Response of Recently Metamorphosed Anadromous Parasitic Lamprey (*Lampetra tridentata*) to Confinement in Fresh Water

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Recently metamorphosed *Lampetra tridentata* were collected from six rivers in British Columbia in early autumn and held in fresh water in the laboratory at ambient temperature and simulated natural photoperiod. Ability to survive in fresh water varied considerably among populations, ranging from the Babine River population which did not survive beyond February to the Chemainus River population which survived until July. Associated with the onset of mortality was a decrease in plasma sodium concentrations. Plasma sodium concentrations in individual lampreys were correlated with condition factor, indicating that osmoregulatory failure may have resulted from depletion of body energy reserves. In a separate experiment, postmetamorphic lamprey sampled from two rivers fed poorly in fresh water and feeding did not prolong their survival. We conclude that confinement of *L. tridentata* in fresh water does not easily result in the formation of landlocked populations.

Des *Lampetra tridentata* récemment métamorphosées ont été capturées dans six rivières de la Colombie-Britannique au début de l'automne et gardées en laboratoire dans les conditions suivantes : eau douce, température ambiante et photopériode simulant la photopériode naturelle. La capacité de survie en eau douce a varié considérablement selon les populations, les extrêmes étant la population de la rivière Babine qui n'a pas survécu après février et la population de la rivière Chemainus qui a survécu jusqu'en juillet. Le début de la mortalité coïncidait avec une baisse du taux de sodium plasmatique. Les taux de sodium plasmatique chez les lamproics individuelles étaient corrélés avec le coefficient de conditions, ce qui indique que l'insuffisance de l'osmorégulation pourrait résulter de l'épuisement des réserves énergétiques de l'organisme. Dans une autre expérience, des lamproics métamorphosées provenant de deux rivières s'alimentaient peu en eau douce et l'alimentation n'a pas prolongé leur survie. On conclut donc que le confinement de *L. tridentata* en eau douce n'aboutit pas facilement à la formation de populations landlockées.

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Anadromous parasitic lamprey enter salt water after metamorphosis where they feed on other fishes. Entry into salt water can occur almost immediately after metamorphosis, be delayed for up to 10 mo from the onset of metamorphosis, or occur in two stages (Beamish and Potter 1975; Potter et al. 1980; R. J. Beamish 1980; Maitland et al. 1984). Migration into salt water is associated with increased stream discharge (Potter 1970; Potter and Huggins 1973; Beamish and Youson 1987) and with the opening of the foregut during metamorphosis (Hardisty et al. 1970; Potter et al. 1980; Richards and Beamish 1981; Beamish and Youson 1987).

Although there have been studies of the ability of anadromous lamprey to adapt to salt water (Potter and Huggins 1973; F. W. H. Beamish 1980; Beamish and Youson 1987), there are very few reports of the consequences of retaining an anadromous species in fresh water after metamorphosis (Beamish and Youson 1987; R. J. Beamish 1980). Such studies are relevant because it is generally believed that freshwater parasitic lamprey arise when anadromous species invade a new freshwater habitat or are prevented from entering the sea. Because of the abundance of anadromous parasitic lampreys and the adverse effect that freshwater parasitic lamprey can have on other fishes (Applegate 1950; Birman 1950; Nikol'ski 1956; Gritsenko 1968; Beamish 1982; Smith and Tibbles 1980; Holcik 1986), it is important to know if the confinement of postmetamorphic anadromous parasitic lamprey in fresh water could result in the establishment of freshwater feeding for the duration of the trophic phase. This knowledge is particularly important in areas such as British Columbia where *Lampetra tridentata* is common (R. J. Beamish, unpubl.) and there are numerous proposals for the construction of hydroelectric dams.

There are two species of anadromous parasitic lamprey in British Columbia (*L. ayresi* and *L. tridentata*). Recently, Beamish and Youson (1987) showed that it was possible to keep a few *L. ayresi* in fresh water for their entire postmetamorphic phase. This study examines the response of *L. tridentata* from a number of populations to confinement in fresh water.

Materials and Methods

In September 1981, samples of recently metamorphosed *L. tridentata* were collected from the Babine River. Twenty-five lamprey were acclimated to salt water at ambient temperature over a 3-d period in November. Juvenile coho (*Oncorhynchus kisutch*) and sockeye salmon (*O. nerka*) were added to the tank to provide food. The number of lamprey that were attached to salmon were noted daily for the first month and dead salmon were replaced. Another 48 lamprey were held in a separate tank of fresh water without food and samples of five lamprey were taken each month for analysis of plasma sodium concentrations. Blood was collected into heparinized microhematocrit tubes from a transverse incision behind the last branchial opening (Beamish et al. 1978). The tubes were centrifuged to separate the plasma which was diluted for analysis of sodium concentrations (Blackburn and Clarke 1987). Lamprey were measured at the beginning of the experiment and at the end of February 1982.

In September 1982, samples of recently metamorphosed lamprey were again collected in the Babine River. Half were held in fresh water without food and samples of five lamprey were taken monthly for analysis of plasma sodium concentrations. Another 20 lamprey were held in a separate tank of fresh water; small Pacific herring (*Clupea harengus pallasi*) were added to provide food. Herring were used as prey in the freshwater experiment to avoid the problem of fungus infections which may be induced by nipping of the lamprey by juvenile salmon. The number of lamprey that were attached to the herring were noted daily and dead herring were replaced. A second sample of 25 recently metamorphosed lamprey from the Big Qualicum River was held in fresh water with herring provided as food.

Recently metamorphosed lamprey were collected in September and early October 1983 from six rivers in British Columbia (Fig. 1) using electroshockers and transported to the laboratory. Lamprey from each population were distributed among three tanks in mid-October. The number of lamprey at the start of the study ranged from 145 for the Babine River population to 66 for the Kanaka Creek population. Sand and rocks were placed on the bottom to provide suitable shelter to reduce the amount of movement. Since provision of prey failed to enhance survival in the 1982 experiments, lamprey were held without food under simulated natural photoperiod at ambient water temperature (see Table 2). Samples of five lamprey from each population were taken at approximately monthly intervals from mid-October until February and at approximately 3-wk intervals thereafter; they were anesthetized in 2-phenoxyethanol, blotted dry on a damp chamois, and measured in length and weight. Condition factor was calculated as weight (g)/length $(mm)^{2.08} \times 10^6$. The exponent 2.08 calculated from a regression of log weight on log length was used instead of the power 3 used by Potter and Beamish (1977). Six 24-h seawater challenge tests (Blackburn and Clarke 1987) were performed at approximately monthly intervals from November to June using lamprey from the Big Qualicum, Puntledge, and Babine populations to determine their ability to adapt to seawater. Samples of five lamprey were transferred directly from the freshwater holding tanks to a tank of flowing seawater at the same temperature.

Results

In the 1981 experiment, recently metamorphosed Babine River lamprey acclimated to 30‰ seawater commenced feeding on November 25, 9 d after juvenile salmon were provided. Thereafter, feeding occurred daily. Apart from a single mortality in November, no further deaths occurred in salt water for the duration of the experiment through February 1982. During this period, the lamprey grew an average of 0.6 cm.

In the 1982 experiment, Babine River lamprey held in fresh water commenced feeding on October 28, 1 d after juvenile herring were presented. Some feeding occurred almost daily during November and early December. Feeding was less frequent thereafter. The number of attacks and the average daily herring mortalities per lamprey were considerably lower than in lamprey feeding in salt water. The first lamprey died on November 8, half were dead by mid-December, and all were dead by December 29. All moribund lamprey had fungus which could not be cured by malachite green treatments. Big Qualicum River lamprey held in fresh water commenced feeding on December 3, 1 d after being presented with live herring. Feeding continued daily until late December and then declined. The first lamprey died on December 9, half were dead by mid-January 1983, and all were dead by January 21, 1983.

The mean length of lampreys for all six populations in the 1983 experiment was 13.2 cm; at 15.2 cm, the Babine River population was largest and differed significantly ($p < 0.05$) from the smallest group from the Puntledge River (12.3 cm). Mean weight ranged from 3.4 g for the Babine River population to 2.4 g for the Somass River one. The average condition factor for all populations was 1.44 in mid-October, declining to 1.30 in the November sample; it differed significantly among populations, ranging from 1.41 in the Puntledge River to 1.17 in the Babine River population (Table 1).

There were no mortalities during the first month of the 1983 study, with the exception of a single lamprey from the Puntledge River population. Mortalities increased sharply in the Babine River population during the second half of November and continued until mid-February when all fish had died (Fig. 2). Mortalities in the Somass River and Kanaka Creek populations commenced early in December and most fish died by mid-March. Mortalities for the other populations started later and occurred over a longer period. Mortality was most delayed in the Chemainus River population where it increased in late April and peaked in July. In most populations, mortality rose to a maximum and then declined until the remaining animals died. Cumulative percent mortality to the end of March was highest in populations with the lowest average plasma sodium concentration from October to March (Spearman Rank correlation coefficient 0.93, $n = 6$, $p < 0.05$). The Babine and Somass River populations also had the lowest condition factor; however, the overall Spearman rank correlation coefficient between mean condition factor from October to March and cumulative percent mortality to the end of March ($r_s = 0.47$, $n = 6$) was not significant.

Plasma sodium concentrations did not differ among populations in mid-October 1983; the average for all six populations was 120 mmol/L (Table 2). Plasma sodium levels declined significantly in January in four populations but not in the Puntledge and Chemainus River samples (Table 2). Lampreys in the Babine River population were the least able to maintain blood sodium concentrations in fresh water, followed by those in the Somass River, Kanaka Creek, and Big Qualicum River populations. Samples of the Babine River population taken in 1981, 1982, and 1983 exhibited a consistent pattern of declining plasma sodium levels during November and December followed by low and variable levels during December to February (Fig. 3). No significant decline in plasma sodium concentrations was observed in the Puntledge River population; the mean for 12 samples taken from October to July was 109.5 mmol/L

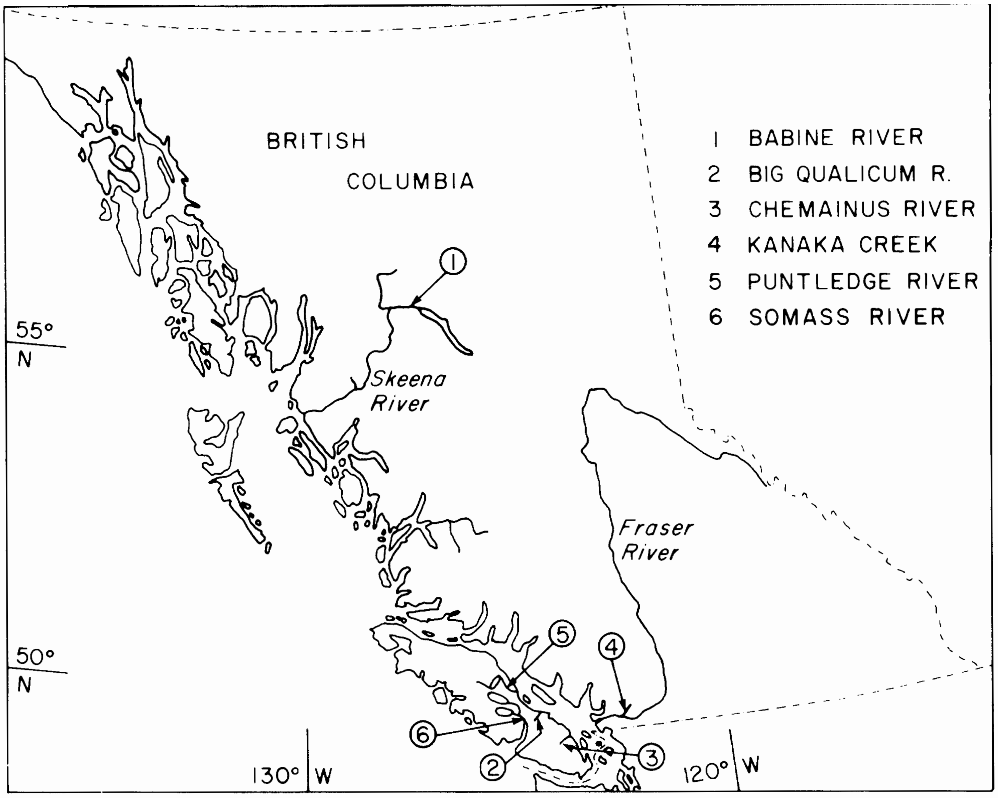

FIG. 1. Locations of British Columbia rivers from which lamprey were collected.

TABLE 1. Condition factor of lamprey from six populations held in the laboratory and sampled from October to March. Values are arithmetic mean (SE) of five fish per group (except March Babine sample where $n = 1$). Population or monthly means followed by the same letter are not significantly different by Tukey's Studentized range test at the 0.05 level.

	October	November	January	February	March	Means
Big Qualicum R.	1.68 (0.10)	1.36 (0.10)	1.36 (0.11)	1.38 (0.07)	1.32 (0.09)	1.42 a
Puntledge R.	1.59 (0.05)	1.49 (0.05)	1.39 (0.06)	1.30 (0.02)	1.30 (0.07)	1.41 a
Kanaka C.	1.46 (0.09)	1.36 (0.06)	1.49 (0.07)	1.31 (0.06)	1.27 (0.02)	1.38 ab
Chemainus R.	1.35 (0.08)	1.27 (0.03)	1.31 (0.04)	1.26 (0.04)	1.19 (0.04)	1.27 bc
Somass R.	1.38 (0.05)	1.20 (0.03)	1.10 (0.10)	1.14 (0.06)	1.09 (0.08)	1.18 c
Babine R.	1.19 (0.08)	1.11 (0.07)	1.26 (0.06)	1.15 (0.05)	0.98	1.17 c
Mean	1.44 a	1.30 b	1.32 b	1.26 b	1.22 b	

with a minimum of 102 mmol/L in January. Over the same period, the mean plasma sodium concentration measured in the Chemainus River population was 113 mmol/L; a minimum of 101 mmol/L was reached in late June but this was not a statistically significant drop. For all six populations, sodium concentrations were positively correlated with monthly mean holding temperature ($r_s = 0.90$, $n = 5$, $p = 0.05$) and condition factor ($r = 0.25$, $n = 135$, $p < 0.01$) but negatively correlated with length ($r = -0.272$, $n = 135$, $p < 0.01$). However, there was no significant correlation between sodium concentrations and body weight ($r = -0.099$, $n = 135$). The mean plasma magnesium concentration in freshwater lamprey was 0.85 mmol/L; it did not differ significantly among populations and was not significantly correlated with plasma sodium ($r = 0.075$).

Seawater adaptability did not differ appreciably among the three populations tested (Table 3). However, all three exhibited a decline in seawater adaptability at the time of the January challenge test as evidenced by elevated plasma sodium concentrations. The Big Qualicum River population suffered mortality after seawater challenge in January, February, and March. In contrast, the Puntledge River population showed no mortality until the June challenge test.

Discussion

This is the first study comparing the ability of metamorphosed lamprey from different populations of an anadromous species to survive in fresh water. The only known report of anadromous parasitic lamprey being kept to maturity in fresh water is for *L. ayresi* from one population in the Fraser River (Beamish and Youson 1987). Other laboratory studies have shown that it is difficult to maintain metamorphosed *Petromyzon marinus* (Potter and Beamish 1977) and *Geotria australis* (Potter et al. 1980) in fresh water. Our 1983 study showed that the ability of metamorphosed *L. tridentata* to survive in fresh water differed considerably among the populations tested. The most dramatic difference occurred between the Babine River population and the Chemainus River population. No

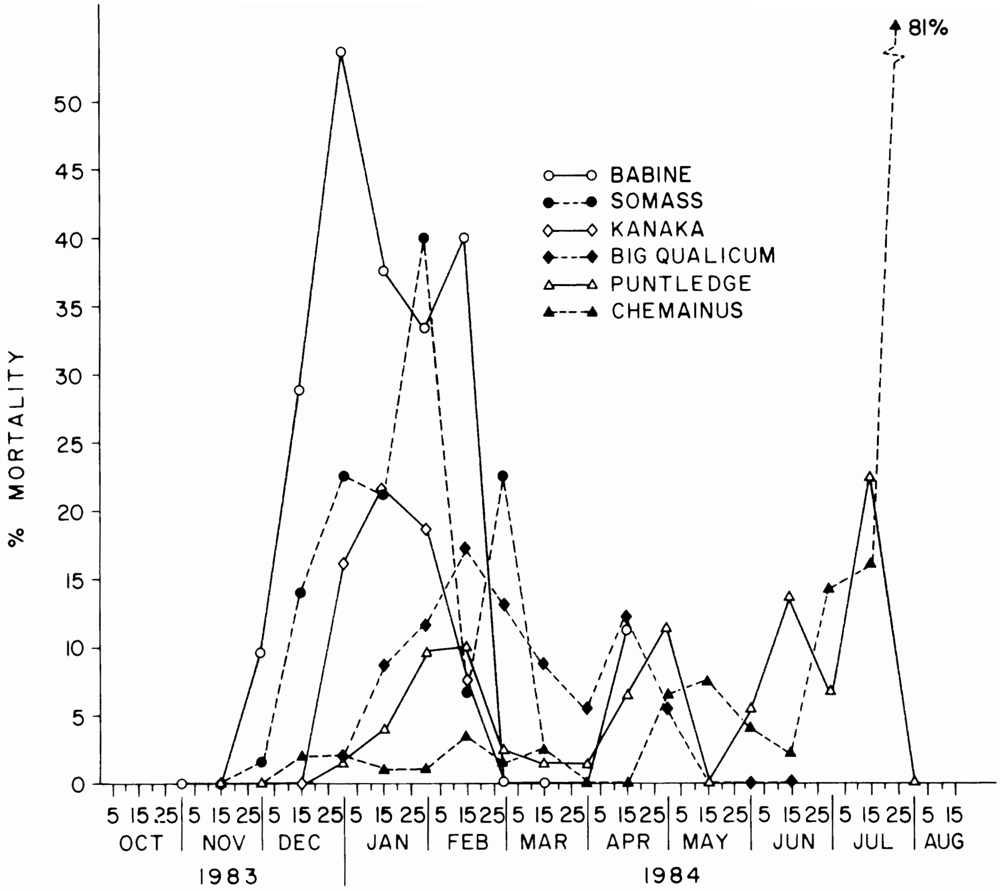

FIG. 2. Biweekly mortality in six populations of *L. tridentata* held in fresh water.

TABLE 2. Plasma sodium concentrations (mmol/L) in lamprey from six populations held in the laboratory and sampled from October 1983 to March 1984. Values are arithmetic mean (SE) of five fish per group (except March Babine River sample where $n = 1$). Population or monthly means followed by the same letter are not significantly different by Tukey's Studentized range test at the 0.05 level.

	October	November	January	February	March	Means
Babine R.	119.5 (4.2)	102.8 (4.6)	75.7 (5.6)	86.0 (12.2)	93.4	95.4 a
Somas R.	124.7 (2.4)	116.1 (3.7)	93.2 (5.0)	101.4 (7.5)	95.5 (8.8)	106.2 b
Kanaka C.	120.1 (2.0)	118.3 (2.4)	79.1 (10.0)	112.6 (10.6)	103.9 (5.7)	106.8 b
Big Qualicum R.	123.9 (3.6)	120.5 (1.1)	103.3 (5.9)	97.7 (4.1)	103.0 (3.7)	109.7 bc
Puntledge R.	116.3 (1.2)	123.7 (1.7)	101.9 (6.7)	111.7 (7.2)	110.8 (2.2)	112.9 bc
Chemainus R.	117.1 (3.0)	119.5 (2.5)	110.1 (8.5)	122.0 (5.5)	121.7 (6.6)	118.1 c
Mean	120.2 a	116.8 a	93.9 b	105.2 c	104.7 c	
Mean holding temperature (°C)	10.6	9.1	4.5	5.6	6.9	

Babine River lamprey survived beyond mid-February, while most of the Chemainus River lamprey survived until July. Possibly this variation in ability to survive in fresh water results from adaptations for different seasonal timing of downstream migration among local populations.

Because food was not provided and temperature was not controlled, it was not determined if any of the lamprey in the 1983 experiment, particularly those of the Chemainus River population, could survive in fresh water if given the opportunity to feed. However, the 1982 experiment demonstrated that feeding by lamprey from the Babine and Big Qualicum rivers in fresh water was not as intense as that observed for lamprey of the same age transferred to seawater in 1981; despite some feeding, these groups did not survive as long in fresh water as unfed ones from the same populations in the 1983 experiment. Our results are in agreement with those of Richards and Beamish (1981) who reported that lamprey from the Chemainus River failed to feed in fresh water during a 75-d experiment, while other groups transferred to salt water fed well.

Mortality was associated with a decline in plasma sodium concentrations. The ability to maintain plasma sodium concentrations in fresh water was independent of body weight but was negatively correlated with length. One possible cause of the observed decline in plasma sodium concentrations is depletion

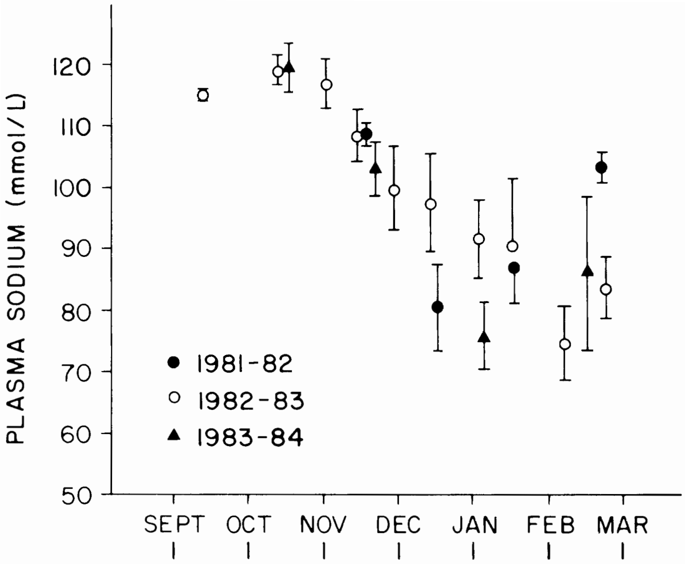

FIG. 3. Plasma sodium concentrations in Babine River lamprey held in fresh water in the laboratory in 1981–82, 1982–83, and 1983–84.

of body lipid reserves. Depending on timing of entry into salt water, anadromous parasitic lamprey may spend up to 10 mo in fresh water without feeding before they enter salt water (Beamish et al. 1979; Gritsenko 1968; Potter et al. 1980; Potter and Beamish 1977; Beamish and Youson 1987). A histological study of *P marinus* revealed that lipid levels declined through the winter and were extremely low in young adults at the end of the nontrophic period in May (Youson et al. 1979). Beamish et al. (1979) measured a lipid level of only 1.3% in a similar group of *P. marinus*. In the present study, we did not measure body lipid levels, but all populations exhibited a significant decline in condition factor during the experiment which suggests that lipid levels also decreased. Condition factor was correlated with plasma sodium concentration and all populations maintained similar sodium concentrations in October; the difference in timing of the decline in sodium concentrations and subsequent increase in mortality may be related to the time at which body lipid reserves became depleted in the various populations. The sharp drop in plasma sodium concentrations in early January may have resulted from the low water temperature at this time. A possible explanation for variation in plasma sodium levels among stocks after October is that there are genetic differences in osmoregulatory ability among populations. Differences in osmoregulatory ability are known between landlocked and anadromous *P. marinus* (Mathers and Beamish 1974) and between *L. tridentata* and the closely related *L. macrostoma* (R. J. Beamish 1980).

Mortalities in the anadromous *L. ayresi* held in fresh water increased sharply in June, about 2 mo after the opening of the foregut and about 10 mo after the onset of metamorphosis (Beamish and Youson 1987). This species normally enters the ocean in May and June and commences feeding immediately (R. J. Beamish 1980; Beamish and Youson 1987). The sharp increase in mortality in fresh water in mid-June coincided with the initiation of feeding in salt water and may be related to the depletion of lipid reserves as we have suggested for *L. tridentata* in the present study.

Variation in the timing of opening of the foregut could contribute to osmoregulatory variability (F. W. H. Beamish 1980). However, in the Chemainus River population which survived the longest, the foregut is known to be open by September (Richards and Beamish 1981). Furthermore, R. J. Beamish (1980) has shown that *L. tridentata* from five populations including those from the Babine and Big Qualicum rivers feed by the end of October when held in salt water in the laboratory. In the present study, lamprey from Big Qualicum, Puntledge, and Babine rivers were able to hypoosmoregulate well in a

TABLE 3. Plasma sodium concentrations (mmol/L) and mortality of lamprey 24 h after transfer to 29‰ seawater. Values are arithmetic mean (SE) of surviving fish in sample of five for each test.

	Population		
	Big Qualicum R.	Puntledge R.	Babine R.
November 22			
Plasma sodium	123.7(2.9)	122.1(1.4)	124.1(2.0)
Mortality	0/5	0/5	0/5
January 5			
Plasma sodium	153.3(8.4)	148.5(13.7)	138.3(9.1)
Mortality	1/5	0/5	0/5
February 16			
Plasma sodium	129.4(17.1)	117.0(2.9)	—
Mortality	1/5	0/5	—
March 20			
Plasma sodium	134.8(9.5)	117.8(0.8)	—
Mortality	2/5	0/5	—
April 26			
Plasma sodium	145.6(13.4)	139.5(17.6)	—
Mortality	0/5	0/5	—
June 8			
Plasma sodium	—	143.8(15.9)	—
Mortality	—	1/5	—

24-h seawater challenge test at the end of November, indicating that the foregut was open (Richards and Beamish 1981). Accordingly, we believe that it is unlikely that variability in the time of the opening of the foregut contributed significantly to the ability of the various populations to survive in fresh water.

From our results, it is evident that postmetamorphic *L. tridentata* sampled from six populations in British Columbia do not readily remain in fresh water. However, we cannot exclude the possibility that a very few individuals from a population could survive and feed in fresh water; it seems possible that the closely related freshwater parasitic species *L. macrostoma* (Beamish 1982) and *L. minima* (Bond and Kan 1973) evolved in this manner. Our conclusion that the confinement of *L. tridentata* in fresh water does not easily result in the formation of landlocked populations is corroborated by the observation that no landlocked populations of *L. tridentata* have been found in British Columbia (R. J. Beamish, unpubl. obs.) and only a few have been reported throughout its entire range (Hubbs 1971; Vladykov and Kott 1979).

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