and the largest measured 72 cm. Adults may spend $3\frac{1}{2}$ yr in salt water before returning to freshwater from April to June and completing their upstream migrations by late September. Stocks that return in the spring exhibit exceptional migratory instincts often migrating considerable distances in freshwater to the uppermost regions of tributary streams before they spawn from April to July in the following year. After entry into freshwater and prior to spawning, adults shrink in length by approximately 20%. The average life span from the onset of metamorphosis until death following spawning probably is 5 yr. A nonanadromous form that appears to be a new species exists in lakes and attacks a large percentage of resident salmonids.

Key words: Pacific lamprey, river lamprey, life history, fish parasites, Pacific fishes

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La métamorphose de la lamproie fluviatile américaine (*Lampetra ayresi*) a lieu fin juillet, la migration en aval se produisant de mai à juillet de l'année suivante. Aussitot arrivés en eau salée, les adultes commencent à se nourrir de morceaux de chair arrachés en grande partie à des harengs et de jeunes saumons. De juin à septembre, les lamproies croissent d'environ 11 à 14 cm et 12 à 18 g. On avait estimé en 1975 qu'il y avait 667 000 lamproies dans le détroit de Géorgie, entraînant la mort de 60 millions de jeunes poissons. Les lamproies fluviatiles américaines retournent en eau douce entre septembre et la fin de l'hiver. La fraie a lieu au printemps, d'avril à juin, après quoi les adultes meurent. La durée de vie adulte, depuis le début de la métamorphose jusqu'à la mort suivant la fraie, est de 2 ans. La lamproie du Pacifique (*Lampetra tridentata*) commence à se métamorphoser en juillet et, en autant qu'on le sache, pénètre en eau salée de décembre à juin. Elle peut commencer à se nourrir en eau douce ou en eau salée vers la mi-octobre. Les lamproies du Pacifique se dirigent vers des eaux de profondeur dépassant 20 à 70 m et sont présentes sur tous les principaux lieux de pêche du large de la côte occidentale canadienne. On a observé une incidence relativement haute d'attaques de lamproies sur des saumons nerka et roses réunis en bancs avant leur retour en eau douce. La plus petite lamproie mature ou en voie de maturation rencontrée dans la présente étude mesurait 16 cm, et la plus grande 72 cm. Les adultes peuvent passer $3\frac{1}{2}$ ans en eau salée avant

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de retourner en eau douce entre avril et juin, cette migration en amont étant terminée fin septembre. Les stocks qui retournent au printemps exhibent des instincts migrateurs exceptionnels, parcourant souvent des distances considérables en eau douce pour atteindre les régions supérieures des cours d'eau tributaires avant de frayer entre avril et juillet de l'année suivante. Après leur entrée en eau douce et avant la fraie, les adultes rapetissent d'environ 20%. La durée de vie moyenne, depuis le début de la métamorphose jusqu'à la mort suivant la fraie, est probablement de 5 ans. Une forme non anadrome, apparemment une espèce nouvelle, existe dans les lacs et attaque un fort pourcentage de salmonidés résidents.

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Two species of parasitic lampreys are found off Canada's west coast. Very little is known about the biology of the Pacific lamprey (*Lampetra tridentata*) and almost nothing is known about the biology of the river lamprey (*Lampetra ayresi*). The purpose of this report is to present new information about the adult phase of the life cycle of these two species, including a description of metamorphosis and spawning.

Materials and Methods

Collections were obtained in freshwater using electroshockers, fish weirs that trapped fish moving downstream and occasionally upstream, purse seines, and small midwater trawls. In salt water, samples were obtained using purse seines with small mesh, plankton nets, and large commercial-size midwater trawls with small mesh liners in the codend. Lamprey maintained in the laboratory were held in a variety of tanks ranging in size from 800 to 4250 L. Salt water was obtained directly from the Strait of Georgia and the salinity ranged from 27 to 30‰ annually. Freshwater was dechlorinated city of Nanaimo water. Except for an experiment to induce river lamprey to spawn, no attempt was made to regulate temperature. Lamprey in the laboratory tanks were fed on a variety of species of fishes but primarily Pacific herring (*Clupea harengus pallasi*) and sockeye salmon (*Oncorhynchus nerka*). Ammocoetes were fed 200 mL of dry yeast suspension (200 cm^3 of brewers yeast in 1 L) twice a week (Hanson et al. 1974). Adult river lamprey gut contents were examined in the laboratory by recovering the entire gut content, measuring the volume and examining the contents with a microscope. All weights of live specimens were determined after lampreys were anesthetized in MS-222. All lengths are total lengths and were made using fresh specimens unless indicated. Additional details of most methods are described in Beamish and Williams (1976) and Beamish and Scarsbrook (1979). When appropriate, special comments about methodologies will be included in the descriptions of the life histories.

Identification of Adults

The tooth pattern clearly separates adult Pacific lamprey from the river lamprey and the western brook lamprey (*L. richardsoni*). River lamprey in salt water can also be identified by the lighter color, presence of countershading, and less robust appearance. However, separation of metamorphosing stages of river and western brook lamprey was not possible as recently metamorphosed western brook lamprey have rather prominent cusps and a dentition pattern similar to the parasitic river lamprey. Confirmation of the identity of some western brook lampreys was obtained by holding recently metamorphosed adults over winter in freshwater, and confirming that they matured and in some cases spawned in the early spring of the year following metamorphosis. Characters that will enable the separation of these two species during the macrophthalmia stage have not been identified because up to the present all but two of the recently metamorphosed specimens, captured in the fall and tentatively identified as river lamprey, proved to be western brook lamprey. Therefore, at present, the separation of metamorphosed river and western brook lamprey from samples collected in the fall remains uncertain.

In the spring, immature adult river lamprey in freshwater can be distinguished, in most cases, by the silver color of the body, the prominence and sharpness of teeth, the immature state of the gonads and the advanced state of development of the gut. In the late fall and early spring, river lamprey returning from sea and found in freshwater can be separated from recently transformed western brook lamprey by their advanced stage of maturity and the sharpness of their teeth.

At present, the identification of ammocoetes of river and western brook lamprey are also in doubt. Identifications of ammocoetes were made according to original published descriptions (Pletcher 1963; Vladykov and Follett 1958, 1965); however, not one of the ammocoetes thought to be a river lamprey developed into a river lamprey in the holding tanks.

In some streams adult lamprey were found that possessed characteristics common to both river lamprey and western brook lamprey. These lamprey were silver and possessed a well-defined gut, but the gonad development although more advanced than samples of river lamprey from other streams, was much less advanced than western brook lamprey found in the same stream. Two of these forms died when an attempt was made to acclimate them to salt water. There also was some variation in the morphology of western brook lamprey. Comparative studies of eye diameters, prebranchial lengths, and the number and morphology of velar tentacles confirmed that there are important variations in river and western brook lampreys found in the various rivers.

Results and Discussion

Biology of Adult River Lamprey

Since ammocoetes and recently metamorphosed river lamprey could not be separated from western brook lamprey, it could only be assumed that river lamprey ammocoetes begin metamorphosis in July, at the same time as the other two species. River lamprey have been

TABLE 1. Length frequency of juvenile adult river lamprey caught in downstream traps, in three British Columbia rivers.

Length (cm)	Fraser River[a] June 6–9, 1978	Fraser River[a,b] April 24–June 5, 1979	Morrison Creek[b] May 20–June 11, 1978	Quinsam River[b] April 26, 1978
4	1	—	—	—
5	—	—	—	—
6	—	—	—	—
7	—	—	—	—
8	—	—	—	—
9	3	6	—	—
10	28	23	—	1
11	28	56	4	—
12	15	76	8	—
13	4	31	5	—
14	—	6	—	—
15	—	2	—	—
16	—	1	—	—
17	—	—	—	—
18	—	—	—	—
19	—	1	—	—
Total	79	202	17	1

[a]Samples from 2.5 m^2 small-mesh midwater trawls fished at depths from 0 to 6 m and 3 to 20 km from the mouth of the river. Lengths from samples in 1978 were from previously frozen specimens.

[b]Lengths from preserved samples.

recorded moving downstream from the end of April to mid-June in three rivers in British Columbia. The length of the downstream migrants ranged from 4 to 19 cm with a mean length of 11 cm (Table 1). In 1979, small mesh midwater trawls were fished in the Fraser River starting March 13–16 but river lamprey were not captured until the end of April. Sampling continued until June 5 when the project was terminated because of decreased salmon abundance. While river lamprey occurred in greatest abundance during the last 2 wk of May, they were still present in early June and it is suspected that river lamprey migration into salt water continued throughout June. In 1979, there was no significant difference (t-test, $P > 0.05$) in the mean length of migrants during the main portion of the migration; however, the mean length of the June sample was 0.8 cm smaller than the mean length in the other sampling periods. Most lamprey were found at the 3–6 m depth range in the day samples. Day and night sets were made on May 3 and 17 and while catches were small (9 and 20 river lamprey, respectively), compared to catches during the day, one more river lamprey was captured in the night sets on May 3 and four more in the night sets on May 17 indicating downstream migration continues day and night with a possible preference for the night.

As part of another study, extensive fishing operations using small-mesh surface nets were conducted in the Strait of Georgia in the vicinity of the mouth of the Fraser River from the end of April to mid-July (Robinson et al. 1968a, b; Robinson 1969; Barraclough and Fulton 1967). The earliest recorded catch of river lamprey was on May 4, and catches of river lamprey in the size range of the downstream migrants listed in Table 1 continued to be present in the samples until mid-July, indicating that migration into salt water continued through June and perhaps into early July. A survey of 40 sites among the Gulf Islands in the Strait of Georgia in mid-May 1978 using a small-mesh purse seine (Beamish and Scarsbrook 1979) did not capture any river lamprey. Thus it appears that river lamprey begin to enter salt water late in April or early May and continue moving into salt water possibly as late as early July.

Withler (1955) observed a 162 mm river lamprey feeding on a young coho salmon fingerling in the Skeena River (54°10′N, 130°11′W) in mid-July, 1955. This specimen was larger than most downstream migrants observed in this study and was found in freshwater at about the same time as the maximum abundance of river lamprey was observed in the Strait of Georgia. While migration into salt water may be later for more northern areas, it is possible that the large size and the apparent delayed entry into salt water was related to the initiation of feeding in freshwater.

In June 1976, 50 juvenile sockeye salmon were captured at depths of 190 and 54 m in the northern portion of the Strait of Georgia (Scarsbrook et al. 1980). Seven of these fish had fresh, severe lamprey wounds some of which were identified from the tooth pattern as resulting from river lamprey attacks. The sockeye had an average length of 10 cm and thus had recently entered salt water. Since river lamprey have never been captured in deep water it is probable tha

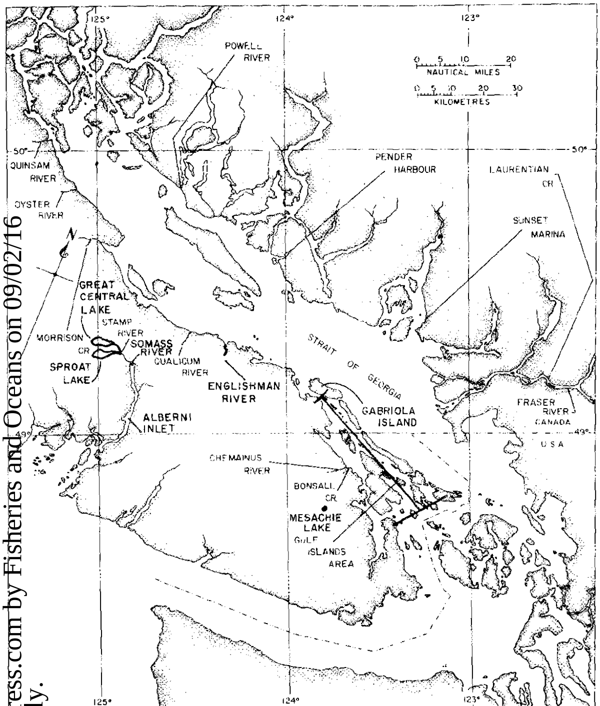

FIG. 1. Strait of Georgia showing areas mentioned in this report.

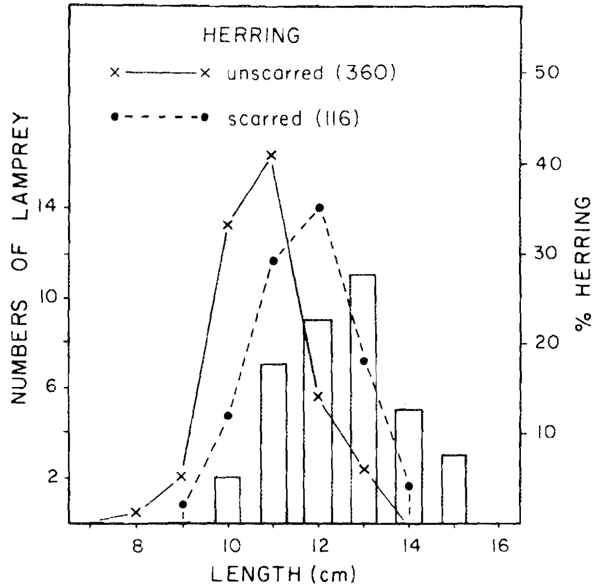

FIG. 2. Length distribution of river lamprey found actively feeding on herring and other fishes in large herring schools in Howe Sound. The length frequency of scarred and unscarred herring is also shown.

the attacks on the young salmon occurred during the downstream migration or in the estuary. These observations and the observations by Withler (1955) indicate that some river lamprey commence feeding in freshwater.

Early Adult Life in Salt Water

In this study the earliest catches of adult river lamprey in salt water were made on May 31 and June 2, 1978 in Sunset Marina in Howe Sound just north of the mouth of the Fraser River (Fig. 1). An entire school of fishes was purse seined and a sample estimated to be about one-third of the total school was removed with dip nets. This subsample contained 18 river lamprey, 1009 Pacific herring, 17 northern anchovy (*Engraulis mordax mordax*), and 5 unidentified salmon. A total of 116 herring (11.5%), 2 northern anchovies (11.8%), and one salmon (20%) were wounded from lamprey attacks. Approximately 75% of the wounds were estimated to be sufficiently severe to cause death. There was a disproportionate number of larger herring that had wounds and fresh scars (Fig. 2). This might be the result of a slightly higher survival rate of the larger fish after an attack rather than a preference for large hosts.

After the subsample was removed, an attempt was made to catch the remaining lamprey. A total of 40 lamprey were obtained and the mean length (Fig. 2) was 1 cm larger than the mean length found for the 1978 Fraser River sample (Table 1) indicating that these lamprey started feeding immediately on entry into salt water. The occurrence of actively feeding river lamprey in schools of Pacific herring is commonly observed for several weeks from several areas in the Strait of Georgia at this time of year. Therefore, it appears that some river lamprey begin their parasitic existence in salt water by associating themselves with schools of Pacific herring and voraciously feeding while remaining part of the school.

Growth and Distribution of Adults in Salt Water

During 1974, purse seine surveys for river lamprey were conducted in the central portion of the Strait of Georgia during July and August. In 1975 the surveys were repeated and extended into September. In 1976, the effort in the main portion of the Strait of Georgia was reduced but a number of standard locations were fished in the Gulf Islands area (Fig. 1) from April through October. In 1974, 1975, and 1976 the range in length of river lamprey from all the samples was 14–23, 12–29, and 9–28 cm, respectively (Fig. 3). In all years there was a wide range in lengths during July and August with little difference observed among the mean lengths (Fig. 3). The September samples did show an increase in mean length although the number of individuals present in the catch was greatly reduced. The Gulf Islands sample in 1976 does indicate that

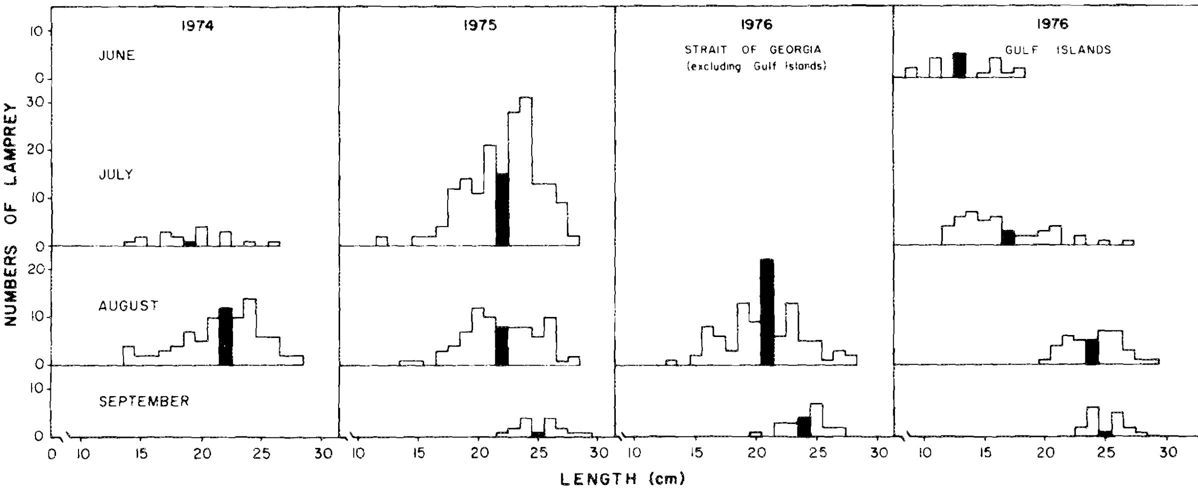

FIG. 3. Length frequency of all river lamprey caught in the Strait of Georgia from 1974 to 1976. In 1976 catches from the Gulf Islands area were separated from the total catch. The shaded bar indicates the mean length of the distribution.

mean length increased from 14 cm in mid-June to 24 cm in mid-August. Increases in length were reduced during late July and August when rapid increases in weight occurred (Fig. 4). The interpretation of growth from length frequencies was complicated by several factors including the time required to complete a survey, the mixing of lamprey from different rivers, and the time of entry into salt water.

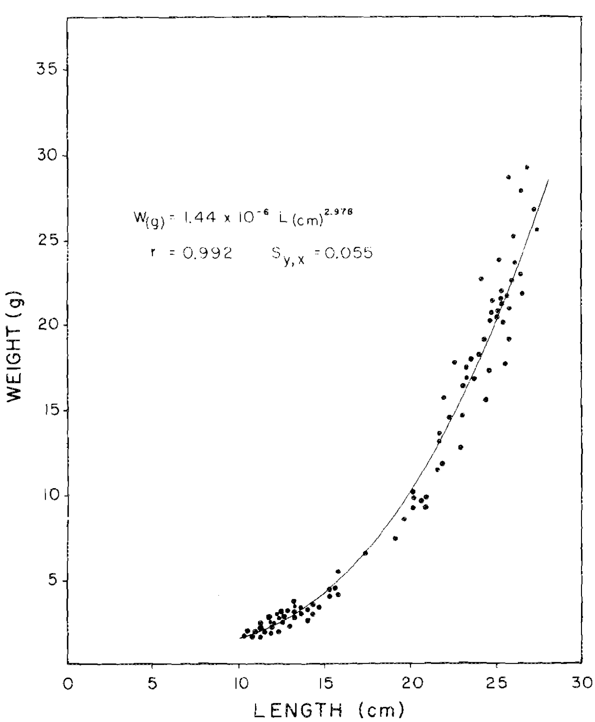

FIG. 4. Relationship between length and weight for adult river lamprey in salt water. The calculated curve does not appear to adequately represent the relationship for length and weight for the largest individuals.

During 1975 and 1976, 229 river lamprey were sexed and sampled for length (Table 2). The mean length of females sampled throughout their salt water residence ranged from being almost identical to being 2.5 cm longer than males. Except for the July 1976 sample there was no significant difference in the mean length of male and female lamprey (t-test, $P > 0.05$).

Sex ratios of adult river lamprey were determined by microscopic examination in 1975 and 1976 when the gut contents were examined. In July 1975 a sample of 50 lamprey consisted of 60% males. In 1976, the sex ratio for the total sample of 182 lamprey examined was 60% females. During July and early August 1976, the ratio of males to females was almost identical. However, in a sample of 59 lamprey collected in late August, there were 64% males and of 17 lamprey found in early September, 74% were females. Thus the adult sex ratios are about equal, but females appear to remain in the surface waters longer.

River lamprey are present in the surface waters from May to September and are most abundant in July. From 1974 to 1979 approximately 500 midwater trawls have been made in the Strait of Georgia at various depths and at various times of the year. While 66 Pacific lamprey were found, only one river lamprey was captured and that was near the surface. (Data are contained in numerous cruise reports, published by the Fisheries and Marine Service, Canada.) Lamprey were most abundant in the surface waters in July and absent after September. No lamprey were found at the surface in the October survey of the Gulf Islands in 1976 or in the 4-day and 4-night purse seine sets made in the Gulf Islands in November 1974. Also a comparison of 20-day and 17-night sets made in the Gulf Islands in

TABLE 2. Mean length (cm) of river lamprey sampled for length and sex in 1975 and 1976. Sample size is in parenthesis.

	1975	1976				
	July 29	June 21–26	July 5–9	Aug. 3–10	Aug. 24–Sept. 2	Sept. 8–15
Male	20.3 (30)	13.9 (6)	15.3 (23)	23.0 (18)	21.8 (21)	24.6 (4)
Female	19.8 (20)	12.0 (12)	17.8 (23)	23.1 (21)	22.7 (38)	25.3 (13)

1976 showed that catches during the day were significantly higher than during the night (t-test, $P < 0.05$, Beamish and Scarsbrook 1979). At night some may move into water deeper than the depth of the purse seine (26–33 m), or move inshore, but they seldom occur at depths greater than 50 m during the day or night. The strong countershading first noted by Kan (1975) is further evidence that this species prefers surface waters.

There seems to be little doubt that a few major rivers such as the Fraser River and its tributaries are a major source of river lamprey in the Strait of Georgia (Fig. 1). By dividing the Strait of Georgia into 7-km squares and plotting the average catch per set for each of these squares (Fig. 5) the areas of concentration were in the vicinity of Pender Harbour, Howe Sound, and the area from the mouth of the Fraser River to Gabriola Island and the Southern Gulf Islands area (Fig. 1).

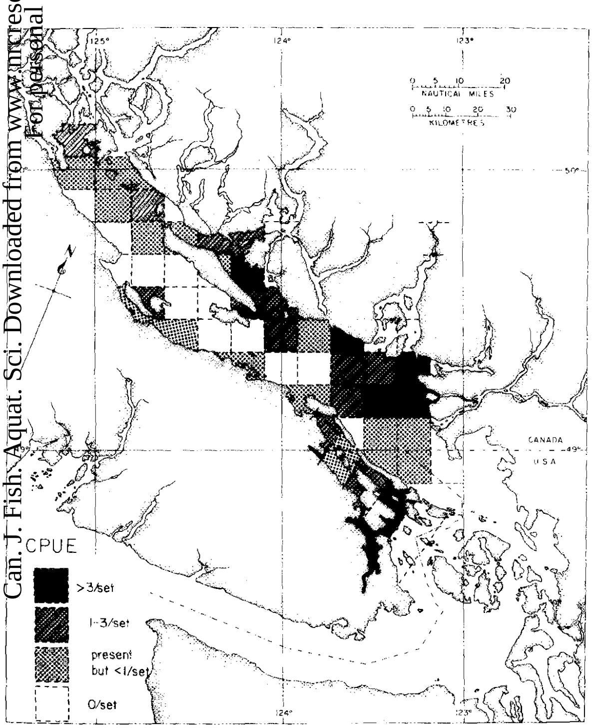

FIG. 5. Catch of river lamprey per unit of effort (CPUE) for all sets made in the Strait of Georgia.

During the summer months the salinity at depths from 10 to 50 m in the Strait of Georgia has an average range of approximately 26–30‰ (Waldichuk 1957). Compared to offshore salinities of approximately 32‰, the salinities in the Strait of Georgia can be considered to be of reduced concentration. The accumulation of river lamprey in the vicinity of major rivers and their distribution throughout the surface waters may indicate a preference for water of reduced salinities.

FEEDING

Gut contents from 182 river lamprey caught in 1976 and from a sample of 50 caught in 1975 were examined in the laboratory. Because river lamprey remove portions of flesh from their hosts (Fig. 6) it was often possible to identify the prey by scales, fin segments, or internal organs such as pyloric caeca. Since much of the gut contents could not be identified, results are expressed as the number of lamprey that contained a particular prey species.

All the identifiable items in each gut were from one prey species. Several guts contained more than one caudal fin or scales from fish of different ages indicating more than one individual had been attacked. Of the 182 guts examined, 38 (22%) were empty and 9 (5%) contained unidentifiable remains. The most frequently occurring species, Pacific herring, was found in 115 (63%) of the guts. Salmon remains were the second most abundant food item occurring in 18 (10%) of the guts. The percent occurrence of salmon remains decreased from 50% in June to 9% in September, while the percent occurrence of herring increased correspondingly. The decrease in the presence of salmon may be related to the movement of young salmon out of the estuaries and the Strait of Georgia. The mean volume of the gut contents was highest in August, averaging 0.8 mL. Because river lamprey often remove pieces of tissue and internal organs, survival of hosts was unlikely. It was estimated from the number of lamprey that contained food, relative to those that were empty, that from June to September each lamprey attacked and fed on 0.8 fish/d.

In laboratory experiments river lamprey fed on a variety of species including Pacific herring, salmonids, shiner perch (*Cymatogaster aggregata*), English sole (*Parophrys vetulus*), on two occasions other river lam-

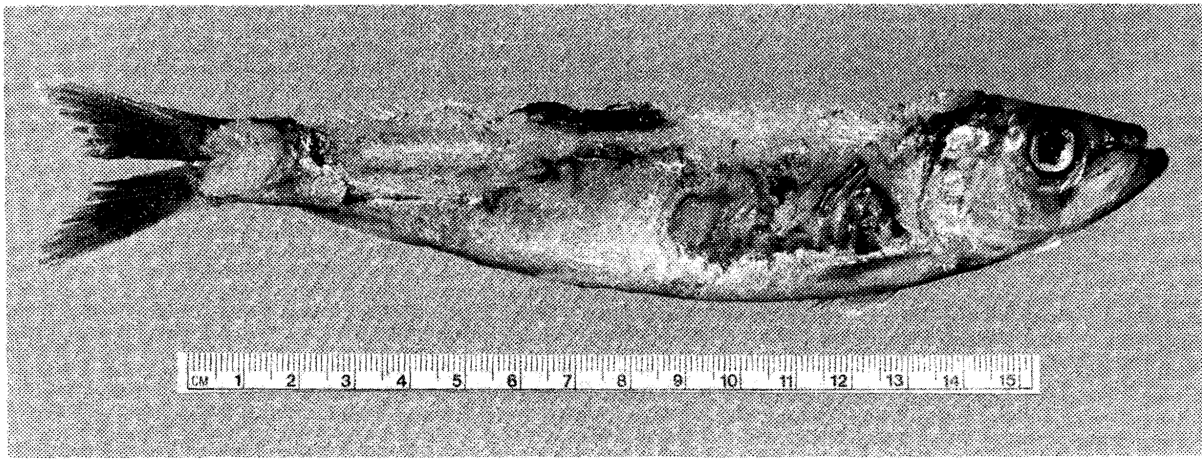

FIG. 6. Pacific herring consumed by river lamprey. The fish was taken from a laboratory feeding experiment and it is apparent from the extensive damage to the body cavity that feeding continued after the death of the host.

prey and one occasion a dead Pacific lamprey. It was not known whether the river lamprey fed on live or dead river lamprey as only a partially consumed carcass was found on the bottom of the tank. On several occasions river lamprey attacked and fed on fish that were already dead. While such attacks were rare, continued feeding on fish that died during an attack was not uncommon. Herring was the preferred species in laboratory experiments and often the addition of fresh herring to a tank would initiate an immediate feeding response. In the laboratory experiments the frequency of feeding was reduced after September. Although river lamprey kept in salt water of the same salinity as the Strait of Georgia started dying in October, those that survived until the following June fed as late as mid-May.

Recreational fishermen have reported that river lamprey attacked their baits and consumed portions of flesh in the length of time it took to retrieve the line. In the laboratory, river lamprey could consume between one-eighth and three-quarters of the body of a small herring (10 cm), exclusive of the head and tail in a single meal of 30–40 min duration. Smaller fish were usually subjected to more general damage with an average of about one-half the trunk tissue being consumed. Larger salmon usually sustained round, deep wounds, often in the anterior dorsal region. Fish smaller than 15 cm seldom survived a lamprey attack for more than a few days or were attacked and killed by another lamprey. During an active 4-wk feeding period in a laboratory experiment, an average of 1.3 fish were killed per lamprey per day (Beamish and Williams 1976). Although it is difficult to relate the results of the number of fish killed in this series of experiments to natural feeding conditions, because lamprey did not feed when first brought into the laboratory, the killing rate of 1.3 fish per lamprey per day is similar to the attacking rate of 0.8 fish per lamprey per day estimated from the analysis of gut contents.

Based on scarring data, Roos et al. (1973) reported that attacks by river lamprey were confined exclusively to the dorsal area. In this study the majority of attacks were dorsal and anterior but some ventral attacks were observed. Ventral attacks probably kill many prey by penetrating the body cavity and would not normally be observed unless large numbers of prey species were examined. There was no question that the majority of attacks observed on fishes in the Strait of Georgia were dorsal, but anterior, posterior, lateral, and ventral attacks were observed in this study. Ventral attacks were more common in laboratory experiments.

At present there is little evidence of predation by other animals on river lamprey. As reported, river lamprey fed on other river lamprey in the laboratory and there is one report of a river lamprey being found in the gullet of a lingcod (Vladykov and Follett 1958). In laboratory experiments in freshwater, salmon fed on small adult western brook lamprey, so predation on river lamprey by other fishes may occur.

ABUNDANCE OF ADULT RIVER LAMPREY IN THE STRAIT OF GEORGIA

As part of the 1975 survey, an approximate estimate of the number of river lamprey in the Strait of Georgia was made by dividing the surface area of the study area in the Strait of Georgia by the total surface area fished in all sets during July to September and multiplying by the total catch of lamprey. From a total survey area estimated to be 4690 km^2, a total area fished of 1.49 km^2, and a catch of 282 river lamprey, it was estimated that 667 000 river lamprey were present in the Canadian portion of the Strait of Georgia (Beamish and Williams 1976). By combining the feed-

TABLE 3. Number of deaths by month for maturing river lamprey held in salt water and freshwater.

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Salt water												
No. of deaths	4	2	3	1	0	2	1	1	6	2	—	22
(male, female)[a]			(1, 1)			(0, 2)	(1, 0)	(0, 1)	(3, 2)	(2, 0)		
Approximate %	18	9	13	5	0	9	5	5	27	9	—	100
Freshwater												
No. of deaths	—	—	5	9	6	4	3	7	26[b]	6[b]	1[c]	67
(male, female)			(5, 0)	(6, 3)	(4, 2)	(4, 0)	(0, 3)	(1, 1)	(9, 15)	(1, 5)	(0, 1)	
Approximate %	—	—	8	14	9	6	4	10	39	9	1	100

[a]No. of males and females may not add to total as sex was not determined for all fish.
[b]Died after spawning.
[c]Mature female that did not spawn.

ing rate of 0.8 fish per lamprey per day and the killing rate of 1.3 fish per lamprey per day, a killing rate of 1 fish per day per lamprey was assumed. Using this killing rate and assuming that each prey is attacked by only one lamprey it was estimated that 60 000 000 juvenile fish would be killed during the 90-d feeding period from mid-June to mid-September. Since many variables had to be estimated it is obvious that the technique provides only a very approximate estimate of population size. For example, if only the portion of the seine that had a mesh size that could retain lamprey was considered, the effective fishing area would be reduced by 90%. Sets could not always be made in a standard manner in randomly selected locations and it is doubtful that all lamprey remained in the study area during the study period. The estimate does indicate that river lamprey could be an important predator of small fishes particularly herring and salmon.

Return to Freshwater, Spawning, Death

No river lamprey were found in salt water after September, but to date no adult river lamprey have been found in rivers in the fall. Using a small midwater trawl, one maturing 14-cm female river lamprey was caught in Nimpkish Lake on November 30, 1978, indicating that in one river the timing of the upstream migration corresponds with the timing of the disappearance from salt water. Pletcher (1963) recorded the presence of *Lampetra planeri* (now called *L. richardsoni*) in two rivers in British Columbia in February 1957 and May 1942. These lamprey ranged in length from 13 to 20 cm and the largest individuals were larger than any adult western brook lamprey found in this study. It is probable that some of the specimens described by Pletcher were river lamprey and that these were the first recorded observations of maturing river lamprey in British Columbia rivers. Vladykov and Follett (1958) recorded adult river lamprey in San Francisco Bay in the United States in November and February. They also recorded adult river lamprey in Lakes Sammamish and Washington in October and December, respectively. The specimen found in Lake Washington was attached to and possibly feeding on a Kokanee salmon (*Oncorhynchus nerka*). They also reported specimens in spawning condition from the Sacramento River, approximately 240 km from the ocean, in April. From the size of the eggs in these specimens they concluded that the spawning period would be April through May.

In this study, some of the specimens captured in late August and September showed signs of early gonad development. Lamprey held in salt water in the laboratory stopped feeding or fed infrequently after September and died over the period from September to mid-June (Table 3). Individuals that died in November and December were maturing, the gut and eyes were degenerating and there was a noticeable reduction in the postanal length and in the space between the dorsal fins. Such changes are associated with the onset of maturity and onset of upstream migration in other parasitic species (Hardisty and Potter 1971) and suggest that some river lamprey move into freshwater during this time of year. Because a loss of marine osmoregulatory mechanisms occurs with the onset of maturity (Morris 1971), some of the deaths recorded in Table 3 probably are related to changes in osmoregulatory mechanisms. All river lamprey that died in the salt water tanks from February to mid-June were mature. Some river lamprey fed infrequently during this period with the last feeding occurring in mid-May. Although mortalities occurred from September to June, the greatest number occurred in May (Table 3), indicating that some river lamprey can remain in salt water until just before the spawning period. This observation is consistent with that of Vladykov and Follett (1958) who recorded river lamprey in San Francisco Bay at the same time as they were found in some lakes.

In a second experiment, river lamprey were acclimated to freshwater over a period of 6 d in early November and maintained in freshwater. In freshwater,

TABLE 4. Mean length (cm) of Pacific lamprey during metamorphosis and downstream migration (number of fish in sample in parentheses).

	Downstream migrants (trapped)				Metamorphosis adults (electro-shocked)											
	M	A	M	J	J	F	M	A	M	J	J	A	S	O	N	D
Qualicum R. 1977	12 (5)	13 (3)	0	—	—	13 (1)	0	0	0	0	0	—	12 (2)	13 (4)	0	—
Qualicum R. 1978	0	13 (4)	12 (4)	—	—	—	0	0	—	—	—	—	—	—	—	—
Oyster R. 1977	—	—	—	—	—	—	—	—	—	—	—	12 (43)	12 (30)	13 (6)	0	—
Oyster R. 1978	—	—	—	—	—	—	—	—	—	—	—	10 (6)	—	12 (39)	—	—

the pattern of mortalities was similar to that observed for the lamprey held in salt water but by the end of February none of the dead showed advanced signs of maturity and none had fed on any of the salmonids that were kept in the freshwater tanks.

At this time, it can be concluded only that some river lamprey can survive in salt water of approximately 28–30‰ until spawning and that some river lamprey can adapt to freshwater shortly after they disappear from the surface waters in the Strait of Georgia. Separate stocks may exist and some stocks may remain in salt water, possibly in estuaries or below the tide level in rivers during the winter, while others move into lakes and rivers in the fall. Since no spawning occurred in salt water, it appears that a return to freshwater is essential for successful spawning.

River lamprey were acclimated to freshwater in early November 1978, and on April 1, 1979 the water temperature in the tanks was heated to 1–2°C above ambient to correspond with the temperature of rivers known or suspected to contain river lamprey. These lamprey spawned in the holding tanks during May 1979 when the water temperature was 12°C. The nesting and spawning behavior observed in the laboratory was similar to the behavior of most lampreys (Hardisty and Potter 1971). Prior to spawning, lamprey constructed nests approximately 15 cm in diameter in the gravel by lifting rocks out of the nest area with the oral disc and by vigorous digging movements. Just prior to spawning a male would glide up and down the body of the female with his oral disc and eventually attach dorsally behind the head of the female, twisting his tail around the body of the female. The actual release of eggs and sperm was not observed. Males appeared to exert considerable pressure when twisting around the body of females as many spawned females were severely bruised. Most females died within hours of spawning while most males survived for approximately 3 wk.

There was a considerable decrease in length during the period in freshwater from early November until spawning in May. The average length of the 29 spawning lamprey was 18.3 cm. The average length of lamprey in this experiment was 23.8 cm in mid-August and while lengths determined in August were not compared with the length of the same individual measured in May, it is probable that the 21% reduction in length is representative of the amount of shrinkage that occurs during the residence in freshwater prior to spawning. The average length of 14 males was 18.9 cm, about 1 cm longer than the average length of 17.8 cm for 15 females suggesting that females may shrink more than males.

If the temperature at which river lamprey spawned in this study is representative of the temperatures river lamprey initiate spawning in rivers, it can be assumed that most spawning occurs in May and could extend from April to June. Since river lamprey survived only a few weeks after spawning, the average duration of adult life from the onset of metamorphosis in July to death following spawning is 2 yr.

Biology of Adult Pacific Lamprey

Metamorphosis and Movement into Salt Water

Metamorphosing Pacific lamprey were first observed in July. Pletcher (1963) also concluded that metamorphosis started in July. Recently an intensive study of the staging of the metamorphosis of Pacific lamprey in the Chemainus River (Richards 1980) confirmed that metamorphosis begins in July and was complete by October. From August to September in the Qualicum River on Vancouver Island (Fig. 1), metamorphosing Pacific lamprey were observed to move from a mud–silt habitat in lentic waters to silt covered large gravel (1 to 4 cm in diameter) in moderate currents. Movement into the large gravel was complete by early September or Stage 6 (teeth blunt, cusps not present on the tongue, oral fimbriae well developed; Richards 1980; Youson and Potter 1979). A survey of other rivers during September, 1979 showed that Pacific lamprey in an advanced stage of metamorphosis characteristically were found in gravel or boulder substrate where currents were moderate to strong. Metamorphosing Pacific lamprey from a nonanadromous population in Mesachie Lake (Fig. 1) were found in similar substrate along the edge of the lake close to the inlet stream.

The mean size of downstream migrants from the Qualicum River was 12.5 cm (Table 4). The mean size of metamorphosing Pacific lamprey, collected from July through to October in the Qualicum and Oyster rivers was 12.0 cm and was not significantly different from the mean size of the total sample of downstream migrants (t-test, $P > 0.05$). The average size of eight metamorphosed Pacific lamprey from Morrison Creek was 7.8 cm with the smallest metamorphosed lamprey measuring 4.7 cm. Downstream migrating Pacific lamprey captured with small mesh midwater nets in the Fraser River from May 3 to June 5, 1979 ranged in length from 11 to 16 cm with a mean length of 14 cm for the 43 specimens captured. It appears that, while there is some variation among rivers, the average size of Pacific lamprey when they first enter salt water is approximately 13 cm.

Downstream trapping operations from February to June for salmon often capture lamprey, but unfortunately only in recent years have catches of lamprey been preserved and identified. The earliest reported capture of a juvenile adult Pacific lamprey, moving downstream, was in February (Table 4) and the latest capture was in June, both in the Qualicum River. Unpublished downstream trap catches from the Qualicum River indicate that unidentified lamprey were caught as late as August indicating that the period of migration of Pacific lamprey into salt water may extend past June. In the Fraser River in 1979, no metamorphosed Pacific lamprey were captured in March and April, but 43 were captured in May and June. Pacific lamprey adults are thought to be more abundant than river lamprey adults, yet this number of metamorphosed Pacific lamprey was only 21% of the number of river lamprey caught in the same nets. Because of this apparently small catch of Pacific lamprey it was suspected that the main downstream migration occurred earlier than April and that the catches in May and June resulted from the migration of Pacific lamprey from only a few of the tributary rivers of the Fraser River. The capture of a 12-cm adult Pacific lamprey at a depth of 90 m in December (Fig. 7) in the Strait of Georgia, near the mouth of the Fraser River indicates that migration into salt water can occur at least as early as December. Also, the presence of young adults in areas in the stream with moderate to strong currents, during the periods of low water in September and October suggests that some entry into salt water may occur when water levels and current velocities increase in November. Richards (1980) believed Pacific lamprey go to sea in November.

In a laboratory experiment in 1978, metamorphosing Pacific lamprey were acclimated to salt water in late September and started feeding in mid-October (Richards 1980). This experiment was repeated in late September, 1979 using five metamorphosing Pacific lamprey recently captured from each of five rivers. The stage of metamorphosis was noted and lamprey from each river were marked with an injection of colored latex into the dorsal fin fold. Twenty of the 25 lamprey survived the 3-d period of gradually increasing salinity. The five lamprey that did not survive in full strength salt water were from two rivers and either had not reached stage 6 or had just reached the 6th stage of metamorphosis. None of the lamprey in stage 5 survived in salt water. Live herring (6–10 cm) were added to the tank on October 1 when full strength seawater was achieved. First attachment to a herring was observed in 4 d and the first confirmed feeding on herring occurred in 10 d. By the end of October, 20 herring had been attacked and killed.

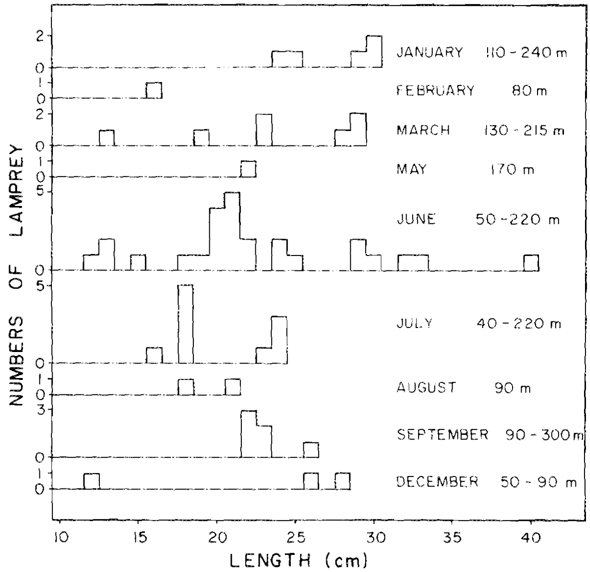

FIG. 7. Length frequency of Pacific lamprey captured in midwater trawls in the Strait of Georgia.

In experiments conducted in 1977/78, 1978/79, and 1979/80, metamorphosed Pacific lamprey in freshwater did not survive past mid-July and most perished by the end of January. In the 1978/79 experiments, salmonids were introduced into the tanks in early February; feeding started in late February to early March and lamprey continued feeding until several weeks prior to death. In 1979/80 experiments, salmonids were introduced into tanks in early October. In three separate experiments, each containing 25–35 lamprey, feeding commenced in mid-October, about the same time as the lamprey from the same rivers commenced feeding in salt water. While the frequency of attacks was lower in freshwater (R. J. Beamish unpublished data), it was apparent that feeding can commence in freshwater and salt water at the same time. The cause of death in these experiments was not determined but if it was related to osmoregulatory problems it may indicate that most stocks of Pacific lamprey must enter salt water soon after metamorphosis is complete and no later than July. Thus the known period of migration into salt water is from December to June and the actual period of migration probably is longer.

Hardisty and Potter (1971) have identified the stage in metamorphosis, after the more obvious external changes have taken place, as the macrophthalmia stage. They consider that in a parasitic species this stage ends with the onset of feeding. Since metamorphosis of Pacific lamprey was complete by mid-October and individuals commenced feeding immediately in freshwater or salt water, it appears that Pacific lamprey metamorphose directly into juvenile adults and the macrophthalmia stage is either very short or it does not exist.

In some locations in British Columbia, lamprey do not migrate into salt water but remain and feed in freshwater (Carl 1953). Mesachie Lake (Fig. 1) contains nonanadromous parasitic lamprey as indicated by the freshly wounded fish that were observed throughout the year. The lamprey captured were immature, feeding, and were larger than most downstream migrants from other rivers. Two lamprey captured in June were acclimated to full strength salt water over a period of 3 d. They were kept in salt water of 6 d indicating that the freshwater residence had not impaired their ability to acclimate to salt water. In subsequent studies these lamprey have been maintained in salt water for several months. Since no physical barrier prevents the adult Pacific lamprey in Mesachie Lake from entering salt water, the term "nonanadromous" rather than "landlocked" more accurately describes their confinement to freshwater. These individuals are morphologically different from other Pacific lamprey and may represent a new species. When recently metamorphosed Pacific lamprey from a number of locations were held in freshwater all Pacific lamprey eventually died except those from Mesachie Lake. While these preliminary experiments show that Mesachie Lake lamprey are different from other Pacific lamprey, it remains unknown if the ability to remain in freshwater is the result of genetic differences or is common to other individuals that traditionally migrate into salt water.

When Pacific lamprey enter salt water they do not remain on or near the surface or in shallow water but move to water deeper than 70 m. Robinson and Barraclough (1968a, b) caught only six Pacific lamprey in surface nets in the vicinity of the Fraser River, and in the present study no Pacific lamprey were found in any surface fishing except in the vicinity of the Fraser River. Pacific lamprey slightly larger than the size of the average downstream migrant have been captured at fishing depths of 100–250 m. Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) commonly found at these depths were occasionally found with fresh lamprey wounds. Off the west coast of Vancouver Island during the summer of 1979, salmon fishermen reported small lamprey attached to pink salmon (*Oncorhynchus gorbuscha*) caught a few km to 40 km offshore and at fishing depths of 20–90 m in water of depths to 180 m. By mid-September 1979, nine Pacific lamprey, ranging in size from 16 to 42 cm with an average length of 23 cm had been returned by fishermen and 35 fishermen observed lamprey attached to salmon. The length of the smaller lamprey that were captured was very close to the average size of 17 cm, estimated by these 35 fishermen, and is very similar to the size of Pacific lamprey in their first year of salt water residence in laboratory experiments (R. J. Beamish unpublished data). It appears that the small lamprey found in the Strait of Georgia and off the west coast of Vancouver Island are in their first year of salt water residence and are located at depths in the range of 20 to 250 m.

In laboratory experiments, metamorphosed Pacific lamprey that were maintained in freshwater without food until March, and then acclimated to salt water over a 3-d period, initiated feeding within hours of being introduced into a tank containing Pacific herring. Therefore, it appears that juvenile Pacific lamprey leaving freshwater, move directly into deeper water and probably start feeding immediately.

Feeding

Rarely are Pacific lamprey observed attached to prey, but the scar or wound that remains on fish frequently has impressions of the teeth, clearly indicating that the wound was caused by a Pacific lamprey. A common prey observed in this study was walleye pollock. Pollock were routinely examined for lamprey attacks from all of the major fishing grounds from 1975 to 1979 and of 21 000 fish examined, 124 fish or about 0.6% were found to have wounds or scars caused by lamprey. The highest incidence of attacks on pollock was observed in Dixon Entrance (54°30′N, 132°39′W), where 10% of a sample of 145 pollock were wounded. More scars or wounds have been observed on the left side of pollock but it is difficult to determine if this apparent preference for the left side is real, as lamprey marks on fish are often observed incidentally to some other project and the degree of sampling bias is unknown at this time. Pacific hake were also examined and of the 50 000 examined 51 or 0.01% were wounded. Pacific hake and walleye pollock are midwater fish that often are found in association with layers of plankton (Beamish et al. 1976) and the attacks on these fish may indicate a preference for this plankton layer by young Pacific lamprey.

Scarring on sockeye salmon by Pacific lamprey in the vicinity of the Fraser River was examined by Williams and Gilhousen (1968) and again in this study. Williams and Gilhousen found that approximately 66% of the sockeye and 20% of the pink salmon sampled had marks of lamprey attacks. Six percent of the wounds on sockeye and 2% of the wounds on pink salmon were considered to be severe. They estimated that mortality due to lamprey wounds after fish moved upstream to the spawning grounds was between 1.6 and 1.8% and was of minor significance. In this study a sample of 681 sockeye from a commercial catch was examined in 1978 for wounds and scars and 27% of the fish were found with evidence of lamprey attacks. Sixty-six percent of the attacks penetrated the skin and 2.4% were severe wounds that penetrated deep into the muscle or body cavity. A sample of 140 sockeye

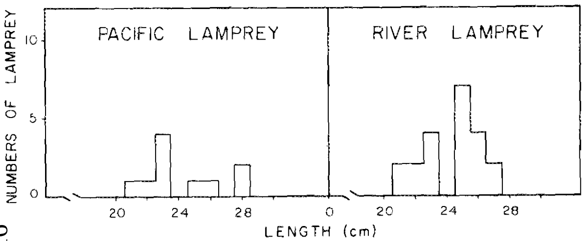

FIG. 8. Length frequency of river lamprey and Pacific lamprey captured in the mouth of the Fraser River Estuary in August–September 1978.

salmon captured during a research cruise, several weeks prior to the examination of the commercial sample contained 17% scarred fish. The higher incidence of scarring in the commercial sample cannot be explained but may be related to the increased time spent in the estuary or may be related to increased attacks on fish that are caught in gill nets. In a combined sample of 821 salmon, 96 attacks were on the right side, 66 were on the left side, 4 were dorsal and 59 were ventral. No explanation for the apparent preference for the right side is possible.

The use of a small mesh purse seine during research cruises in the vicinity of the Fraser River resulted in the capture of Pacific lamprey and river lamprey (Fig. 8) in addition to small and large salmon. On the large sockeye salmon none of the scars in which a tooth pattern could be recognized, appeared to result from river lamprey attacks but many of the smaller salmon had been attacked by river lamprey.

Mason (1974) observed that 61 of 539 coho salmon (14%) returning to Lymn Creek in 1971 had lamprey scars and 137 of 348 in 1972 (45%) had scars. Female coho had significantly more scars than males. Six of 30 sockeye salmon returning to Sproat Lake and 10 of 68 sockeye salmon returning to Great Central Lake had evidence of lamprey attacks. Six fish from the two samples suffered more than one attack and four of the fish had suffered attacks that did not penetrate the skin. Most wounds did penetrate the skin and were approximately 5 mm in diameter, indicating attacks by small, young lamprey. No lamprey were observed on any of the 60 000 sockeye salmon that were counted entering these lakes. Birman (1950) also noted a high percentage (44%) of scars caused by Pacific lamprey on pink salmon in the Amur estuary.

Because the sockeye salmon were returning to spawn and some of the attacks had not penetrated the skin it might appear that the lamprey were also aggregating in preparation to return to freshwater. Soldatov (1934) considered that lampreys gathered in estuaries of larger rivers and attached to salmon that were moving upstream in order to accelerate their own movement into freshwater. However, two of nine Pacific lamprey that were collected in the Fraser River estuary in August in 1976 and measured 20 and 23 cm, were alive in the laboratory in August 1979. The presence of young lamprey in these aggregations, the failure to observe lamprey attached to migrating maturing salmon in freshwater and the observation that maturing Pacific lamprey enter freshwater in the spring, indicates that the aggregations of Pacific lamprey contain younger lamprey and not adults preparing to migrate immediately into freshwater unlike the river lamprey that were captured at the same time.

Pacific lamprey in this study were observed to attack rockfish (*S. aleutianus* and *S. reedi*), Pacific cod (*Gadus macrocephalus*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lingcod (*Ophiodon elongatus*), and sable fish (*Anoplopoma fimbria*). Pike (1950, 1951) recorded lamprey attacks on steelhead trout (*Salmo gairdneri*), Pacific halibut (*Hippoglossus stenolepis*), and whales. In the Bering Sea Pacific lamprey fed on the greenland turbot (*Reinhardtius hippoglossoides*), the arrowtooth flounder (*Atheresthes stomias*), the Kamchatka flounder (*Atheresthes evermanni*), sablefish, Pacific ocean perch (*Sebastes alutus*), and Pacific cod (Novikov 1963; Abakumov 1964). In one study in the Bering Sea, Pacific lamprey attacks were observed on about one-third of all greenland turbot examined (Novikov 1963) and as many as 55% in some hauls had scars or fresh lamprey wounds (Abakumov 1964). The lamprey attacks were almost exclusively on the blind side.

Unlike river lamprey, Pacific lamprey feed in a manner similar to the sea lamprey (Parker and Lennon 1956). Pacific lamprey attacked ventrally and anteriorly leaving 1–3 cm holes in the flesh. A common place of attachment on pollock was just behind the pectoral fin. The anterior ventral area was a common scarring location on sockeye salmon. In the laboratory and in the ocean, multiple attachments occur especially by young metamorphosed lamprey. In the laboratory, lamprey will remain attached to a host for varying periods that last up to several days. Feeding in the laboratory continued throughout the year suggesting feeding in the ocean continues throughout the year.

Distribution

From 1975 to mid-1979, 66 Pacific lamprey were captured during fishing operations on research cruises in the Strait of Georgia. In addition, fishermen frequently captured Pacific lamprey attached to sockeye salmon caught in troll and gill nets in the Strait of Georgia. For example, on August 26 to 27, 1979 one fisherman landed 17 Pacific lamprey that ranged in size from 16 to 20 cm. Only nine Pacific lamprey have been obtained from other areas off British Columbia; however, scars or wounds have been observed during research cruises off the west coast of the Queen Charlotte Islands, in Dixon Entrance, Hecate Strait, Queen Charlotte Sound, and off the west coast of Vancouver Island. The relatively large number of lamprey attacks reported in the area off the west coast of Vancouver Island may indicate a relatively high abundance in this area. It is expected that other areas of high relative abundance will be identified in the future because observations of lamprey attacks and collections of lamprey have been solicited from fishermen only in the last few years. Despite the relatively few accounts of lamprey attacks, Pacific lamprey have been observed in all the important commercial fishing areas off Canada's west coast and their number and distribution certainly are greater and more widespread than indicated by current reports.

Predation on Pacific Lamprey

The extent that other animals feed on Pacific lamprey is unknown but various accounts of animals feeding on lamprey indicate that lamprey may be consumed more often than formerly thought. Eighty-two percent of the observed feedings of Steller sea lions (*Eumetopias jubatus*) feeding at the mouth of the Klamath River, California were on Pacific lamprey. Two sea lions that were shot had stomach contents composed entirely of Pacific lamprey (Jameson and Kenyon 1977). One of a group of seals thought to be feeding on sockeye salmon smolts in the Skeena River was shot as part of a program to reduce the nuisance to salmon net fishermen (the program was terminated about 1962). The stomach of the seal contained two lamprey apparently from a group of nearby spawning lamprey (A. Peden, British Columbia, Provincial Museum, personal communication). A fishery officer in the Skeena River area reported that in January he observed a mink (*Mustela vison*) with a live lamprey in its mouth. Pacific lamprey have also been found in the stomach of a sperm whale (*Physeter catodon*) (Pike 1950) and fur seals (Hubbs 1967). In the present study, portions of tails of upstream migrating adult lamprey in freshwater occasionally were missing. In a laboratory experiment, a spiny dogfish (*Squalus scanthias*) bit off the posterior 2–3 cm of the tail of a lamprey and the lamprey survived. As part of another study, spiny dogfish and sablefish fed actively on freshly killed adult Pacific lamprey, consuming about two to three lamprey each in a 15-min period.

Movements and Duration of Saltwater Life

Little evidence is available to indicate whether or not Pacific lamprey from Canadian rivers migrate extensive distances. Larkins (1964) recorded catches of Pacific lamprey during a high seas salmon sampling program suggesting that Pacific lamprey do actually move into the high seas. However, the catches were made 60–150 km south of the Aleutian Islands and possibly were fish from local rivers on the Aleutian Islands. Pacific lamprey have been observed in the central and western regions of the Bering Sea (Novikov 1963) and in rivers in Japan (Hubbs 1971). It is unknown if Pacific lamprey spawn in Asiatic rivers but it is possible that at least some of the observed specimens migrated or were carried into these waters and were endemic to North America. Pletcher (1963) felt that total length might be related to the length of the migratory journey as proposed by Lack (1954) for anadromous fishes. If this is true, then the larger Pacific lamprey that are found in the Fraser, Skeena, and Stamp rivers (40–72 cm range) may range farther than some stocks of smaller Pacific lamprey. It is also possible that size may be related to the duration of feeding, and that lamprey spending longer periods in salt water grow to larger sizes. Certainly Pacific lamprey move offshore and it is probable that some lamprey or some stocks of lamprey migrate considerable distances.

The length of time spent by Pacific lamprey in salt water is unknown and possibly is different for different stocks. Since traditional methods of age determination or tagging could not be used to estimate the time spent in salt water, a simple laboratory holding and feeding experiment was initiated in October 1975 using 15 Pacific lamprey that were captured during midwater trawling operations in June 1975 in the Strait of Georgia (Fig. 7). These lamprey ranged in length from 18 to 40 cm and in weight from 13 to 83 g. They were given salmon and a variety of other species to feed on and were left untouched. By December 1975, 12 lamprey remained alive; in December 1976, 7 remained; in December 1977, 4 remained and in December 1978, 3 were alive. One died and one was lost in January 1979 and the remaining fish died in May 1979. Some lamprey died as a result of culture problems, but most dead fish were mature and presumably ready to spawn. If December can be considered to approximate the time of entry into salt water, the three lamprey alive in December 1978 completed at least 4-yr residence in salt water. Similar experiments were repeated in 1976, 1977, 1978, and 1979 and the results to date are similar.

It is possible that the remaining fish in December 1978 were older than one year in December 1975 and it also can be argued that if these lamprey had been in a natural system they would return to freshwater at an earlier date. River lamprey held in tanks in this study did not survive past the normal spawning time indicating laboratory observations were representative of the natural life cycle. Most landlocked sea lamprey (*Petromyzon marinus*) held in laboratory tanks, matured and showed signs of irreversible physical degeneration (Parker and Lennon 1956) at about the same time as reported for wild fish (Applegate 1950). However, Parker and Lennon (1956) did observe that a few lamprey survived longer than others. Thus it appears that holding in the laboratory may extend the parasitic life of some lamprey. It is also possible that some lamprey do have a longer parasitic period than other individuals of the same species since variation in the duration of saltwater life is known to occur

TABLE 5. Size of maturing Pacific lamprey in freshwater.

Location		Mean length (cm)	Range (cm)	No.
Quinsam River	1978[a,h]	20	18–26	7
Chemainus River	1978[b,h]	27	17–38	131
Bonsall Creek	1978[b,h]	26	13–31	18
Qualicum River	1978[a,h]	19	16–24	6
Kennedy Lake tributary river	1979[a,c,h]	29	23–45	5
Robertson Creek	1978[a,d,j]	28	22–40	11
Babine Lake unnamed creek	1979[a,c,j]	49	42–59	52
	1979[i]	48	41–56	255
	total	48	41–59	307
Babine Lake	1979[b,e,i]	64	55–67	14
Bulkley Falls	1979[b,f,j]	60	55–69	32
	1979[i]	58	48–65	46
	total	59	48–69	78
Moricetown Falls	1979[b,g,i]	64	56–72	9
Stamp River	1979[b,j]	29	23–51	1226

[a]Sampled during spawning period.
[b]Sampled during upstream migration.
[c]49°35′N, 125°30′W.
[d]Robertson Creek is located in the vicinity of Stamp River (Fig. 1).
[e]54°N, 126°W.
[f]54°29′N, 129°16′W.
[g]55°02′N, 127°41′W.
[h]Measured after preservation in 5% formalin.
[i]Measured after freezing.
[j]Measured with no preservation.

for other anadromous fishes such as sockeye and chinook salmon (Hart 1973). If the laboratory observations are representative of a natural life cycle, Pacific lamprey remain and feed in salt water for a period up to 3½ yr if they return to freshwater in the spring.

There is a wide range in the size of adult Pacific lamprey. This difference in size is most obvious when the sizes of returning adults are examined (Table 5). The sizes recorded in freshwater probably underestimate the maximum size because maturing adult lamprey decrease in length as observed in this study and for other species (Beamish 1980; Larsen 1973). While the sample size in Table 5 is small it is apparent that mature Pacific lamprey range in length from 13 to at least 72 cm. Pletcher (1963) also describes a wide range of lengths for Pacific lamprey. The 66 specimens captured in this study in the Strait of Georgia and the 9 specimens found in other areas off the west coast of Canada ranged in size from 12 to 42 cm. It is possible that the very small mature Pacific lamprey found in the Qualicum and Quinsam rivers may not remain in salt water as long as the larger lamprey and some may even remain in freshwater. Until more information is available it might be assumed that the moderate to large lamprey (25–50 cm) spend approximately 3½ yr in salt water.

SEX RATIO

Little information was available concerning the sex ratio of adults captured at sea. Thirty-nine of the 61 specimens captured in the Strait of Georgia were sexed and the ratio was 1.4 males to 1 female. The sex ratios of males to females returning to the Stamp River, Bulkley River, Babine Lake, Chemainus River and Bonsall Creek were 2:1, 0.8:1, 1:1, 1:1, 1:1, respectively. Except for the Stamp River sample, the ratio of males to females was equal, thus it is probable that sex ratios at sea are about equal.

RETURN TO FRESHWATER

Since larger Pacific lamprey are found in only some rivers such as in the Skeena River system, it is probable that at least some lamprey return to their native streams to spawn. However, more information about the size compositions of adults from more rivers is needed before the importance of homing can be assessed.

Pacific lamprey have been reported to return to freshwater from May to September, overwinter in freshwater and spawn April to June and possibly as late as July (Pletcher 1963, Carl et al. 1967, Moffett and Smith 1950). In the Chemainus River, except for a few days, upstream traps were in place close to the mouth of the river from April 20 until June 27. A total of 131 adult lamprey were captured during the period April 23 to May 31 with 94% of the catches occurring between May 5 and 10. Sixty males and 64 females were captured with about equal numbers of males and females in the daily catches. In Bonsall Creek, the upstream trap close to the mouth of the river captured 18 adult Pacific lamprey from May 1 until May 17. The trap was in operation from April 15 until June 1 and equal numbers of males and females were captured.

In the Stamp River, Pacific lamprey were collected in an artifical river bypass or fishway, 14 km from the mouth of the river. The first sample was collected in mid-June, 1979 from an estimated 2500 individuals and at the end of August approximately 300 lamprey were still migrating through the fishway. Observations of movements of tagged lamprey confirmed that the lamprey were actually migrating through the fishway. By the end of September the fishway contained about 250 lamprey. While some lamprey tagged in August were still migrating through the fishway in September it appeared that most lamprey had completed their migration by mid-August. In 1980 no migration was observed until May and since the fishway is approximately 14 km from the ocean it is probable that upstream migrations commenced in April. At a fish counting fence, 400 km from the mouth of the Skeena River and 13 km downstream from Babine Lake, upstream migrating Pacific lamprey were first observed in mid-August at about the same time Pacific lamprey were observed in other tributaries of the Skeena River (Table 5). It was interesting that Pacific lamprey were observed spawning in the Babine Lake area in early July 1979 only 4–6 wk prior to the arrival of next year's spawning individuals. Since these sites are approximately 400 km from the mouth of the Skeena River it is probable that entry into freshwater occurred in April-May as observed in other rivers. Migration into one of the smaller headwater streams of the Skeena River was completed by the end of September 1979. The lamprey apparently remain in the uppermost region of the stream or in a small lake until they spawn in mid-June. Richards (1980) observed young-of-the-year ammocoetes in the uppermost regions of the tributary streams of the Chemainus River indicating adults migrated well upstream prior to spawning. The movement of adult Pacific lamprey into the headwater areas, often through rapids and over waterfalls indicates the species has exceptional migratory instincts. Spawning in the uppermost areas also allows for maximum usage of suitable stream habitats assuming young ammocoetes gradually migrate downstream.

Ovaries from upstream migrating lamprey in the Stamp River in August and the Skeena River in September occupied less than one-third to about two-thirds of the body cavity, respectively. Egg diameters for lamprey from the Stamp and Skeena rivers were approximately 1.0 and 0.7 mm, respectively. The abdomens of all females were not distended and there was no evidence of postanal length reductions or dorsal fin space reductions. Although the females were maturing there was little doubt that they were not close to spawning condition, indicating spawning would not occur until the following spring. Upstream migrants from the Stamp River, held in the laboratory in 1979/80, did not spawn until the spring following entry into freshwater.

It is important that a distinction is made between the time upstream migrations occur in freshwater and the time Pacific lamprey enter freshwater. The observations in this study indicate that entry into freshwater occurs from April to June while most migrations in freshwater streams probably are complete by late September. The statement that the return to freshwater occurs from May to October (Moffett and Smith 1950; Pletcher 1963; Hart 1973) fails to acknowledge that most lamprey enter freshwater early in the spring. This can result in the incorrect assumption mentioned earlier, that Pacific lamprey feeding on maturing salmon in estuaries migrate upstream with the salmon.

Spawning lamprey in June and July in Babine Lake averaged 48 cm in length (Table 5). Lamprey returning to Babine Lake, Bulkley Falls, and Moricetown Falls in August and September, all migrate up the Skeena River and had a similar mean length of 60 cm (Table 5). If average lengths are similar each year, Pacific lamprey in the Skeena River system decrease approximately 12 cm in length from the postmigration period until spawning is complete. This 20% average decrease in length is similar to the 21% decrease previously described for river lamprey, but undoubtedly underestimates the actual amount of shrinkage since the lengths at the time of entry into freshwater were unknown. As reported for other species (Beamish 1980) there was a disproportionate reduction in length of females (23%) compared to males (15%).

Pletcher (1963) observed that April to May was the main spawning period for Pacific lamprey. In this study, Pacific lamprey were observed spawning in a small stream flowing into Babine Lake in early July, 1979 and Pacific lamprey have been observed spawning in the Stamp River in April and in the Englishman River (Fig. 1) in June. Since entry into freshwater occurs from April to June and spawning occurs from April until early July, the average residence of maturing adults in freshwater is about 1 yr. If the period of saltwater residence is about 3½ yr for adults returning to freshwater in the spring, then the period of adult life from the onset of metamorphosis in July to death following spawning is 5 yr.

In smaller rivers, smaller Pacific lamprey were observed to spawn several kilometres from the mouth of the river. It is possible that entry into such rivers occurs in the same year as spawning and the length of saltwater residence may be shorter or longer than 3½ yr.

The spawning and nesting behavior of the Pacific lamprey has been described by Pletcher (1963) and appears to be similar to that of other lamprey. Following spawning, Pacific lamprey have been reported to survive until July (Moffett and Smith 1950). In this study dead, spawned Pacific lamprey were observed in Robertson Creek on Vancouver Island in late April and in Babine Lake in July. A sample of eight live

Pacific lamprey of various sizes that had recently spawned, died when they were reintroduced to full strength salt water in the laboratory over a 3-d period. A sample of six upstream migrating adult lamprey, collected in August 1979 from the fishway at Stamp River also could not be acclimated to salt water over a 3-d period. Thus, after Pacific lamprey enter freshwater in preparation for spawning, they do not return to salt water.

Effect on Commercially Important Fishes in Waters off Canada's West Coast

Very little is known about the size of stocks of Pacific lamprey, however, casual observations at fish counting fences and by commercial fishermen indicate that the numbers of Pacific lamprey may be increasing, at least in some areas. No Pacific lamprey were observed at the fish counting fence near Babine Lake from 1956 to 1962. From 1963 to the present the number of lamprey at the fence has been increasing (F. Jordan, Pacific Biological Station, Nanaimo, B.C., personal communication) and in 1977 I received the first unconfirmed report of a lamprey attacking a fish in Babine Lake. Williams and Gilhousen (1968) reported that fishermen first reported cases of severe lamprey parasitism on Fraser River sockeye in 1967. In 1979 several fishermen reported their first observations of lamprey attacking salmon off the west coast of Vancouver Island, while others reported the incidence of lamprey attacks on salmon was higher than in the past.

The number of streams and rivers that contain Pacific lamprey is unknown. However, Carl et al. (1967) believed Pacific lamprey may be present in all coastal streams and in this study all of the 10–20 streams that have been examined have contained Pacific lamprey. If all or almost all of the coastal streams and rivers contain Pacific lamprey, the numbers of adults may be large, and if Pacific lamprey remain in salt water for 3½ yr they may be an important and overlooked predator of juvenile and adult marine fishes.

Pacific lamprey contribute to the mortality of young salmon but the relative importance of this mortality is unknown. Active predation on juvenile sockeye salmon was observed in this study in the Strait of Georgia and some preliminary unpublished trapping information indicates that in some rivers the movements of Pacific lamprey and juvenile sockeye salmon into salt water are synchronous. Preliminary results from laboratory feeding experiments indicate that one Pacific lamprey in its first year in salt water can kill one salmon of 15–20 cm in length about every 2–4 d. Thus the attacks and in some cases resulting mortalities may be more important than formerly thought. The non-anadromous parasitic lamprey in Mesachie Lake attack a significant number of the resident salmonids. A sample of 221 salmonids contained 122 fish with lamprey attacks and 32 of these attacks (15%) penetrated the body cavity or penetrated deeply into the muscle and probably would result in the death of the fish. Salmonids that were killed by lamprey attacks have been found on the bottom of Mesachie Lake from June until September when observations were terminated. It is apparent that Pacific lamprey are an active predator of marine and sometimes freshwater fishes; however, their role as a predator of commercially important species in relation to other predators is difficult to assess until better estimates of their abundance and food preferences can be determined.

Comparisons and Conclusions

While there is much more to learn about river and Pacific lampreys, it is apparent that the two species differ greatly in many aspects of their adult biology. It is suspected that the date of metamorphosis is similar but it appears that Pacific lamprey enter salt water earlier and perhaps over a longer period. Downstream trapping and fishing in salt water suggested that Pacific lamprey enter salt water in late fall or early winter and continue to enter salt water into the summer. The bulk of river lamprey catches occurred in downstream traps in late May and June and no river lamprey were found in salt water in April or May.

Once in salt water, river lamprey were found in the surface waters and concentrated in the general vicinity of the larger rivers suggesting river lamprey preferred water of reduced salinity. Pacific lamprey were found at greater depths often associated with layers of plankton. Pacific lamprey were more abundant than river lamprey but river lamprey could not be considered to be rare. While Pacific lamprey or evidence of Pacific lamprey attacks were observed on fishes associated with the midwater depths, the evidence of rather substantial predations on greenland turbot from the Bering Sea indicates that this species occurs throughout a wide depth range when at sea. Pacific lamprey or animals attacked by Pacific lamprey were caught well offshore indicating that Pacific lamprey migrated greater distances than river lamprey. River lamprey had a more restrictive diet preferring smaller herring and some smaller salmon. They attacked dorsally and anteriorly and consumed chunks of tissue. Pacific lamprey may feed on herring when first in salt water but generally feed on a variety of fishes and mammals. Pacific lamprey attacked ventrally or laterally apparently preferring body fluids to chunks of flesh.

Adult Pacific lamprey can be much larger than river lamprey, partly as a result of the longer period Pacific lamprey spend in salt water. Pacific lamprey can remain in salt water for 3½ yr while river lamprey may spend only 3–4 mo in salt water. River lamprey may return to freshwater over the period September to May but stocks of Pacific lamprey enter freshwater from April to June. The period of freshwater residence for most maturing Pacific lamprey is about 1 yr but it may be shorter for some other stocks. The period of freshwater residence for maturing river lamprey may be about 8 mo or shorter. Both species decrease in length during the prespawning residence in freshwater and in this study both species decreased in length by approximately 20%. Both species die following spawning.

Predators on adult river lamprey appear rare while Pacific lamprey may be a more common food item of fishes, seals, sea lions, and mammals. It is possible that ammocoetes of both species are consumed by other fishes.

Lampetra ayresi was considered to be conspecific with the European river lamprey *Lampetra fluviatilis* before Vladykov and Follett (1958) reviewed the systematics of those two forms and concluded that they were separate species. Even though these two forms are now considered to be distinct species there are some remarkable similarities in their adult biology. *Lampetra fluviatilis* may prefer water of reduced salinity (Bahr 1952) and feeds on small fish apparently preferring herring species (Bahr 1933; Eglite 1958a, b). When feeding, chunks of muscle, pieces of fins, and internal organs are consumed and attacks frequently occur in the dorsal region (Eglite 1958a). Adults returning to freshwater average 31–34 cm (Berg 1948) but a wide range in sizes of adults has been found. The smaller forms have been described by Berg (1948) as being distinct "praecox" varieties. Berg (1948) noted that some adults return to freshwater in the fall and some in the spring. Hardisty and Potter (1971) consider that from metamorphosis to spawning the duration of adult life of *Lampetra fluviatilis* is about 2½ yr. This is slightly longer than the period of 2 yr observed for *Lampetra ayresi* in this study.

All of the preceding adult characteristics of *Lampetra fluviatilis* were similar to *Lampetra ayresi*. The similarities in form and the biology of the adults of these two species clearly suggest a close relationship at some time in the past.

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ABAKUMOV, V. A. 1964. Some data on the ocean period in the life-cycle of lamprey (*Entosphenus tridentatus* Richardson). Trudy vses. nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49: 253–256. (In Russian)

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus* in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

BAHR, K. 1933. Das Flussneunauge (*Lampetra fluviatilis*) als Urheber von Fischverletzungen. Mitt. Dtsch. Seefisch. Ver. 49(1): 3–8.

1952. Beitraege zur Biologie des Flussneunauges, *Petromyzon fluviatilis* L. (Lebensraum und Ernaehrung). Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere. 81: 408–436.

BARRACLOUGH, W. E., AND J. D. FULTON. 1967. Data record. Number, size composition and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–8, 1966. Fish. Res. Board Can. MS Rep. 940: 82 p.

BEAMISH, F. W. H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

BEAMISH, R. J., AND J. R. SCARSBROOK. 1979. Data for the study of the distribution and feeding habits of lampreys in the surface waters of the Gulf Islands and in the vicinity of the Fraser River, British Columbia. Fish. Mar. Serv. Data Rep. 136: 353 p.

BEAMISH, R. J., M. SMITH, R. SCARSBROOK, AND C. WOOD. 1976. Hake and pollock study, Strait of Georgia cruise G. B. REED, June 16–27, 1975. Fish. Mar. Serv. Data Rec. 1: 174 p.

BEAMISH, R. J., AND N. E. WILLIAMS. 1976. A preliminary report on the effects of river lamprey (*Lampetra ayersii*) predation on salmon and herring stocks. Fish. Mar. Serv. Res. Dev. Tech. Rep. 611: 26 p.

BERG, L. S. 1948. Freshwater fishes of the USSR and adjacent countries. Acad. Sci. USSR. Zool. Inst.: Guide to the Fauna of the USSR, No. 27. (Transl. from Russian for Nat. Sci. Found., Wash., D.C. by the Israel Program for Scientific Translations, Jerusalem, 1962. Vol. 1: 18–52, 494.)

BIRMAN, I. B. 1950. Parasitism of salmon of the genus *Oncorhynchus* by the Pacific lamprey. Vladivostok. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) Izv. 32: 158–160. (Transl. from Russian by Fish. Res. Board. Can., Transl. Ser. 290 (1960): 3 p.)

CARL, G. C. 1953. Limnobiology of Cowichan Lake, British Columbia. J. Fish. Res. Board Can. 9: 417–449.

CARL, G. C., W. A. CLEMENS, AND C. C. LINDSEY. 1967. The freshwater fishes of British Columbia. B.C. Prov. Mus., Handbook No. 5: 192 p.

EGLITE, R. 1958a. Feeding habits of *Lampetra fluviatilis* L. in the sea. Zool. Zh. 37(10): 1509–1514.

1958b. The biology of the river lamprey in the Latvian SSR. Gidrobiol. Issled., Tartu 1: 234–269.

HANSON, L. H., E. L. KING JR., J. H. HOWELL, AND A. J. SMITH. 1974. A culture method for sea lamprey larvae. Prog. Fish-Cult. 36(3): 122–128.

HARDISTY, M. W., AND I. C. POTTER [ed.]. 1971. The biology of lampreys. Academic Press. London, New York. Vol. 1: 424 p.

HART, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180: 740 p.

HUBBS, C. L. 1967. Occurrence of the Pacific lamprey, *Entosphenus tridentatus*, off Baja California and in streams of Southern California; with remarks on its nomenclature. Trans. San Diego Soc. Nat. Hist. 14: 301–312.

1971. *Lampetra* (*Entosphenus*) *lethophaga*, new species, the nonparasitic derivative of the Pacific lamprey. Trans. San Diego. Soc. Nat. Hist. 16: 125–164.

JAMESON, R. J., AND K. W. KENYON. 1977. Prey of sea lions in the Rogue River, Oregon. J. Mammal. 58(4): 672.

KAN, T. T. 1975. Systematics, variation, distribution and biology of lampreys of the genus *Lampetra* in Oregon. Ph.D. thesis, Oregon State Univ., Corvallis, OR. 194 p.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 p.

LARKINS, H. A. 1964. Some epipelagic fishes of the North Pacific Ocean, Bering Sea, and Gulf of Alaska. Trans. Am. Fish. Soc. 93: 286–290.

LARSEN, L. O. 1973. Development in adult, freshwater river lampreys and its hormonal control. Starvation, sexual maturation and natural death. Copenhagen. 172 p.

MASON, J. C. 1974. Movements of fish populations in Lymn Creek Vancouver Island: a summary from weir operations during 1971 and 1972 including comments on species life histories. Fish. Mar. Serv. Tech. Rep. 483: 35 p.

MOFFETT, J. W., AND S. H. SMITH. 1950. Biological investigations of the fishery resources of Trinity River, California. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 12: 70 p.

MORRIS, R. 1971. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

NOVIKOV, N. P. 1963. Attacks of *Entosphenus tridentatus* on halibut and other fish of the Bering Sea. Vopr. Ikhtiol. 3(28): 567–569.

PARKER, P. S., AND R. E. LENNON. 1956. Biology of the sea lamprey in its parasitic phase. U.S. Fish. Wildl. Serv. Res. Rep. 44: 32 p.

PIKE, G. C. 1950. Stomach contents of whales caught off the coast of British Columbia. Fish. Res. Board Can. Prog. Rep. Pac. Coast Stations 83: 27–28.

1951. Lamprey marks on whales. J. Fish. Res. Board Can. 8(4): 275–280.

PLETCHER, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. MSc. thesis, Univ. British Columbia, Vancouver, B.C. 195 p.

RICHARDS, J. E. 1980. Freshwater life history of the anadromous Pacific lamprey *Lampetra tridentata*. M.Sc. thesis, Univ. Guelph, Guelph, Ont., Canada. 99 p.

ROBINSON, D. G. 1969. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–6, 1967. Fish. Res. Board Can. MS Rep. 1012: 71 p.

ROBINSON, D. G., W. E. BARRACLOUGH, AND J. D. FULTON. 1968a. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia May 1–4, 1967. Fish. Res. Board Can. MS Rep. 964: 105 p.

1968b. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 5–9, 1967. Fish. Res. Board Can. MS Rep. 972: 109 p.

ROOS, J. F., P. GILHOUSEN, S. R. KILLICK, AND E. R. ZYBLUT. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia by the river lamprey (*Lampetra ayresi*). J. Fish. Res. Board Can. 30: 565–568.

SCARSBROOK, J. R., R. J. BEAMISH, AND M. S. SMITH. 1980. Hake and pollock study, Strait of Georgia, G. B. REED cruise May 31–June 18, 1976. Can. Data. Rep. Fish. Aquat. Sci. (In press)

SOLDATOV, V. K. 1934. Fishery Ichthyology. Part I. Cited by I. B. Birman. 1950. Fish. Res. Board Can., Transl. Ser. 290: 3 p.

VLADYKOV, V. D., AND W. I. FOLLETT. 1958. Redescription of *Lampetra ayresii* (Günther) of western North America, a species of lamprey (Petromyzontidae) distinct from *Lampetra fluviatilis* (Linnaeus) of Europe. J. Fish. Res. Board Can. 15(1): 47–77.

1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 22: 139–158.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 14: 321–486.

WILLIAMS, I. V., AND P. GILHOUSEN. 1968. Lamprey parasitism on Fraser River sockeye and pink salmon during 1967. Int. Pac. Salmon. Fish. Comm. Prog. Rep. 18: 22 p.

WITHLER, F. C. 1955. Coho salmon fingerling attacked by young lamprey. Fish. Res. Board Can. Pac. Prog. Rep. 104: p. 15.

YOUSON, J. H., AND I. C. POTTER. 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 57: 1808–1817.