Feeding of Larval Lamprey

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Feeding of Larval Lamprey[1]

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The feeding mucus in larval lamprey is produced by the lateral walls of the pharynx and by glandular goblet cells on gill filaments. The mucous complex has 14 lateral branches which move inward to the middle of the pharynx, where they are collected and directed back to the esophagus. Mucus, which is carried by intrapharyngeal ciliary tracts and water currents, fills virtually every space in the pharynx, resulting in high (75%) entrapment efficiency. Based on indirect calculations, algae accounted for only 0.14–1.5% of the gut contents in larvae of European brook lamprey (*Lampetra planeri*). Although the bacterial film associated with algae, detritus, and sand grains may be an energy source for ammocoetes, suspended bacteria cannot support growth in laboratory experiments. Selective feeding on different species of algae is common among lampreys and is based on three factors: (1) susceptibility to capture in the feeding–respiratory flow differs among particles, (2) filtration of long filaments by the oral cirri, and (3) selective agglutination at the mucous filter. *Fragilaria*, *Cocconeis*, and *Oscillatoria* species are present in relatively low numbers in the gut whereas *Navicula* species are ingested with greater frequency than they occur in the environment. The size distribution of ingested particles is, in general, independent of the size of the ammocoete. Feeding rate depends on temperature and to a lesser extent, food density. In the laboratory, ammocoetes digest and assimilate only 30–40% of the protein, lipid, and carbohydrate (excluding cellulose) and 6–7% of the cellulose in their food. Therefore, larvae of many species pass large quantities of undigested algae and other food through their guts, particularly at low temperatures.

Key words: algae, ammocoetes, assimilation efficiency, bacteria, detritus, feeding, lamprey, mucous complex

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Le mucus alimentaire de la lamproie larvaire est produit par les parois latérales du pharynx et par des cellules caliciformes glandulaires situées sur les filaments branchiaux. Le complexe muqueux comprend 14 branches latérales qui se déplacent à l'intérieur vers le milieu du pharynx où elles sont collectées et ramenées vers l'oesophage. Le mucus, transporté par des faisceaux ciliaires intrapharyngiens et des courants d'eau, remplit pratiquement tout le pharynx avec, comme résultat, une grande efficacité (75%) d'emprisonnement. Des calculs indirects indiquent que le contenu du tractus digestif de larves de *Lampetra planeri* ne comprenait que 0,14–1,5% d'algues. Bien que la pellicule bactérienne associée aux algues, aux détritus et aux grains de sable puisse être une source énergétique pour les ammocètes, les bactéries en suspension ne peuvent supporter la croissance dans des expériences de laboratoire. On observe communément chez les lamproies une alimentation sélective à même trois espèces différentes d'algues, fondée sur 3 facteurs : (1) la susceptibilité à la capture dans le courant alimentaire-respiratoire diffère d'une particule à l'autre, (2) la filtration des longs filaments par les cirri buccaux et (3) l'agglutination sélective au filtre muqueux. Les espèces de *Fragilaria*, *Cocconeis* et *Oscillatoria* se rencontrent en nombres relativement faibles, alors que celles de *Navicula* sont absorbées à une fréquence supérieure à celle où elles se trouvent dans le milieu. La répartition des tailles des particules absorbées est en général indépendante de la taille des ammocètes. Le taux d'alimentation dépend de la température et, à un degré moindre, de la densité des aliments. En laboratoire, les ammocètes ne digèrent et assimilent que 30–40% des protéines, lipides et hydro-

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carbures (cellulose non comprise) et 6–7% de la cellulose contenus dans la nourriture. Les larves de plusieurs espèces éliminent donc par leur tractus digestif de grandes quantités d'algues et autres aliments non digérés, en particulier aux basses températures.

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LARVAL lampreys are filter feeders, which usually inhabit burrows in the soft sediments of streams. Potential food items are carried by the unidirectional respiratory current through a ring of coarse oral cirri into the pharynx (Randall 1971; Sterba 1961, 1962). The meshwork of cirri acts as a sieve, preventing large particles from entering the pharyngeal chamber. These particles are enmeshed in mucus on the cirri and are periodically expelled through a "coughing" action (Applegate 1950). The purpose of this paper is to review the literature on the feeding biology of larval lampreys; included are a description of the feeding mechanism, source and composition of food, selective feeding, and feeding rates, entrapment, and digestion efficiency.

The Feeding Mechanism

It was suggested in previous studies (Kieckebusch 1928; Newth 1930; Balabai 1950; Young 1950; Sterba 1961, 1962) that suspended food particles are trapped by a mucous cord (the food cord) extending the length of the central portion of the pharynx. The mucus was thought to be secreted by the subpharyngeal gland or endostyle. However, Mallatt (1980) showed that glandular goblet cells, occupying the lateral portion of each gill filament, and the lateral walls of the pharynx, produce the feeding mucus. The mucus is secreted in large quantities and forms an intricate complex which fills virtually every space within the pharynx. The mucous complex has 14 similar lateral branches (one per gill pouch) which move inward to the central part of the pharynx. Here, they are collected into a longitudinal band (the food cord of previous authors) and directed back to the esophagus. The mucus is directed primarily by intrapharyngeal ciliary tracts, but also by water currents. Particle entrapment occurs throughout the mucous complex, although the largest particles (100 to 300 μm in diameter) are trapped most centrally. Particles and mucus aggregate as they move inward across the gill pouches. Thus, the mucous complex serves the multiple functions of trapping, aggregating, and transporting food particles. This manner of feeding seems to be common to ammocoetes of all sizes and genera.

Since the entrapping mucus originates in the lateral part of the pharynx, the medially situated endostyle is evidently not its source. The function of this gland is to add secretions such as digestive enzymes and iodoproteins (Clements-Merlini 1960; Hoheisel 1969) to the highly condensed central portion of the mucous complex.

Source of Food

Because ammocoetes are filter feeders, much of their food is suspended material. Creaser and Hann (1929) indicated that the food was drawn from the water immediately above the substrate where microorganisms are particularly dense. Although subsequent studies (Wigley 1959; Manion 1967) have confirmed that ammocoetes feed primarily on suspended material, the constant shifting of sediments and movement of larvae indicate that benthic organisms are consumed to a varying degree. Furthermore, since the burrows at the substrate surface are sometimes closed off, lamprey cannot consume suspended food at that time. Thus, food may be drawn from the water or a combination of the water and sediments, depending on environmental conditions and activity of the ammocoetes.

Composition of Food

There is little quantitative information on the relative importance of various foods in the nutrition of larval lampreys. On the basis of cell counts, Creaser and Hann (1929) concluded that diatoms and desmids were frequently eaten by American brook lamprey (*Lampetra lamottenii*) (*Entosphenus appendix* of Creaser and Hann) during the summer. Although ciliated protozoans were also believed to be ingested, these could not be identified because of their rapid digestion. Subsequent studies, using semiquantitative methods such as cell counts, and determinations of surface areas have reemphasized that algae, particularly diatoms, are found in ammocoetes (Sterba 1953; Manion 1967; Schroll 1959; Alvarez del Villar 1966; Potter et al. 1975). Predominant taxa in the guts of lampreys usually include *Navicula*, *Cymbella*, *Gomphonema*, *Nitzschia*, *Pinnularia*, and *Achnanthes* species. These forms are also common in the water and sediments of temperate zone streams (Hynes 1972).

Detritus is frequently reported in the gut contents of all species of lampreys, although its relative abundance may vary with season and locality (Hardisty and Potter 1971). For example, Schroll (1959) found that the quantity of ingested detritus (<65% of gut contents) in European brook lamprey (*Lampetra planeri*) was greatest in the winter when algal densities were low in the environment. Although Sterba (1962) recorded significant amounts of ingested detritus in *L. planeri* during the summer, this material was rare in the guts of the Australian lamprey *Mordacia mordax* collected from a stream in Australia (Potter et al.

TABLE 1. Percentage contribution of algae to the gut contents of several species of herbivores. Data expressed in terms of weight,[1] volume,[2] or caloric content.[3]

Species	Algal abundance (%)	Habitat	Reference
Lamprey			
Lampetra planeri[1]	0.14	Woodland stream (England)	This study
Insects			
Ephemeroptera (several species)[3]	3.5–92.1	Woodland streams (Pennsylvania, Kentucky)	Cummins (1973)
Plecoptera (several species)[2]	1–45	Woodland streams (Wisconsin)	Shapas and Hilsenhoff (1976)
Oligochaetes			
Lumbriculus variegatus[2]	70–85	Great Slave Lake	Moore (1978)
Mollusks			
Lymnaea auricularia[1]	85	Lake Zurich	Knecht and Walter (1977)

1975). Based on laboratory experiments, Moore and Potter (1976a) showed that, at 15°C, larvae of *L. planeri* gained ~2% in wet body weight when fed detritus for 60 d. Since the detritus used in their studies was not presterilized, some growth may have been attributable to the associated bacterial film. Detritus, a poor energy source, is very high (90–95%) in cellulose, lignin, and ash (Calow 1973; Monk 1976).

Because of the difficulties involved in separating microscopic particles in the gut contents, gravimetric estimates of the relative abundances of algae and detritus have not been made for ammocoetes. Therefore, current estimates of the quantities of ingested algae and detritus are probably subject to error and should be considered tentative. Although biochemical techniques of estimating the biomass of ingested microorganisms are available (Moriarty 1976, 1977), they have not been used to estimate good consumption ammocoetes.

To obtain a better (albeit indirect) estimate of the relative abundance of algae and detritus in *L. planeri* inhabiting Highland Water in southern England (Moore and Potter 1976b), the maximum volume of ingested algae (9×10^6 μm^3) reported for a 1.0-g ammocoete can be transformed into an estimate of biomass, assuming a specific gravity of 1. This transformation, based on direct microscopic measurements of the length, width, and depth of algae to estimate volume, is frequently used in phycological studies. Therefore, the wet weight of ingested algae in *L. planeri* was 0.009 mg per animal, which is equivalent to ~0.006 mg in terms of dry weight. Since the maximum dry weight of gut contents was 4.3 mg, algae comprised only 0.14% of dry gut contents. For the flora to constitute 50% of the ingested material, 3.2×10^9 μm^3 would have to be found in a 1.0-g ammocoete, which is approximately equivalent to 10×16^6 cells per animal. Such large numbers have not been found in any species. In most cases the number of ingested cells is $<0.5 \times 10^6$ per animal (Potter et al. 1975). In a eutrophic agricultural stream in southern England, the microflora accounted for 1.5% by volume of the gut contents of *L. planeri* (Moore and Potter 1976b). Based on these results, larvae of *L. planeri* contain far less algae in their guts than other herbivorous species (Table 1). Since microphagous feeders, including ammocoetes, pass mixtures of different food items through their gut at the same rate (Moore and Beamish 1973), it is not necessary to include a time factor in the analysis of the preceding data.

Although there are no estimates of the importance of attached bacteria and fungi in the feeding of larval lampreys, such nutriment supports the growth and reproduction of many other herbivorous species. Smyly and Collins (1975) showed that the cladoceran *Ceriodaphnia quadrangula* could be maintained solely on the bacteria associated with the alga *Scenedesmus*. Their studies also demonstrated that, while algae were frequently ingested, they played no part in the nutrition of *C. quadrangula*. Similarly Brinkhurst et al. (1972) considered that attached bacteria were the only significant food source for oligochaetes whereas Moriarty (1976) reported that 30% of the carbon in the guts of the prawn *Metapenaeus bennettae* was of bacterial origin and that algae were unimportant in the food of most specimens. Based on these comparisons and the small contribution of algae to the gut contents of *L. planeri*, the bacteria and fungi attached to detritus, sand grains, and algae are probably more important to the nutrition of larval lampreys than has been previously thought.

Planktonic bacteria are a potential food source, which may partially govern the distribution of larvae. Hardisty and Potter (1971), for example, found relatively high densities of ammocoetes in the vicinity of decaying animal carcasses. However, in experimental tanks with a slight (<5 cm·s^{-1}) current, *L. planeri* gained only 0.5% in wet weight when fed *Escherichia coli* at a concentration of 1×10^8 cells·mL^{-1} for 60 d (Moore and Potter 1976a). Such densities are extremely high and would not be encountered in a lamprey stream. The preceding experiments also demonstrated that lamprey lost weight when fed at 1×10^6 and 1×10^5 bacteria·mL^{-1}. In contrast, Freeden (1964) reared *Simulium* in the laboratory on nothing but bacteria.

Protozoans, nematodes, and rotifers are occasionally found among the gut contents of lamprey. Since the total number of organisms in the gut is generally small, often <10 per animal, they cannot be an important food source in most streams (Moore and Beamish 1973; Potter et al. 1975). In addition, nematodes and rotifers often show little indication of digestion in *P. marinus* and *L. lamottenii* (Moore and Beamish 1973).

Selective Feeding

Although the importance of the various dietary items of lamprey is not known, there have been some examples of selective feeding on different species of algae. Manion (1967) found that the diatom *Navicula* made up 32.9% of the flora in sea lamprey (*Petromyzon marinus*) larvae measuring 70–72 mm in length, while corresponding values for 33–35 mm specimens and in the water were 19.1 and 11.5%, respectively. This same species rarely consumed algae attached to sand grains (*Cocconeis* and *Amphora* species) and very long diatoms such as *Diatoma* and *Oscillatoria*, even though these forms were common on the sediments and in the water (Moore and Beamish 1973).

Because potential food items are drawn towards the larvae in a unidirectional respiratory current, selective feeding (Fig. 1) depends on the susceptibility of algae to capture in the respiratory current. This accounts for the scarcity in *P. marinus* of large algae (Fig. 1) and species attached to sand grains (Moore and Beamish 1973). Once inside the oral hood, microscopic algae probably have little difficulty in passing through the oral cirri. The cirri are coarse and, although they afford a mechanical limitation based on size, their main function is to limit large detrital particles and algal filaments from entering the pharynx. Manion (1967) demonstrated that filaments of *Fragilaria* species were rarely consumed by *P. marinus*, presumably due to filtration at the oral cirri. Similarly, Moore and Beamish (1973) found that 1-mm-long filaments of *D. vulgare* and *O. limosa* and *O. tenuis* could not pass through the cirri.

Once inside the pharyngeal chamber, the primary site of selection is the mucous complex. Schroll (1957, 1959) demonstrated that diatoms, sand grains, and carbon readily adhered to the mucus in larvae of *L. planeri* and Hungarian lamprey (*Eudontomyzon danfordi*), whereas certain species of protozoans and parts of oligochaetes were not taken up by the filter. In addition, Potter et al. (1975) suggested that the spines on *Scenedesmus* readily embedded in the mucus of *Mordacia* and consequently this alga appeared in disproportionately large numbers in the gut.

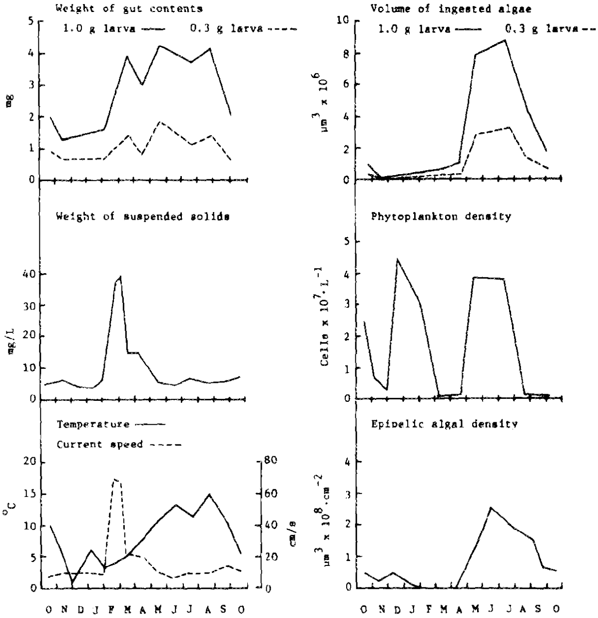

FIG. 1. Length distribution of algae in the guts of sea lampreys of different length and in the water and sediments of Shelter Valley Creek (Ont.) during September 1971. (Data recalculated from Moore and Beamish 1973.)

Algae within the diatom genus *Navicula* usually appear more frequently in the gut contents than in the environment (Manion 1967; Moore and Beamish 1973). Although this may result from selective agglutination (Schroll 1959), the exclusion of other algae from the gut due to size selection implies that all other species must be ingested with greater frequency than their abundance in the environment. Therefore, the apparent selection for *Navicula* is the result of exclusion of other genera based on size. Similarly, *Scenedesmus* species represented 31.2% by numbers of the gut contents of *Mordacia mordax* and only 0.9% of the flora in the environment (Potter et al. 1975). This suggested that there was a selective mechanism preventing the consumption of all species of diatoms. However, the abundance of ingested diatoms in the absence of *Scenedesmus* indicates that the relative proportion of diatoms in the gut was similar to that in the environment.

Although size selection limits the consumption of large particles (>340 μm), algae which are 5–340 μm were particularly common in both large and small ammocoetes and were also prevalent in the environment. Furthermore, taxa of 21–30 and 51–70 μm were also less abundant in the environment. The largest algae (*Nitzschia sigmoidea*) found in the gut of larvae >10.5 cm averaged 313 μm in length whereas in specimens of less than 3.5 cm, the corresponding average was 340 μm. Based on these data, we conclude that the size distribution of particles ingested by ammocoetes of <3.5 cm is similar to that recorded for specimens >10.5 cm, and that there is no selection based on size within the 5- to 340-μm range.

Since the main species of algae in streams measure

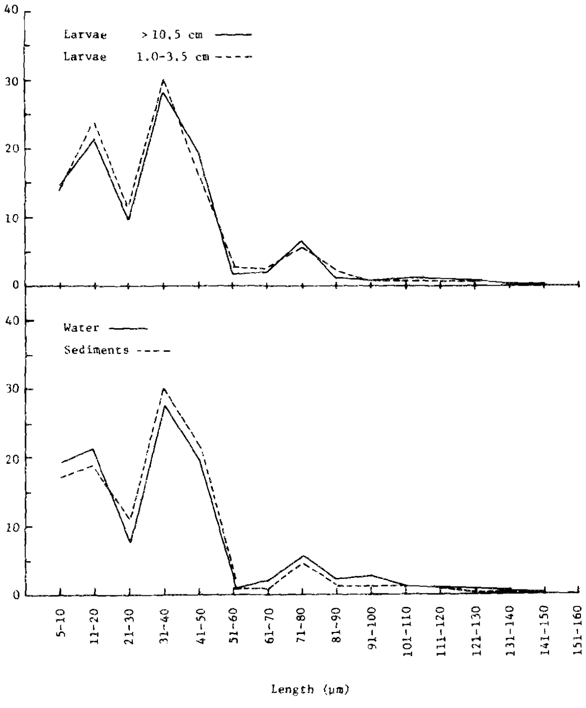

FIG. 2. Seasonal changes in the dry weight of gut contents and the number of ingested cells in *Lampetra planeri*, and in environmental conditions in Highland Water (southern England). (Data from Moore and Potter 1976b.)

>5 μm at all stages of their life cycle, there have been no examples of selection by lampreys for small algae. Since particle entrapment involves capture by impaction on mucus rathar than filtration by fixed pore size, there is no priori reason why there should be an abrupt lower size limit to particles ammocoetes can trap (see Rubenstein and Koehl 1977). However, most of the smallest particles, such as suspended bacteria, probably pass out of the pharynx into the water which would explain the inability of larvae to gain weight on this food source. Overall, therefore, most examples of selective feeding are based on particle size.

Feeding Rates, Entrapment, and Digestion Efficiencies

There is a seasonal variation in the feeding rate of ammocoetes in northern temperate zone streams. In Highland Water in southern England, *L. planeri* began feeding intensively in March as the water temperature increased from 5 to 12°C (Moore and Potter 1976b) (Fig. 2). Since the spring bloom of algae occurred about 2 mo after this increase, the availability of algae was not involved in the initiation of increased feeding activity. There was also an inverse relationship between the quantity of material suspended in the water and the weight of the gut contents. This implied that the total amount of food potentially available in the environment had little influence on the quantity of ingested matter. During the summer in Highland Water, the quantity of ingested matter remained relatively constant and declined in October at a temperature of 10°C. Therefore the intensity of feeding was less during the fall than in the spring, despite the similarity in water temperatures. It is not known if there is an optimal temperature for food intake in lampreys.

Like other suspension feeders (Lam and Frost 1976), ammocoetes regulate food intake according to availability. For example, Mallatt (1979), found that within the range 0.5 to 85 mg dry yeast$\cdot$L^{-1} (*Saccharomyces cereviseae*) the flow of water into the pharynx (F) in *P. marinus* increases with yeast concentration (C) according to the formula: $F = 31 + 5.2\,C^{0.3}$ mL$\cdot$h$^{-1}\cdot$g^{-1} for a 1.6-g animal at 12.5°C. If C exceeds 85 mg$\cdot$L^{-1}, however, flow rate decreases presumably because ingested material interferes with normal feeding and respiration The data suggest that, except at high concentrations of food, ammocoetes consume more food as their abundance increases as observed for other suspension feeders. However, while the flow rates of most other suspension feeders begin declining at 2–10 mg$\cdot$L^{-1}, ammocoete flow rates do not begin to decline until concentrations much higher than this. Mallatt (1979) also demonstrated that flow rate in ammocoetes is much slower, on a unit weight basis, than that of other suspension feeders such as copepods and mollusks This partially reflects the relatively low metabolic rate of lamprey (Hill and Potter 1970) and implies that ammocoetes may need relatively high concentrations of food to sustain growth.

From laboratory experiments, the rate of evacuation of food from the gut of larval sea lampreys required an average of 54 h (range 51–58 h) at 16°C and 70 h (range 60–90 h) at 2.5°, regardless of larval length (Moore and Beamish 1973). There were no differences in the rates at which various species of algae passed through the gut at either temperature.

As in most species of aquatic herbivores (Ivlev 1939; Levanidov 1949; Brown 1961), ammocoetes digest only part of the food in their guts. At 15°C, the larvae of *L. planeri* utilized an average of 39.5% of the lipid in their food, 33.8% of the protein, 35.2% of the carbohydrates (excluding cellulose), and 6.5% of the cellulose (Table 2). The corresponding values for animals maintained at 5°C were 8.0, 3.9, 6.2, and 0.5%. The considerable variation in assimilation efficiency in the different experiments recorded in Table 2 was probably due to the degree of activity of the animals prior to analysis, as noted in other herbivores (Prus 1971; Nilsson 1974). For example, in an active animal (Hardisty and Potter 1971), food passes through the gut much more rapidly than when at rest. Under natural conditions, digestion efficiency is probably relatively high, particularly during low water periods in summer. However, spring floods would likely increase the level of activity in ammocoetes, thereby decreasing digestion efficiency.

TABLE 2. Percentage contribution by weight of the different nutritional components assimilated by larvae of *Lampetra planeri* (data from Moore and Potter 1976a).

Component	Percentage absorbed						
	Expt. 1	2	3	4	5	6	Mean
15°C							
Lipid	5.4	45.5	87.3	62.1	22.7	14.1	39.5
Protein	4.5	44.2	69.9	42.4	31.7	10.3	33.8
Carbohydrate (excluding cellulose)	9.7	38.5	62.4	58.1	9.7	9.7	35.2
Cellulose	6.1	9.5	10.2	3.2	4.5	5.2	6.5
5°C							
Lipid	5.5	10.5					8.0
Protein	1.5	6.3					3.9
Carbohydrate (excluding cellulose)	5.1	7.3					6.2
Cellulose	0.2	0.8					0.5

The inefficient utilization of food by ammcoetes is attributable to the thick cellulose walls that many species of algae possess which are not easily broken down by digestive enzymes. In addition, detritus, potentially the most abundant material in the gut, consists primarily of ash, cellulose, and lignin, which are also not easily broken down. Finally, food embedded in the mucous band may be more resistant to digestion than the material attached to the surface. This poor utilization of food suggests that large quantities of algae must pass thruogh the gut undigested, a view substantiated by work on *P. marinus*, where survival of diatoms was about 45% during the summer and 95% in the winter (Moore and Beamish 1973).

Contrasting with this low efficiency of food utilization is a high efficiency of food entrapment. *Petromyzon marinus* larvae removed an average of 75% of both yeast (diameter = 5 μm) and algal cells (*Chlorella pyrenoidosa*, diameter = 8 μm) from the water passing through the pharynx (Mallatt 1979).

APPLEGATE, V. C. 1980. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Rep. U.S. Fish. Wildl. Serv. 55: 237 p.

ALVAREZ DEL VILLAR, J. 1966. Ictiologia michoacana, IV. Contribution al Conocimiento Biologico y Sistematico de las Lampreas de Jacona, Mich., Mexico. An. Esc. Nac. Cienc. Biol. Mexico City 13: 107–144.

BALABAI, P. 1950. Observations on the feeding of the ammocoete. Dokl. Akad. Nauk SSSR 72: 341–344. (In Russian)

BRINKHURST, R. O., K. E. CHUA, AND N. K. KAUSHIK. 1972. Interspecific interactions and selective feeding by tubificid oligochaetes. Limnol. Oceanogr. 17: 122–131.

BROWN, D. S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). J. Anim. Ecol. 30: 55–75.

CALOW, P. 1973. On the nature and possible utility of epilithic detritus. Hydrobiologia 46: 181–189.

CLEMENTS-MERLINI, M. 1960. The secretory cycle of iodoproteins in ammocoetes. J. Morphol. 106: 337–356.

CREASER, C. W., AND C. S. HANN. 1929. The food of larval lampreys. Pap. Mich. Acad. Sci. Arts Lett. 10: 433–437.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 18: 183–206.

FREEDEN, F. J. H. 1964. Bacteria as a source of food for blackfly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Can. J. Zool. 42: 527–538.

HARDISTY, M. W., AND I. C. POTTER. 1971. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter (ed.) The biology of lampreys. Academic Press, London.

HILL, B. J., AND I. C. POTTER. 1970. Oxygen consumption in ammocoetes of the lamprey *Ichthyomyzon hubbsi* Raney. J. Exp. Biol. 53: 47–57.

HOHEISEL, B.1969. Untersuchungen zur functionellen Morphologie des Endostyls und der Thyreoiden vom Bachneunauge (*Lampetra planeri* Bloch). I. Untersuchungen am Endostyl. Gegenb. Morphol. Jahrb. 114: 204–237.

HYNES, H. B. N. 1972. The ecology of running waters. Univ. Toronto Press, Toronto, Ont.

IVLEV, V. S. 1939. Transformation of energy by aquatic animals. Coefficient of energy consumption by *Tubifex tubifex* (Oligochaeta). Int. Rev. Gesamten Hydrobiol. Hydrogr. 38: 449–458.

KIECKEBUSCH, H. H. 1928. Beiträge zur Kenntnis des Baues und der Entwicklung der Schilddrüse bei den Neunaugenlarven (*Lampetra fluviatilis* L. and *Lampetra planeri* Bl.) Z. Morphol. Oekol. Tiere 11: 350–354.

KNECHT, V. A., AND J. E. WALTER. 1977. Vergleichende Untersuchung der Diäten von *Lymnaea auricularia* und *L. peregra* (Gastropoda: Basommatophora) im Zurichsee Schweiz. Z. Hydrol. 39: 299–305.

LAM, R. K., AND B. W. FROST. 1976. Model of copepod filtering response to changes in size and concentration of food. Limnol. Oceanogr. 21: 490–500.

LEVANIDOV, U. YA. 1949. Significance of allochthonous material as a food resource in a water body as exemplified by the nutrition of the water louse *Asellus aquaticus* L. Tr. Vses Gidrobiol. Ova. 1: 100–117.

MALLAT, J. 1980. Surface morphology of structures within the pharynx of the larval lamprey *Petromyzon marinus*. J. Morphol. (In press)

1979. The feeding biology of the larval lamprey, *Petromyzon marinus*; mechanisms and regulation of feeding. Ph.D. thesis, Department of Anatomy, Univ. Chicago, Chicago, IL.

MANION, P. J. 1967. Diatoms as food of larval sea lampreys in a small tributary of Northern Lake Michigan. Trans. Am. Fish. Soc. 96: 224–226.

Monk, D. C. 1976. The distribution of cellulose in freshwater invertebrates of different feeding habits. Freshwater Biol. 6: 471–475.

Moore, J. W. 1978. Importance of algae in the diet of the oligochaetes *Lumbriculus variegatus* (Müller) and *Rhyacodrilus sodalis* (Eisen). Oecologia 35: 357–363.

Moore, J. W., and F. W. H. Beamish. 1973. Food of larval sea lamprey (*Petromyzon marinus*) and American brook lamprey (*Lampetra lamottei*). J. Fish. Res. Board Can. 30: 7–15.

Moore, J. W., and I. C. Potter. 1976a. A laboratory study on the feeding of larvae of the brook lamprey *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 81–90.

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

Moriarty, D. J. W. 1976. Quantitative studies on bacteria and algae in the food of the mullet *Mugil cephalus* L. and the prawn *Metapenaeus bennettae* (Racek & Dall). J. Exp. Mar. Biol. Ecol. 22: 131–143.

1977. Quantification of carbon, nitrogen and bacterial biomass in the food of some penaeid prawns. Aust. J. Mar. Freshwater Res. 28: 113–118.

Newth, H. G. 1930. The feeding of ammocoetes. Nature 126: 94–95.

Nilsson, L. M. 1974. Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). Oikos 25: 35–42.

Potter, I. C., D. Cannon, and J. W. Moore. 1975. The ecology of algae in the Moruya River, Australia. Hydrobiologia 47: 415–430.

Prus, T. 1971. The assimilation efficiency of *Asellus aquaticus* L. (Crustacea; Isopoda). Freshwater Biol. 1: 287–305.

Randall, D. J. 1971. Respiration. *In* M. W. Hardisty and I. C. Potter (ed.) The biology of lampreys. Academic Press, London.

Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111: 981–994.

Schroll, F. 1957. Zur Ernährungsphysiologie der Ammocoetesslarven der Cyclostomen. Zool. Anz. 159: 75–78.

1959. Zur Ernährungsphysiologie der steirischen Ammocöten *Lampetra planeria* (Bloch) and *Eudontomyzon danfordi* (Regan). Int. Rev. Gesamten Hydrobiol. Hydrogr. 44: 395–429.

Shapas, T. J., and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Tricoptera. Great Lakes Entomol. 9: 175–188.

Smyly, W. J. P., and V. G. Collins. 1975. The influence of microbial food sources and aeration on the growth of *Ceriodaphnia quadrangula* (O. F. Müller) (Crustacea: Cladocera) under experimental conditions. Freshwater Biol. 5: 251–256.

Sterba, G. 1953. Die Physiologie und Histogenese der Schilddrüse und des Thymus beim Bachneunauge (*Lampetra planeri* Bloch — *Petromyzon planeri* Bloch) als Grundlagen phylogenetischer Studien über die Evolution de innersekretor-ischen Kiemandarm Derivate. Wiss. Z. Friedrich-Schiller-Univ. Jena Math.-Naturwiss. Reihe 2: 239–298.

1961. Zur Phylogenese des Kiemendarmes der Chordaten. Int. Rev. Gesamten Hydrobiol. Hydrog. 46: 105–113.

1962. Die Neunaugen (Petromyzonidae), p. 263–352. *In* R. Demoll and H. Maier (ed.) Handbuch der Binnenfischerei Mitteleuropas. E. Sschwizerbart, Stuttgart.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish. Bull. U.S. Fish. Wildl. Serv. 59: 559–617.

Young, J. Z. 1950. The life of vertebrates. The MacMillan Company, New York.