Abundance and Freshwater Migrations of the Anadromous Parasitic Lamprey, Lampetra tridentate, in a Tributary of the Fraser River, British Columbia

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Abundance and Freshwater Migrations of the Anadromous Parasitic Lamprey, *Lampetra tridentata*, in a Tributary of the Fraser River, British Columbia

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The migration of young adult *Lampetra tridentata* out of the Nicola River during 1984–85 through 1987–88 was estimated to be approximately 176 000, 19 000, 90 000, and 102 000; at the same time, approximately 749 000, 909 000, 920 000, and 605 000 large ammocoetes, age 4 and 5 yr, left the river. Migration of young adults started in September, with the largest number migrating from mid-March to mid-May. Ammocoetes behaved similarly except that movement continued throughout the year. Most young adults metamorphosed at age 4 or 5 and were age 5 or 6 when they migrated to sea. It was not determined when lamprey from the Nicola River reached salt water; however, *L. tridentata* entered the Strait of Georgia from the Fraser River from March until July. Maturing adults first returned to the Nicola River from the ocean in August when water levels in the river were at their lowest. This is the first estimate of abundance of young adult *L. tridentata* in any river in the Fraser River drainage. The very large number of young adults and older ammocoetes leaving the Nicola River indicate that parasitic lamprey are abundant in the Fraser River and that they are potentially a common predator of commercially important fishes.

Selon nos estimations, environ 176 000, 19 000, 90 000 et 102 000 jeunes *Lampetra tridentata* de stade adulte sont sortis de la rivière Nicola de 1984–1985 à 1987–1988; durant la même période, il est aussi parti environ 749 000, 909 000, 920 000 et 605 000 grands ammocètes de 4 et 5 ans. La migration des jeunes adultes a commencé en septembre; les plus gros contingents ont migré de la mi-mars à la mi-mai. Il en a été de même pour les ammocètes, sauf que leur migration s'est poursuivie toute l'année. La plupart des jeunes adultes se sont métamorphosés à 4 ou 5 ans et avaient 5 ou 6 ans lorsqu'ils ont migré vers l'océan. Nous n'avons pas déterminé quand les lamproies de la rivière Nicola arrivent en eau salée; nous savons néanmoins que *L. tridentata* est entré au détroit de Géorgie, arrivant du Fraser, de mars jusqu'à juillet. Les adultes en maturation ont commencé à migrer de l'océan jusqu'à la Nicola en août, lorsque le niveau de l'eau de la rivière était au plus bas. C'est la première fois que l'on estime l'abondance du jeune *L. tridentata* de stade adulte dans une rivière du bassin du Fraser. Le fait que le nombre de jeunes adultes et d'ammocètes plus âgés quittant la Nicola soit aussi élevé indique que la lamproie parasite est très abondante dans le Fraser et qu'elle pourrait être un prédateur répandu de poissons commercialement importants.

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The Pacific lamprey, *Lampetra tridentata*, is a wide-ranging anadromous parasitic lamprey that occurs in coastal rivers from southern California to the Aleutian Islands in Alaska. In British Columbia, Pacific lamprey occur in most rivers, including the large Fraser River and Skeena River drainages (R. J. Beamish, unpubl. data). Despite the wide distribution in British Columbia, little is known about its abundance or the number and type of prey that are killed during the marine feeding phase. This lack of knowledge probably is related to the difficulty of observing or capturing metamorphosed lampreys.

Pacific lamprey reside as ammocoetes in the fine sediments in shallow backwater areas of streams for approximately 5 yr before they metamorphose into the adult form (Russell 1986; Beamish and Northcote 1989). After migrating to sea between the fall and the spring, Pacific lamprey feed on marine fishes for at least 1 yr (Beamish 1980). Adults return to fresh water in the spring. After migrating into headwater areas, adults spawn and die in the following spring (Pletcher 1963; Beamish 1980; Farlinger and Beamish 1984). It is only during brief periods in the upstream migration and the few weeks of spawning that metamorphosed Pacific lamprey are easily observed.

The relative absence of observations has created the impression that this lamprey is not commonly found and consequently is relatively unimportant as a source of mortality of commercially important fishes. If abundance of either downstream or upstream migrating lamprey were known, it would be possible to begin to estimate the relative importance of lamprey preda-

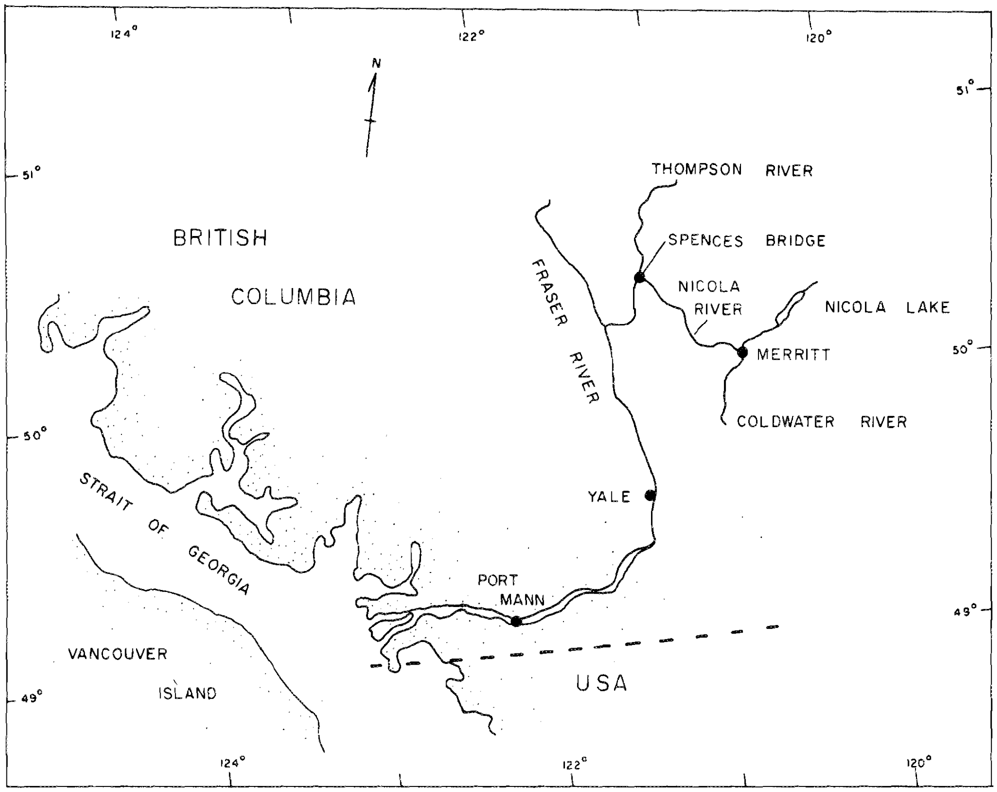

FIG. 1. Location of study and sampling sites.

tion. Unfortunately, it is still difficult to catch lampreys during the upstream migration of adult Pacific lamprey. It is possible to sample the downstream migration. Downstream-migrating lamprey are often captured with salmon. As part of a study of winter movements of juvenile salmon, we extended sampling beyond the normal period of juvenile salmon trapping and obtained information about lamprey movements and abundance.

The information collected in this study was obtained during a study of chinook salmon, *Oncorhynchus tshawytscha*, in the Nicola River (Levings and Lauzier 1989). Sufficient data were obtained to provide the first estimates of abundance of young adult Pacific lamprey from a major west coast river. In addition, we obtained information on the timing of migration in and out of the Nicola River, a tributary of the Thompson River which flows into the Fraser River. The Fraser River has the largest drainage area in British Columbia of approximately 230 400 km^2 and contributes more salmon to the commercial fishery than any other watershed. The Fraser River is 1253 km long with more than 300 rivers and streams in the watershed. Because Pacific lamprey are frequently found in the same rivers as salmon, we suspect that Pacific lamprey occur in a number of these 300 rivers.

Materials and Methods

Migrating lamprey were trapped using floating inclined plane traps (Conlin and Tutty 1979) with a 0.61 × 0.92 m (2 × 3 ft) opening. The stainless steel mesh of the inclined plane and live box has a 4-mm mesh size. The traps were suspended from a block and cable system attached to a bridge near the town of Spences Bridge, B.C. The bridge over the Nicola River is 300 m upstream of the confluence of the Nicola and Thompson rivers. Sampling began on March 21, 1985, and continued until freeze-up on November 9, 1985. Sampling resumed on March 10, 1986, and continued until December 1, 1986. Sampling resumed on February 9, 1987, and terminated on May 15, 1987. In 1988, two sites were sampled. Sampling at the mouth of the Nicola River started on March 10 and continued until August 19. Inclined plane trap sampling was also carried out from February 18 until July 20 on the Nicola River at Merritt (Fig. 1). This site is 4 km above the confluence of the Nicola and Coldwater rivers. Except during extreme freshets, two traps were used at Spences Bridge, one within 2 m of the shoreline and another closer to the centre of the river, about 5 m from shore. The block and cable system allowed adjustment of the position of each trap in the river to fish slow or fast water as streamflow conditions changed. During freshet, only the trap closest to the stream bank was used because debris has to be continually removed. Under average flow conditions, the river was approximately 20 m wide. At Merritt the river was usually 8 m wide.

Under normal conditions, traps were checked and catches were enumerated in the morning (06:00–09:00) and evening (18:00–21:00). Surface water temperature and water height were taken in the morning.

At extreme freshet, the trap was fished between 21:00 and 02:00 because of excessive debris. Results of 24-h test fishing during freshet conditions gave the proportion of lamprey caught in a particular time during the 24-h period. The catch of a reduced sample period was divided by the calculated expected proportion for a particular flow regime for a 24-h period, resulting in a standardized 24-h catch.

Total numbers of lamprey leaving the river were estimated using the volume passing through the traps. A Marsh-McBirney electromagnetic current meter (model 201) was used to measure water velocities at both sides and at the centre of the trap mouth. The water volume was calculated from the depth of the trap mouth floor and the water velocities. Nicola River streamflow was obtained from the Water Survey of Canada gauge No. 08LG006 located 13 km upstream of the trap site. There is negligible addition of water from tributaries between the gauging station and the trap site. The volume passing through the trap was divided by the discharge of the Nicola River to determine the proportion of the Nicola River discharge the traps were sampling.

The 24-h catch was divided by the fraction of discharge sampled by the trap to estimate the total number of migrants. We assumed a homogeneous distribution of lamprey across the river and averaged the catches from the two traps. On days the traps were not fished, a mean was taken of the previous day's estimate and the following day's estimate.

Samples of young adult lamprey and ammocoetes were collected during the periods of maximum migration and preserved in 5% formalin. Specimens were measured and examined for sex in the laboratory. Sex was determined by visual examination and a subsample was checked histologically. Live young adults and ammocoetes were sampled in the laboratory for age determination. Statoliths were removed using the procedure of Volk (1986). Age was determined using the criteria of Volk (1986) and Russell (1986). Ages of lamprey sampled after January 1 were assigned assuming a January 1 birthday. This means that a statolith from a lamprey sampled in April that had a translucent edge and had five opaque zones or annuli was aged as 6 yr. All ages were assigned without knowledge of the size of the lamprey. Ages were determined by two readers, and any statoliths that were not aged identically were reexamined. Final ages were compared with the lengths of the lamprey. At this stage, 15% of the age estimates appeared anomalous and were aged again.

A banding pattern was most obvious when statoliths were examined immediately after they were removed from the lamprey and placed in immersion oil. The position of the statoliths that produced the optimal contrast between translucent zones and opaque zones was found by manipulating the statolith within the beam of transmitted light (see Beamish and Northcote (1989) for photograph of a statolith).

Two samples of young adults were collected (February 2 at Merritt and March 8 at Spences Bridge) from the traps for age determination in 1988. Lamprey from the February sample were weighed and sex was determined in addition to sampling the statoliths and measuring lengths. Samples of ammocoetes and young adults were collected from the mouth of the Nicola River using electroshockers on October 8–11 and 23–24, 1986, and measured without preservation. The combined length–frequency of lamprey collected by electroshocking was aged using a running average of five. Statoliths were removed from a few of the smaller ammocoetes. Ages estimated from these statoliths were not recorded using the January 1 birthday because it was assumed growth was completed, that is, a 1+ ammocoete was recorded as age 2. Adjusting the age estimate in this manner facilitates the comparisons of growth and age at metamorphosis in this study.

In 1986, adults migrating upstream were captured at a site 6 km upstream of the mouth of the Nicola River. A modified fyke net was set on the margin of the river with the wings and opening facing downstream. The wings were made of 0.5-cm wire mesh and the trap was covered with netting of similar mesh size. The width of the wings at the widest point fished approx-

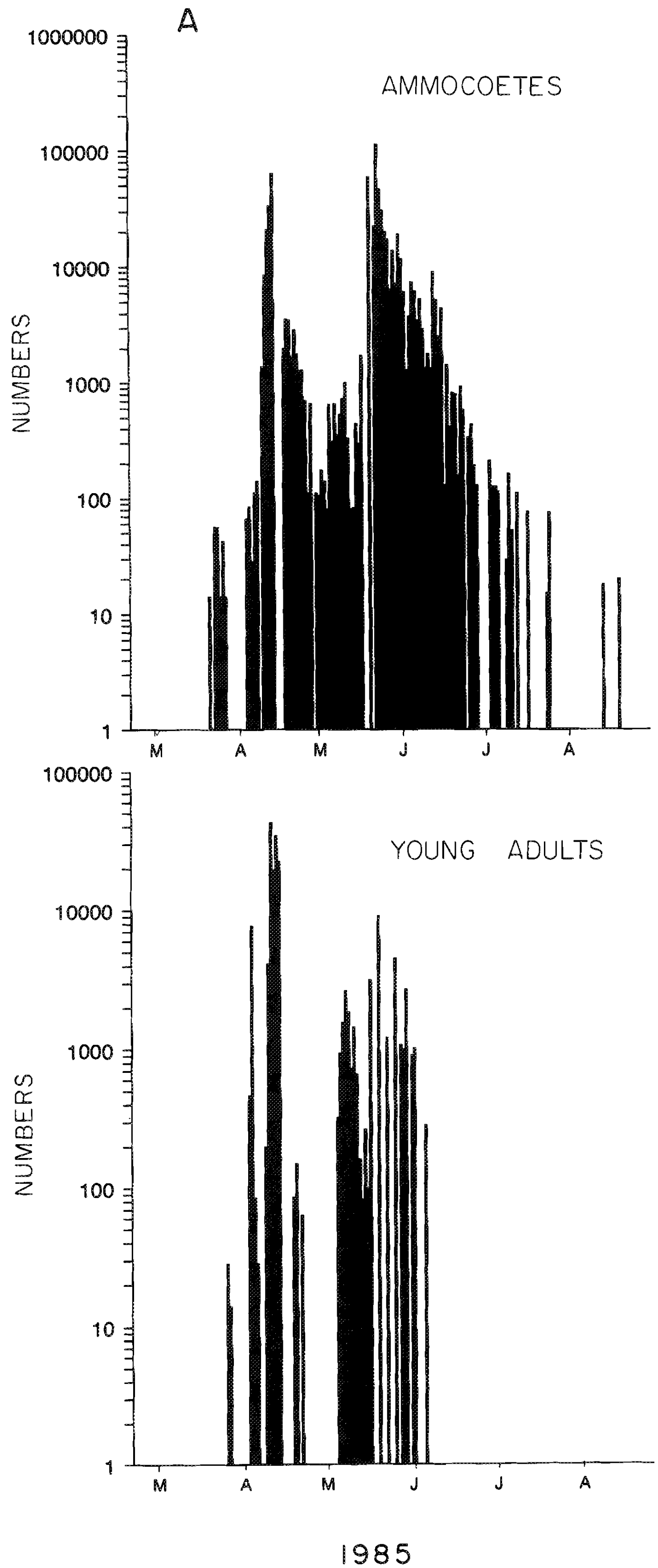

FIG. 2. Calculated daily numbers of young adults and ammocoetes migrating downstream. (A) 1985; (B) September 1, 1985, to August 31, 1986; (C) September 1, 1986, to August 31, 1987; (D) 1988; (E) 1988 at the Merritt site. (*Fig. 2 continued next page*)

(Fig. 2 continued next page)

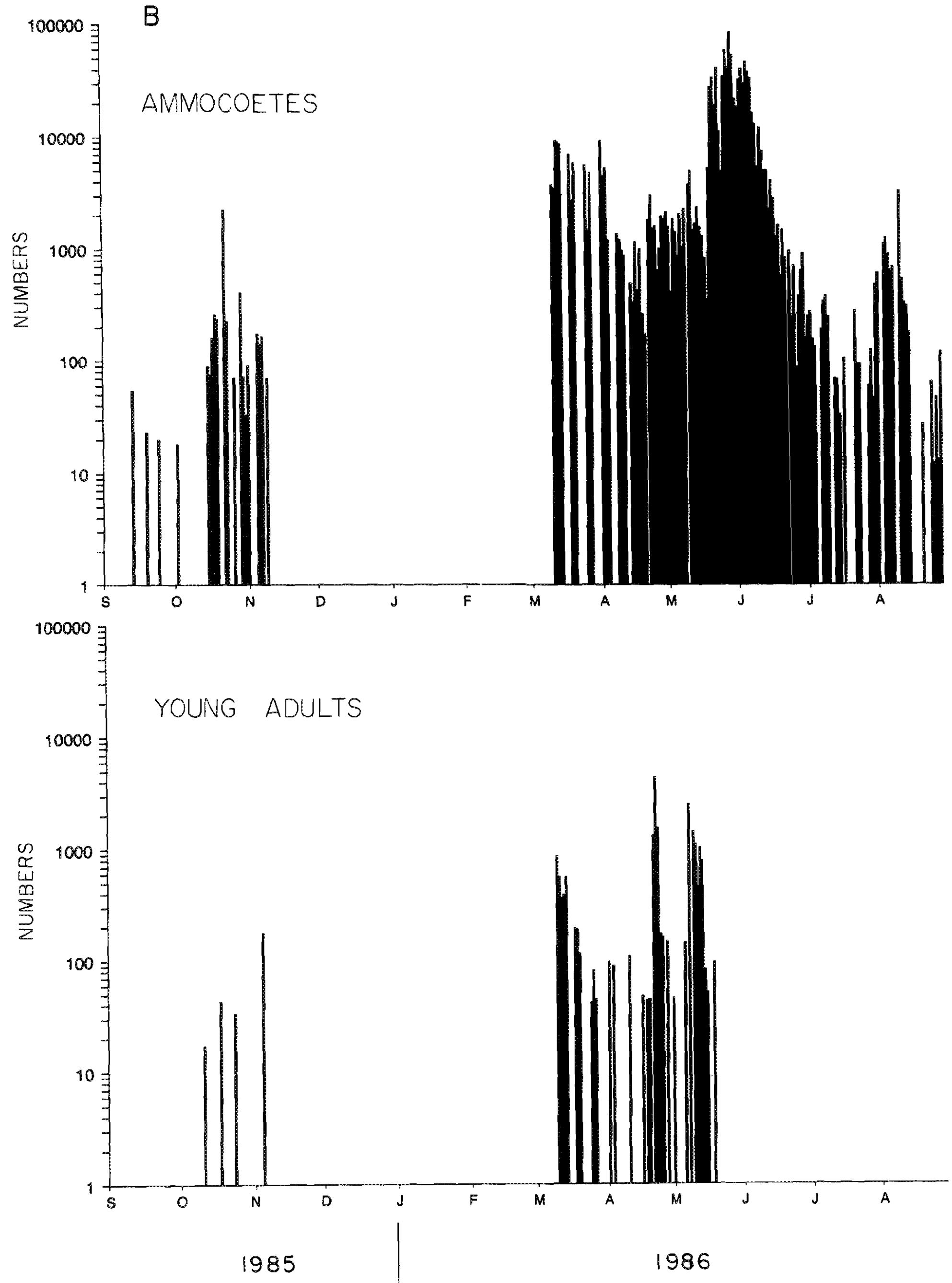

FIG. 2. (*Continued*)

imately 10% of the width of the river. The trap was operated from July 25 until mid-October and was checked daily.

Mature adults migrating up the Fraser River were sampled in 1983 at Yale, 170 km from the mouth of the Fraser River and 118 km downstream from the mouth of the Nicola River. Adult lamprey were jigged as they migrated upstream along the edge of the river in a steep gorge. Jigs were 2-m poles with 8–10 three-pronged fish hooks lashed along the top of the pole.

Lamprey were also collected in 1988, 36 km from the mouth of the Fraser River at Port Mann. A surface trawl with a 0.3-cm codend mesh was fished from February 25 until August 3. The net was fished twice a week according to the procedures described by Whitehouse et al. (1989).

Results

Young Adults

Downstream migration

Lampetra tridentata begin metamorphosis in the summer and complete metamorphosis, including the ability to osmoregulate in salt water, in the fall (Richards and Beamish 1981). Short periods of downstream migration of young adults started in September. In 1985 and 1986 the first downstream migrations occurred on October 11 and September 25, respectively (Fig. 2B, 2C). It is unknown if migration out of the river continued under the ice (November–February 1985–86). In 1986, the ice

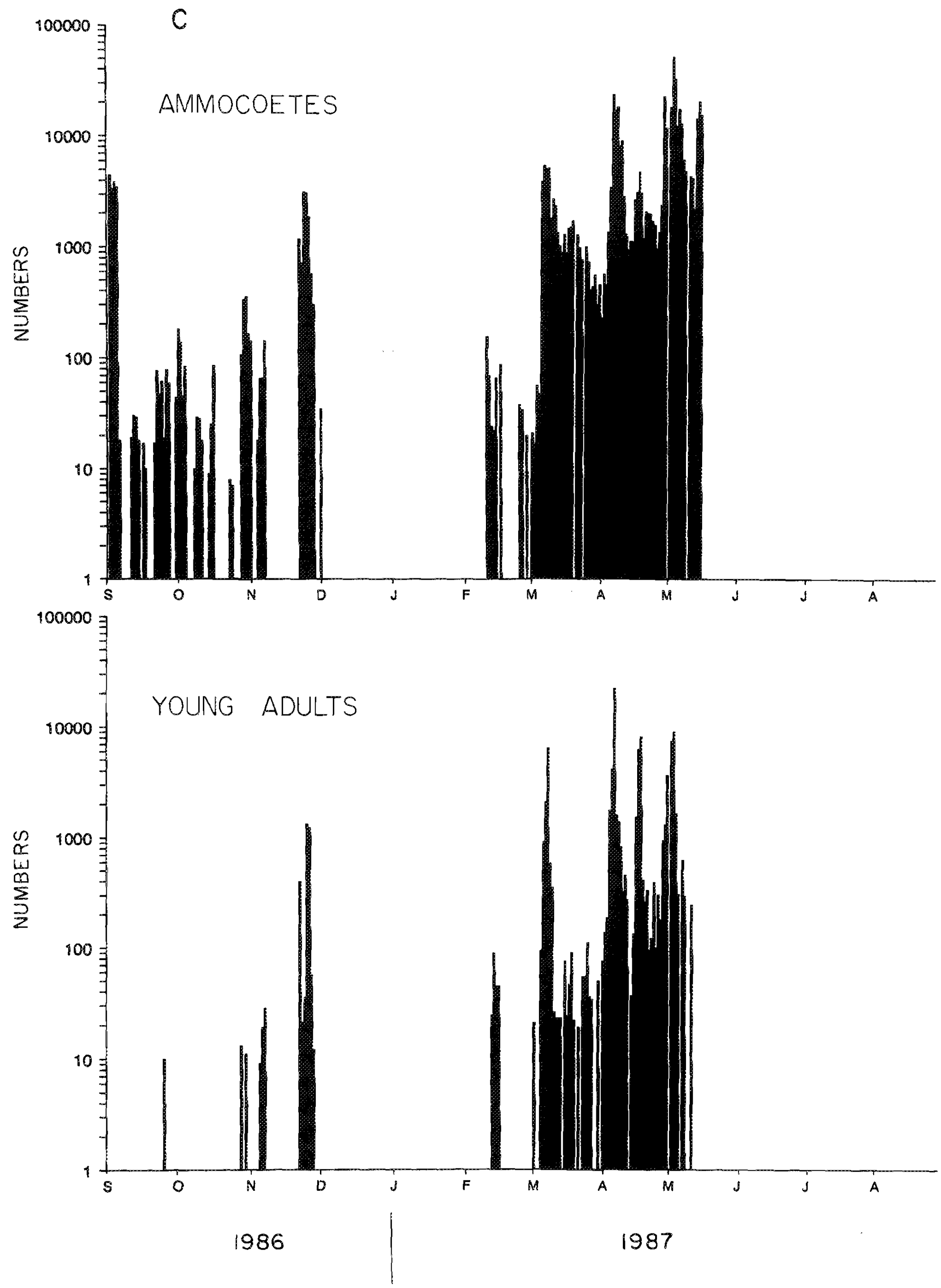

FIG. 2. (*Continued*)

left the river in November after a brief freezing period in early November. Trapping during this ice-free period caught young adults. Traps installed shortly after ice breakup in the late winter immediately captured young adult lamprey. The earliest catches after ice left the river occurred in mid-February in 1987 and 1988 (Fig. 2C, 2E). In 1985 (Fig. 2A), 99% of the all young adults left the river in April and May; 82% left during these two months in 1985–86 (Fig. 2B) and it is possible that a similar pattern of migration occurred during these two months in 1986–87 (Fig. 2C). In 1988, 99.5% of the young adults passed by the trapping site at the mouth of the Nicola River (Fig. 2D) and 92% at the Merritt site (Fig. 2E) in April and May. The downstream migrations from 1985 to 1987 ended abruptly in mid-May or early June. In 1988, metamorphosed lamprey were captured up to July 29 at Merritt, when trapping stopped (Fig. 2E). However, no lamprey were caught in July or August downstream at Spences Bridge.

The correlation between the numbers of downstream migrants, morning temperature, and discharge was examined for the spring–summer migration in 1985 (Fig. 3, 4). The multiple regression identified discharge as the only parameter that showed a significant relationship with the young adults migrating each day ($p < 0.01$). For example, in 1985 the downstream migrants were most numerous on April 3–5, April 10–16, May 5–13, and May 16–22. Abrupt increases in discharge occurred on April 3 and 10 and May 7 and 17 (Fig. 3). None of the parameters showed a significant relationship with ammocoete migration ($p > 0.05$). At Merritt, the large

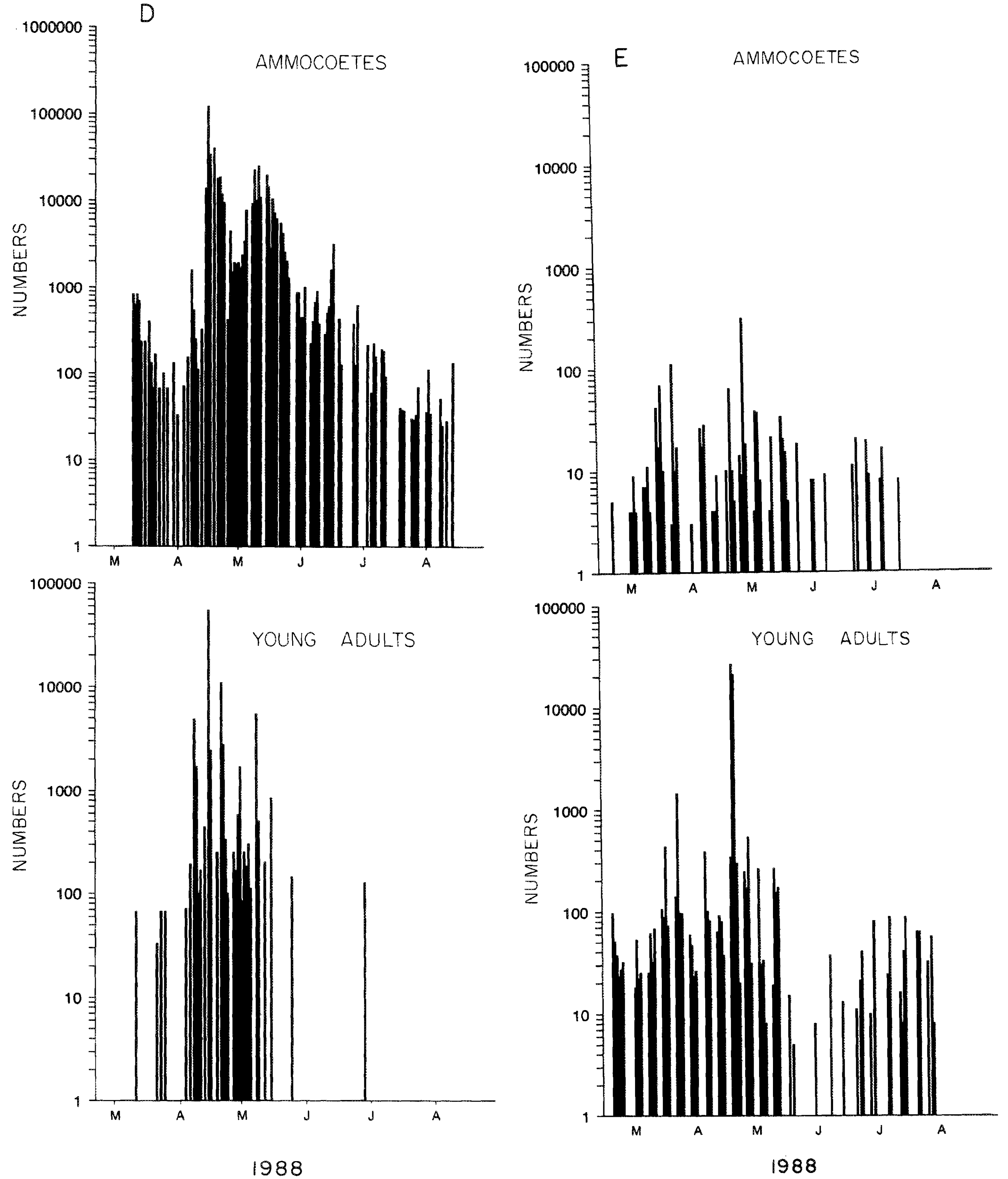

FIG. 2. (*Concluded*)

migrations on April 20 and 21 were not preceded by major increases in discharge. Discharge at this site is controlled by a dam on Nicola Lake.

Lengths

In 1985, the average length of 1331 young adults collected throughout the spring migration was 12.1 cm. In 1986, a sam-

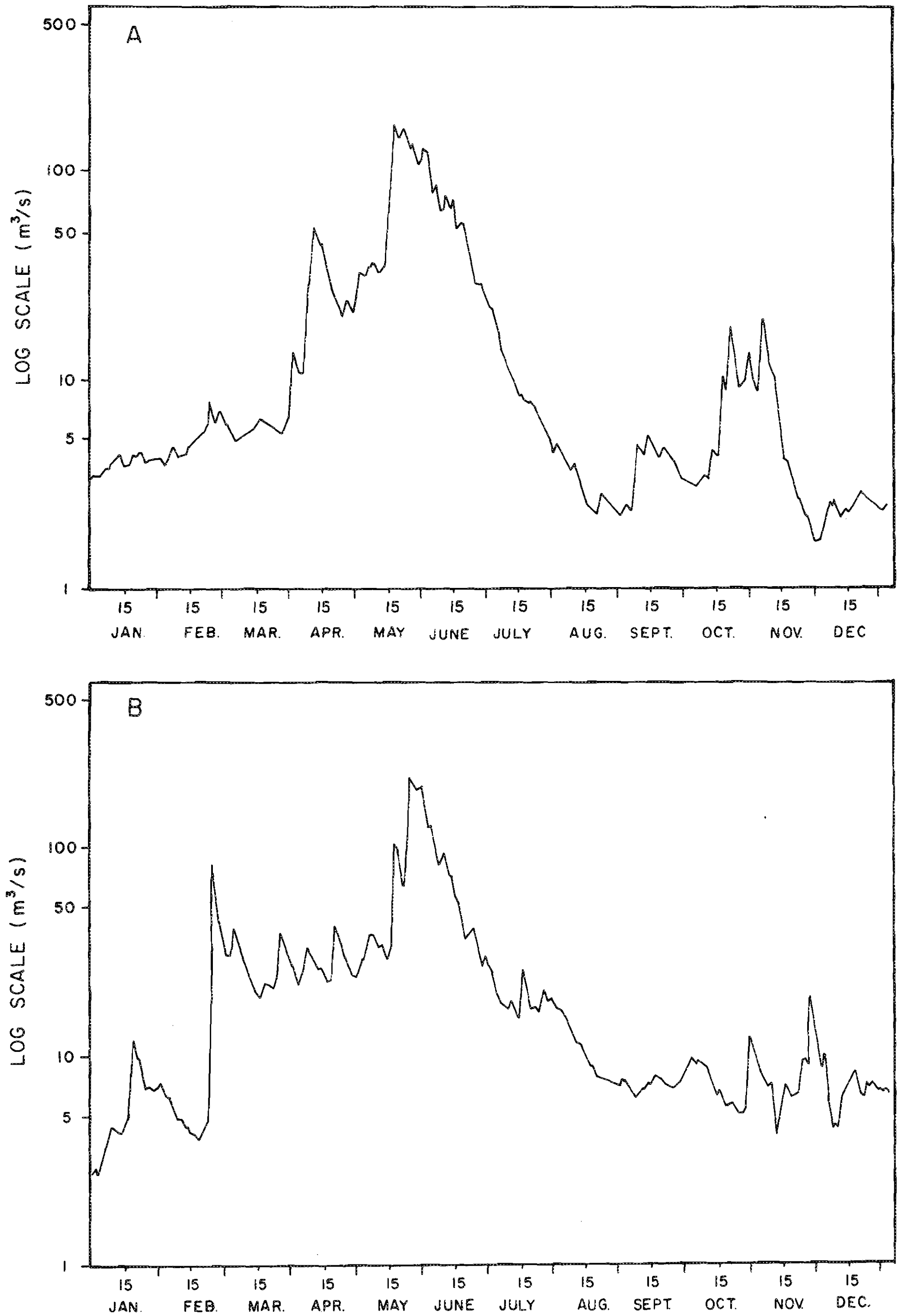

FIG. 3. Nicola River discharge at Spences Bridge as measured by the water survey of Canada. (A) 1985; (B) 1986; (C) 1987; (D) 1988. *(Fig. 3 concluded next page)*

ple of 240 young adults collected from March to mid-May was 10.6 cm. In 1987, 698 lamprey sampled from early April until early May had an average length of 12.3 cm. In 1988 the mean lengths of a sample of 412 young adults from the Merritt trap and 67 from the Nicola River trap were 14.0 and 13.7 cm, respectively. The length–weight relationship for a sample of 651 young adults sampled in April 1987 was $W = 8.5 \times 10^{-6} \times L^{3.093}$.

Abundance

Catches at night accounted for 99% of the total catches. There was considerable variation in the estimated number of young adult lamprey that left the river over the 4-yr study. The migration in 1984–85 was the largest, with an estimated 175 968 young adults leaving the river (Table 1). Because there was no trapping in the fall of 1984, this estimate would underestimate the total number leaving the river. In 1985–86, 1.4% of the

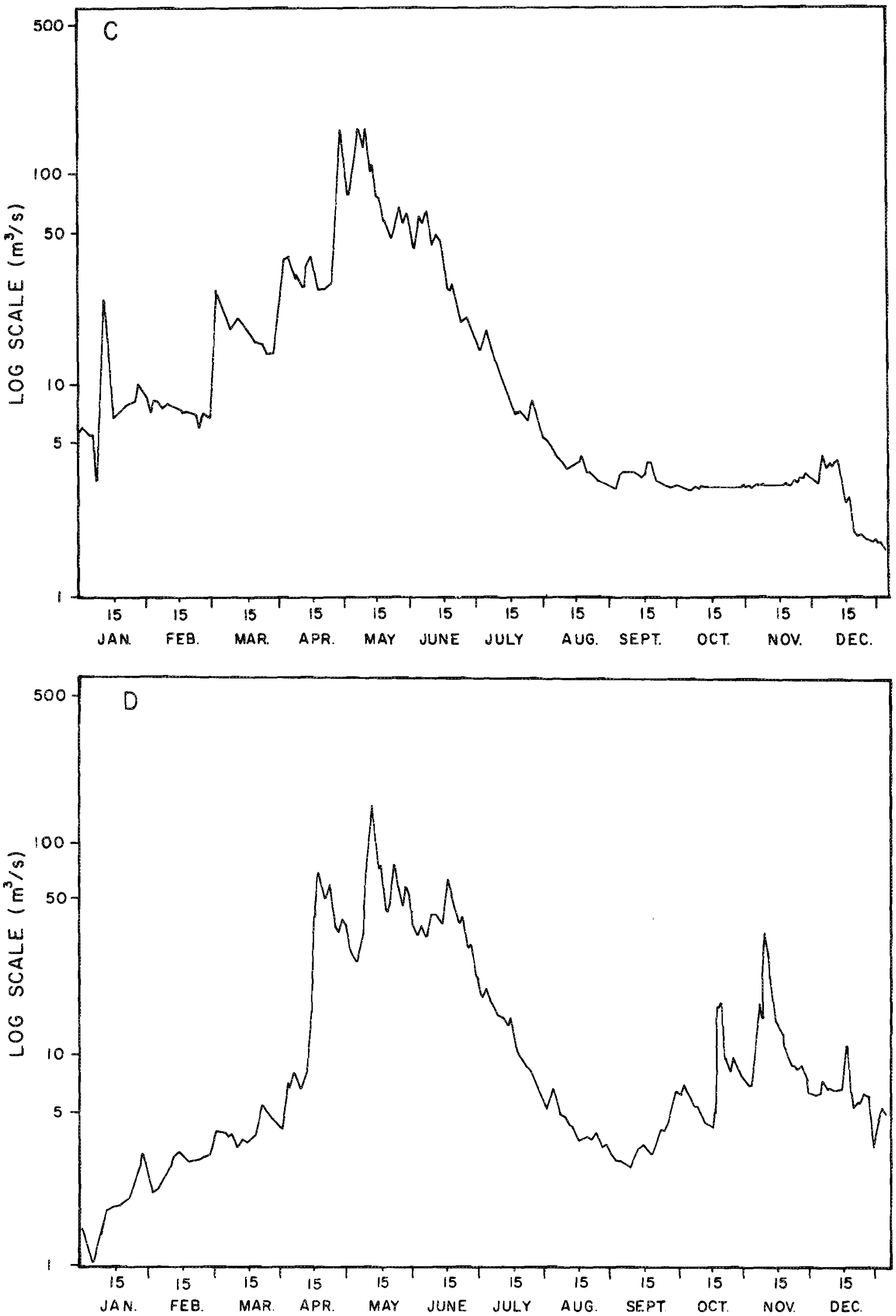

FIG. 3. (*Concluded*)

migration occurred in the fall, and in 1986–87 at least 3.4% occurred in the fall. If the average percentage of these two migrations occurred in 1984–85, there would be 4400 more young adults or a total of 180 367. In 1985–86 the number of young adult migrants was 19 283 or 11% of the previous migration. In 1986–87, 72 199 young adults left the river by the end of April. Because traps were not fished in May and because the catches in May in the previous two years were quite high, we estimated that the 1986–87 estimate was low by about 36%, the average percentage migration for this period in the previous two migrations. An adjusted estimate of approximately 98 191 is approximately one half of the 1984–85 migration and five times larger than the 1985–86 migration.

In 1988, an estimated 99 352 young adults migrated out of the river. This estimate includes the lamprey that were sampled at Merritt and not returned to the river. Because there was no sampling in the fall of 1987, an estimate of the fall migration was made using 2.4% of the total migration, as was done for

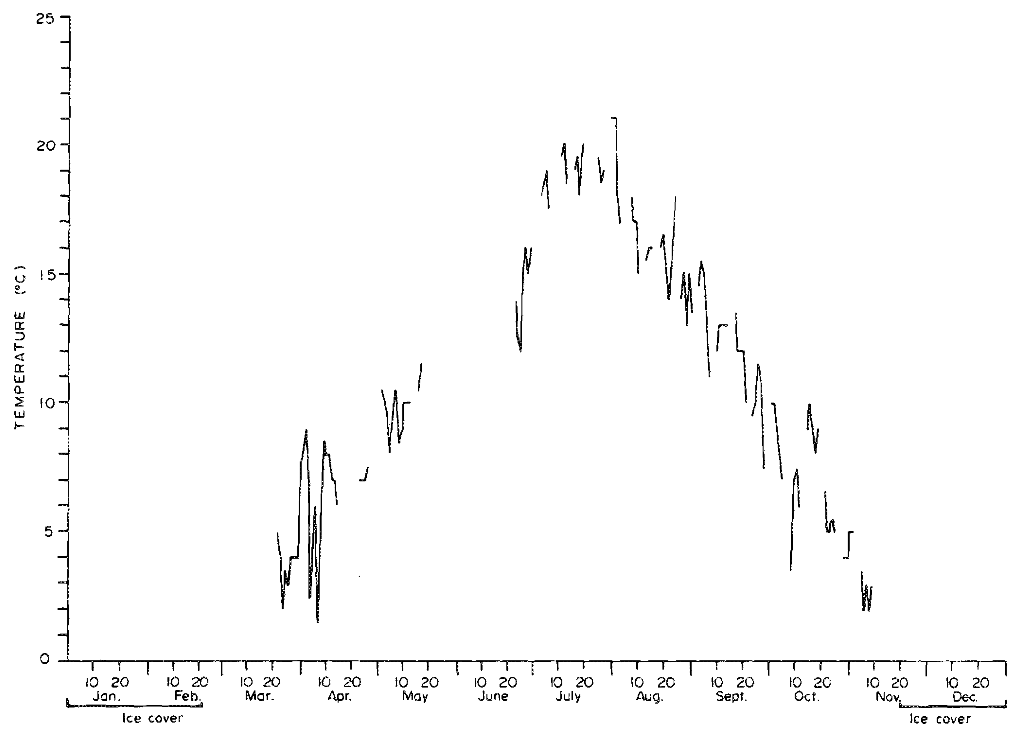

FIG. 4. Temperature at Spences Bridge, 1985.

the 1985 migration. When this estimate is added to the total, there were 101 736 young adults that left the river.

Ammocoetes

The mean length of approximately 3000 ammocoetes measured was 11.7 cm. Approximately 8% were smaller than 100 mm and less than 1% ranged from 75 to 90 mm.

In contrast with young adults, ammocoetes moved out of the river at all sampling times throughout the year (Fig. 2). Large numbers of ammocoetes moved at the same time as most young adults, but the largest numbers moved downstream in May and June. This movement occurred after the main migration of young adults. We added the mean number leaving the river in the fall of 1985–86 and 1986–87 to the 1985–86 and 1987–88 migrations because no observations were made in the fall of 1985 and 1987. We also added the mean number leaving in the spring of 1985 and 1985–86 to the number leaving in 1986–87. The total estimated numbers of ammocoetes were 749 210 for 1984–85, 908 985 for 1985–86, 920 328 for 1986–87, and 605 032 in 1987–88 (Table 1).

In 1988, 1383 ammocoetes were captured in the traps at the mouth of the Nicola River, 318 of which (23%) were captured at night. At the Merritt site, 68% (172) of the total catch of 254 ammocoetes were captured at night. In 1988, at the mouth of the Nicola River, there were approximately six times as many ammocoetes as young adults. At Merritt, there were approximately 43 times as many young adults as ammocoetes.

Lower Fraser River Sampling

Both metamorphosed *L. tridentata* and *Lampetra ayresi* were caught in the trawl sampling, 36 km upstream from the mouth of the Fraser River. A total of 97 lamprey were captured from March 25 until August 8, 1988: 28 metamorphosed *L. tridentata*, 56 metamorphosed *L. ayresi*, eight *L. ayresi* ammocoetes, and seven that were not saved for identification (Table 2). Most lamprey (67) were captured between April 17 and 20 in both day and night sets.

Age Determination

A total of 93 young adults and 33 ammocoetes were used for age determination, six of which could not be aged. The first annulus was located in an area of the statolith where an abrupt change in the shape occurred. This abrupt change frequently formed a distinct notch in the profile of the statolith. If there was doubt about the location of the first annulus, it was assumed to be located in this notch. In general, the opaque zones were clear for ages up to 3 and 4. The opaque zones were closer together, and contrast between opaque and translucent zones was reduced for older ages.

Metamorphosed lamprey ranged in age from 4 to 8 (Table 3). The mean lengths of young adult lamprey aged 5, 6, 7 were not significantly different (*t*-test, $p > 0.05$). Most lamprey began metamorphosis at age 4+ or 5+ and were age 5 or 6 when sampled in the year following metamorphosis (Table 3). The average length of the few young adults that were estimated to be age 7 and 8 was smaller than those lamprey that metamorphosed at a younger age (Fig. 5). One lamprey metamorphosed at age 3+. Sex was only determined from the March 1988 sample. Of 66 young adults sampled March 1988, 30 were female and 36 were male. There was no significant difference in the average lengths of male and female lamprey of similar age (*t*-test, $p > 0.05$). However, there were more age 7 males than females (Table 4).

The oldest ammocoetes were age 6. The average size of age 5 ammocoetes was significantly smaller (*t*-test, $p < 0.05$) than the average size of age 5 metamorphosed individuals.

The length–frequency analysis indicated that more ammocoetes would be in the older age groups than indicated by the

TABLE 1. Numbers of young adult lamprey and ammocoetes estimated to move out of the Nicola River.

	1984–85				1985–86				1986–87				1987–88							
													Young adults				Ammocoetes			
	Young adults	%	Ammocoetes	%	Young adults	%	Ammocoetes	%	Young adults	%	Ammocoetes	%	Merritt	%	Nicola	%	Merritt	%	Nicola	%
September	—		—		0		97	—	10	0.01	15 641	6.9	—		—		—		—	
October	—		—		93	0.5	3 898	0.4	23	0.03	1 379	0.6	—		—		—		—	
November	—		—		174	0.9	639	0.1	2 468	3.4	9 835	4.3	—		—		—		—	
December	—		—		—		—		—		—		—		—		—		—	
January	—		—		—		—		—		—		—		—		—		—	
February	—		—		—		—		—	0.3	514	—	417	0.7	—		5	0.4	—	
March	42	0.02	196	—	3 202	16.6	60 347	6.6	11 327	15.7	43 943	19.3	3 368	0.6	333	0.3	343	26.3	5 084	0.9
April	133 215	75.7	149 397	20.4	6 737	34.9	42 415	4.7	58 171	80.6	156 285	68.7	50 593	89.4	89 146	89.7	610	46.8	358 290	60.8
May	40 518	23.0	503 247	68.6	9 077	47.1	468 223	51.5	—		—		1 410	2.5	9 748	9.8	220	16.9	211 620	35.9
June	2 193	1.3	79 493	10.8	0		319 939	35.2	—		—		232	0.4	125	0.1	94	7.2	15 384	2.6
July	0		1 095	0	0		3 055	0.3	—		—		544	1.0	0		32	2.6	1 493	2.5
August	0		38	—	0		10 372	1.1	—		—		—		0				417	0.1
Total	175 968		733 466		19 283		908 985		72 199		227 597		56 563		99 352		1 304		589 288	
Estimated annual abundance	180 367		749 210		19 283		908 985		98 191		920 328				101 736				605 032	

statolith method (Tables 3, 5; Fig. 6). Specifically, the length–frequency method indicated that the largest percentage of ammocoetes in the sample should be age 7 (Table 5; Fig. 6). Because ages produced using the length–frequency analysis were not similar to ages estimated from the statolith method, we had to select one age determination method and reject the other. We based our analysis on the statolith method because length–frequency analysis is a less accurate method (Beamish and McFarlane 1983).

Adults

Adult lamprey migrating upstream were first caught at Yale (Fig. 1) on July 25, 1983. Records of lamprey collected by a commercial sturgeon fishermen (lamprey are used for bait for sturgeon fishing) for 3 yr prior to our sampling indicated that the upstream migration first occurred at this site at the end of July or the first week in August. On all nights, we caught lamprey from 22:30 to 03:00. On July 25, 50 lamprey were caught, and on July 30, over 100 lamprey were captured. Commercial fishing continued after our sampling until mid-August when catches became quite small. The total lengths of a sample of 48 adults ranged from 27.3 to 45.3 cm, with an average length of 33.7 cm and weight of 72.7 g. There were equal numbers of males and females.

The first adult lamprey in the Nicola River were captured on August 14, 1986. Over the period August 14–28, seven females and one male were captured with an average length of 30.0 cm and weight of 55.9 g. No more lamprey were captured until October 1–7 when two females and two males were captured with an average length of 27.7 cm and weight of 50.7 g. The trap was removed in mid-October.

Discussion

Migration of Young Adults

There are only a few studies of the downstream migration of young adults and ammocoetes that have monitored movements throughout the year. One of the earliest and most extensive studies (Applegate 1950) reported that recently metamorphosed landlocked sea lamprey, *Petromyzon marinus*, began moving out of rivers late in October or early in November. Movement continued throughout the winter, with most movement occurring in late March and early April. Migratory activity was closely associated with increases in discharge and not with temperature changes. This association between increases in discharge and the initiation of downstream movement of juvenile adults has been reported for a number of other species: *L. ayresi* (Beamish and Youson 1987), *Geotria australis* (Potter 1980), *Mordacia mordax* (Potter 1970), and anadromous *P. marinus* (Beamish and Potter 1975). In this study, discharge initiated downstream movement of young adults even though movement at the Merritt site started without a major fluctuation in flow rate. We think that the migration at Merritt indicates that even small increases in flow rate are sufficient to initiate downstream migration.

The pattern of a small migration in the fall followed by a spring migration of metamorphosed *L. tridentata* is similar to patterns observed from other species (Applegate 1950; Bird and Potter 1979). The migration in the Nicola River, therefore, started as early as late September in one year and continued to late May or early June in the next year except in 1988 when a small migration occurred late in July. Any bimodality in the

TABLE 2. Catches of lamprey at the mouth of the Fraser River.

	L. tridentata	*L. ayresi*	Not identified	*L. ayresi* ammocoetes
February 25	1	—	—	—
April 6	1	—	—	—
April 19–28	10	6	2	—
May 5–6	0	6	1	—
May 10–15	3	9	—	—
May 16–19	5	23	1	2
May 25 – June 20	6	9	—	4
June 24 – July 4	2	3	—	2
August 8	—	—	1	—
Total	28	56	5	8

TABLE 3. Age composition of Nicola River *L. tridentata* (combined sexes).

	Age (yr)	*n*	Mean length (mm)	SD	Range in length (mm)
Ammocoetes	2[a]	4	60	4.5	56–66
	3[a]	8	80	6.7	80–100
	4	6	115	11.8	98–132
	5	13	115	7.6	100–127
	6	2	119	4.2	116–122
Adults	4	1	127	—	—
	5	37	138	10.2	117–157
	6	35	140	11.5	118–175
	7	10	132	13.2	113–156
	8	3	121	10.6	113–133

[a]From electroshocking sample.

pattern of migration appears to be a result of stream conditions and the timing of observations rather than two distinct and separate migration periods.

In this study and others, downstream migration occurred mostly at night (Long 1968; Hardisty and Potter 1971; Potter and Huggins 1973; Potter 1980). For example, at the Merritt trap in 1988, 2060 young adults were captured from April 15 to 17. All but four were captured at night. By the time young adults were close to the mouth of the Fraser River, they migrated both at night and during the day. Movement throughout the 24-h period at the mouth of the Fraser River was also reported for *L. ayresi* (Beamish and Youson 1987).

The migratory behaviour near the mouth of the Fraser River differed from that observed in the Nicola River. Young adult *L. tridentata* were not caught until late March and the daily catches were more uniform over the period of migration that occurred from March 25 until July 4. Thus, the characteristics of the migration depend on the sampling location. At the beginning of the migration, in the headwaters of the various rivers, young adults begin the downstream migration at night when discharge increases abruptly. Most leave the substrate over a very short period. As the migration proceeds towards salt water, more groups amalgamate, resulting in a more uniform migration that continues day and night. In this study, the young adults that left the stream first were longer than those that migrated later. We also observed that young adults were smaller in some years that others.

Migration of Ammocoetes

Ammocoetes that move out of the Nicola River do not migrate into salt water because they are unable to osmoregulate

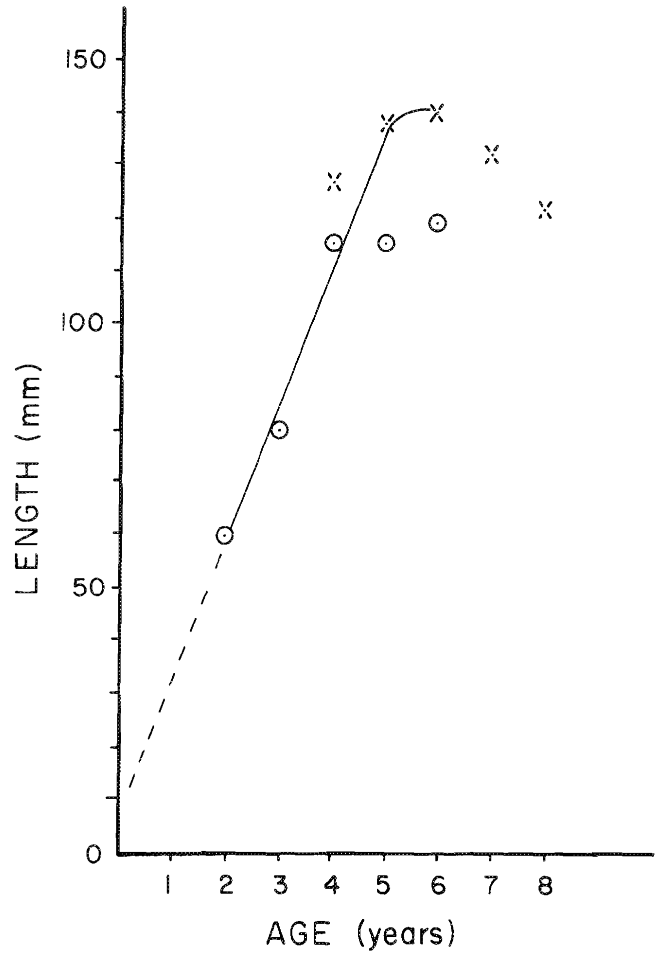

FIG. 5. Mean size at age of ammocoetes (○) and young adults (×).

TABLE 4. Mean length of male and female young adult lamprey.

Age (yr)	Mean male length (mm)	*n*	SD	Mean female length (mm)	*n*	SD
4	127	1	—	—	—	—
5	142	16	7.7	140	13	7.1
6	141	13	7.1	143	16	11.3
7	135	6	8.5	158	1	—

Table 5. Comparison of ages of ammocoetes using statoliths and length–frequency analysis.

Age (yr)	Statolith mean length (mm)	Length–frequency mean length (mm)
1	—	33
2	60	64
3	80	74
4	115	84
5	115	94
6	119	105
7	—	115
n	33	685

in salt water (Hardisty 1956; Morris 1972). It is believed that this downstream movement disperses larval lamprey throughout the watershed and is common among lamprey (Potter 1980). We did not observe a seasonal movement, as observed in other studies (Manion and Smith 1978; Potter 1980; Gritsenko 1968); however, most downstream movement occurred in the spring when the discharge was the highest, consistent with other studies (Manion and McLain 1971; Manion and Smith 1978). Smaller numbers of ammocoetes moves out of the river in the summer even though flows were reduced, water levels were low, and temperatures were high. The 10°C "barrier" reported by Manion and Smith (1978) for the Big Garlic River study was not observed in our study. Movement of ammocoetes occurred primarily at night, as observed in other studies (Gritsenko 1968; Manion and Smith 1978; Potter and Huggins 1973).

It is interesting that migration of young adults was almost always associated with an increase in abundance of larger ammocoetes moving downstream except in 1988 at the Merritt site. In the upper Nicola above Merritt, discharge was very constant in April 1988, as a consequence of the controlled flow from Nicola Lake (Fig. 1). The relative absence of any ammocoete movement may be related to discharge or may indicate low ammocoete abundance in this area. If there are few ammocoetes, the large number of young adults could only be produced by an upstream migration of ammocoetes prior to metamorphosis or an upstream migration of young adults prior to their downstream migration. We think that this is unlikely because of the strong tendency for ammocoetes to move downstream. We believe that the controlled flow in the area of the Merritt traps did not provide the stimulation for ammocoetes to move downstream. Therefore, larger increases in discharge may be required to stimulate movement of ammocoetes than required to stimulate the migration of young adults.

Age

Ages assigned using statoliths have not been validated. An indication that accurate ages may be produced by this method was found in a study of a population of *L. tridentata* that was prevented from going to sea (Beamish and Northcote 1989). The method was also valid for younger age groups of some populations of some other species of lamprey (Medland and Beamish 1987). However, the differences in mean size and age estimates between the statolith and length–frequency age determination methods indicate that the ages produced by the statolith method must be validated before it is considered to be accurate.

The age composition of the population, estimated using statoliths, was similar to the population of *L. tridentata* from the Ash River (Beamish and Northcote 1989). The mean lengths of similarly aged lamprey were larger for lamprey from the Nicola River than the Ash River, but the ages at metamorphosis and the number of age groups of young adults were similar.

In this study, there was an indication of a relationship between slower growth and age at metamorphosis. The average size of some lamprey that metamorphosed at an older age was

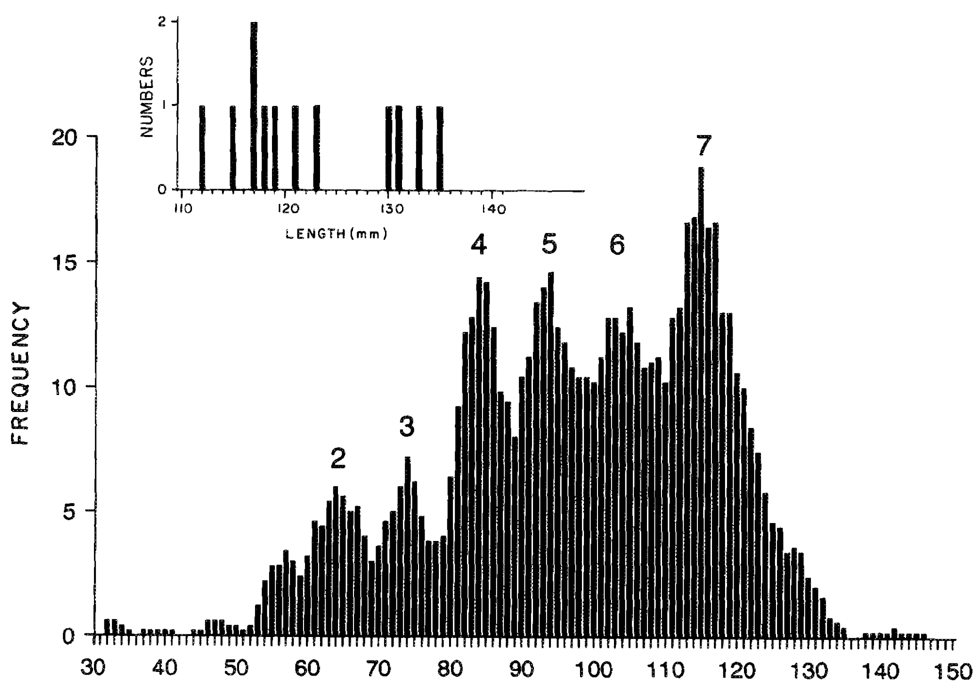

Fig. 6. Length–frequency of ammocoetes using a running average of five. Age estimates are shown above the modes. Lengths of metamorphosed lamprey (n = 12) are inserted in the upper left corner.

smaller than those that metamorphosed earlier, suggesting that slower growing ammocoetes may metamorphose at older ages.

The existence of four age groups in the metamorphosing population indicates more age groups of young adult Pacific lamprey than the two age classes reported for young adult *Lampetra fluviatilis* (Potter and Huggins 1973). The presence of at least two major age groups from the four age groups indicates that the interannual variation in the abundance of young adults, discussed earlier, may be related to environmental conditions. In the absence of a fishery and with the inevitable influence of the environment on survival, it is unlikely that a population can maintain cycles of abundance when young adults are from more than one age group. Unless cycles are produced by an association with cyclic abundance of predators, it is probable that the variation in the numbers of young adults leaving the Nicola River is related to conditions within the river.

Spawning Migration

Adult *L. tridentata* first returned to the Nicola River in August. This was unexpected because water levels were very low and it might be expected that adults would not enter the river until discharges were higher. For example, in the Chemainus River, adults entered the river when discharge was close to its annual maximum (Richards 1980). If the lamprey sampled at Yale in August form any part of the migration into the Nicola River, lamprey move upstream from Yale to the Nicola River, approximately 112 km, in about 2 wk or about 8 km/d. This would suggest that the lamprey entered the Fraser River, 170 km downstream of Yale, towards the end of June. This is about the time of maximum discharge of the Fraser River and would indicate that lamprey may in fact return during maximum discharges, as observed in the Chemainus River, but reach the Nicola River at low discharge.

Length of Life after Metamorphosis

Using the growth rates determined in the laboratory (R. J. Beamish and C.-E. Neville, unpubl. data), it would take about 12 mo for young adult lamprey to reach the size of the adults sampled at Yale. Assuming that metamorphosis is complete by about the end of September, the average young adult would spend 8 mo in fresh water, enter the sea in April–May, spend about 12–14 mo in salt water, returning to fresh water in June or July. It would then spend about 4 mo returning to the Nicola River and 7–9 mo more in fresh water before spawning and dying. The length of life after metamorphosis, therefore, is about 32 mo or approximately 2.5 yr.

Abundance

The number of young adults leaving the Nicola River varied considerably among the four years. The 1985 migration of approximately 176 000 was the largest and about 9 times greater than that of 1985–86. The 1986–87 and 1987–88 migrations were of intermediate size. We are not aware of any studies that have estimated the abundance of anadromous lamprey migrating out of larger rivers. Thus, it is unknown if the large variation in abundance is common. To estimate the potential amount of predation on marine fishes by young adult lamprey produced in the Nicola River, we considered the average migration to be 100 000 young adults.

The abundance of young adult lamprey produced in the Nicola River is the sum of the number of young adults leaving the river and those produced by the ammocoetes that left the river in previous years. Most ammocoetes leaving the river were age 4 and 5, about 1 yr from metamorphosis. There are no estimates of mortality that can be used to estimate how many of these ammocoetes survive and metamorphose. However, for most fishes, the period of highest mortality occurs immediately after hatching, suggesting that mortality rates may not be high at age 4 and 5. We used a very high mortality rate of 0.5 to estimate the total production of young adult lamprey so that it would not appear that we are attempting to inflate the estimate of young adults produced. If about one half of the average migration of about 800 000 ammocoetes leaving the river survive and metamorphose, then these young adults can be added to the average migration of about 100 000 young adults. The total annual production of young adults would be approximately 500 000.

If the abundance of *L. tridentata* relative to *L. ayresi* is representative of the actual proportion in all years, then it is also possible to estimate the total numbers of *L. tridentata* using abundance estimates for *L. ayresi* (Beamish and Youson 1987). In 1979, it was estimated that 6 500 000 young adult *L. ayresi* left the Fraser River. In this study, approximately one *L. tridentata* was captured for every two *L. ayresi*, indicating that total *L. tridentata* abundance in the Fraser River drainage may be about 3 000 000 young adults. Obviously this estimate is little better than a guess; however, until proper abundance estimates are made, it is useful to have some appreciation of the numbers of *L. tridentata* that leave the Fraser River and to show that the Nicola River is a major producer of *L. tridentata* in the Fraser River drainage.

Impact on Commercial Fishes

There are no laboratory studies that identify the feeding preference of Pacific lamprey. In laboratory studies that compared the preference between salmon and herring, it was observed that more herring were eaten than salmon (R. J. Beamish, unpubl. data). Scarring information (Gilhousen 1989; Beamish 1980) indicated that salmon were attacked by Pacific lamprey, but the relationship between scarring and mortality was unknown.

The relative importance of Pacific lamprey as predators can be assessed by comparing their abundance with the abundance of landlocked sea lamprey (*P. marinus*) in the Great Lakes because the impact of this landlocked sea lamprey is known and because the Pacific lamprey and the anadromous form of the sea lamprey may be similar in their predatory behaviour. At the peak of the destruction of the commercial fishery in the 1950s, approximately 750 000 spawning sea lamprey were in three Great Lakes (Lake Huron, Lake Michigan, and Lake Superior; Walters et al. 1980). There are no recent estimates of abundance for all of these lakes, but an estimate of spawning lamprey in 1987 in all of Lake Superior was 47 662 (Dustin et al. 1988). Our estimate of 3 000 000 young adult Pacific lamprey leaving the Fraser River each year or 500 000 young adults produced by the Nicola River does not account for marine phase mortalities. If we use an 80% mortality rate used to estimate the number of feeding landlocked sea lamprey that survive to spawn (Walters et al. 1980), the Nicola River would produce 100 000 spawning lamprey and the Fraser River 600 000 spawning lamprey. If the average number of spawning adults produced by the Nicola River is compared with the Great Lakes, this single river produces approximately twice the number of spawning lamprey currently in Lake Superior. The estimate of 600 000 spawning lamprey produced by the Fraser River is 80% of the estimate of the maximum numbers of spawning lamprey in all three Great Lakes, during the peak abundance in the 1950s. The high abundance relative to landlocked sea lamprey abundance in the Great Lakes indicates that the Pacific lamprey should be recognized as an important predator of marine fishes.

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