Significance of Organic Detritus in the Diet of Larval Lampreys in the Great Lakes Basin

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Larval sea lamprey (*Petromyzon marinus*) and northern brook lamprey (*Ichthyomyzon fossor*) were collected monthly from three streams in the Upper Peninsula of Michigan from May 1992 through May 1993 and larval sea lampreys were collected during summer months from sites throughout the Great Lakes basin. Organic detritus made up most of the diet ash-free-dry-mass (AFDM) throughout the year, averaging 97.79%, with algae (2.12%) and bacteria (0.09%) making up the remainder of the diet AFDM. Assimilation efficiency for AFDM averaged 72% during warmer months and 53% during cooler months (annual mean = 61%). Gut fullness (amount of AFDM in the anterior one-tenth of the intestine) was low (mean = 0.10 mg diet AFDM$\cdot$g^{-1} ammocoete). There were no significant differences in these measures between ammocoetes collected from the Upper Peninsula and those collected throughout the Great Lakes basin. From a laboratory-determined relationship between gut fullness and feeding rate, feeding rate in the field was estimated to be extremely slow, ranging from 4.2 to 5.5 mg diet AFDM$\cdot$g^{-1} ammocoete$\cdot$d^{-1}. These observations indicate that larval lampreys efficiently utilize a diet of organic detritus during warmer months when stream temperatures and food quality are more favorable for feeding, digestion, and growth.

Des larves de lamproie de mer (*Petromyzon marinus*) et de lamproie du nord (*Ichthyomyzon fossor*) ont été collectées mensuellement dans trois cours d'eau de la haute péninsule du Michigan de mai 1992 à mai 1993; des larves de lamproie de mer ont aussi été collectées durant les mois d'été dans des sites du bassin des Grands Lacs. Les détritus organiques représentatient la plus grande partie du poids sans cendre (PSC) des aliments au cours de l'année (moyenne de 97,79 %), les algues (2,12 %) et les bactéries (0,09 %) constituant le reste. L'efficacité de l'assimilation était en moyenne de 72 % pendant les mois les plus chauds et de 53 % pendant les mois les plus froids (moyenne annuelle de 61 %). La plénitude intestinale (PSC des aliments présents dans le dixième antérieur de l'intestin) était faible (moyenne = 0,10 mg de PSC des aliments par gramme d'ammocète). Il n'existait aucune différence appréciable quant à ces mesures entre les ammocètes collectés dans la haute péninsule et ceux qui provenaient du bassin des Grands Lacs. À partir d'un lien établi en laboratoire entre la plénitude intestinale et le taux d'alimentation, on a estimé que le taux d'alimentation était extrêmement lent (de 4,2 à 5,5 mg de PSC des aliments par gramme d'ammocètes par jour). Ces observations indiquent que les larves de lamproies utilisent efficacement leur alimentation en détritus organiques pendant les mois les plus chauds lorsque la température des cours d'eau et la qualité des aliments sont plus favorables à l'alimentation, à la digestion et à la croissance.

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Larval lampreys (ammocoetes) are suspension feeders that inhabit burrows in the soft sediment of streams. The larval phase may last from 3 to 13 yr. Their diet consists of a mixture of algae (primarily diatoms), organic detritus, and bacteria (Manion 1967; Moore and Beamish 1973). Although most investigators have focused their attention on the algal component (Creaser and Hann 1929; Schroll 1959; Manion 1967), algae actually comprise little of the diet. Based on indirect calculations, Moore and Potter (1976b) estimated that algae accounted for only 0.14 to 1.5% by volume of the diet of larval European brook lamprey (*Lampetra planeri*) in a eutrophic stream in England. They concluded that because algae contributed so little to the diet, ingested detritus and bacteria are probably more important to the nutrition of these animals.

Although organic detritus is frequently reported in the gut contents of all species of larval lampreys (Schroll 1959; Sterba 1962; Hardisty and Potter 1971), there are few estimates of its importance as a nutritional resource. A laboratory experiment by Moore and Potter (1976a) found that *L. planeri* ammocoetes increased in wet weight by 2.1% when fed 20–30 mg$\cdot$L^{-1} detritus for 60 d at 15°C, but lost weight at this concentration over the same period at 5°C. Thus, the significance of organic detritus in ammocoete diets remains unclear.

The purpose of the present study was to directly quantify each dietary component (algae, bacteria, and detritus) and measure total diet assimilation over a thirteen month period for two species of larval lampreys to identify their principal nutritional resource. Feeding rate, estimated from gut fullness,

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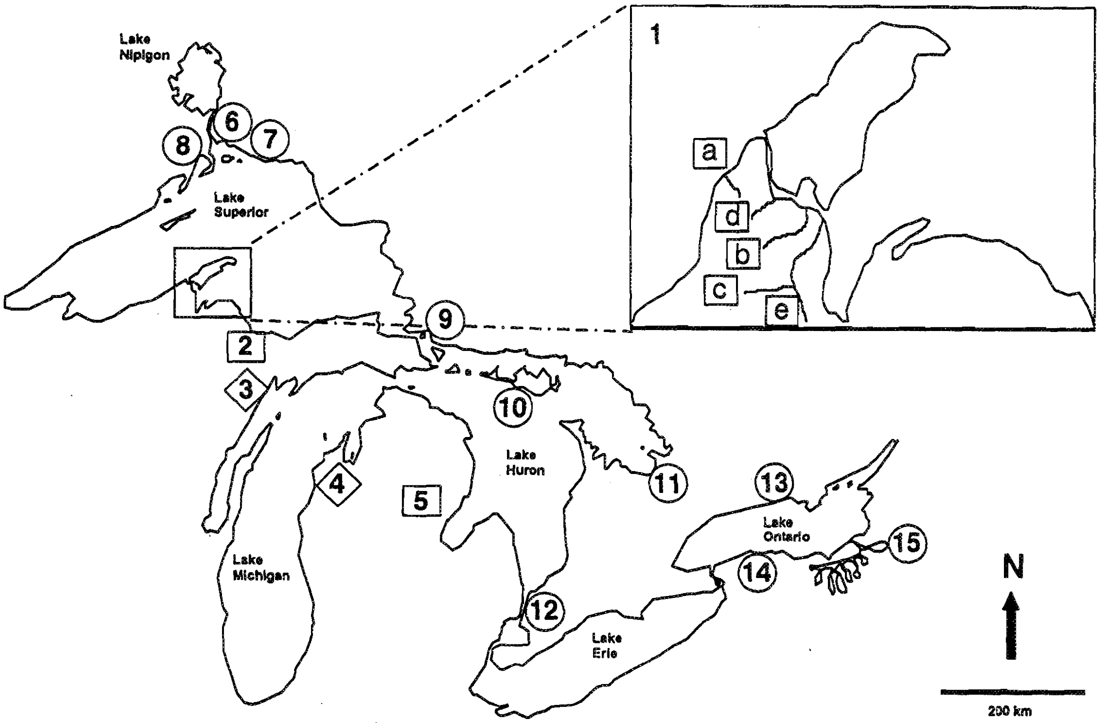

FIG. 1. River sites sampled for lamprey ammocoetes throughout the Great Lakes basin. Sites denoted with squares were sampled by Michigan Technological University, diamonds by the U.S. Fish and Wildlife Service, and circles by the Canadian Department of Fisheries and Oceans. Keweenaw sites are as follows: 1a-Misery River, 1b-Pike River, 1c-West Branch of the Sturgeon River, and 1d-Pilgrim River. For the remainder of site designations, see Table 1.

was also determined to further interpret the annual cycle of ammocoete feeding.

Methods

Sample Collection

Both sea lamprey (*Petromyzon marinus*) and northern brook lamprey (*Ichthyomyzon fossor*) ammocoetes were collected by electrofishing at monthly intervals from three streams in the Upper Peninsula of Michigan (hereafter termed Keweenaw sites) from May 1992 through May 1993 (Fig. 1; sites 1a, 1b, and 1c). Preliminary examination showed no differences in diet composition, assimilation efficiency, or gut fullness for samples collected at 4-h intervals over 24-h periods on two streams, so survey collections were made during morning hours for convenience. Due to prolonged flooding in all three streams as a result of ice and snow melt, ammocoetes were not sampled in April. At other sites throughout the Great Lakes basin, ammocoetes were obtained on single dates during the summer and fall of 1991 and 1992 by the U.S. Fish and Wildlife Service (Fig. 1; sites 3 and 4) and the Canadian Department of Fisheries and Oceans (Fig. 1; sites 1e-2 and 5-15).

Because ammocoetes are not responsive to electrofishing at temperatures <2°C (J. Weisser, U.S. Fish and Wildlife Service, Marquette, Mich., personal communication), diet samples during winter months (December–March) were obtained by placing lampreys in a cage in each stream. Cages were constructed of 1.27-cm plywood with outside dimensions: 0.3-m high × 0.6-m long × 0.45-m wide, providing a surface area of about 0.3-m^2. Openings in the front and back of the cages (0.3-m wide × 0.15-m high) were covered by 3-mm mesh netting that allowed flow through the cages but retained the lampreys. The cages were placed in areas of favorable ammocoete habitat and soft sediment was added to a depth of 0.15-m in each cage. Prior to introduction, ammocoetes were allowed to acclimate in the laboratory to ambient stream temperatures for two weeks. At monthly intervals, all ammocoetes were removed for analysis and replaced. As ammocoete density in each cage (ten per cage) was similar to densities observed in the field, no density-dependent cage effects should have occurred. This was confirmed in a field test conducted in May 1993, as diet composition, assimilation efficiency, and gut fullness of caged lampreys did not differ from those collected from streams by electrofishing (t-test; all $p > 0.25$).

For each sampling period and stream, ten freshly caught lampreys were held on ice until quiescent and anaesthetized with MS-222 (Sigma Chemical Corp.). This resulted in no loss of ingested material by regurgitation (Doxtater 1963). Lampreys were then fixed in 10% buffered formalin for 24 h and placed in Carosafe post-fixation preservative (Carolina Biological Supply) pending analysis.

Gut Content Analyses

The ammocoete digestive tract is a straight, undifferentiated tube approximately 45% of total body length (n = 305; SE = 0.01). Preliminary examination using yeast as a marker for detritus-fed ammocoetes indicated that there was no mixing or differential movement of diet contents. Thus, it can be assumed that ingested food material moves along the length of the intestine as plug flow. Contents were removed from the

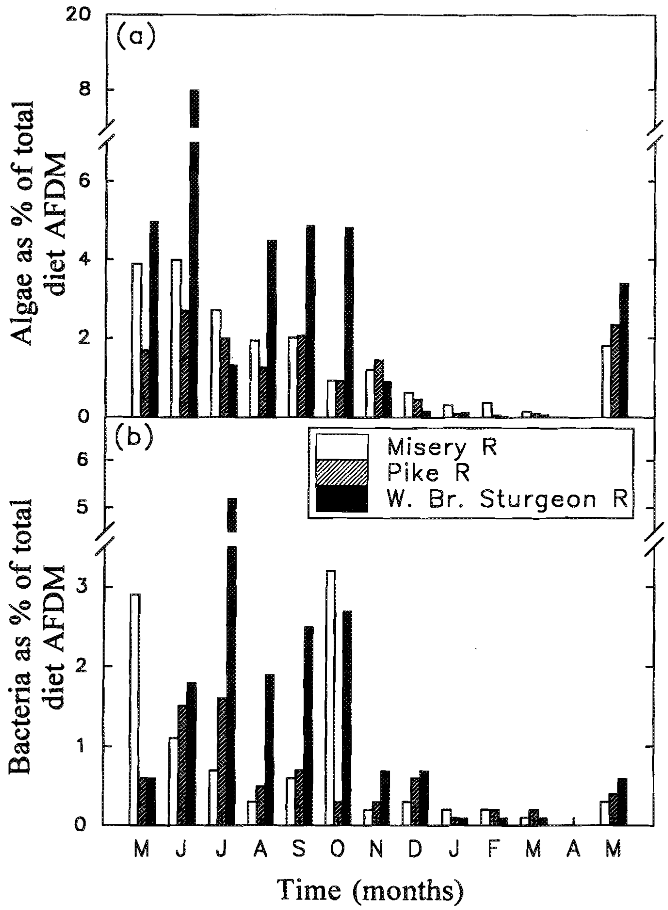

FIG. 2. Seasonal variation in the contribution of (a) algae and (b) bacteria ingested in ammocoete diets as a percentage of total diet AFDM for the Keweenaw sites from May 1992 through May 1993. Values for each month and stream are means of five individual ammocoetes.

anterior one-fourth of the intestine for five lampreys per sampling period per stream and a 50-μL subsample was analyzed by quantitative microscopy according to Ahlgren (1990a). Algal biovolume was estimated and converted to ash-free-dry-mass (AFDM) with an empirically determined weight/volume conversion factor (0.3633 mg AFDM$\cdot$mm^{-3}) that is similar to ratios reported by Nalewajko (1966).

Contribution of bacteria to total diet AFDM was determined by staining a 50-μL subsample of the contents from the anterior one-fourth of the intestine with acridine orange (0.1 mg$\cdot$mL^{-1} in 0.1 M potassium phosphate buffer, pH 7.5) according to Hobbie et al. (1977). Bacterial biomass per sample (mg AFDM$\cdot$mL^{-1}) was calculated as [cells$\cdot$mL^{-1}] × [mean biovolume (1 μm$^3\cdot$cell^{-1}; vanDuyl and Kop 1990)] × [2.2×10^{-10} mg C$\cdot$μm^{-3}; carbon conversion factor of Bratback and Dundas 1984] × [0.5 AFDM$\cdot$mg C^{-1}].

The remainder of the sample was dried to constant weight at 110°C and total sample AFDM was calculated as weight loss after combustion at 550°C. The AFDM of organic detritus was calculated indirectly as total AFDM minus microorganism AFDM (Bowen 1979a).

Assimilation Efficiency

Assimilation efficiency (%AE), the net amount of food assimilated through the gut wall expressed as a percentage of the amount ingested, was determined for total organic matter as described by Conover (1966). AFDM in gut contents taken separately from the first and last tenths of the digestive tract were compared, using diet ash as an unassimilated reference material. The assumption that ash is not assimilated is reasonable inasmuch as most of the ash appears to be small sand grains and diatom frustules. To the extent that this assumption is incorrect, assimilation efficiency will be underestimated. Because there was not enough food in the first and last tenth of the intestine to calculate individual assimilation efficiencies, gut contents of five lampreys per sampling period per stream were pooled for this analysis.

Feeding Rate

Gut fullness

As an index of feeding rate, fullness of the anterior one-tenth of the intestine was measured for ammocoetes caught in the field as mg diet AFDM$\cdot$g^{-1} ammocoete wet weight. The same five lampreys per sampling period per stream used in determining assimilation efficiency were used to estimate gut fullness.

Laboratory feeding experiment

Sea lamprey ammocoetes were obtained from the Hammond Bay Biological Station (U.S. Fish and Wildlife Service), Millersburg, Mich., in December 1992 and were acclimated to laboratory conditions for 3 wk on a diet of stream detritus.

Detritus was collected from an area in the Pilgrim River known to support ammocoetes. The upper 2.5 cm of sediment were removed using a plastic scoop, sieved, and the fraction >45-μm allowed to settle for 10 min. Suspended detritus was poured off and fed to 36 groups of three ammocoetes (average 3.21 ± 0.64 g live weight per aquaria; 0.21–0.32 g$\cdot$L^{-1}). Ammocoetes were held in aerated, glass aquaria with 12 L of conditioned water. Each aquarium contained sieved sand (<1 mm) to a depth of 7.5 cm and photoperiod was maintained on a 12 h L:12 h D cycle. To control temperature, twelve glass aquaria were held in each of three Living Stream refrigerated tanks with constant water circulation (Frigid Units Inc.). Experiments were conducted at 2, 9, and 16°C, simulating average winter, spring/fall, and summer temperatures, respectively, in Upper Peninsula streams.

To measure feeding rate, Red 40 Alum Lake (a water insoluble, particulate food dye; Warner-Jenkinson Inc.) was used as a visible tracer. Preliminary experiments showed that a concentration of 100 mg$\cdot$L^{-1} of the dye was needed to allow detection in ammocoete guts. This concentration appeared not to disturb the normal feeding behavior of ammocoetes. Because ammocoetes normally feed on particles at much lower concentrations (<40 mg$\cdot$L^{-1}), it appears that their feeding mechanism has a low capture efficiency for these dye particles. Detritus was added to the aquaria at a concentration of 30 mg$\cdot$L^{-1}, as this is comparable to that found suspended in depositional areas in many natural waterways (Moore and Potter 1976a).

The detritus/dye mixture was added to each aquarium and ammocoetes were allowed to feed for several hours before being removed and sacrificed. Each digestive tract was removed and preserved in 10% buffered formalin and the distance the detritus/dye mixture traveled was measured to the nearest millimetre. Contents were removed, dried to

TABLE 1. Means (SE) for percent AFDM in the diet, percent contribution of algae and detritus to diet AFDM, assimilation efficiency of AFDM, and gut fullness of AFDM for sea lamprey ammocoetes sampled throughout the Great Lakes basin.

Site No. (Fig. 1)	Stream	Date	AFDM	Algae	Detritus	Assimilation efficiency	Gut fullness
8	Black Sturgeon R	08-13-92	54.42 (3.72)	0.64 (0.16)	99.36 (0.16)	86.44	0.31 (0.06)
2	Chocolay R	09-06-91	61.76 (5.19)	2.15 (0.38)	97.85 (0.38)	—	—
2	Chocolay R	09-12-91	44.20 (9.96)	7.83 (1.07)	92.24 (1.05)	—	—
15	Fish Cr	09-17-92	65.32 (6.93)	0.81 (0.10)	99.19 (0.10)	63.57	0.44 (0.08)
7	Gravel R–Mtn Bay	08-15-92	58.94 (7.38)	0.44 (0.22)	99.56 (0.10)	78.63	0.18 (0.05)
6	Nipigon R–Lake Helen	08-28-92	63.83 (10.63)	0.91 (0.31)	99.09 (0.31)	69.05	0.19 (0.04)
11	Nottawasaga R	09-09-92	68.04 (1.29)	1.90 (0.57)	98.10 (0.57)	49.06	0.34 (0.06)
4	Platte R	03-23-92	85.20 (4.91)	0.82 (0.07)	99.18 (0.07)	66.44	—
4	Platte R	04-29-92	62.35 (7.61)	2.87 (0.34)	97.13 (0.34)	77.92	—
4	Platte R	06-23-92	62.23 (3.40)	1.49 (0.23)	98.51 (0.23)	76.26	0.14 (0.01)
3	Rapid R	10-24-91	73.83 (7.34)	1.66 (0.59)	98.34 (0.59)	—	—
5	Rifle R	07-21-92	57.66 (6.59)	4.23 (1.27)	95.77 (1.27)	79.11	—
13	Salem Cr	09-19-92	74.43 (5.57)	1.80 (0.45)	98.20 (0.45)	62.33	0.27 (0.03)
14	Salmon Cr	09-11-92	59.93 (6.00)	1.97 (0.72)	98.03 (0.72)	70.69	0.41 (0.12)
12	St. Clair R	07-27-92	61.39 (7.29)	1.13 (0.46)	98.79 (0.54)	81.36	0.37 (0.10)
9	St. Marys R	08-27-92	76.61 (3.61)	0.20 (0.07)	99.80 (0.07)	85.58	0.21 (0.14)
1e	Sturgeon R	08-20-91	46.72 (9.44)	2.49 (0.55)	97.52 (0.54)	—	—
1e	Sturgeon R	08-31-91	44.35 (5.16)	5.53 (1.74)	94.50 (1.75)	—	—
10	Timber Bay Cr	07-07-92	39.77 (7.04)	0.53 (0.12)	99.47 (0.12)	56.93	0.10 (0.01)
	Mean		61.10 (6.26)	1.98 (0.43)	98.03 (0.43)	71.67 (2.95)	0.25 (0.04)

constant weight at 110°C, combusted at 550°C, and reweighed. Gut fullness and feeding rate were measured as mg diet AFDM in the anterior one-tenth of the intestine·g^{-1} ammocoete wet weight, and mg diet AFDM ingested·g^{-1} ammocoete wet weight·h^{-1}, respectively.

Results

Diet Composition

Throughout the Great Lakes basin, for all sites and months sampled, organic detritus made up most of the diet, averaging 97.79% of total diet AFDM. Algae contributed 2.12%, with diatoms alone comprising 1.79%. Bacteria were limited to 0.09% (data collected for Keweenaw sites only) of the total diet AFDM. Diets of sea lamprey and northern brook lamprey ammocoetes were made up of algae, bacteria, and detritus in proportions that were not significantly different (ANOVA; all $p > 0.25$).

Algal and bacterial abundance in streams sampled at monthly intervals at the Keweenaw sites from May 1992 through May 1993 followed distinct seasonal patterns. As a percentage of diet AFDM, algal abundance peaked in May/June and September for all three sites (two-factor ANOVA; both $p < 0.001$; Fig. 2a). The cycle of bacterial abundance lagged about one month behind algal abundance, with peaks in July and October (two-factor ANOVA; both $p > 0.25$; Fig. 2b). Abundance of algae and bacteria in the diet declined in all three streams from November through March (Fig. 2). Winter samples (November–March) contained a significantly lower algal and bacterial biomass than samples collected during warmer periods (May–October) in all three streams (t-test; all $p < 0.001$). Algal and bacterial abundance in the diet, as a percentage of total AFDM, increased in May following the spring thaw as streams resumed more typical flows, temperatures warmed, and light levels increased (Fig. 2).

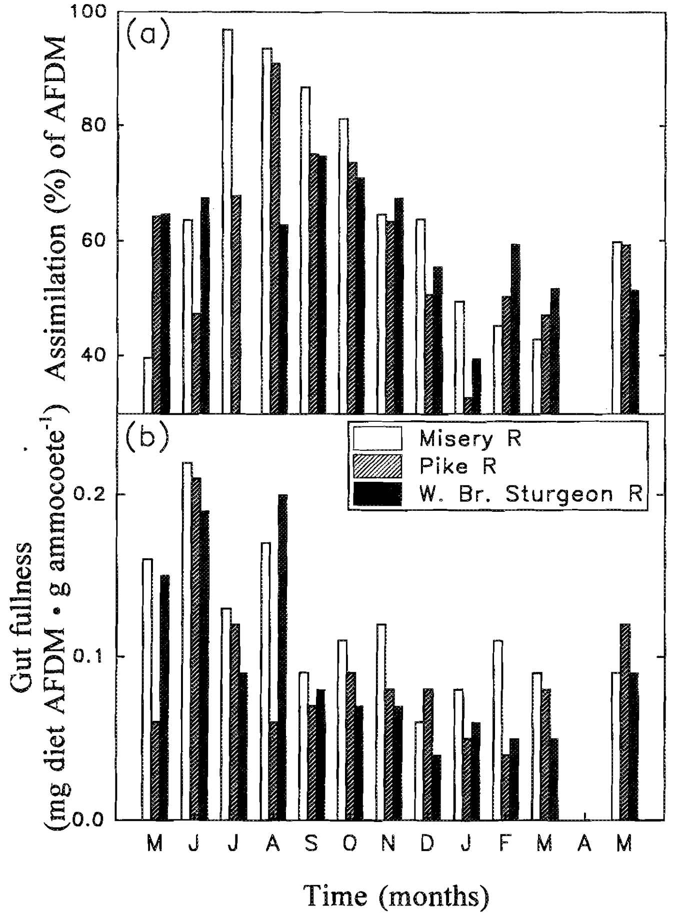

FIG. 3. Seasonal variation in the (a) assimilation and (b) gut fullness of organic matter ingested by ammocoetes for the Keweenaw sites from May 1992 through May 1993. Estimates for each month and stream consist of five pooled ammocoetes for assimilation efficiency and means of five individual ammocoetes for gut fullness.

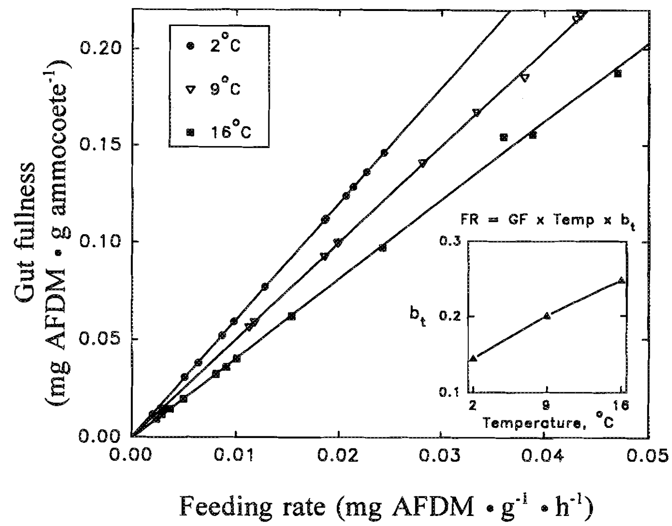

FIG. 4. Relationship between feeding rate and gut fullness at 2, 9, and 16°C as determined from the laboratory feeding experiment.

From May through October 1992, the amount of algal AFDM in the diet was higher, on average, in the West Branch of the Sturgeon River (6.46%), which has a canopy that remains relatively open, than in either the Misery (2.57%) or Pike (1.77%) rivers, which have closed canopies (ANOVA; $p < 0.001$). An unusually large spate in the Sturgeon River in July appears to have swept away much of the algae, resulting in a lower algal abundance in the diet for that month relative to all other summer months in that stream (ANOVA; $p < 0.01$; Fig. 2a).

Ammocoetes sampled from the remainder of the Great Lakes basin showed similar diet composition to ammocoetes sampled at Keweenaw sites (ANOVA; $0.15 < p < 0.20$; Table 1). Riparian canopy was categorized as open or closed by field personnel of the Canadian Department of Fisheries and Oceans Sea Lamprey Control Centre. The amount of algal AFDM in the diet was typically higher for streams with open canopies (Fig. 1; sites 1d, 2, 3, 4, 5; Table 1). Algal abundance in open canopy streams was, on average, 3.98% of total diet AFDM, whereas closed canopy streams had an algal abundance averaging only 1.27% (t-test; $p < 0.02$). Four deep-water sites were unshaded by riparian vegetation but ammocoetes collected from these contained little algae. Two were lentic environments (Fig. 1; sites 6 and 7) and two were in large rivers (Fig. 1; sites 9 and 12). Both habitat types have low light penetration to bottom substrate which impedes the development of algae. However, a suitable environment exists for ammocoetes (Wagner and Stauffer 1962).

Assimilation Efficiency

In July 1992, we determined assimilation efficiencies for nine large individual northern brook lamprey ammocoetes (range 120–155 mm TL) from the Pike River. Mean %AE was 78.08% with a relatively low level of variation (range 71.01–84.38%; CV = 5.92%). More typically, ammocoetes collected were too small (60–90 mm TL) to provide adequate gut samples to determine individual %AE. As there was little variation between ammocoetes collected at the same time within a stream, we pooled samples from five individuals for monthly measures of %AE.

Throughout the year, lamprey ammocoetes assimilated, on average, 61% of organic detritus ingested. For the Keweenaw sites, %AE followed a seasonal cycle, peaking in July or August (Fig. 3a). Percent AE was higher during warmer months (May–October; mean = 72%) than during colder sampling periods (November–March; mean = 53%) (t-test; $p < 0.05$). Flooding in the West Branch of the Sturgeon River in July caused a change in diet composition resulting in no assimilation of ingested material (Fig. 3a). Assimilation efficiency estimates from the remainder of Great Lakes basin sites (Table 1) fall within the range of values for ammocoetes sampled during late summer at the Keweenaw sites (Fig. 3a).

Feeding Rate

For the Keweenaw sites, gut fullness followed a seasonal cycle, peaking in June and decreasing through the remainder of the year (Fig. 3b). During warmer months (May–October), gut fullness was higher (0.13 mg diet AFDM·g^{-1} ammocoete wet weight) than in colder sampling periods (November–March; 0.07 mg diet AFDM·g^{-1} ammocoete wet weight) (t-test; $p < 0.02$; Fig. 3b). Ammocoetes sampled from the remainder of Great Lakes basin sites typically had gut fullness values (Table 1) within the range found for ammocoetes sampled at the Keweenaw sites during late summer (Fig. 3b).

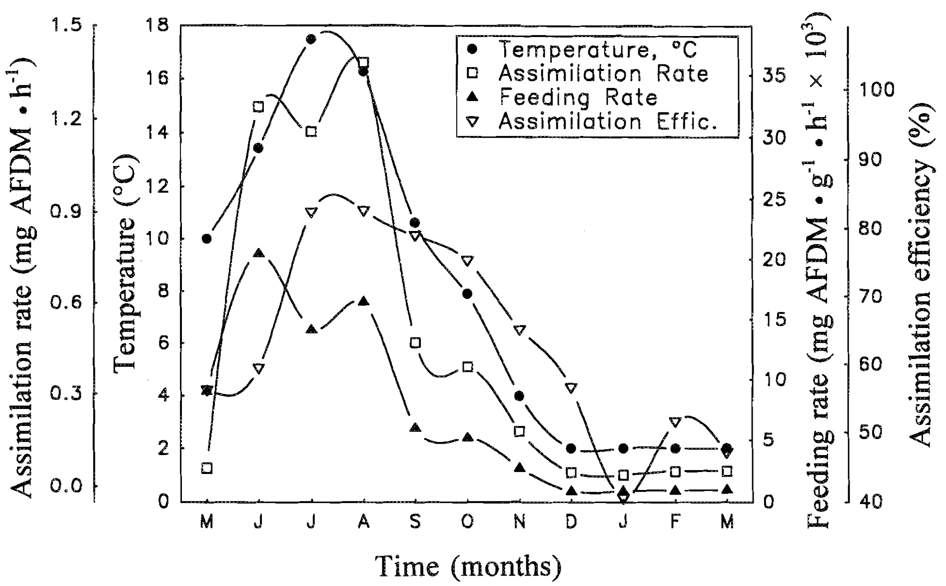

FIG. 5. Seasonal variation in stream temperature, assimilation rate, feeding rate, and %AE as estimated for the Keweenaw sites.

In the laboratory feeding experiment, mean feeding rates were 1.43×10^{-2}, 3.67×10^{-2}, and 3.21×10^{-2} mg diet AFDM·g^{-1} ammocoete wet weight·h^{-1} at 2, 9, and 16°C, respectively. Gut fullness values at these temperatures were 0.08, 0.11, and 0.07 mg diet AFDM·g^{-1} ammocoete wet weight. Although within-treatment variance was relatively high (CV = 58.51%), regression slopes of feeding rate and gut fullness between temperature treatments were significantly different (ANCOVA; both $p < 0.001$).

From field gut fullness estimates and the experimentally determined slope of the regression relationship between gut fullness and feeding rate (b_t; Fig. 4), we calculated feeding and assimilation rates for wild populations of lamprey ammocoetes from the Keweenaw sites for the period May 1992 through March 1993. Feeding rate (FR) was estimated as the product of gut fullness (GF), stream temperature (Temp), and the slope (b_t) (Fig. 4). Assimilation rate (AR) was estimated as the product of feeding rate (FR) and field determined %AE.

Discussion

Seasonal Variation in the Abundance of Algae and Bacteria

Variation in the abundance of algae in ammocoete diets follows the general annual cycle described for north temperate streams (Hynes 1970). Algae in diets peaked in late spring and early autumn when light availability and stream temperatures support high levels of diatom production (Chapman and Demory 1963; Hynes 1970). A similar cycle of algal abundance in ammocoete diets has also been reported in other studies (Moore 1972; Moore and Beamish 1973; Moore and Mallatt 1980). Bacterial abundance in the diet also followed a seasonal cycle, lagging about a month behind peaks in algal abundance. This may reflect the time required for bacterial population growth that is fueled by organic substrates from physiologically mature or senescent algae. Thus, variation in the abundance of algae and bacteria in ammocoete diets is consistent with the expected pattern of their availability in the annual stream cycle.

Sources of Nutrients Supporting Lamprey Larvae

Organic detritus is the principal trophic resource supporting the metabolism and growth of both sea lamprey and northern brook lamprey larvae in the populations studied. Microorganisms averaged only 2.2% of diet AFDM. Even if these are digested with 100% efficiency, their low concentration means they could account for no more than 4% of the organic matter assimilated. Because detritus makes up an average of 98% of diet AFDM and diet AFDM is assimilated with a mean efficiency of 61%, it is necessarily the case that most organic matter assimilated is detritus. The same conclusion was reported for two teleosts, *Oreochromis* (*Sarotherodon*) *mossambicus* (Bowen 1981) and *Prochilodus lineatus* (*platensis*) (Bowen et al. 1984), that feed on similar mixtures of aggregated detritus and microorganisms.

Although microorganisms provide a small fraction of the digesta, they may be important as sources of specific nutrients, especially vitamins, or as supplementary sources of digestive enzymes. Of much greater significance, they may play a critical role in production of the detrital fraction of the diet. There is a strong correlation between microorganism abundance and the digestibility of detritus, with assimilation efficiency lagging about one month behind microorganism abundance. Algal and bacterial abundances in ammocoete diets peaked in June and July, respectively, whereas peak %AE occurred in July and August. After October, %AE and microorganism abundance declined as stream temperatures cooled. Percent AE reached a low in January, increasing slightly in February before declining again in March (Fig. 3a). This February increase coincided with a period of warmer air temperatures from mid-January to early February 1993 that caused some stream ice melt, allowing light penetration to the stream bottom in some reaches for approximately two weeks.

The correlation in the annual cycles of microorganism abundance and assimilation efficiency points to algae and bacteria as agents responsible for the production of more digestible detrital aggregate. At the Keweenaw sites, the four- to six-week-long period of high discharge following spring snow melt either buries or scours from the system much of the algae, bacteria, and organic detritus. This is followed in May and June by a spring diatom bloom during which cells begin to lay down layer upon layer of extracellular polymer matrix. Production of extracellular matrix is greater after the stationary growth phase as diatom cells become more physiologically mature (Decho 1990). This material entraps existing particles, adsorbs dissolved organic matter (DOM) and gradually builds up a "biofilm" layer (Decho 1990) comprised of "detrital aggregate" (Bowen 1979b). We speculate that the lag between peaks in diatom abundance and detritus digestibility (%AE) reflects the time required for detrital aggregate to accumulate, be dislodged by physical erosion, sloughing (Decho 1990), and invertebrate activity (Allanson 1973), and become a significant component of suspended particulate organic matter (POM) in streams. These newly produced particles are likely to be less degraded and refractory, and to have a higher food value than older particulate matter, especially that derived from vascular plant debris (Bowen 1979b). Not only do biofilms potentially represent a highly labile carbon source because they are more abundant in easily hydrolyzable polysaccharides, but the DOM adsorbed to their surface provides a reservoir of nutrients and organic compounds that are otherwise not available to particulate feeding organisms (Decho and Lopez 1993). Thus, we believe that the peak in %AE is likely due to increased availability of recently produced, more digestible detrital aggregate relative to other sources of detrital particles in streams. The correlation between bacterial abundance and the digestibility of detrital aggregate for lamprey larvae suggests that both heterotrophs derive their nutrition from labile detrital aggregate.

This interpretation of the annual cycle is consistent with the effects of the July flood in the West Branch of the Sturgeon River. Flood waters appear to have swept away both algae and detritus, leaving only indigestible sediment in suspension for ammocoete feeding. This heavy bedload movement resulted in ammmocoete diets containing an extremely high percentage of mineral matter compared with other months of the year. Typically, ammocoete diets contained, on average, 35% mineral matter (range 14.80–61.25%; SE = 2.06). However, in July, ammocoete diets contained 75% mineral matter. After stream discharge returned to normal, algal abundance increased in August and diet digestibility peaked later in September. Thereafter, the pattern for the Sturgeon River was comparable to the other two streams.

Seasonal Variation in Gut Fullness and Feeding Rate

Gut fullness and feeding rate appear more closely associated with stream temperature than with diet digestibility. An increase in stream temperature up to 15°C in early summer was associated with an increase in gut fullness, feeding rate, %AE, and assimilation rate (Fig. 5). Peak stream temperatures in July coincided with a decrease in feeding and assimilation rate, but a peak in %AE. Reduced feeding at this time may have been a response to the increased availability of digestible detrital aggregate, allowing the larvae to meet their nutritional needs while ingesting a smaller quantity of food. As stream temperature declined after the peak, feeding and assimilation rates increased again before declining through the remainder of the year (Fig. 5). This pattern points to the annual temperature cycle as a major influence on ammocoete feeding in north temperate streams (R^2 = 0.60 and 0.57 for %AE and gut fullness, respectively; both $p < 0.001$). Malmqvist and Brönmark (1981) reported a similar response, in that stream water temperature has a significant effect on the rate of particle filtration in *L. planeri* ammocoetes. However, the availability of a higher quality food source in biofilm detritus during the summer makes it difficult to separate the relative contribution of both temperature and food quality on ammocoete feeding.

Ammocoete Adaptations to Detritivory

Compared with other detritivorous fishes, the digestive tract of lamprey ammocoetes is unspecialized (Hardisty and Potter 1971). It consists of little more than a simple tube about half as long as the animal's body, with some differentiation into esophagus and intestine. As no mucosal folds or lateral caeca are evident, the surface area for absorption appears to be small. Also, the pH in the intestine of ammocoetes is circumneutral, typically around 7.5 (Barrington 1972). Other detritivorous fishes studied to date show morphological adaptations for digestion of detritus (Bowen 1980, 1984; Mundahl and Wissing 1988). Yet lamprey ammocoetes assimilate an average of 61% of the organic matter in their diets, a percentage similar to that reported for other detritivorous fishes (Bowen 1981; Bowen et al. 1984; Mundahl and Wissing 1988; Ahlgren 1990b). The question remains, how can lamprey ammocoetes so efficiently utilize a low quality food resource such as detritus while having no apparent morphological adaptations of their digestive tract?

Ammocoetes feed very slowly. We estimate from gut fullness data and the experimentally determined gut fullness/feeding rate relationship that at between 9 and 15°C, ammocoetes feed at rates ranging from 4.2 to 5.5 mg diet AFDM$\cdot$g^{-1} ammocoete$\cdot$d^{-1}. This is far below the 60 mg diet AFDM$\cdot$g^{-1} fish$\cdot$d^{-1} typical of other juvenile fishes fed highly digestible diets *ad libitum* (Brett and Groves 1979, *inter alia*). Slow feeding is consistent with observations that ammocoetes' respiratory pumping rate and metabolic rate are both slower than those observed for other fishes (Mallatt 1982; Sterba 1962; Hill and Potter 1970) and with the long time period required for gut clearance in ammocoetes (Moore and Mallatt 1980). In the absence of discernable morphological adaptations for digestion of detritus, it appears that ammocoetes achieve a high assimilation efficiency with an extraordinarily long period of digestion. This suggests that natural selection may have favored a low metabolic rate as an adjustment to the limited nutrient assimilation rate associated with this digestive strategy. In turn, low metabolism is linked to slow growth and the extended length of the detritivorous larval phase (3–13 yr; Applegate 1950; Lowe et al. 1973). Thus, many of the life history characteristics of lamprey larvae can be interpreted as adaptations to organic detritus as a food resource.

The destructive impact of sea lamprey predation on Great Lakes fishes is currently partially controlled by chemical treatment of streams to kill larvae before most metamorphose into the parasitic form. Due to both cost and limited effectiveness, the level of control in many parts of the basin is not adequate to support management objectives. There is a growing need to supplement or replace the current control technology with less expensive, more effective, and more environmentally benign technologies. Identification of the link between the detritus food resource and larval lamprey production may provide a step toward identifying opportunities for new control strategies.

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