Nutritional Condition of the Pacific Lamprey (*Lampetra tridentata*) Deprived of Food for Periods of Up to Two Years

John N. C. Whyte, Richard J. Beamish, Norma G. Ginther, and Chrys-Ellen Neville

Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada

Whyte, J. N. C., R. J. Beamish, N. G. Ginther, and C.-E. Neville. 1993. Nutritional condition of the Pacific lamprey (*Lampetra tridentata*) deprived of food for periods of up to two years. Can. J. Fish. Aquat. Sci. 50: 591–599.

The anadromous parasitic Pacific lamprey (*Lampetra tridentata*) does not feed during metamorphosis or its spawning migration. To assess the utilization of body reserves, we compared the compositions of an adult lamprey held for 2 yr without food, recently metamorphosed lampreys, and lampreys starved for 6 mo. Moisture was higher and soluble ash and lipid levels were lower in tissue of the 2-yr-starved than in metamorphosed lampreys (2.67 and 3.39 kJ·g^{-1}, respectively). Fatty acid profiles of 2-yr-starved and metamorphosed lampreys were qualitatively similar except for the presence of 15:0 in the latter. Substantially lower levels of 14:0 and 16:1*n*7 and higher levels of polyunsaturated fatty acids occurred in starved lampreys. Changes in composition of lampreys starved for 6 mo were similar to changes between the 2-yr-starved and metamorphosed lampreys. Maintenance energy in a normalized 1-g lamprey starved for 6 mo was derived from catabolism of 71% lipid and 29% protein; total loss was 2.56 kJ or 49% of the original energy. The ability to survive extended periods on endogenous reserves, which may have allowed *L. tridentata* to survive past environmental catastrophes, allows it to migrate considerable distances to spawning areas in the headwaters of rivers.

La lamproie du Pacifique parasite anadrome (*Lampetra tridentata*) ne s'alimente pas durant sa métamorphose ni durant sa migration de frai. Pour évaluer ses réserves corporelles, nous avons comparé la constitution de lamproies adultes privées de nourriture pendant 2 ans, des lamproies récemment métamorphosées et des lamproies privées de nourriture pendant 6 mo. La teneur en eau était plus élevée et la concentration de cendres solubles et de lipide étaient plus faibles dans les tissus des lamproies privées pendant 2 ans que dans ceux des lamproies récemment métamorphosées (respectivement 2,67 et 3,39 kJ·g^{-1}). Les profils des acides gras chez les lamproies privées pendant 2 ans et les lamproies récemment métamorphosées étaient semblables du point de vue qualitatif, sauf pour ce qui est de la présence d'acides 15:0 chez ces dernières; chez les lamproies privées d'aliments, on a observé des concentrations d'acide 14:0 et 16:1*n*7 substantiellement plus faibles et des concentrations d'acides gras polyinsaturés plus élevées. Les modifications dans la constitution des lamproies privées d'aliments pendant 6 mo étaient semblables aux modifications que l'on observe entre les lamproies privées pendant 2 ans et les lamproies métamorphosées. L'énergie d'entretien chez une lamproie normalisée de 1 g privée pendant 6 mo a été obtenue à partir du catabolisme lipidique (71 %) et protéique (29 %); les pertes totales ont été de 2,56 kJ ou 49 % de l'énergie initiale. La capacité de survivre pendant longtemps sur des réserves endogènes, qui peut avoir aidé *L. tridentata* à survivre à des catastrophes environnementales dans le passé, lui permet d'entreprendre de longues migrations pour aller frayer dans les eaux d'amont.

Received April 9, 1992
Accepted August 26, 1992
(JB465)

Reçu le 9 avril 1992
Accepté le 26 août 1992

The Pacific lamprey (*Lampetra tridentata*) is a common anadromous fish, ranging from California to the Aleutian Islands, along the eastern coast of Russia and south to Japan. Larvae of the Pacific lamprey live up to 7 yr before metamorphosing into young adults (Russell 1986; Beamish and Northcote 1989; Beamish and Levings 1991). Larval lamprey live in burrows in the silt deposits of rivers, where they filter-feed on algae, detritus, bacteria, and protozoa (Moore and Mallatt 1980). The energy reserves accumulated during this larval stage are used during metamorphosis, the nontrophic period, when the characteristic features of the adult are developed. All parasitic and nonparasitic species of lamprey stop feeding during metamorphosis. However, the nonparasitic species no longer feed and spawn approximately 10 mo after metamorphosis.

Most larval Pacific lamprey metamorphose at age 4–5 yr. After metamorphosis the young adults begin to migrate into the salt water over an 11-mo period starting in September (Beamish and Northcote 1989; Beamish and Levings 1991). In the Nicola River in British Columbia, over 90% of the young adults migrate out of the river in early spring (Beamish and Levings 1991). Young adults feed parasitically on saltwater fish for a period generally considered to be about 1 yr (Beamish and Levings 1991). However, the trophic phase of development in salt water may differ among populations, as mature Pacific lamprey range widely in size and some have continued to feed in salt water in the laboratory for 4 yr (Beamish 1980). The return migration into fresh water can occur immediately before spawning or almost 1 yr prior to spawning, and although spawning occurs mainly in spring, it has been recorded as late as July (Beamish 1980).

When adult anadromous parasitic lamprey return to fresh water, they stop feeding and lose the ability to osmoregulate in salt water (Youson 1981). Cessation of feeding, or starvation,

is accompanied by rapid atrophy of the intestine, and any further assimilation of exogenous reserves, at least by intestinal absorption, is impossible (Youson 1981). The endogenous reserves accumulated during saltwater feeding are then used for upstream migration to the spawning area and for gonadal maturation and spawning. During the period from entry into fresh water until spawning occurs the Pacific lamprey shrinks about 20% in length (Beamish 1980). As Pacific lamprey do not feed on reentering fresh water or while being held in fresh water in the laboratory, the term "starved" used throughout the text expresses only the natural state of the fish and not any intentional deprivation of food. Nothing is known of the changes in body reserves of the Pacific lamprey during the period of prolonged starvation.

Changes in body reserves have been studied in the trophic and nontrophic stages of the anadromous parasitic sea lamprey (*Petromyzon marinus*) (Lowe et al. 1973; Beamish et al. 1979; Farmer 1980), river lamprey (*Lampetra fluviatilis*) (Moore and Potter 1976; Heikkala et al. 1984), and the Southern Hemisphere lamprey (*Geotria australis*) (Bird and Potter 1981, 1983a, 1983b). Anabolic and catabolic changes have also been investigated in the life cycle of the nonparasitic European brook lamprey (*Lampetra planeri*) (Moore and Potter 1976) and southern brook lamprey (*Ichthyomyzon gagei*) (Beamish and Legrow 1983). These studies indicated that the major source of maintenance energy during periods of food deprivation was derived from lipid, although some protein was also catabolized.

Pacific lamprey captured during upstream migration in June 12, 1986, survived in fresh water in the laboratory for 2 yr, the longest starvation period recorded for this fish. To assess the body reserves used during nontrophic stages of the Pacific lamprey, the biochemical composition, caloric content, and energy reserves of different tissues of the 2-yr-starved lamprey were compared with those from recently metamorphosed lampreys and with those from lampreys analyzed during a 6-mo holding, or starvation, period.

Materials and Methods

Lamprey Collection, Holding, and Processing for Analysis

Pacific lamprey (150) returning to the Somass River drainage system (Beamish and Northcote 1989) were captured at a fish bypass on June 12, 1986, and transported directly to the Pacific Biological Station, Nanaimo, British Columbia. They were kept in tanks containing well-aerated fresh water at 10 ± 2°C. The tank bottoms were covered with sand and rocks to provide cover and spawning areas. Lampreys were checked daily for mortalities and for the development of fungal disease. All but three males had either spawned or died by June 1987, and only two survived to the spring of 1988 when one was preserved. On May 10, 1988, the remaining lamprey was killed and the body dissected into head (that portion from mouth to just behind the last gill pouch), body (the remainder of the exterior body), liver, and remaining internal organs. There were insufficient gonads for separation and analysis. The body parts were freeze-dried, homogenized, vacuum packed, and stored at −80°C for subsequent analysis as parts of the "2-yr-starved" lamprey.

Recently metamorphosed Pacific lamprey were collected from the Fraser River on June 24, 1988. On return to the laboratory, two specimens were dissected into head, body (the remainder of the exterior body), liver, and remaining internal organs. Body parts were combined, freeze-dried, and homogenized for analysis as "metamorphosed" lamprey. Sufficient liver was available only for fatty acid analysis, and the gonads were insufficient in amount to be separately analyzed.

On October 27, 1988, a small sample of Pacific lampreys, which probably entered the Somass River in late July, was collected at Stamp Falls. Specimens (six) were held in tanks, as mentioned previously, and sampled for analysis after 0, 91, and 182 d of holding, and starvation. Lampreys collected were dissected into head, body (the remainder of the exterior body), liver, gonad, and remaining internal organs. The body parts were freeze-dried, homogenized, vacuum packed, and stored at −80°C until analyzed.

Biochemical Analysis

Analysis of chemical components in freeze-dried tissue has been described in detail previously (Whyte and Englar 1982; Whyte et al. 1986, 1987). Energy conversion factors used for lipid, carbohydrate, and protein were 35.24, 17.16, and 18.00 kJ·g dry weight^{-1}, respectively (Beukema and De Bruin 1979).

Methyl esters of fatty acid components of total lipids in freeze-dried lamprey parts were prepared by in situ saponification and methylation with methanolic boron trifluoride (Whyte 1988). Analyte solutions were separated on a Supelcowax 10 fused silica capillary column (30 m × 0.32 mm ID, 0.25-μm film) maintained at 190°C for 32 min and then programmed to 240°C at 2°C·min^{-1} and held at 240°C for 16 min. Helium carrier gas was controlled at 21 cm·s^{-1} with a split ratio of 100:1. Identification was made by comparison with standards and peaks assigned in accord with the data presented by Ackman (1986). Peaks of less than 0.2% of the total area were omitted from the profile. Fatty acid structure is represented as (L:B*n*X) where L = chain length, B = number of ethylenic bonds, and *n*X = position of the double bond closest to the terminal methyl group in monomer or *cis* methylene-interrupted structures. The expression Σ4-6,*n*3/poly. represents the ratio of the sum of higher unsaturated fatty acids (HUFA's) with four to six double bonds in the *n*3 series of acids to the sum of polyethylenic acids. Linear regression was performed on arcsine-transformed data (Zar 1984).

Results

The six lamprey (four males, two females) starved for 6 mo lost weight at a linear rate of 0.1628 g·d^{-1} (r^2 = 0.7571, p = 0.024) (Table 1). The head and body of the male lampreys formed a higher percentage of the whole body weight than that of the females (Table 1). This resulted from the higher content of gonads in the females. The gonadosomatic ratio of the males declined with starvation whereas that of the females increased (Table 1). Under starvation conditions the percentage of liver, the hepatosomatic ratio, increased (Table 1). The percentage of other internal body organs was much higher in the recently metamorphosed lamprey than in the other growth phases of the lamprey (Table 1).

The procedures used for compositional analysis accounted for 96.4–99.3% of the components in the body parts of 2-yr-starved and recently metamorphosed lampreys, respectively (Table 2). Lipid content was higher and soluble ash, sugars, and glycogen contents lower in the head than in the body sections of both the starved and metamorphosed lampreys. The

TABLE 1. Whole weight and percentage distribution of body parts of the 2-yr-starved, metamorphosed, and 6-mo-starved *L. tridentata*. N/S = not separated because gonad content minimal.

Lamprey (sex)	Wet weight (g)	Head (%)	Body (%)	Liver (%)[a]	Gonad (%)[b]	Remainder (%)
Starved 2 yr (m)	48.02	35.86	59.95	2.46	N/S	1.73
Metamorphosed (m)	1.92	35.14	47.52	1.20	N/S	16.14
Starved						
0 d (m)	43.48	33.39	62.26	1.43	2.18	0.74
0 d (f)	56.57	28.60	60.84	1.19	8.72	0.65
91 d (m)	20.87	32.44	61.52	2.35	2.25	1.44
91 d (f)	38.25	28.25	51.65	2.19	16.38	1.52
182 d (m)	19.28	37.81	57.00	2.91	1.35	0.93
182 d (m)	21.50	40.84	55.53	2.19	0.42	1.02

[a]Hepatosomatic ratio.
[b]Gonadosomatic ratio.

TABLE 2. Biochemical composition and energy content of body parts of a 2-yr-starved and recently metamorphosed *L. tridentata*. ND = not determined because of insufficient quantities.

	Parts of lamprey starved for 2 yr				Parts of metamorphosed lamprey[a]		
Parameter	Head	Body	Liver	Remainder	Head	Body	Remainder
Component (% wet weight)							
Moisture	86.1	84.8	72.3	80.9	81.7	82.6	86.8
Insoluble ash	0.06	0.04	ND	ND	0.01	0.06	ND
Soluble ash	0.50	0.68	ND	ND	0.70	0.73	ND
Lipids	1.37	1.21	16.52	11.37	4.95	4.68	1.67
Sugars	0.06	0.10	0.18	0.07	0.10	0.18	0.14
Glycogen	0.23	0.23	0.26	0.30	0.24	0.28	0.24
Protein	10.57	11.35	9.49	5.74	11.52	10.40	7.49
Caloric content of wet tissue ($kJ \cdot g^{-1}$)							
Lipid	0.48	0.43	5.82	4.01	1.74	1.65	0.59
Carbohydrate	0.05	0.06	0.08	0.07	0.06	0.08	0.07
Protein	1.90	2.04	1.71	1.03	2.07	1.87	1.35
Total	2.43	2.53	7.61	5.11	3.87	3.60	2.01
Energy in parts of a normalized 1-g lamprey (kJ)[b]	0.87	1.52	0.19	0.09	1.36	1.71	0.32

[a]Insufficient liver for complete analysis, although separated from other internal organs.
[b]Calculated from the caloric content of wet tissue and the corresponding percentage distribution of the body part in the lamprey from Table 1.

moisture, insoluble ash, and protein levels between the head and body parts were not consistently higher or lower in either the starved or metamorphosed lampreys. The 16 and 11% of lipid in the liver and remaining internal organs of the 2-yr-starved lamprey contrasted with the 2% in the internal organs of the metamorphosed lamprey. This resulted in a higher total caloric value for the internal organs of the starved lamprey.

Higher moisture levels and lower soluble ash, lipid, and carbohydrates in the head and body sections of the 2-yr-starved lamprey relative to the metamorphosed lamprey were consistent with the prolonged period of starvation (Table 2). The total caloric content of the head and body of the metamorphosed lamprey was at least 1.2 $kJ \cdot g^{-1}$ higher than that of the starved lamprey, principally from higher content of lipid. With the weight of the 2-yr-starved and metamorphosed lampreys being so dissimilar, a normalized 1-g lamprey was used for energy comparisons. Total energy per 1 g of the 2-yr-starved and metamorphosed lampreys was 2.67 and 3.39 kJ. The more energetically favoured metamorphosed lamprey reflected a high storage of lipid in the head tissue (Table 2).

Fatty acid profiles of lipids in the head and body of the 2-yr-starved and metamorphosed lampreys were qualitatively similar, differing mainly in the 4% of 15:0 acid in the latter (Table 3). The starved lamprey exhibited higher percentages of 18:0, 18:1*n*9, 20:4*n*6, 20:5*n*3, 22:5*n*3, and 22:6*n*3 acids and lower percentages of 14:0 and 16:1*n*7 acids than the metamorphosed lamprey. Higher levels of 20:5*n*3 in the liver than in the body walls of both starved and metamorphosed lampreys suggested either enzymatic capability to synthesize this acid from lower carbon fatty acids or that this acid was available in freshwater organisms. The latter is more probable, as the unexpected 21% 22:6*n*3 in the other internal organs of the metamorphosed lamprey suggested a source from dietary freshwater organisms. Lower contents of saturated and monoethylenic fatty acids in the starved relative to the metamorphosed lampreys conferred to the former a high proportion of polyethylenic acids which were principally polyunsaturated *n*3 acids (Table 3).

To determine that the biochemical differences between the 2-yr-starved and metamorphosed lampreys were more a function of starvation than influences of the preceding trophic envi-

TABLE 3. Fatty acid composition (relative %) in the lipids of body parts of a 2-yr-starved and recently metamorphosed *L. tridentata*.

	Body parts of lamprey starved for 2 yr				Body parts of metamorphosed lamprey			
Fatty acid	Head	Body	Liver	Remainder	Head	Body	Liver	Remainder
12:0	0.20	0.20	0.23	0.31	2.54	3.69	0.21	0.23
14:0	1.12	0.52	0.61	0.79	15.73	15.42	6.33	2.97
15:0	—	—	—	—	3.59	4.44	0.93	0.67
16:0	12.90	15.15	5.61	25.11	12.77	12.40	12.88	13.78
16:1*n*9	0.24	0.23	0.24	0.25	0.21	0.20	0.88	0.32
16:1*n*7	3.79	2.82	1.69	9.46	24.01	23.77	12.88	8.42
16:3*n*4	0.20	0.20	0.23	0.50	4.92	4.94	0.86	1.81
16:4*n*1	1.93	2.40	0.90	0.59	—	—	—	—
18:0	5.91	7.40	4.09	4.24	2.33	2.17	5.45	6.72
18:1*n*9	15.90	17.78	31.00	29.47	14.63	13.53	25.49	11.38
18:1*n*7	3.87	4.16	4.02	7.04	2.43	1.99	3.83	3.87
18:2*n*9	0.69	0.78	0.24	0.48	0.28	0.29	0.27	0.20
18:2*n*6	0.77	1.29	0.38	0.59	0.47	0.48	0.42	0.70
20:1*n*11	0.34	0.43	0.90	0.20	0.26	0.25	0.46	3.46
20:1*n*9	0.56	0.58	1.61	0.43	0.33	0.29	0.47	1.28
20:2h	0.64	0.73	0.56	0.36	0.34	0.47	0.93	0.50
20:4*n*6	6.35	6.57	3.90	2.52	0.75	0.98	1.85	2.18
20:4*n*3	0.36	0.31	1.58	0.28	0.21	0.22	0.21	0.30
20:5*n*3	12.36	12.33	20.30	1.96	1.36	1.43	5.31	7.02
22:4*n*6	0.46	0.44	1.20	0.28	0.20	0.25	0.23	0.23
22:5*n*3	3.09	1.69	4.49	0.82	0.66	0.73	1.67	2.92
22:6*n*3	19.71	15.03	9.47	6.27	2.85	2.71	9.69	21.06
Saturated	20.13	23.27	10.54	30.45	36.96	38.12	25.80	24.37
Monoethylenic	24.70	26.00	39.46	46.85	41.87	40.03	44.01	28.73
Polyethylenic	46.56	41.77	43.25	14.65	12.04	12.50	21.44	36.92
Σ4-6,*n*3/poly.	76.29	70.29	82.87	63.69	42.19	40.72	78.73	84.78
Σ4-6,*n*6/poly.	14.63	7.70	11.79	19.11	7.89	9.84	9.70	6.53

ronment, other specimens of upstream-migrating lampreys were analyzed over a 6-mo holding period (Table 4). The variation in composition of head and body sections of the male lampreys after 182 d was greater than those demonstrated between male and female lampreys taken earlier in the starvation period (Table 4). Other studies on lampreys have shown no significant differences between components in body tissue of males and females at the same stage of development (Bird and Potter 1983b). Linear regression was therefore fitted only to the data from head and body tissue irrespective of gender.

Starvation of lampreys in the laboratory for 182 d resulted in a linear increase in the moisture content in the head by $0.0354\%\cdot d^{-1}$ ($r^2 = 0.8711$) and in the body by $0.0387\%\cdot d^{-1}$ ($r^2 = 0.9368$). Insoluble ash as a minor component in head and body of lampreys averaged 0.05 and 0.07% wet weight, respectively, and showed no linear trend. Conversely, soluble ash decreased linearly in starved head and body tissue by $0.0028\%\cdot d^{-1}$ ($r^2 = 0.7235$) and $0.0033\%\cdot d^{-1}$ ($r^2 = 0.7177$), respectively. Lipid in the head of the lamprey was catabolized linearly at $0.0426\%\cdot d^{-1}$ ($r^2 = 0.9038$) and in the body at $0.0451\%\cdot d^{-1}$ ($r^2 = 0.8718$). No consistent loss in low molecular weight or polymeric carbohydrate was evident with starvation of the lamprey. Protein in the head and body was catabolized linearly during starvation at $0.0187\%\cdot d^{-1}$ ($r^2 = 0.8108$) and $0.0153\%\cdot d^{-1}$ ($r^2 = 0.8588$), respectively.

Substantial differences in the composition of internal organs of male and female lampreys resulted from starvation (Table 4). Lipid was stored to a greater extent in the liver of males than in females and the converse for gonadal tissue. Lipid content was higher in the tissue of liver than in all other body parts of the lamprey, but carbohydrate and protein levels were quite similar (Table 4). Lipid was also higher in ovaries than in the other parts of the lamprey.

The caloric content of lipid in the head and body tissue declined linearly with time of starvation, $0.0094\ kJ\cdot g^{-1}\cdot d^{-1}$ ($r^2 = 0.9022$) and $0.0098\ kJ\cdot g^{-1}\cdot d^{-1}$ ($r^2 = 0.8752$), respectively. A linear decline in the caloric content of protein in the head tissue, $0.0132\ kJ\cdot g^{-1}\cdot d^{-1}$ ($r^2 = 0.9270$), and body tissue, $0.0131\ kJ\cdot g^{-1}\cdot d^{-1}$ ($r^2 = 0.9181$), occurred with starvation. Caloric content of carbohydrate in the head and body tissue was reasonably constant at $0.11\ kJ\cdot g^{-1}$ (SD ± 0.04) and $0.11\ kJ\cdot g^{-1}$ (SD = ± 0.03), respectively. The caloric content of liver and gonad tissue fluctuated during starvation.

Energy derived from lipid and protein in a normalized 1-g lamprey declined with starvation at $0.0101\ kJ\cdot d^{-1}$ ($r^2 = 0.7878$) and $0.0040\ kJ\cdot d^{-1}$ ($r^2 = 0.8320$), respectively. Energy from carbohydrate was constant at 0.10 kJ (SD ± 0.03). Total energy required to maintain a 1-g lamprey during 6 mo of starvation was 2.56 kJ or 49% of the starting energy (whole energy $d_{(0-182)} = 5.2725 - 0.0141\cdot d$ ($r^2 = 0.7970$)). The total energy lost was derived 71% from lipid and 29% from protein catabolism.

Differences in relative proportions of fatty acids in tissue of male and female lampreys, other than gonads, were minor and mean values are presented in Table 5 for 0-, 91-, and 182-d specimens. Starvation caused a decrease in 14:0 and 16:1*n*7 acids in all tissues and a decline in 18:1*n*9 only in the head and body tissue, presumably as energy sources. The percentage of 18:0, 20:4*n*6, 20:5*n*3, 22:5*n*3, and 22:6*n*3 acids increased in the head and body, and 18:1*n*9 and 20:5*n*3 increased in the liver with prolonged starvation. The remaining internal organs, excluding gonads, showed a general increase in 16:0, 18:0,

TABLE 4. Biochemical composition, caloric content of body parts, and energy in *L. tridentata* held in fresh water under starvation conditions for 182 d.[a] ND = not determined because of insufficient quantities.

	Starved 0 d		Starved 91 d		Starved 182 d	
Parameter	Male	Female	Male	Female	Male	Male
Component (% wet weight)						
Moisture						
Head	77.1	76.8	83.8	80.5	84.2	87.0
Body	75.2	74.8	81.2	79.1	83.4	86.1
Liver	61.3	75.9	67.5	76.0	67.9	71.3
Gonad	84.2	53.6	ND	56.6	ND	ND
Insoluble ash[b]						
Head	0.05	0.03	0.07	0.06	0.03	0.03
Body	0.01	0.08	0.08	0.05	0.11	0.08
Soluble ash[b]						
Head	0.74	0.82	0.64	0.65	0.65	0.61
Body	0.99	0.94	0.82	0.79	0.82	0.78
Lipids						
Head	6.42	6.10	2.26	4.20	1.69	1.09
Body	6.63	5.99	2.37	4.92	1.58	0.90
Liver	26.24	8.76	19.00	6.91	19.61	15.74
Gonad	4.37	18.42	ND	15.22	ND	ND
Sugars						
Head	0.10	0.11	0.06	0.07	0.10	0.08
Body	0.27	0.27	0.15	0.22	0.11	0.12
Liver	0.21	0.11	0.10	0.15	0.25	0.23
Gonad	0.10	0.10	ND	0.43	ND	ND
Glycogen						
Head	0.40	0.37	0.41	0.84	0.68	0.29
Body	0.37	0.27	0.48	0.55	0.60	0.19
Liver	0.51	0.65	0.37	1.00	0.41	0.37
Gonad	0.34	0.43	ND	0.50	ND	ND
Protein						
Head	13.11	14.55	12.38	11.60	10.97	9.02
Body	15.27	14.86	13.18	12.32	12.37	11.15
Liver	11.37	14.26	12.84	15.60	11.31	11.39
Gonad	10.00	24.62	ND	25.20	ND	ND
Caloric content of wet tissue ($kJ \cdot g^{-1}$) (energy in a normalized 1 g lamprey (kJ)[c])						
Lipid						
Head	2.26 (0.75)	2.15 (0.61)	0.80 (0.26)	1.48 (0.42)	0.60 (0.23)	0.38 (0.16)
Body	2.34 (1.46)	2.11 (1.28)	0.84 (0.52)	1.73 (0.89)	0.56 (0.32)	0.32 (0.18)
Liver	9.25 (0.13)	3.09 (0.04)	6.70 (0.16)	2.44 (0.05)	6.91 (0.20)	5.55 (0.12)
Gonad	1.54 (0.03)	6.49 (0.57)	ND ND	5.36 (0.88)	ND ND	ND ND
Whole	— (2.37)	— (2.50)	— (0.94)	— (2.24)	— (0.75)	— (0.46)
Carbohydrate						
Head	0.09 (0.03)	0.09 (0.03)	0.09 (0.03)	0.17 (0.05)	0.15 (0.06)	0.07 (0.03)
Body	0.12 (0.07)	0.10 (0.06)	0.12 (0.07)	0.14 (0.07)	0.13 (0.07)	0.06 (0.03)
Liver	0.13 (0.00)	0.14 (0.00)	0.09 (0.00)	0.22 (0.01)	0.12 (0.00)	0.11 (0.00)
Gonad	0.08 (0.00)	0.10 (0.01)	ND ND	0.17 (0.03)	ND ND	ND ND
Whole	— (0.10)	— (0.10)	— (0.10)	— (0.16)	— (0.13)	— (0.06)
Protein						
Head	2.36 (0.79)	2.62 (0.75)	2.23 (0.72)	2.09 (0.59)	1.97 (0.74)	1.62 (0.66)
Body	2.75 (1.71)	2.67 (1.52)	2.37 (1.46)	2.22 (1.15)	2.23 (1.27)	2.01 (1.12)
Liver	2.05 (0.03)	2.57 (0.03)	2.31 (0.05)	2.81 (0.06)	2.04 (0.06)	2.05 (0.05)
Gonad	1.80 (0.04)	4.43 (0.39)	ND ND	4.54 (0.74)	ND ND	ND ND
Whole	— (2.57)	— (2.79)	— (2.23)	— (2.54)	— (2.07)	— (1.83)
Total						
Head	4.71 (1.57)	4.86 (1.39)	3.12 (1.01)	3.74 (1.06)	2.72 (1.03)	2.07 (0.85)
Body	5.21 (3.24)	4.88 (2.97)	3.33 (2.05)	4.09 (2.11)	2.92 (1.66)	2.39 (1.33)
Liver	11.43 (0.16)	5.80 (0.07)	9.10 (0.21)	5.47 (0.12)	9.07 (0.26)	7.71 (0.17)
Gonad	3.42 (0.07)	11.02 (0.96)	ND ND	10.07 (1.65)	ND ND	ND ND
Whole	— (5.04)	— (5.39)	— (3.27)	— (4.94)	— (2.95)	— (2.35)

[a]Linear regression fitted to the data provided levels of significance: $*p < 0.05$; $**p < 0.02$; $***p < 0.005$ (levels in parentheses correspond to data in parentheses).

[b]Insufficient liver and gonad for determination of ash contents.

[c]Calculated from the caloric content of wet tissue and the corresponding percentage distribution of the body part in the lamprey from Table 1.

TABLE 5. Fatty acid composition (relative %) in the lipids of body parts of *L. tridentata* held in the laboratory under conditions of food deprivation for 182 d.

	Head, days starved			Body, days starved			Liver, days starved			Remainder, days starved[a]		
Fatty acid	0	91	182	0	91	182	0	91	182	0	91	182
12:0	1.61	1.54	1.21	1.54	1.81	0.65	0.38	0.21	0.20	0.65	0.34	0.20
14:0	11.79	11.66	8.27	9.89	11.42	1.55	5.54	5.23	2.19	6.27	3.33	1.63
16:0	13.65	10.74	10.53	14.23	10.76	13.38	12.59	8.38	2.97	16.54	22.35	21.15
16:1*n*9	0.33	0.20	0.75	0.33	0.21	0.31	0.31	0.28	0.32	0.53	0.21	0.74
16:1*n*7	16.02	17.40	12.82	16.08	17.13	3.93	9.48	9.39	4.55	11.90	8.57	6.07
16:3*n*4	0.22	0.24	0.20	0.22	0.20	0.20	0.23	0.21	0.20	0.20	0.30	0.21
18:0	2.13	3.50	5.16	2.68	3.22	7.82	2.95	1.87	3.48	3.52	5.30	7.33
18:1*n*9	24.90	22.91	19.86	23.41	23.99	17.59	29.49	33.34	35.58	21.96	23.83	21.64
18:1*n*7	3.16	3.03	3.09	3.07	2.91	4.24	3.95	3.59	3.52	3.57	4.98	4.82
18:2*n*9	0.30	0.71	0.33	0.32	0.61	0.64	0.24	1.30	0.29	0.45	0.63	0.21
18:2*n*6	0.55	0.34	0.30	0.63	0.42	0.75	0.43	0.25	0.25	0.91	0.27	0.35
20:1*n*11	0.64	0.24	0.20	0.84	0.90	1.12	0.34	0.68	1.67	0.67	0.32	0.35
20:1*n*9	0.83	0.48	0.25	0.91	0.49	1.04	0.64	0.91	1.68	0.66	0.43	0.57
20:2h	—	0.79	0.94	0.51	0.73	0.45	1.54	1.65	1.00	0.51	1.13	0.84
20:4*n*6	1.10	2.66	3.18	1.49	2.41	6.70	2.22	3.42	3.36	3.02	4.27	5.48
20:4*n*3	0.38	0.26	0.20	0.41	0.28	0.23	0.20	0.30	0.70	0.50	0.20	0.23
20:5*n*3	5.85	4.89	7.01	5.97	4.55	10.95	7.25	6.32	17.37	6.86	4.02	7.43
22:4*n*6	0.20	0.20	0.20	0.64	0.20	0.37	0.43	0.37	0.45	0.37	0.54	0.46
22:5*n*3	1.76	1.77	1.81	1.88	1.87	2.25	3.56	4.31	3.39	2.73	2.24	2.34
22:6*n*3	9.47	9.16	16.06	11.01	10.72	17.36	12.91	11.32	11.80	12.07	6.92	9.48
Saturated	29.18	27.44	25.17	28.34	27.21	23.40	21.46	15.69	8.84	26.98	31.32	30.31
Monoethylenic	45.88	44.26	36.97	44.64	45.63	28.23	44.21	48.19	47.32	39.29	38.34	34.19
Polyethylenic	19.83	21.02	30.23	23.08	21.99	39.90	29.01	29.45	38.81	27.62	20.52	27.03
Σ4-6,*n*3/poly.	88.05	76.50	82.96	83.49	79.22	77.17	82.45	75.55	85.70	80.23	65.21	72.09
Σ4-6,*n*6/poly.	6.56	13.61	11.18	9.22	11.87	17.72	9.13	12.87	9.82	12.27	23.44	21.98

[a]Excluding gonads, values of which are presented in Table 6.

20:4*n*6, and 20:5*n*3 acids and a decline in the 22:6*n*3 acid. Saturated fatty acids decreased in head, body, and liver tissue but increased in the other internal organs with progressive starvation. The monoethylenic acids declined in the head and body but increased in the liver. The polyethylenic acids increased in head, body, and liver during starvation but mainly from an increase in polyunsaturated *n*6 acids (Table 5).

It would seem prudent for prespawning lampreys not to rob their gonads of energy, thereby ensuring the quality and viability of sperm and eggs. Changes in relative proportions of fatty acids with starvation were more pronounced in testes than in ovaries (Table 6). In the testes the decline in content of 14:0 and 16:0 acids may have resulted from their conversion to, and increase in, the 16:1*n*7 acid. The use of this acid as a source of maintenance energy in the lamprey was alluded to previously. The eicosanoid hormone precursor 20:4*n*6 increased substantially over the 6-mo period in the testes and the content of 18:2*n*6, one of its precursors, declined. It is feasible that this acid could be an indicator of testes maturation in lampreys. The decline in saturated acids in the testes was compensated for by an increase in polyethylenic acids, principally the 20:4*n*6 acid (Table 6). In comparison with the testes, the ovaries showed remarkable stability to starvation, with little change in combined classes of acids (Table 6). The minor decline in 14:0 and 16:0 acids was compensated for by a corresponding increase in the 18:1*n*9 acid, presumably from the elongation and desaturation of the saturated acids. A conservative anabolic rearrangement of relative proportions of fatty acids in the gonads, rather than any catabolic loss, therefore appeared to have occurred during the starvation of the Pacific lamprey.

Discussion

Adult *L. tridentata* migrate into the Stamp River from May to September, with the largest number migrating in July (Beamish 1980). It is probable that the lampreys caught in October and subjected to 6 mo of starvation in the laboratory were caught about 3 mo after they had entered the Somass River. This additional starvation period, when applied to the linear regression equation derived for weight loss on starvation, suggested that the lampreys entered the river at about 63 g. The increase from a 2-g metamorphosed lamprey to an approximately 63-g adult reentering the river is similar to the growth of *L. fluviatilis* which increases from 1–2 g as a downstream migrant to 53 g as an adult after a marine trophic stage of 18 mo (Hardisty and Potter 1971; Abou-Seedo and Potter 1979; Bird and Potter 1979). Calculations for the 2-yr-starved lamprey, which had been caught almost immediately on reentry into the river in June, suggested a reentry weight of about 167 g and a considerably longer trophic phase of development in salt water, as has been suggested previously by Beamish (1980). The higher weight gain for this lamprey is similar to that of anadromous *P. marinus* and *G. australis*, which increase from their downstream migrant weights by about 290 times during the parasitic phases of 23–28 mo (Potter and Beamish 1977; Beamish et al. 1979). The gonadosomatic ratios for *L. tridentata* were similar to the 10.02 and 4.57% recorded for female and male *L. fluviatilis*, and although the hepatosomatic ratio of the Pacific lamprey increased slightly during starvation, values were similar to the 2.02 and 1.29% recorded for female and male *L. fluviatilis* (Heikkala et al. 1984).

TABLE 6. Fatty acid composition (relative %) in the lipids of gonads of *L. tridentata* held in the laboratory under conditions of food deprivation.

	Testes			Ovaries	
Fatty acid	Before starvation	Starved 91 d	Starved 182 d	Before starvation	Starved 91 d
12:0	0.40	0.20	0.20	0.20	0.20
14:0	5.46	2.91	1.49	6.05	5.66
16:0	14.77	9.07	8.21	15.08	13.15
16:1*n*9	0.31	0.24	0.31	0.20	0.20
16:1*n*7	10.66	12.74	15.94	11.78	10.43
16:3*n*4	0.20	0.21	0.20	0.31	0.24
18:0	3.33	7.36	4.72	3.04	3.00
18:1*n*9	24.77	17.63	19.74	17.12	20.07
18:1*n*7	4.83	4.99	4.57	2.63	3.72
18:2*n*9	0.25	0.44	0.21	0.56	0.62
18:2*n*6	0.86	0.21	0.30	0.47	0.40
20:1*n*11	0.46	0.47	0.40	0.39	0.20
20:1*n*9	0.63	0.58	0.50	0.41	0.34
20:2h	0.23	1.79	1.28	0.35	0.43
20:4*n*6	0 20	4.95	5.32	1.92	1.79
20:4*n*3	0.46	0.20	0.20	0.52	0.20
20:5*n*3	7.28	3.52	6.04	10.47	11.05
22:4*n*6	0.23	0.32	0.35	0.20	0.22
22:5*n*3	2.31	2.30	2.82	3.61	2.76
22:6*n*3	13.79	20.10	19.82	19.44	19.11
Saturated	23.96	19.54	14.62	24.37	22.01
Monoethylenic	41.66	36.65	41.46	32.53	34.96
Polyethylenic	25.81	34.04	36.54	37.85	36.82
Σ4-6,*n*3/poly.	92.37	76.76	79.04	89.93	89.95
Σ4-6,*n*6/poly.	1.67	15.48	15.51	5.60	5.45

Biochemical differences between the 2-yr-starved and metamorphosed lampreys reflected the extent of food deprivation. Increased hydration of tissue in the 2-yr-starved lamprey, relative to the metamorphosed lamprey, is a common function of starvation in many species (Mayzaud 1976; Taylor and Venn 1979; Cuzon et al. 1980; Beninger and Lucas 1984; Whyte et al. 1986; Whyte et al. 1990). The soluble ash content declined with starvation. The generally low ash content in *L. tridentata* was similar to the 0.8% reported in *P. marinus* and *G. australis* but about four times that found for *I. gagei* (Beamish et al. 1979; Bird and Potter 1981; Beamish and Legrow 1983). The glycogen content was constant in all tissue from the starved and metamorphosed lamprey, but the minor yet variable content of sugars suggested a constant metabolic use of the low molecular weight carbohydrate pool throughout starvation. In the citric acid cycle, carbohydrate is the main source of oxaloacetate, an intermediate in the cycle essential for complete oxidation of lipid. Although comprising 0.5% or less of the total tissue, carbohydrate was maintained constant for metabolic processes in starved *L. tridentata*, as in other lampreys during nontrophic phases (Beamish et al. 1979).

The protein level in recently metamorphosed Pacific lamprey, about 11%, was similar to the 12–13% level found in *P. marinus* during metamorphosis (Lowe et al. 1973). During metamorphosis, anabolic processes for protein formation must provide for enlargement of fins, eyes, suctorial disc, teeth, and tonguelike piston (Hardisty and Potter 1971). Any catabolism of protein as an energy source during this anatomical rearrangement would not be metabolically expedient.

The fatty acid profiles of the 2-yr starved and metamorphosed lampreys differed qualitatively in the presence of 16:1*n*4 in the former and 15:0 in the latter. The odd-carbon saturated acid was also exclusive to the larval stages of *G. australis* and is apparently derived from a freshwater organism rich in this acid (Bird and Potter 1983a). The decrease in 14:0 and 16:1*n*7 acids, particularly in the body, and the lack of change in appropriate higher isomers suggest their oxidation as major energy sources during starvation.

Hydration occurred in the lamprey tissue during 6 mo of starvation, similar to the increased hydration noted between the 2-yr-starved and metamorphosed lampreys. Increase of moisture with starvation is normally accompanied in marine species by the uptake of chloride salts to compensate for ionic imbalance (Whyte et al. 1990). In fresh water with low elemental concentration, ion uptake is less probable. A decline in plasma sodium was reported previously in starved *L. tridentata* by Clarke and Beamish (1987). The 2-yr-starved lamprey had 0.5–0.7% soluble ash as opposed to 0.7–1.0% in the 6-mo-starved lampreys and suggested that cellular ionic imbalance may be the ultimate cause of death.

In the head and body of the lamprey starved for 6 mo, a significant linear decline in caloric content derived from lipid and protein occurred, but the carbohydrate content remained constant. These changes were reflected in the differences between the 2-yr-starved and metamorphosed lampreys. Values reported by Beamish and Legrow (1983) for the caloric content of the carcass of male and female adult *I. gagei* when recalculated for wet tissue gave 4.30 and 6.01 $kJ \cdot g^{-1}$, respectively, in close agreement with the 4.71–5.21 $kJ \cdot g^{-1}$ for the head and body tissue of male and female *L. tridentata*. As Beamish and Legrow (1983) in their study on *I. gagei* did not provide the moisture content of the liver and gonads, the caloric contents of these organs in the Pacific lamprey were recalculated (as kilocalories) on a dry weight basis. Liver and gonads of male

and female Pacific lampreys contained 7.06 and 5.75 and 5.17 and 5.68 kcal·g dry tissue^{-1}, respectively. In reasonable agreement were the 6.13 and 6.05 and 5.37 and 6.62 kcal·g dry weight^{-1} of the liver and gonads in the male and female *I. gagei* (Beamish and Legrow 1983). The energy loss from linear regression analysis of starved lamprey on a wet tissue basis was 0.0141 kJ·g^{-1}·d^{-1}, derived 71% from lipid and 29% from protein catabolism. The average 2.66 kJ·g wet tissue^{-1} of the 6-mo-starved lamprey, in reality starved for about 9 mo from entering the river, and 2.67 kJ·g^{-1} in the 2-yr-starved lamprey was slightly higher than the average 2.35 kJ·g wet weight^{-1} reported by Beamish and Legrow (1983) for spent adult *I. gagei*. The recently metamorphosed male Pacific lamprey had an energy level of 3.39 kJ·g wet weight^{-1}, in contrast with the 5.50 kJ·g^{-1} reported for metamorphosed male *I. gagei* (Beamish and Legrow 1983).

The decrease or increase in the relative proportions of the fatty acids between the 2-yr-starved and metamorphosed lampreys was reflected in changes of corresponding fatty acids in the 6-mo-starved lampreys. Both 14:0 and 16:1*n*7 were used as energy sources in the lamprey; the latter acid is a major constituent of marine and freshwater fish (Ackman 1967; Whyte 1988). The decline with starvation, in an otherwise high content of 18:1*n*9, particularly in the enzymatically active liver, indicates the inability of the cartilagenous lamprey to convert this acid readily to 18:2*n*6, as is the case with most vertebrates. The decline in content of C-14 and C-16 fatty acids on starvation resulted in an increase in the C-20 and C-22 polyunsaturated isomers, which originate largely from marine particulate matter (Mayzaud et al. 1989). The presence of arachidonic acid, 20:4*n*6, in substantial amounts in all body parts of the lamprey suggests its requirement in the formulation of pharmacologically active eicosanoids, such as prostaglandins and thromboxanes, which regulate many different cell functions (Ruggeri and Thoroughgood 1985). Bird and Potter (1983a) reported 6–8% 20:4*n*6 in the phospholipid fraction of *G. australis*. Both eicosapentaenoic, 20:5*n*3, and docosahexaenoic, 22:6*n*3, acids, which are common to most marine species, have been regarded as nutritionally essential for growth and to maintain membrane fluidity and permeability characteristics in cold-water environments (Castell 1970; Watanabe et al. 1983). The buildup of these acids in the body wall of the starved Pacific lamprey and their high content in phospholipids of *G. australis* (Bird and Potter 1983a) tend to support a structural role in the cartilaginous lamprey, which, unlike skeletal fish, can shrink in size and slowly catabolize tissue for maintenance energy.

The longest recorded period of survival of a fish deprived of food is 3.5 to just over 4 yr for the African lungfish (*Protopterus annectens*) (Coates 1937; Smith 1939; El Hakeem 1979). African lungfish aestivate generally for 9 mo in underground cocoons in dry river beds in Central Africa during the dry season. The ability to slowly catabolize its tissue for maintenance energy is an adaptive physiology to ensure its survival should the dry season be prolonged (El Hakeem 1979). The ability of lampreys in general, and the Pacific lamprey in particular, to survive prolonged periods without feeding must also be a natural adaptation for survival. In northern British Columbia, the Pacific lamprey migrates 402 km up the Skeena River into Babine Lake where spawning lampreys have been deprived of food for about 14 mo (Farlinger and Beamish 1984). Spawning in the headwaters of large rivers allows for distribution of the larval lamprey throughout the watershed and access to vast areas of rearing habitat.

Present-day lampreys are presumably descendants of primitive lampreys that existed in the Carboniferous period at least 300 million yr ago (Janvier and Lund 1983). During the later Permian period, about 230 million yr ago, the union of the continents to form Pangaea drained shallow seas, exposed continental shelves, and reduced favoured marine environments, resulting in the extinction of many marine species. The ability of lamprey to withstand prolonged periods of starvation by using endogenous reserves may have been an important adaptation to survival during this later Palaeozoic period, which now allows it to survive extended periods of nontrophic development.

References

ABOU-SEEDO, F. S., AND I. C. POTTER. 1979. The estuarine phase in the spawning run of the river lamprey *Lampetra fluviatilis*. J. Zool. Lond. 188: 5–25.

ACKMAN, R. G. 1967. Characteristics of the fatty acid composition and biochemistry of some fresh-water fish oils and lipid in comparison with marine oils and lipids. Comp. Biochem. Physiol. 22: 907–922.

1986. WCOT (capillary) gas–liquid chromatography, p. 137–206. *In* R. J. Hamilton and J. B. Rossell [ed.] Analysis of oils and fats. Elsevier Applied Science Publishers Ltd., New York, NY.

BEAMISH, F. W. H., AND M. LEGROW. 1983. Bioenergetics of the southern brook lamprey, *Ichthyomyzon gagei*. J. Anim. Ecol. 52: 575–590.

BEAMISH, F. W. H., I. C. POTTER, AND E. THOMAS. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus*, in relation to feeding, migration and reproduction. J. Anim. Ecol. 48: 1–19.

BEAMISH, R. J. 1980. 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 C. D. LEVINGS. 1991. Abundance and freshwater migration of the anadromous parasitic lamprey, *Lampetra tridentata*, in a tributary of the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 48: 1250–1263.

BEAMISH, R. J., AND T. G. NORTHCOTE. 1989. Extinction of a population of anadromous parasitic lamprey, *Lampetra tridentata*, upstream of an impassable dam. Can. J. Fish. Aquat. Sci. 46: 420–425.

BENINGER, P. G., AND A. LUCAS. 1984. Seasonal variation in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in a common habitat: *Tapes decussatus* L. (Jeffreys) and *Tapes phillippinarum* (Adams and Reeve). J. Exp. Mar. Biol. Ecol. 79: 19–37.

BEUKEMA, J. J., AND W. DE BRUIN. 1979. Calorific values of the soft parts of the tellinid bivalve *Macoma balthica* (L.) as determined by two methods. J. Exp. Mar. Biol. Ecol. 37: 19–30.

BIRD, D. J., AND I. C. POTTER. 1979. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 2. Quantitative data for the body proportions, weights, lengths and sex ratios. J. Linn. Soc. Lond. (Zool.) 65: 145–160.

1981. Proximate body composition of the larval, metamorphosing and downstream migrant stages in the life cycle of the Southern Hemisphere lamprey, *Geotria australis*. Environ. Biol. Fishes 6: 285–297.

1983a. Changes in the fatty acid composition of triacylglycerols and phospholipids during the life cycle of the lamprey *Geotria australis* Gray. Comp. Biochem. Physiol. 75B: 31–41.

1983b. Proximate composition at various stages of adult life in the Southern Hemisphere lamprey, *Geotria australis* Gray. Comp. Biochem. Physiol. 74A: 623–633.

CASTELL, J. D. 1970. The essential fatty acid requirement of rainbow trout (*Salmo gairdneri*). Ph.D. thesis, Oregon State University, Corvallis, OR. 116 p.

CLARKE, W. C., AND R. J. BEAMISH. 1987. Response of recently metamorphosed anadromous parasitic lamprey (*Lampetra tridentata*) to confinement in fresh water. Can. J. Fish. Aquat. Sci. 45: 42–47.

COATES, C. W. 1937. Slowly the lungfish gives up its secrets. Bull. N.Y. Zool. Soc. 40: 25–34.

CUZON, G., C. CAHU, J. F. ALDRIN, J. L. MESSAGER, G. STEPHAN, AND M. MEVEL. 1980. Starvation effect on metabolism of *Penaeus japonicus*, p. 410–423. *In* J. W. Avault [ed.] Proc. World Maric. Soc. 11, Louisiana State University, Baron Rouge, LA.

EL HAKEEM, O. H. 1979. A lungfish that survives over three and a half years of starvation under aquatic conditions. Zool. Anz. Jena 202: 17–19.

FARLINGER, S. P., AND R. J. BEAMISH. 1984. Recent colonization of a major salmon-producing lake in British Columbia by the Pacific lamprey (*Lampetra tridentata*). Can. J. Fish. Aquat. Sci. 41: 278–285.

FARMER, G. J 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

HARDISTY, M. W., AND I. C. POTTER. 1971 The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

HEIKKALA, R. M., A. T. LAUKKANEN, AND A. V. MIKKONEN. 1984. Proximate composition of the river lamprey, *Lampetra fluviatilis*, during the spawning run. Can. J. Zool. 62: 2272–2279.

JANVIER, P., AND R. LUND. 1983. *Hardistiella montanensis* n. gen. et sp. (Petromyzonitida) from the lower carboniferous of Montana, with remarks on the affinities of the lampreys. J. Vertebr. Paleontol. 2: 407–413.

LOWE, D. R., F. W H. BEAMISH, AND I. C. POTTER. 1973. Changes in the proximate body composition of *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish Biol. 5: 673–682.

MAYZAUD, P. 1976. Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and biochemical composition of some species. Mar. Biol. 37: 47–58.

MAYZAUD, P., J. P CHANUT, AND R. G. ACKMAN. 1989. Seasonal changes of the biochemical composition of marine particulate matter with special reference to fatty acids and sterols. Mar. Ecol. Prog. Ser. 56: 189–204.

MOORE, J. W., AND J. M. MALLATT. 1980. Feeding of larval lampreys. Can. J. Fish. Aquat. Sci. 37: 1658–1664.

MOORE, J. W., AND I. C. POTTER. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

POTTER, I. C., AND F. W. H. BEAMISH. 1977. The freshwater biology of adult anadromous sea lamprey *Petromyzon marinus*. J. Zool. Lond. 181: 113–130.

RUGGERI, B., AND C. A. THOROUGHGOOD. 1985. Prostaglandins in aquatic fauna: a comprehensive review. Mar. Ecol. Prog. Ser. 23: 301–306.

RUSSELL, J. E. 1986. Ecology of the Pacific lamprey (*Lampetra tridentata*) colonizing Babine Lake, British Columbia, Canada. M.Sc. thesis, University of Guelph, Guelph, Ont. 90 p.

SMITH, H. W. 1939. The lungfish. Nat. Hist. N.Y. 44: 214–225.

TAYLOR, A. C., AND T. L. VENN. 1979. Seasonal variation in weight and biochemical composition of the tissue of the queen scallop *Chlamys operculatis*, from the Clyde sea area. J. Mar. Biol. Assoc. U.K. 59: 605–621.

WATANABE, T., C. KITAJIMA, AND S. FUJITA. 1983. Nutritional value of live organisms used in Japan for mass propagation of fish: a review. Aquaculture 34: 115–143.

WHYTE, J. N. C. 1988. Fatty acid profiles from direct methanolysis of lipids in tissue of cultured species. Aquaculture 75: 193–203.

WHYTE, J. N. C., N. BOURNE, AND C. A. HODGSON. 1987. Assessment of biochemical composition and energy reserves in the larvae of the scallop *Patinopecten yessoensis*. J. Exp. Mar. Biol. Ecol. 113: 113–124.

WHYTE, J. N. C., AND J. R. ENGLAR. 1982. Seasonal variation in the chemical composition and condition indices of Pacific oyster, *Crassostrea gigas*, grown in trays or on the sea bed. Can. J. Fish. Aquat. Sci. 39: 1084–1094.

WHYTE, J. N. C. J. R. ENGLAR, AND B L. CARSWELL. 1990. Biochemical composition and energy reserves in *Crassostrea gigas* exposed to different levels of nutrition. Aquaculture 90: 157–172.

WHYTE, J. N. C., J R. ENGLAR, B. L. CARSWELL, AND K. E. MEDIC. 1986. Influence of starvation and subsequent feeding on body composition and energy reserves in the prawn *Pandalus platyceros*. Can. J. Fish. Aquat. Sci. 43: 1142–1148.

YOUSON, J. H. 1981. The alimentary canal, p. 95–189. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. 3. Academic Press Inc., London.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NY. 718 p.