Lampetra macrostoma, a New Species of Freshwater Parasitic Lamprey from the West Coast of Canada

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BEAMISH, R. J. 1982. ***Lampetra macrostoma***, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39: 736 – 747.

Lampetra macrostoma n.sp., a freshwater parasitic lamprey, is distinguished from related species *L. tridentata*, *L. lethophaga*, *L. folletti*, *L. minima*, and *L. similis* by its parasitic habit and very large disc. Other characters distinguishing the species from *L. tridentata* are its longer prebranchial length, large eye, weakly pigmented velar tentacles, and its ability to remain in freshwater. The recently metamorphosed form readily survives in freshwater and probably is non-anadromous even though it can survive in salt water. The new species has been discovered in two lakes on Vancouver Island, British Columbia, Canada, where it attacks large numbers of resident salmonids. Because of its ability to survive and feed in freshwater, it poses a definite threat to freshwater fishes.

Key words: lamprey, new species, non-anadromous lamprey, salmonid parasitism

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Lampetra macrostoma n.sp., une lamproie parasite d'eau douce, se distingue des espèces apparentées *L. tridentata*, *L. lethophaga*, *L. folletti*, *L. minima* et *L. similis* par son mode de vie parasitaire et son disque buccal très grand. Les autres caractères qui différencient cette espèce de *L. tridentata* sont une longueur prébranchiale plus grande, un oeil plus grand, des tentacules vélaires faiblement pigmentées et sa capacité à demeurer en eau douce. La forme récemment métamorphosée survit facilement en eau douce et est probablement non anadrome, même si elle peut survivre en eau salée. La nouvelle espèce a été découverte dans deux lacs de l'île Vancouver, en Colombie-Britannique (Canada), où elle attaque de grands nombres de salmonidés résidants. Capable de survivre et de se nourrir en eau douce, l'espèce est une réelle menace pour les poissons d'eau douce.

Received March 10, 1981
Accepted January 27, 1982

Reçu le 10 mars 1981
Accepté le 27 janvier 1982

LAMPREYS possessing a supraoral lamina with 3 well-developed cusps, 4 innerlaterals on each side of the disc, and an infraoral lamina with 5 cusps (or a 3–4–5 formula) have been included in the genus *Entosphenus* by Gill (1862), Jordan and Evermann (1896), Berg (1931), Hubbs (1967), Vladykov and Follett (1965), McPhail and Lindsey (1970), and Vladykov and Kott (1976a). Others (Hubbs 1971; Hubbs and Potter 1971; Kan 1975) have combined this group with lampreys that have a supraoral lamina with 2 cusps, 3 innerlaterals on each side of the disc, and an infraoral lamina with 7 cusps (or a 2–3–7 formula) into the genus *Lampetra*. In this second system, *Entosphenus* may or may not be considered to be a subgenus of *Lampetra*. In this report, the genus *Lampetra* is used in the sense of Hubbs and Potter (1971) to conform with the terminology adopted by the American Fisheries Society (Robins et al. 1980). As more becomes known about the relationships of lampreys on the west coast of North America it is possible that the terminology of Vladykov and his co-workers will become popular again and the new species will be placed in the genus *Entosphenus*.

The new species described in this paper belongs to the group with the 3–4–5 formula and is readily distinguished from the group with the 2–3–7 formula. Previously there were six known species that possess the 3–4–5 formula: *Lampetra tridentata*, *L. minima*, *L. similis*, *L. lethophaga*, *L. folletti*, and *L. hubbsi*. *Lampetra tridentata*, a parasitic species, was first described by Gairdner 1836 (in Richardson 1836, p. 293). *Lampetra minima* Bond and Kan, 1973 is a dwarfed parasitic derivative of *L. tridentata* that has been reported from only one lake and is now believed to be extinct; *L. minima* was distinguished from *L. tridentata* by its dwarfed size at maturity, a low number of trunk myomeres, the shape and number of the posterials, larger eye, a longer prebranchial region, and a paler, simpler coloration (Bond and Kan 1973). A third parasitic species, *L. similis* (Vladykov and Kott, 1979) differs from *L. tridentata* by having fewer velar tentacles and myomeres and a larger disc, and from *L. minima* by its larger size at maturity and its larger disc.

There also are three nonparasitic derivatives of *L. tridentata*. *Lampetra lethophaga* Hubbs, 1971, *L. folletti* (Vladykov and Kott, 1976b), and *L. hubbsi* (Vladykov and Kott, 1976c) are easily distinguished from the parasitic species by the nonfunctional digestive tract. *Lampetra letho-*

Printed in Canada (J6426)
Imprimé au Canada (J6426)

phaga frequently has a bicuspid supraoral lamina in addition to a tricuspid and a quadricuspid one (Hubbs 1971). The distinctions among these three non-parasitic species have been described by Vladykov and Kott (1976b, c).

It was not until the biology of adult and postlarval *L. tridentata* on the west coast of Canada was reexamined (R. J. Beamish 1980) that the very distinctive morphometric features of the new species were noted. At present the new species has been found in Lake Cowichan (124°17'W, 48°52.6'N) and the connected Mesachie Lake (124°07'W, 48°48.7'N) on Vancouver Island, British Columbia. The term non-anadromous rather than landlocked is used to describe the habit of this species as there currently are no physical barriers in these two lakes that prevent access to the sea.

Material and Methods

Postlarval or immature specimens were obtained using beach seines, purse seines, gill nets, traps, and from sports-caught fish that were landed with lamprey attached. Mature adults were trapped on a gravel bar at the inlet to Mesachie Lake. A 5-mm-square-mesh-galvanized wire fence was placed on the gravel bar at right angles to the shore. Unbaited minnow traps (mesh-covered cylinders of various sizes with conical entry tunnels at each end) were placed on the bottom along both sides and ends of the fence. Lamprey entered the openings of these traps apparently in an attempt to find passage around the fence.

Ammocoetes and recently metamorphosed individuals were collected using electroshockers in Mesachie Lake and Lake Cowichan. They were most plentiful along the edge of the lakes, rather than in outlet or inlet streams, and they were seldom found in any abundance.

Sixteen immature lamprey were obtained from Mesachie Lake in 1979 and 1 from Lake Cowichan in 1980. Ninety-four mature adults were captured from Mesachie Lake in 1980. Seventeen recently metamorphosed specimens were collected from Mesachie Lake in 1979 and maintained in the laboratory. A sample of 16 ammocoetes was examined from a collection made in Mesachie Lake during September 1979. A portion of the sample was kept alive using the procedures described in R. J. Beamish (1980).

Samples of *L. tridentata* were collected from two locations in British Columbia, Canada, for comparison with ***L. macrostoma*** n.sp. Between 1978 and 1980 one sample of 22 feeding adults was collected from the Strait of Georgia. All these lamprey were immature and were caught during research cruises or commercial fishery operations (R. J. Beamish 1980). A sample from Stamp River, collected at an artificial river bypass or fishway 14 km from the mouth of the river, was subsampled. The sample was obtained in June 1979 and consisted of individuals that had just entered freshwater prior to spawning in the spring of 1980. The gonads of all specimens were maturing. The body cavity of most juveniles was one third to about two thirds full of eggs, but there was no distention of the abdomen that is characteristic of females just prior to spawning.

Measurements and counts were made from the left side of specimens that had been previously preserved in 5% Formalin unless otherwise indicated. The procedures described by Vladykov and Follett (1965) were used. Tail length, trunk length, branchial length, prebranchial length, disc length, eye length, postorbital length, total length, and the height of the first and second dorsal fins were measured for each specimen. Myomeres were counted from the posterior branchial opening (first myomere not touching the posterior of the branchial opening) to the last myomere, whose lower posterior angle lies in part or wholly above the cloacal slit. Velar tentacles were examined and counted according to the procedures described by Vladykov and Kott (1979). Terminology used for the dentition was according to Vladykov and Follett (1967). All measurements except total length were expressed as a fraction of total lengths.

Experiments were conducted to compare the ability of recently metamorphosed ***L. macrostoma*** n.sp. and *L. tridentata* to remain in freshwater and to determine if feeding ***L. macrostoma*** n.sp. captured in a lake would acclimate and feed in full-strength seawater.

During September 1979, recently metamorphosed *L. tridentata* were collected from Robertson Creek (124°58.5'W, 49°19.8'W), Oyster River (125°07'W, 49°52.3'N), Qualicum River (124°37'W, 49°24'N), Haslam Creek (123°53'W, 49°04'N), and Babine Lake (126°W, 54°N). Recently metamorphosed ***L. macrostoma*** n.sp. were collected from Mesachie Lake in late September and early October 1979. At the end of September, five *L. tridentata* from each location were held in an 800-L tank with flowing freshwater of ambient temperature. A second similar experiment contained 48 *L. tridentata* with a minimum of 5 from each location. Five ***L. macrostoma*** n.sp. were added to the second experiment in November and five were held separately in a third tank. Small salmonids were maintained in all tanks for food for the duration of the experiments, except that all fish were removed from the first experiment at the end of October to determine if there might be some relationship between the presence of the fish and the observed lamprey mortalities.

In two other experiments, 37 and 40 recently metamorphosed *L. tridentata* from the same five locations were maintained in 800-L tanks in freshwater until mid-October and mid-November, respectively, when they were converted to full-strength salt water over a 3-d period. No salmonids were provided for food while lamprey were in freshwater.

In late September 1979, five recently metamorphosed ***L. macrostoma*** n.sp. were gradually introduced into full-strength salt water over a period of 3 d. This experiment was repeated on November 3 with an additional two lamprey. In December 1980, the experiment was repeated again, this time using four recently metamorphosed ***L. macrostoma*** n.sp.

In all experiments, freshwater was dechlorinated City of Nanaimo water; salt water was obtained directly from the Strait of Georgia and ranged in salinity from 27 to 30‰. Saltwater and freshwater ambient temperatures ranged from 8.5 to 10.5°C and 4.5 to 11.5°C, respectively, during the experiment. Photoperiod was not regulated, and tanks were darkened with opaque plastic covers.

Results and Discussion

Lampetra macrostoma n.sp.

SYNONYM: *E. tridentatus*; of Carl (1953).

ETYMOLOGY: The specific name in Latin means large opening

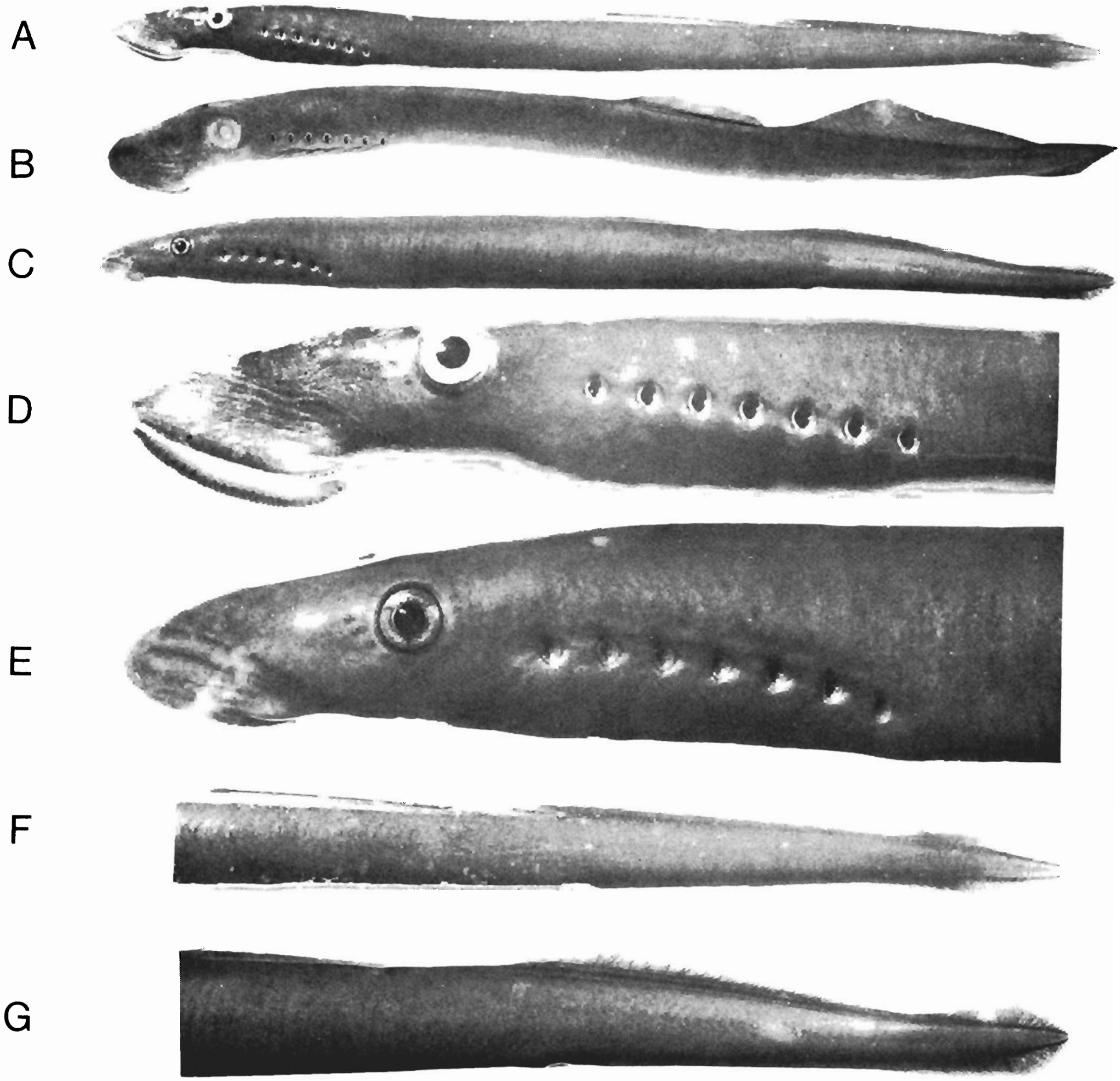

FIG. 1A. Lateral view of the holotype of *L. macrostoma*. B. Holotype after preservation. C. Lateral view of *L. tridentata* (29.0-cm specimen from the Qualicum River. D. Head region of holotype. E. Head region of *L. tridentata* in C. F. Tail region of holotype. G. Tail region of *L. tridentata* in C. All photographs were of live specimens except B.

in reference to the very large disc or mouth, compared to *L. tridentata*.

COMMON NAME: Lake lamprey.

HOLOTYPE: National Museum of Natural Sciences, Ottawa, Canada, No. NMC 81-1219 caught November 14, 1980 in Lake Cowichan, Vancouver Island, British Columbia, attached to a coho salmon (*Oncorhynchus kisutch*).

DESCRIPTION OF HOLOTYPE

Immature male; 22.8 cm total length before preservation (Fig. 1A) and 22.1 cm after preservation (Fig. 1B); preserved weight 19.8 g; preserved measurements (as % TL): tail length 28.8, trunk length 42.4, branchial length 10.8, prebranchial length 15.9, disc length 10.0, eye diameter 2.7, postorbital length 2.7, height of first dorsal fin 2.0, height of second dorsal fin 4.2; supraoral lamina tricuspid. Four inner lateral teeth on each side of disc, first and fourth bicuspid, second and third tricuspid. Infraoral lamina with 6 cusps. Anterials 10, posterials 18. Three anterior posterials on each side of disc bicuspid. Marginals 62. Transverse lingual lamina with 17 cusps, median cusp slightly enlarged. Left longitudinal lingual lamina with 27 cusps. Velar tentacles 14, and myomeres 64.

The new species is known to reside in lakes and probably is non-anadromous even though it can survive in salt water.

PARATYPES

All mature males and females were in spawning condition and were collected by Messrs Mike Smith, Ed Pawlik, John Richards, and myself from a gravel bar in Mesachie Lake from June 1 to August 23, 1980. The sample consists of 53 males and 41 females ranging in length from 17.9 to 25.6 cm. National Museum of Natural Sciences, Ottawa, Canada, No. NMC 81-1220. A sample of 16 immature fish that were collected in 1979 from Mesachie Lake are catalogued as NMC

TABLE 1. Proportional measurements (% TL), number of cusps, velar tentacles, and myomeres from lamprey examined in this and other studies. Range in parentheses.

	L. macrostoma mature	*L. macrostoma* immature	*L. tridentata* maturing,[c] Stamp River	*L. tridentata* immature, St. of Georgia	*L. minima*, Miller Lake, Oregon[d,e]
Total length (TL), cm	20.6 (17.9–25.6)	17.4 (11.8–27.3)	28.6 (24.5–32.1)	25.1 (18.4–33.1)	8.5 (7.2–12.9)
Tail length	28.4 (20.9–31.7)	27.9 (25.7–30.8)	28.4 (24.9–30.1)	26.7 (23.6–28.5)	30.7 (25.9–32.9)
Trunk length	42.3 (37.5–48.2)	42.6 (38.0–46.1)	45.2 (42.1–48.5)	46.7 (43.0–54.0)	45.2 (42.6–51.3)
Branchial length	11.0 (10.0–12.6)	10.5 (9.4–11.1)	10.7 (9.0–11.4)	10.4 (9.6–11.3)	9.2 (7.9–10.8)
Prebranchial length	15.9 (15.2–17.2)	15.4 (14.3–17.6)	13.1 (12.4–13.9)	13.9 (10.9–15.7)	14.8 (13.4–16.4)
Disc length	10.0 (6.5–11.7)	9.7 (8.8–11.4)	7.3 (6.4–8.2)	7.1 (4.6–9.1)	6.2 (5.0–7.4)
Eye diameter	2.8 (2.4–3.5)	2.9 (2.2–3.3)	2.2 (1.9–2.6)	2.5 (1.9–3.2)	2.4 (2.1–3.1)
Postorbital length	2.8 (2.3–4.4)	2.7 (2.5–3.1)	2.8 (2.5–3.2)	2.8 (2.2–3.4)	—
Height of 1st dorsal fin	3.1 (2.2–4.1)	1.9 (1.3–2.4)	2.2 (1.7–2.8)	2.0 (1.4–2.7)	—
Height of 2nd dorsal fin	4.7 (2.6–6.5)	3.3 (2.2–4.2)	3.6 (2.9–4.1)	4.0 (2.6–4.8)	5.0 (4.4–6.1)
No. myomeres	65.1 (62–70)	64.9 (59–68)	65.2 (63–69)	65.2 (60–70)	63.8 (62–65)
No. velar tentacles	13.4 (11–15)	13.2 (11–14)	13.8 (13–17)	14.1 (12–16)	6.3 (5–7)
Supraorals	3.0	3.1 (3–4)	3.0	3.0	3.0 (2–3)
Innerlaterals[a]	2–3–3–2	2–3–3–2	2–3–3–2	2–3–3–2	2–3–3–2
Infraorals	5.1 (5–6)	5.3 (5–6)	5.1	5.0	5.0 (5)
Anterials	8.8 (6–12)	9.9 (8–11)	8.0	8.2 (6–12)	7.1 (6–10)
Posterials	18.1 (16–21)	17.8 (14–21)	17.2	17.1 (16–19)	14.4 (11–17)
Marginals	59.7 (54–67)	—	54.0 (48–60)	54.4 (49–62)	—
Transverse lingual lamina	15.5 (13–19)	16.1 (13–20)	16.1	17.5 (16–20)	25.6 (20–29)
Longitudinal lingual lamina	22.2 (17–25)	23.8 (22–26)	21.0	24.2 (22–27)	22.1 (18–25)
Number examined[b]	94	17	30	22	45

	L. similis,[c] Klamath River		*L. tridentata*[f]		*L. tridentata*,[c] Sprague River, landlocked
	<17.0 cm	17–30.0 cm	Upper Klamath Lake	Pacific Ocean, immature	
Total length (TL) cm	14.7 (13.6–16.3)	22.6 (18.8–26.9)	22.4 (16.1–29.4)	21.0 (18.5–29.2)	25.9 (22.5–28.4)
Tail length	31.8 (30.2–34.9)	29.0 (27.0–32.1)	30.6 (29.2–31.9)	27.8 (24.6–29.6)	32.3
Trunk length	44.7 (42.5–47.8)	47.2 (44.9–52.0)	46.3 (44.2–48.4)	48.1 (43.4–51.6)	46.1
Branchial length	9.2 (8.2–10.6)	9.9 (8.5–11.8)	9.7 (8.6–10.3)	9.7 (8.6–10.3)	9.8
Prebranchial length	15.0 (14.4–16.4)	14.3 (13.0–15.6)	13.4 (12.0–14.6)	13.8 (12.0–16.0)	12.2
Disc length	9.0 (8.5–10.3)	9.3 (7.8–10.4)	6.7 (6.1–7.4)	6.1 (5.0–6.8)	6.6
Eye diameter	2.4 (2.0–2.7)	2.0 (1.4–2.4)	1.7 (1.3–2.0)	2.5 (1.9–3.7)	2.0
Postorbital length	—	—	—	—	—
Height of 1st dorsal fin	—	—	—	—	—
Height of 2nd dorsal fin	—	—	2.8 (2.2–3.2)	3.3 (2.5–5.8)	—
No. myomeres	61.5 (58–65)		63.1 (59–66)	—	64.7 (63–66)
No. velar tentacles	8.0 (7–9)		6.1 (6–8)	—	9.0 (7–11)
Supraorals	3.0 (3)		—	—	3.0
Innerlaterals[a]	2–3–3–2		—	—	2–3–3–2
Infraorals	5.2 (5–6)		—	—	5.2 (5–6)
Anterials	12.8 (10–15)		—	—	14.5 (12–17)
Posterials	18.0 (16–20)		—	—	18.0 (16–20)
Marginals	—		—	—	—
Transverse lingual lamina	22.9 (20–29)		(18–21)	—	19.1 (16–23)
Longitudinal lingual lamina	28.1 (24–33)		(24–28)	—	23.8 (20–26)
Number examined[b]	22		39	12	14

TABLE 1. *(Concluded)*

	L. tridentata,[e] Cultus Lake, landlocked	*L. tridentata*[c] maturing		
		<17 cm	17–30 cm	>30 cm
Total length (TL) cm	20.6	12.6 (9.6–15.9)	24.5 (19.2–30.0)	50.5 (31.2–71.6)
Tail length	28.2	29.9 (26.8–34.9)	29.7 (25.9–31.3)	30.7 (25.6–32.1)
Trunk length	45.2	45.8 (40.3–50.4)	45.9 (42.9–49.3)	47.1 (42.6–50.3)
Branchial length	11.3	9.6 (7.8–12.0)	11.2 (10.3–12.3)	11.0 (9.7–12.3)
Prebranchial length	15.6	14.8 (13.0–18.0)	13.4 (12.1–14.6)	12.1 (9.8–14.5)
Disc length	8.2	7.0 (4.7–8.5)	6.8 (6.0–7.8)	6.2 (4.7–8.0)
Eye diameter	3.4	3.7 (2.4–4.5)	2.6 (2.0–3.1)	1.8 (1.3–2.7)
Postorbital length	—	—	—	—
Height of 1st dorsal fin	—	—	—	—
Height of 2nd dorsal fin	—	—	—	—
No. myomeres	66.3 (65–69)		67.8 (62–71)	
No. velar tentacles	12.6 (11–14)		13.4 (10–17)	
Supraorals	3.0		3.0	
Innerlaterals[a]	2–3–3–2		2–3–3–2	
Infraorals	5.0 (5–6)		5.0 (5–6)	
Anterials	17.6 (5–10)		8.3 (5–11)	
Posterials	17.5 (14–19)		17.8 (12–21)	
Marginals	—		—	
Transverse lingual lamina	17.9 (16–19)		17.9 (14–21)	
Longitudinal lingual lamina	—		22.3 (20–24)	
Number examined[b]	14	90	20	30

[a] Typical formula.

[b] Numbers examined in this study refer to all measurements; however, in other studies, numbers of specimens used for counts are usually less than the number indicated.

[c] Collected during upstream migration in freshwater in June 1979.

[d] Bond and Kan (1973.)

[e] Teeth and velar tentacle counts from Vladykov and Kott (1979).

[f] Kan (1975).

TABLE 2. Comparison of disc lengths of recently metamorphosed *L. macrostoma* and *L. tridentata* sampled in December 1980.

	Total length (cm)	Disc length/ total length	No.
L. macrostoma (Mesachie Lake)	12.3	0.8	7
L. tridentata (Robertson Creek)	11.9	0.6	4

81-1221 and one immature lamprey from Lake Cowichan collected in 1980 is catalogued as NMC 81-1222.

METAMORPHOSED SPECIMENS

Total length (Table 1) — Spawning males and females 20.6 cm (17.9–25.6 cm), immature specimens 17.4 cm (11.8–27.3 cm); five recently metamorphosed specimens collected in Mesachie Lake in September 1979 12.3 cm (11.8–13.9 cm).

Body proportions (Tables 1, 2, 3) — Average measurements (% TL) similar for mature and immature specimens except for the higher dorsal fins of mature fish (Table 1): average measurements expressed as percentage of total length similar for immature males and females (Table 3); mature females had shorter tail length, longer trunk length, and slightly shorter branchial length, prebranchial length, disc length, and higher second dorsal fin than males (Table 3). For average measurements in percentage of the total length, first number refers to mature specimens and second number to immature specimens (Table 1): tail length 28.4, 27.9; trunk length 42.3, 42.6; branchial length 11.0, 10.5; prebranchial length 15.9, 15.4; disc length 10.0, 9.7; eye diameter 2.8, 2.9; postorbital length 2.8, 2.7.

Trunk myomeres (Tables 1, 3) — 65.1 (59–70).

Velar tentacles (Tables 1, 3) — Long and slender with lateral tentacles curving onto dorsal surface: number ranged from 9 to 15 with averages of 13.4 for mature specimens and 11.5 for immature specimens: lower number for immature specimens probably results from difficulties associated with identifying some of the smaller tentacles: base and lower portion of tentacles weakly pigmented.

Dentition (Table 1, Fig. 2E) — Transverse lingual lamina with 13–19 cusps, median cusp enlarged; paired longitudinal lamina with 17–25 cusps; supraoral lamina almost always tricuspid, without exception 4 inner laterals on each side with a cusp formula of 2–3–3–2; infraoral lamina usually 5 cusps but occasional specimen with 6 cusps, all cusps prominent and well developed; 16–21 posterials, outer 3 on each side

TABLE 3. Body proportions (% TL), myomere, and velar tentacle counts of immature and mature male and female *L. macrostoma* (range in parentheses).

	Immature		Mature	
	Male	Female	Male	Female
Total length (TL) cm	17.9 (12.0–23.6)	18.9 (11.8–27.3)	21.1 (17.9–27.2)	20.4 (18.2–25.6)
Tail length	27.7 (26.1–29.2)	28.8 (26.2–30.8)	29.7 (26.9–31.7)	26.8 (20.9–31.5)
Trunk length	42.4 (41.2–44.6)	42.5 (39.9–44.4)	40.4 (37.5–44.0)	44.7 (39.0–48.2)
Branchial length	10.6 (9.8–11.1)	10.4 (9.9–10.9)	11.4 (10.0–12.6)	10.6 (6.9–11.9)
Prebranchial length	15.8 (17.0–14.6)	15.7 (15.0–16.5)	16.1 (15.2–17.2)	15.5 (14.2–17.2)
Disc length	9.7 (8.8–11.4)	9.6 (9.0–10.4)	10.3 (8.1–11.8)	9.6 (6.5–11.7)
Eye diameter	2.9 (2.5–3.3)	2.9 (2.2–3.4)	2.7 (2.4–3.0)	2.9 (2.6–3.5)
Postorbital length	2.7 (2.6–3.0)	2.7 (2.5–2.9)	2.8 (2.3–3.2)	2.9 (2.5–4.4)
Height of 1st dorsal fin	1.9 (1.4–2.3)	2.0 (1.5–2.3)	3.2 (2.2–3.9)	3.1 (2.2–4.1)
Height of 2nd dorsal fin	3.5 (2.3–4.2)	3.5 (2.2–4.4)	4.6 (2.6–5.5)	5.1 (3.8–6.5)
Myomeres	64.3 (59–68)	66.3 (64–69)	64.5 (62–67)	65.9 (63–70)
Velar tentacles	13.1 (11–14)	13.3 (13–14)	13.3 (11–15)	13.6 (11–15)
Number examined[a]	10	5	53	41

[a] Sex of some immature individuals could not be determined.

bicuspid; anterials averaged ~ 9 and ranged 6–12 for all specimens and 9–11 for immature specimens, only the counts of immature specimens were considered to be reliable as some mature specimens lost anterials when touched; 54–67 marginals, easily separated from anterials except in extreme anterior field.

Color (Fig. 1, 2) — Specimens uniformly dark, almost black; both dorsal fins pigmented, although second dorsal fin more heavily pigmented; caudal fin pigmented but flesh above notochord clearly identifiable (Fig. 1A, F, 2C, 3B) and uniformly pigmented.

Sexual dimorphism — Males readily identifiable by presence of an external genital papilla.

Comparisons — Postlarval individuals of *L. macrostoma* are readily distinguished from nonparasitic species by their functional digestive tract and prominent dentition. They differ from the parasitic species that have a supraoral lamina with 2 well-developed cusps, 3 inner laterals on each side of the disc, and an infraoral lamina with 7 cusps in having a supraoral lamina with 3 cusps, 4 innerlaterals on each side of the disc and 5 cusps on the supraoral lamina. Mature individuals were smaller than the average *L. tridentata* from a number of other locations in British Columbia (R. J. Beamish 1980, Table 1), but were larger than the dwarf *L. minima* (Table 1). Sizes were similar to *L. similis*, a subspecies of *L. tridentata* proposed by Kan (1975) and some other populations of reportedly non-anadromous *L. tridentata* (Table 1).

Lampetra macrostoma has a large disc (Fig. 2A, C, E) that is considerably bigger than the discs of *L. tridentata* from the Stamp River, the Strait of Georgia (Table 1), or the Qualicum River (Fig. 2B, D). The flattened disc of *L. macrostoma* (Fig. 2A) has approximately two thirds more surface area than the disc of similar size *L. tridentata* (Fig. 2B). The characteristically large size of the disc readily visible on fresh and preserved specimens (Fig. 1A, B, D) in adult, recently metamorphosed and immature specimens (Fig. 3A, B, Table 2), is the key character distinguishing *L. macrostoma* from *L. tridentata*. The large disc results in relatively large wounds on hosts (Fig. 3G) that can be mistakenly interpreted as attacks by very large *L. tridentata* on small fish.

Lampetra macrostoma has a large eye, a longer prebranchial length, and possibly a shorter trunk length compared to the *L. tridentata* examined in this study (Table 1, Fig. 1D, E).

Lampetra macrostoma differs from *L. minima* primarily by the much larger disc and greater number of velar tentacles. It also is larger at maturity, has a larger eye, fewer transverse lingual laminae, and possibly a shorter trunk length and a longer branchial length. It differs from *L. similis* primarily by the larger number of velar tentacles, but it also appears to have a shorter trunk length, longer branchial length, and a slightly larger eye and disc. The prebranchial appears slightly longer, and there may be more myomeres and fewer cusps on the transverse and longitudinal lingual lamina.

Lampetra macrostoma can be distinguished from a subspecies of *L. tridentata* (Kan 1975) by the larger disc, larger eye, and greater number of velar tentacles. *Lampetra macrostoma* also appears to have a larger prebranchial, shorter trunk and longer branchial region. It is interesting that the major difference between this subspecies identified by Kan (1975) and *L. similis* is the size of the disc (Table 1).

When *L. macrostoma* is compared to samples of *L. tridentata* examined in other studies, the size of the disc remains distinctive. A sample from Cultus Lake that Vladykov and Kott (1979) claimed was landlocked appears similar to *L. macrostoma* although the disc size remains smaller. The larger disc and greater number of velar tentacles separated *L. macrostoma* from a sample of "landlocked *L. tridentata*" described by Vladykov and Kott (1979) from the Sprague River.

It is interesting to note that the major differences between *L. minima* and *L. similis* are the size at maturity and disc size. Because size at maturity is quite variable for other species of fishes (Beamish and Crossman 1977), the size of the disc becomes a principal character for separating these species. Vladykov and Kott (1979) also concluded that disc size was an important character and stated "the principal differences

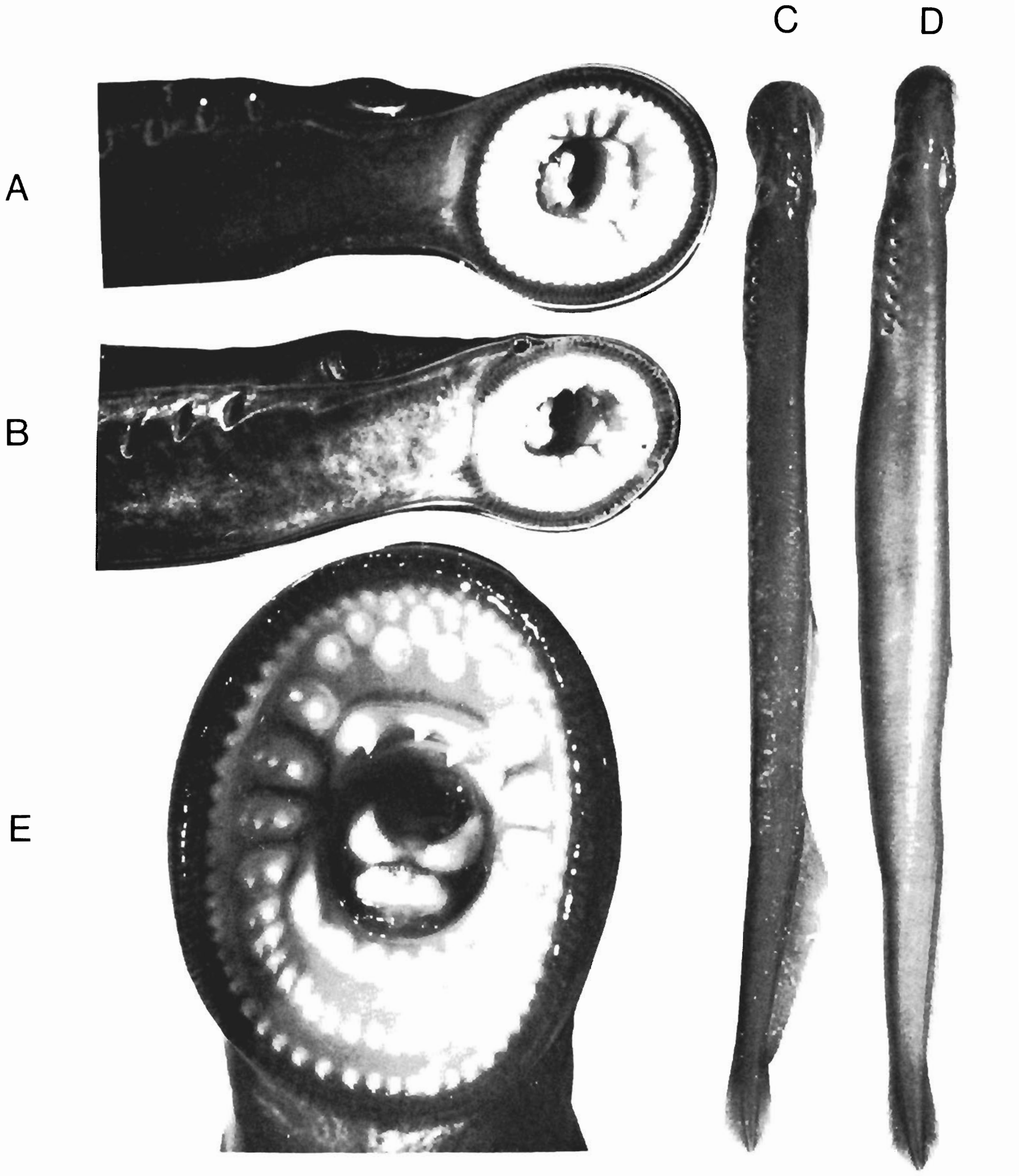

FIG. 2A. Ventral view of holotype. B. Ventral view of *L. tridentata* in Fig. 1. C. Dorsal view of holotype. D. Dorsal view of *L. tridentata* in B. E. Ventral view of disc of holotype. All photographs were of live specimens.

between the parasitic species of *Entosphenus* are in the length of the disc and eye, which are proportionately larger in smaller specimens."

The number of velar tentacles is a useful character for separating species (Table 1). Because of the range in counts in *L. macrostoma*, the number of velar tentacles must be considered to be similar to the number observed for *L. tridentata* (Table 1). There was no obvious difference in the shape of the velar tentacles; however, those of *L. macrostoma* were very weakly pigmented relative to the darkly pigmented base and lower portion of the velar tentacles of *L. tridentata*.

There were apparent differences in dentition among some species in Table 1 such as the higher number of cusps on the traverse lingual lamina for *L. minima* and *L. similis* and possibly a higher number of cusps on the longitudinal lingual lamina for *L. similis*. *Lampetra minima* appears to have fewer posterials, and *L. similis* and the Sprague River landlocked form in Oregon has a greater number of anterials.

Mature *L. macrostoma* males had a larger disc than females, but the eye and second dorsal were slightly smaller. Females had a greater trunk length, but males had a larger tail length. If females decrease in size during maturation more than males as found for other species (F. W. H. Beamish 1980; R. J. Beamish 1980), then the body proportions of females (% TL) might be expected to be greater for mature females than males because they were similar as immature individuals (a comparison of immature males and female fish (Table 3) indicated there was little difference in body proportions). Because there was no consistent trend in changes of body proportions of females, it appears that allometric shrinkage occurs in males and females during maturation.

AMMOCOETES

The sample of 16 ammocoetes examined for body proportions has the National Museum of Natural Sciences No. NMC 81-1223. Body proportions (% TL): tail length 30.0 (28.3–33.1), trunk length 47.8 (45.5–51.4), branchial length 14.4 (12.8–15.7), prebranchial length 9.2 (7.6–10.7), disc length 5.1 (4.8–6.6). Myomere counts averaged 66.1, which is slightly higher than the average of ~ 65 found in this study for adult *L. tridentata* and *L. macrostoma* and slightly lower than the average of 67.5 found for ammocoetes of *L. tridentata* by Pletcher (1963).

The pigmentation of the branchial region from preserved specimens (Fig. 3C) was similar to that reported for ammocoetes of *L. folletti*, *L. lethophaga*, and *L. minima* (Vladykov and Kott 1976b), but not for *L. tridentata* (Vladykov and Kott 1976b; Pletcher 1963). Both Pletcher and Vladykov reported that the latter has a patch of unpigmented area above the first branchial pore. Pletcher showed that the pigmentation extends close to the other branchial pores and Vladykov showed that *L. tridentata* ammocoetes have a broad band of unpigmented area above the branchial pores. The ammocoetes examined in this study did not have a clear patch above the first branchial pore, and a nonpigmented area above the branchial pores was absent (Fig. 3C, D). Despite the differences in the branchial region pigmentation of *L. macrostoma* and *L. tridentata*, the head pigmentation pattern is not characteristic of this new species because there are important variations in the pattern reported for *L. tridentata* (Vladykov and Kott 1976b; Pletcher 1963). The pigmentation of the head region of living specimens (Fig. 3D) was much darker, and it was difficult to identify a clear pattern.

The pigmentation of the tail region (Fig. 3E, F) was similar to the pigmentation of the *L. tridentata* ammocoete shown, but not described in Vladykov and Kott (1976b). We have found that the pigmentation of the tail region is the only method for distinguishing live and preserved ammocoetes of *L. tridentata* and its derivatives in British Columbia (Richards 1980). The pattern also is similar to the pattern shown for *L. tridentata* derivatives (Vladykov and Kott 1976b). The area above the notochord in the caudal fin is uniformly lightly pigmented, often grayish. The dorsal and ventral edge of the caudal ridge has a thin dark band, and the caudal fin is deeply pigmented immediately adjacent to the ridge (Fig. 3E, F). In living specimens (Fig. 3F) the dark bands are accentuated by areas of reduced pigmentation immediately to the interior. The pigmentation in the caudal fin may extend for varying distances, but usually extends about halfway to the edge of the fin. This pattern is readily distinguished from the dark caudal area found on *L. richardsoni* Vladykov and Follett, 1965 and *L. ayresi*.

The bulb of the tongue precursor of *L. macrostoma* is unpigmented, and there is little or no black pigmentation on either side of the elastic ridge. The pigmentation is similar to the tongue precursor shown for *L. tridentata* in Vladykov and Kott (1976b).

Part of the sample collected in September 1979 was kept alive and fed (R. J. Beamish 1980). Four of the larger ammocoetes metamorphosed, and all were *L. macrostoma*. In 1980, a sample of 227 ammocoetes from Lake Cowichan was kept alive and fed. In October 1981, 59 of these had metamorphosed, and all were *L. macrostoma*. Because subsamples of these two samples were preserved and examined in this study, it is probable that they were *L. macrostoma*. Ammocoetes of *L. macrostoma* ranging from 1.6 to 17.0 cm have been found in Lake Cowichan and Mesachie Lake. The larger ammocoetes (10–17 cm) are not unusual in the areas where ammocoetes occur.

BIOLOGY

The life history of this new species is currently being examined. Preliminary results indicate that adults spawn on shallow gravel bars in the lake. Mature males and females in spawning condition have been captured from May to August at two sites, and it is assumed that spawning would occur over this period. Ammocoetes were found primarily in the silt bottom of the lake or in the inlet of streams that flowed into the lake. Few were found at distances greater than 100 m from the lake, indicating that the lake is the principal rearing area for larvae. At this time nothing is known about their depth distribution or the average duration of ammocoete life.

Metamorphosing lamprey have been collected in the two lakes from mid-September until mid-November. The stage of metamorphosis was not as advanced as that of *L. tridentata* collected over the same period from other areas.

Feeding adults readily attack resident fishes. Up to 50% of fish collected throughout the year had some evidence of being attacked by lamprey. In one sample of 221 salmonids, 15% had wounds that penetrated the body cavity (Fig. 3G) or penetrated deeply into the muscle and probably would result in the death of the fish. Carl (1953) reported that 8 of 10 fish examined from Lake Cowichan had been attacked by lamprey. During the summer of 1980, coho salmon that were killed by lamprey were found on the bottom of the lake and washed up along the shore. There was no doubt that this species was a serious predator of resident fishes and an important source of mortality.

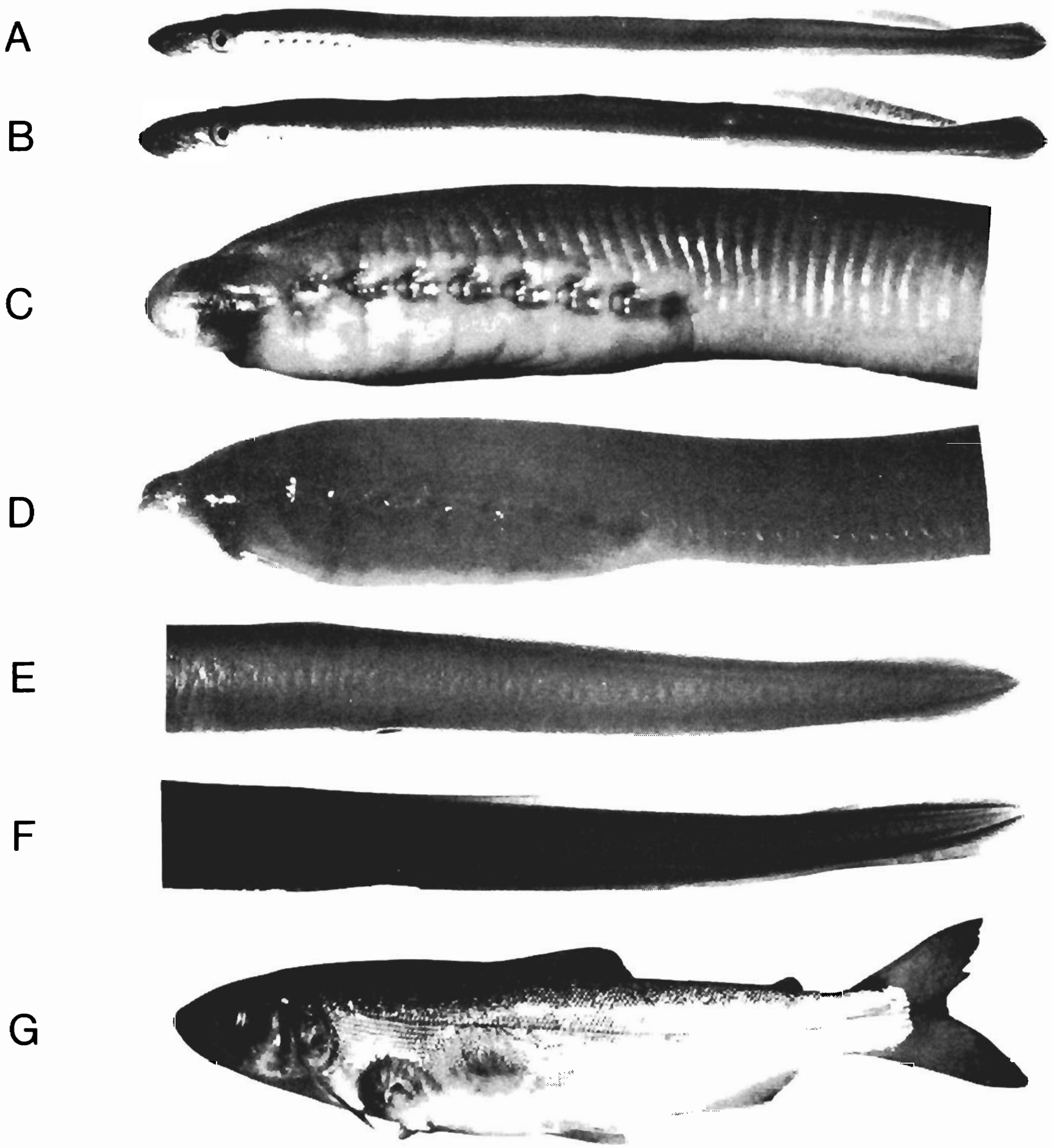

FIG. 3A. Recently metamorphosed live *L. tridentata* from the Stamp River (11.5 cm). B. Recently metamorphosed live *L. macrostoma* from Mesachie Lake (12.0 cm). A and B were photographed in December 1980. C. Anterior of preserved *L. macrostoma* ammocoete (11.4 cm). D. Anterior of live *L. macrostoma* ammocoete from Mesachie Lake (12 cm). E. Tail region of ammocoete in C. F. Tail region of ammocoete in D. G. *Lampetra macrostoma* wound on 19-cm salmonid found dead on the bottom of Mesachie Lake.

The duration of adult life is unknown. It is suspected that postlarval lamprey may begin to feed in the spring following metamorphosis. Feeding continues throughout the year as evidenced by the fresh wounds that were observed on prey throughout the year. Thus the minimum length of life from onset of metamorphosis to death following spawning is 2 yr, but the actual life span probably is longer. All mature adults held in the laboratory died after spawning.

PHYSIOLOGY

When recently metamorphosed *L. macrostoma* were held in freshwater separately and with samples of recently metamorphosed *L. tridentata* from five locations, all *L. macrostoma* survived while 50% of the *L. tridentata* died before the end of November, and none survived past March of the next year (Fig. 4). Both freshwater holding experiments with

L. tridentata produced similar results (Fig. 4). In both experiments feeding was initiated in mid-October. While the cause of death of *L. tridentata* was not determined, there can be no question that *L. macrostoma* was better adapted than *L. tridentata* to survive in freshwater in these experiments. This suggests that the non-anadromous habit of *L. macrostoma* is distinct from the anadromous habit of *L. tridentata*.

In contrast to the total mortality observed for *L. tridentata* in freshwater, there was very little mortality of *L. tridentata* from the same locations once they were acclimated to salt water. In one experiment (Fig. 4, experiment 4) there was an initial death in freshwater; however, there were no deaths from mid-October until shortly after conversion to salt water in mid-November (Fig. 4). After these initial deaths in salt water, no others were observed. These lamprey were maintained in salt water, and many were still alive in December 1981. In experiment 5 in which *L. tridentata* were introduced into salt water in October, there were 10 deaths during conversion, and 2 a few days after full-strength salt water was reached (Fig. 4). There were two deaths in mid-February, and no more mortality until the end of the experiment in March 1980. The deaths during the conversion to salt water probably resulted from forcing the lamprey into full-strength salt water before metamorphosis was completed (Richards 1980). After March 1980 these lamprey were maintained and fed in salt water, and many were still alive in December 1981.

The lamprey held in freshwater in experiment 4 until mid-November (Fig. 4) did not suffer similar mortality rates as the lamprey held in the two freshwater holding experiments. Because the only known difference among these experiments was that the lamprey converted to salt water were not fed while in the other two experiments fish were supplied and feeding commenced in mid-October, it is possible that the rate of mortality in freshwater was related to the onset of feeding. Because the removal of fish at the end of October did not affect the rate of mortality, any relationship may be to the onset, and not the amount, of feeding.

In the final experiments in which five *L. macrostoma* were subjected to increasing concentrations of salt water with five *L. tridentata* from five locations, all died within 3 d while 80% of the *L. tridentata* survived and remained feeding in salt water. The cause of death of all lamprey appeared to be related to the stage of metamorphosis. Those that died had not reached stage 6 or had just reached stage 6 (Richards 1980). On November 3, 1979, an attempt was made to acclimate two more recently metamorphosed *L. macrostoma* to salt water. One died within 2 d (~20‰) and the other survived. In December 1980, four recently metamorphosed *L. macrostoma* were acclimated to full-strength salt water over a 3-d period; two died in the summer of 1981 and two were maintained until November 1981 when the experiment was terminated. The two that remained grew from an average size of 9.5 cm and 1.5 g to 22.8 cm and 11.5 g in 11 mo. It appeared that *L. macrostoma* will not survive in salt water as early as *L. tridentata*, but will acclimate with little difficulty a few months later.

In June 1979, two feeding adult *L. macrostoma* were captured in Mesachie Lake and gradually acclimated to full-strength salt water over a period of 3 d. In November 1979, two feeding adults were captured in Mesachie Lake and acclimated to full-strength salt water over a period of 3 d and maintained in salt water with salmonids used as food. In both experiments the lamprey were probably in their second postlarval year, again indicating that *L. macrostoma* can live and feed in salt water.

Conclusions

Lampreys, which are believed to be at least 280 million yr old, are one of the most primitive groups of living fishes and have few characters that can be used for taxonomy. Dentition characters are used for generic level distinctions (Berg 1940; Vladykov and Follett 1967), and morphological characters along with trophic or life history distinctions form the basis for species or subspecies distinctions (Hubbs and Potter 1971). Often the distinctions may appear trivial and not of sufficient importance to warrant a species designation. For example, the distinction between *L. ayresi* and *L. fluviatilis* (cf. Vladykov and Follett 1958) (expressed as % TL) is based on one species having a larger eye (3.3 compared to 2.2), a larger prebranchial length (12.5 compared to 11.6), and a shorter branchial length (9.0 compared to 10.0). The differences in these body proportions are similar to differences described in Table 1 and may appear of minor significance; however, Hubbs and Potter (1971) heralded this separation as "one of the highlights in clarifying lamprey systematics."

The distinctions separating *L. similis*, *L. minima*, and *L. tridentata* similarly may appear of minor importance, yet these lamprey have been accepted as distinct species. Vladykov and Kott (1979) believe that the disc is "the distinctive character separating species of parasitic lamprey," and it is the size of the disc of *L. macrostoma* that distinguishes it from *L. tridentata*. Therefore, apparently minor differences are considered important, and differences in the size of the disc and eye, prebranchial lengths, and pigmentation of the velar tentacles are sufficient to allow *L. macrostoma* to be called a new species; certainly it is as distinctive as the other derivatives of *L. tridentata*.

The characters used in this study were subjected to multivariate analysis, detailed results of which will be published separately. Discriminant functions were derived to maximize separation between groups using principal components (combinations of characters). The first component (67.7% of variance) separated *L. macrostoma* from *L. tridentata*. Disc length exhibited the strongest loading on the first component. The second component (31% of variance) appeared to differentiate among *L. tridentata* at different life stages. This second component was strongly influenced by the morphological changes females undergo prior to spawning.

Lampetra macrostoma differs physiologically from *L. tridentata*. Postlarval *L. macrostoma* survived in freshwater while all attempts to maintain *L. tridentata* were unsuccessful. As *L. tridentata* from the same locations survived in full-strength seawater, it appeared that *L. tridentata* could survive only temporarily in freshwater after metamorphosis was completed, and after feeding commenced in mid-October. Admittedly the failure to maintain *L. tridentata* in freshwater is an inconclusive experiment because the cause of death was not determined. However, the survival of the non-anadromous species under similar conditions and the survival

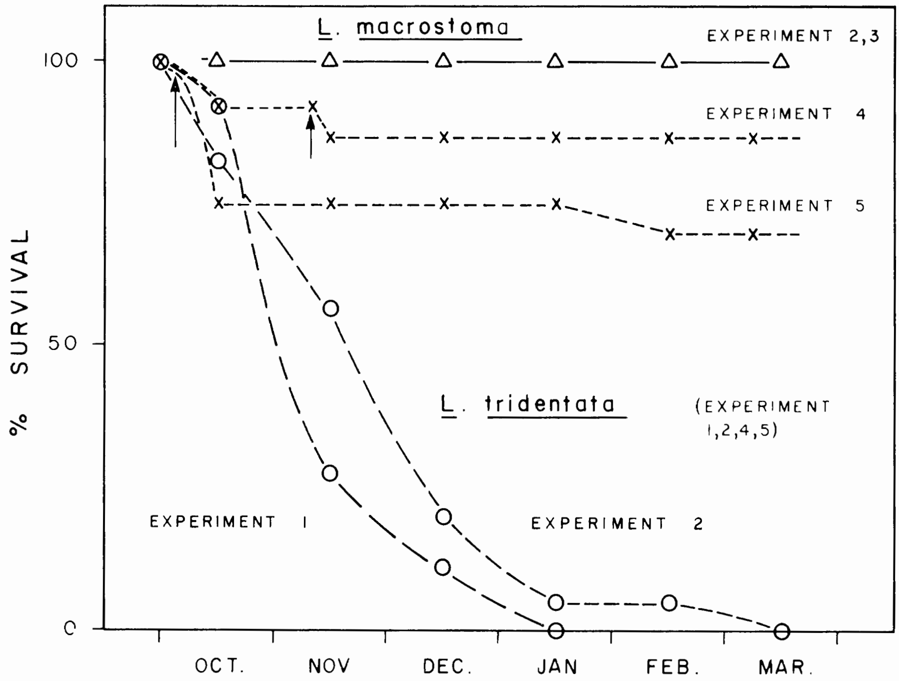

FIG. 4. Survival of *L. macrostoma* and *L. tridentata* in freshwater and *L. tridentata* in salt water. Experiment 1 contained *L. tridentata*, experiment 2 contained *L. tridentata* and *L. macrostoma*, experiment 3 contained *L. macrostoma*, experiment 4 contained *L. tridentata* that were converted from freshwater to salt water in mid-November (position of arrow), and experiment 5 contained *L. tridentata* that were converted to salt water in mid-October (position of arrow).

of *L. tridentata* in seawater strongly suggest that recently metamorphosed *L. tridentata* and *L. macrostoma* differ in their ability to survive in freshwater. It is possible that *L. tridentata* must go to sea while *L. macrostoma* prefers freshwater.

Interestingly, it is not known if the anadromous form of the sea lamprey (*Petromyzon marinus*) can survive in freshwater. It is not an uncommon belief that "landlocked" or non-anadromous forms of the sea lamprey and the Pacific lamprey developed when anadromous forms remained in freshwater and became non-anadromous. Certainly this is one of the theories for explaining the increase in abundance of the sea lamprey in the Great Lakes, yet to my knowledge no one has demonstrated that this is possible within the period being considered. It is possible that the ability to remain in freshwater evolved in the same manner as other specific characteristics (e.g. nonparasitic habits), and that the non-anadromous genotype is not present in the anadromous population.

Lampetra macrostoma as well as the anadromous *L. tridentata* are found in the Lake Cowichan system (Carl 1953). In order that the two species remain distinct, conventional theory would require that some barrier must be present to prevent interbreeding. One possibility is that the spawning of *L. tridentata* occurs earlier than *L. macrostoma* and *L. tridentata* may spawn exclusively in streams while *L. macrostoma* spawn in lakes. Unfortunately, at present there is not enough information to decide if either of these possibilities is valid.

I feel that the morphological and physiological differences are sufficiently distinct and constant to describe this form as a new species. Certainly they are as distinctive as characters currently used to separate other species. However, morphological characters are variable and it is always possible that the specimens examined in this study represent the extremes in the range. While one such study of variations of *L. tridentata* over their geographical range in Oregon concluded that these characters were useful in distinguishing *L. tridentata* from its congeners if fish of similar life history stages were compared (Kan 1975), it is still possible that differences may be found over a broad range. Until more information becomes available to prove or disprove this possibility, I suggest that the new species designation be retained to emphasize the existence of this form and its profound deleterious effect on freshwater fishes, particularly salmonids. When more information becomes available we may conclude that *L. similis*, *L. minima*, and *L. macrostoma* are all subspecies of *L. tridentata*, but until such proof has been produced, I believe it is important to recognize the existence of these distinct forms with a distinct species designation.

Acknowledgments

Much of the information used in this study was collected by a group of volunteers, who used their spare time to study the biology of this new species. I greatly appreciate the interest and enthusiasm of Sue Farlinger, Wendy-Lou Mitton, Heidi Zeis, Mike Smith, Ed Pawlik, Barry Pawlik, John Richards, and Jim Thompson. Other colleagues at the Pacific Biological Station and numerous local residents assisted in the project. Sue Farlinger made many of the measurements. Dr Z. Kabata kindly reviewed the manuscript.

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., 1980. The adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

Beamish R. J., and E.J. Crossman. 1977. Validity of the subspecies designation for the dwarf white sucker (*Catostomus comersoni utawana*). J. Fish. Res Board Can. 34: 371–378.

Berg, L. S. 1931. A review of the lampreys of the northern hemisphere. Ann. Mus. Zool. Acad. Sci. USSR 32: 87–116.

1940. [Classification of fishes both recent and fossil.] (In Russian.) Trav. Inst. Zool. Acad. Sci. USSR 5: 87–517. Reprint (In English) 1974. Edwards Brothers, Ann Arbor, MI.

Bond, C. E., and T. T. Kan. 1973 *Lampetra* (*Entosphenus*) *minima* n. sp., a dwarfed parasitic lamprey from Oregon. Copeia 1973: 568–574.

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

Gill, T 1862. Note on some genera of fishes of western North America. Proc. Acad. Nat. Sci. Philadelphia 14: 329–332.

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: 301–311

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

Hubbs, C. L., and I. C. Potter. 1971 Distribution, phylogeny and taxonomy, p. 1–65. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, Inc., London.

Jordan, D S., and B. W. Evermann 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus. 47: 1–1240.

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.

McPhail, J. D., and C. C Lindsey. 1970 Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Board Can. Bull. 173: 381 p.

Pletcher, F. T 1963. The life history and distribution of lampreys in the salmon and certain other rivers in British Columbia, Canada. M.Sc. 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. 99 p.

Richardson, J. 1836. The fish. Part third. *In* Fauna Boreali–Americana. John Murray, London.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. 4th ed. Am. Fish. Soc. Spec. Pub. 12: 174 p.

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

1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 27: 139–158.

1967. The teeth of lampreys (Petromyzonidae): their terminology and use in a key to the Holarctic genera. J. Fish. Res. Board Can. 24: 1067–1075.

Vladykov, V. D., and E. Kott. 1976a. Is *Okkelbergia* Creaser and Hubbs, 1922 (Petromyzonidae) a distinct taxon? Can. J. Zool. 54: 421–425

1976b. A second nonparasitic species of *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River system, California. Can. J. Zool. 54: 974–989.

1976c. A new nonparasitic species of lamprey of the genus *Entosphenus* Gill, 1862 (Petromyzonidae) from south central California. Bull. South Calif. Acad. Sci. 75: 60–67.

1979. A new parasitic species of the holarctic lamprey genus *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River, in California and Oregon. Can. J. Zool. 57: 808–823.