GREAT LAKES FISHERY COMMISSION
Research Completion Report *

IDENTIFICATION OF THE NUTRITIONAL RESOURCE SUPPORTING GROWTH IN LARVAE OF TWO LAMPREY SPECIES IN THE GREAT LAKES BASIN

by

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ABSTRACT

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The diets of larval sea lamprey (*Petromyzon ma* k lamprey (*Ichthyomyzon fossor*) in three streams in the U n were sampled monthly for thirteen months. Other samples of sea lamprey diets were collected during summer months from streams and lentic sites throughout the Great Lakes Basin. Quantative determination of the organic matter in diet components (algae, bacteria, and detritus) was combined with measurement of total diet digestion and assimilation to identify the principal nutritional resource.

Organic detritus averaged 97.75% of diet AFDW, with algae making up 2.15% and bacteria limited to 0.10%. Detritus was somewhat less abundant during summer (80-97%), but varied little (95-99%) throughout the remainder of the year.

Throughout the Great Lakes basin, assimilation efficiency (%AE) varied with stream temperature ($R^2 = 0.60$) and food quality, averaging 72% during the summer and 53% during the winter (mean = 61%). No differences in %AE were evident between stream or habitat types.

Because organic detritus makes up 98% of the organic matter in the diet, and 61% of the organic matter is digested and assimilatied, it is necessarily the case that this material is the primary nutritional resource supporting the growth of lamprey ammocoetes in the Great Lakes Basin. Given the facts that in some streams ammocoetes grow much faster than in others, and that these differences have been correlated by other researchers primarily with differences in water conductivity, it would be useful to know how conductivity is linked to food quality. This may provide a new basis for predicting growth from a simple measure of the environment useful over a number of time scales: seasonal, yearly, and longer term as changes in land use and water quality continue.

INTRODUCTION

Larval lampreys (ammocoetes) are suspension feeders inhabiting burrows in the soft sediment of streams. Particulate material is transported by a unidirectional respiratory current through a ring of coarse oral cirri into the pharynx (Sterba 1962; Randall 1971). The cirri act as a sieve to prevent larger particles (> 340 μm) and algal filaments from entering the pharyngeal chamber (Hardisty and Potter 1971). These particles are periodically expelled as they accumulate on the cirri (Applegate 1950). Particles passing through the cirri are enmeshed in a mucous complex in the pharynx and aggregate as they are passed by cilia to the intestine (Mallatt 1979, 1981). Thus, the mucous complex serves multiple functions in trapping, aggregating, and transporting food particles.

The diet of lamprey ammocoetes has been reported to consist of algae (primarily diatoms), organic detritus, and bacteria (Manion 1967; Hardisty and Potter 1971; Moore and Beamish 1973). Although most investigators have focused primarily on the algal component (Creaser and Hann 1929; Schroll 1959; Manion 1967; Moore and Beamish 1973; Potter et al. 1975), 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 since algae contributed so little to the diet of *L. planeri*, ingested detritus and bacteria are probably more important to the nutrition of larval lampreys.

Although organic detritus is frequently reported in the gut contents of all species of larval lamprey (Schroll 1959; Sterba 1962; Hardisty and Potter 1971; Potter et al. 1975), there are few estimates of its importance as a nutritional resource. A laboratory experiment by Moore and Potter (1976a) showed that at 15°C, *L. planeri* ammocoetes increased in wet weight by 2.1% when fed on detritus at a concentration of 20-30 mg l^{-1} for 60 d, but lost weight at this concentration over the same period at 5°C. These results indicate that detritus can be sufficient as a nutrient source to enable ammocoete growth at summer temperatures. As the detritus food chain is the principal route of energy flux and material cycling in aquatic ecosystems (Mann 1972; Wetzel 1983), the significance of organic detritus in larval lamprey feeding warrants closer examination.

The objective of the present study was to determine the significance of organic detritus in the diets of ammocoetes of both sea lamprey (*Petromyzon marinus*) and northern brook lamprey (*Ichthyomyzon fossor*) throughout the Great Lakes basin by examination of diet composition and assimilation efficiency.

METHODS

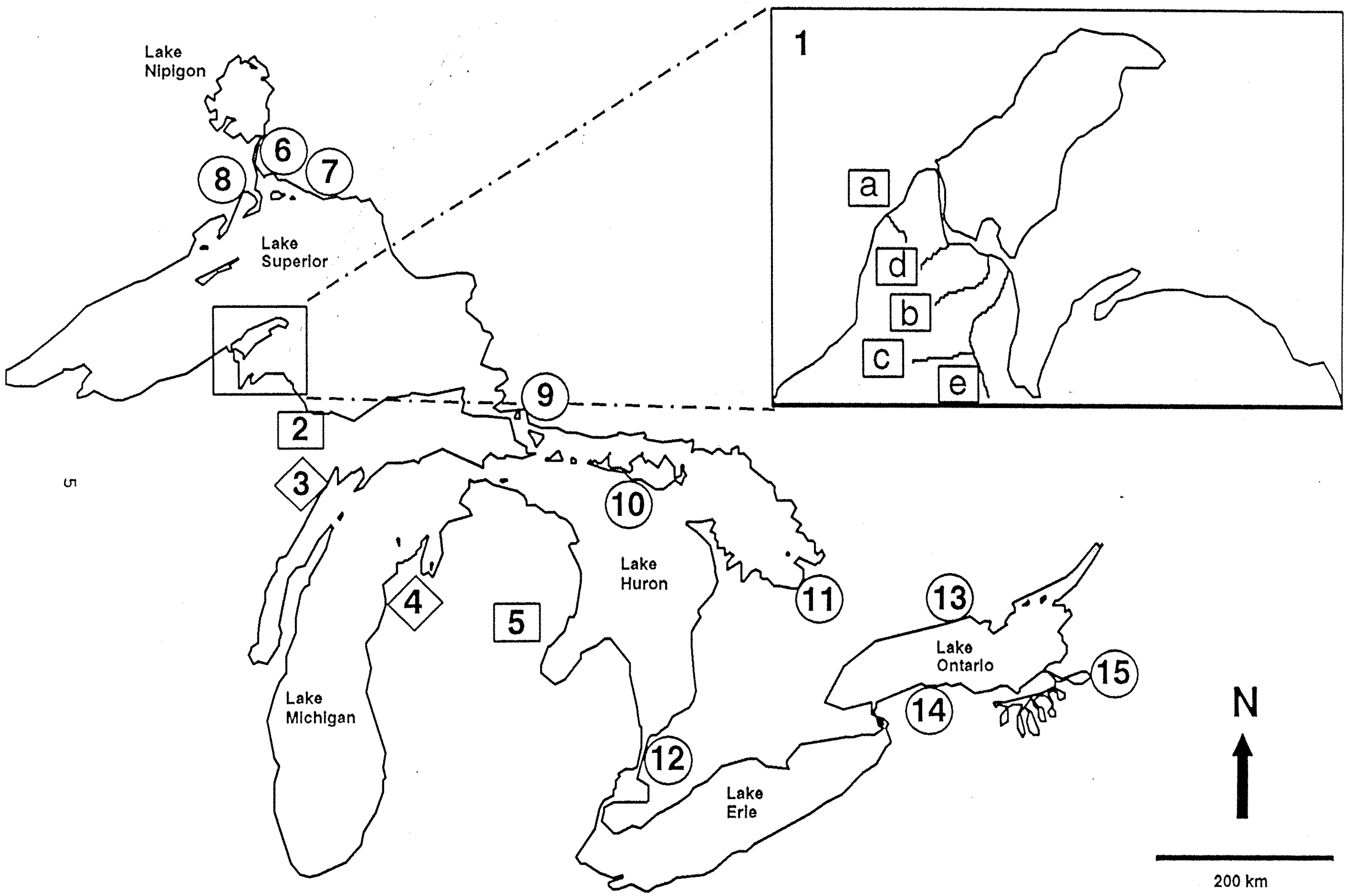
Sample Collection

Seasonal Sampling. - Both sea lamprey and northern brook lamprey ammocoetes were collected by electrofishing at monthly intervals from three streams in the Upper Peninsula of Michigan (Keweenaw sites) beginning May 1992 through May 1993 (Fig. 1, sites 1a, 1b, and 1c). Preliminary work showed no differences in diet composition or assimilation for samples collected every three hours during 24 hour periods on two streams, so survey collections were made during midday for convenience. Due to prolonged flooding in all three streams as a result of ice and snow melt, ammocoetes were not sampled in April. Other samples of ammocoetes were obtained on single dates during the summer and fall of 1991 and 1992 from rivers throughout the Great Lakes basin by the U.S. Fish and Wildlife Service and the Canadian Department of Fisheries and Oceans - Sea Lamprey Control Centre (Fig. 1, sites 1e-15). Monthly sampling during winter (December-March) was limited to Keweenaw sites. Because ammocoetes are not responsive to electrofishing at temperatures < 2°C (J. Weisser, U.S. Fish and Wildlife Service, Marquette, MI, *personal communication*), diet samples were obtained by placing lampreys in cages in each stream. Diet composition of caged lampreys did not differ from those collected from the stream by electrofishing (t-test; $p > 0.25$). The cages were constructed of 1.27 cm plywood with outside dimensions of 30 cm

Fig. 1. River sites sampled for lamprey ammocoetes throughout the Great Lakes basin. Sites denoted with squares were sampled by Michigan Technological University, sites with diamonds by the U.S. Fish & Wildlife Service - Sea Lamprey Control, and sites with circles by the Canadian Department of Fisheries & Oceans - Sea Lamprey Control Centre.

Sites are as follows: 1a. Misery R; 1b. Pike R; 1c. West Branch - Sturgeon R; 1d. Pilgrim R; 1e. Main Branch - Sturgeon R; 2. Chocolay R; 3. Rapid R; 4. Platte R; 5. Rifle R; 6. Nipigon R/Lake Helen; 7. Gravel R/Mountain Bay; 8. Black Sturgeon R; 9. St. Marys R; 10. Timber Bay Cr; 11. Nottawasaga R; 12. St. Clair R; 13. Salem Cr; 14. Salmon Cr; 15. Fish Cr.

All ammocoetes collected were sea lampreys except those from the Pike, Pilgrim, and West Branch - Sturgeon Rivers which contained only northern brook lampreys.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high x 30 cm long x 45 cm wide. Openings in the front and back of the cages (12.5 cm wide x 12.5 cm high) were covered by one-eighth inch mesh Durethene polyethylene marine netting (ADPI Enterprises, Inc.). This mesh size allowed near to ambient stream flow through the cages, but retained lampreys. Soft sediment was added to a depth of 15 cm in each cage before ten ammocoetes were introduced. The cages were placed in areas of favorable ammocoete habitat that were accessible for periodic retrieval of ammocoetes. Prior to introduction, ammocoetes were allowed to acclimate to ambient stream temperatures for two weeks. At monthly intervals, ammocoetes were removed for analysis and replaced with new ammocoetes.

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

Gut Content Analysis

Algae. - The ammocoete digestive tract is a straight, undifferentiated tube that is 45% of total body length (n = 305; SE = 0.001). Contents were removed from the anterior one fourth of the intestine for five lampreys per sampling period per stream and examined by quantitative microscopy. These contents were taken as representative of food material most recently consumed (Moore and Beamish 1973). To quantify algae, foregut contents were agitated in 2 ml of distilled water in a 25 ml erlenmeyer flask using a vortex mixer and suspended with a magnetic stir bar. The volume of water was adjusted so that 50-100 algal cells were contained in a 50 μl subsample which was mounted under a square coverslip on a microscope slide. The entire coverslip was scanned at 160x using a light microscope. Algal cells were outlined to scale on paper using a camera lucida calibrated against a stage micrometer. Viable algae were grouped into one of three categories: diatoms, green algae, and blue-green algae. Nonviable algal cells, i.e., without chloroplasts or visible cytoplasm, were not traced. The remainder of each sample was used in determinations of bacterial biovolume and ash-free-dry-weight (AFDW).

According to Lund et al. (1958), a single count of 50-100 algal cells is an adequate sample, since the precision and accuracy associated with a single count can be estimated for randomly distributed particles that follow a Poisson distribution. Counts of 50-100 vary no more than 20% of the true value at the 95% confidence level. Counts of 200 or 300 do little to increase accuracy, but counts below 50 are subject to significantly greater statistical error.

Biovolume of algae was estimated according to Ahlgren (1990). To convert algal volumes to AFDW (dry organic matter), a weight/volume conversion factor was determined for a culture of diatoms. By following the above procedure, algae were found to be, on average, 0.22 mg AFDW · mm^{-3}. This value is in agreement with literature values (Nalewajko 1966).

Bacteria. - Contribution of bacteria to diet AFDW was determined by staining the contents from the anterior one fourth of the intestine with acridine orange (0.1 mg · ml^{-1} in 0.1 M potassium phosphate buffer, pH 7.5) according to Hobbie et al. (1977). Bacterial cells were counted by mounting the sample under a plastic coverslip on a microscope slide with type B immersion oil and viewing at 1000x using a light microscope with a IV Fl Epiflourescence condenser with LP520 filter (450-490 nm) (Hobbie et al. 1977; Porter and Feig 1980; Wetzel and Likens 1990). Bacteria were enumerated by counting the average number of bacteria per ml in ten randomly chosen microscope fields (Hobbie et al. 1977). Bacterial biomass per sample (mg AFDW · ml^{-1}) was calculated as [cells · ml^{-1}] x [mean biovolume (1 μm^3 · $cell^{-1}$; vanDuyl and Kop 1990)] x [2.2 x 10^{-10} mg C · μm^{-3}; carbon conversion factor of Bratbak and Dundas 1984] x [0.5 AFDW · mg C^{-1}]. Given the low numbers found, bacterial counts were made only for diets of ammocoetes collected from Upper Peninsula streams.

Organic Detritus. - Total sample AFDW was calculated as weight loss after combustion at 550°C (mg AFDW · mg dry $sample^{-1}$). The AFDW of organic detritus was estimated as total sample AFDW minus microbial AFDW (algal AFDW and bacterial AFDW per sample). This method has been shown to be both accurate and precise

(Ahlgren 1990).

Assimilation Efficiency

Assimilation efficiency (%AE = amount of food assimilated through the gut wall as a percentage of the amount ingested) was calculated for total organic matter as described by Conover (1966). This method assumes that only the organic component of ingested food is significantly affected by digestion and that the indigenous ash fraction remains unassimilated in its passage through the gut. Comparison of the different ratios of organic matter to ash in the first tenth of the intestine relative to the last tenth allowed the percentage of organic matter in the food that has been assimilated to be calculated (Fig. 2). Often there was not enough food material in the first and last tenth of the intestine to calculate individual assimilation efficiencies, so the gut contents of five lampreys per sampling period per stream were pooled.

RESULTS

Diet Composition

Seasonal Comparisons in Upper Peninsula Streams. - Diet composition varied with season for those streams sampled in the Keweenaw peninsula from May 1992 through May 1993. Algal abundance, as a percentage of total diet AFDW, was greatest in May/June and September when the spring and autumn diatom blooms are expected (two-factor ANOVA; both $p < 0.001$; Fig. 3). As the deciduous riparian canopies closed in summer, abundance of algae in the diet decreased until canopies began to reopen in September (Fig. 3). From May through October 1992, the amount of algal AFDW in the diet was higher, on average, in the West Branch - 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 canopies that are almost entirely closed (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

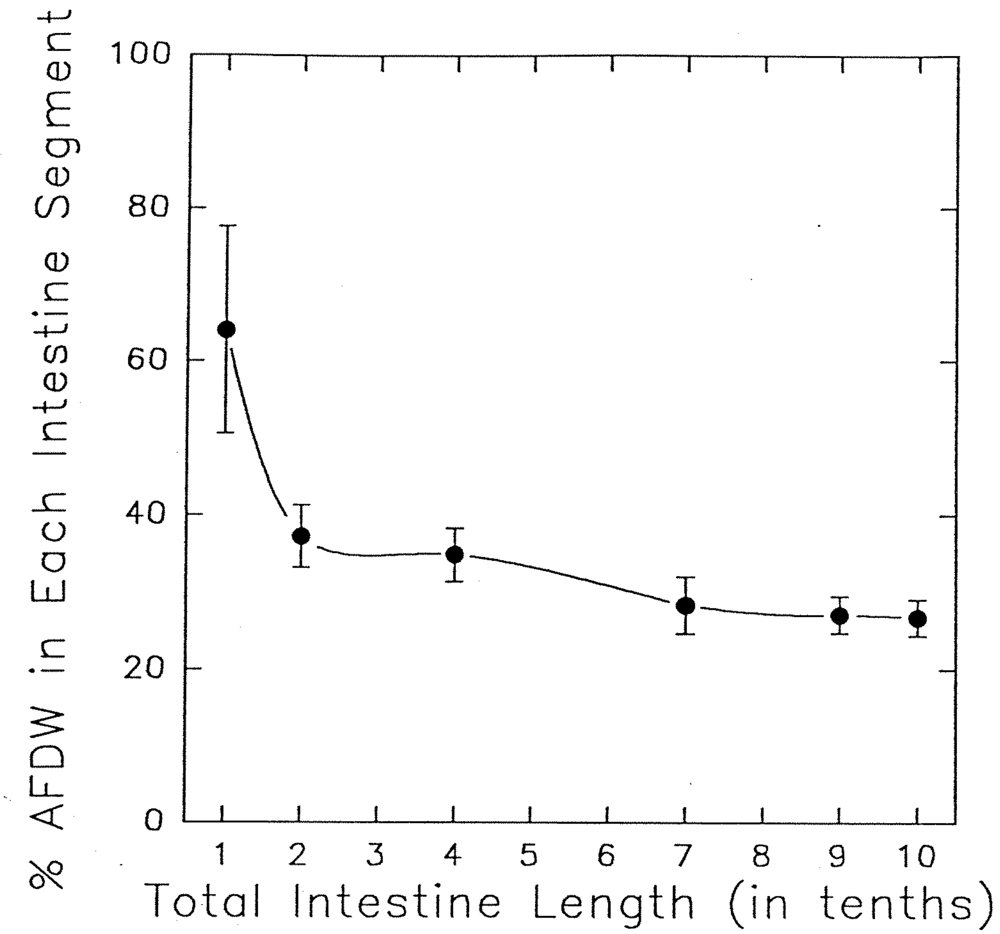

Fig. 2. Assimilation of organic matter (AFDW) by lamprey ammocoetes as it passes from the anterior tenth to the posterior tenth of the intestine. Means and standard errors are for two pooled samples of five lampreys in each (n = 2). The large decrease in organic material between the anterior and posterior tenths represents material that has been assimilated throught the gut wall and this difference allows for the calculation of assimilation efficiency (%AE).

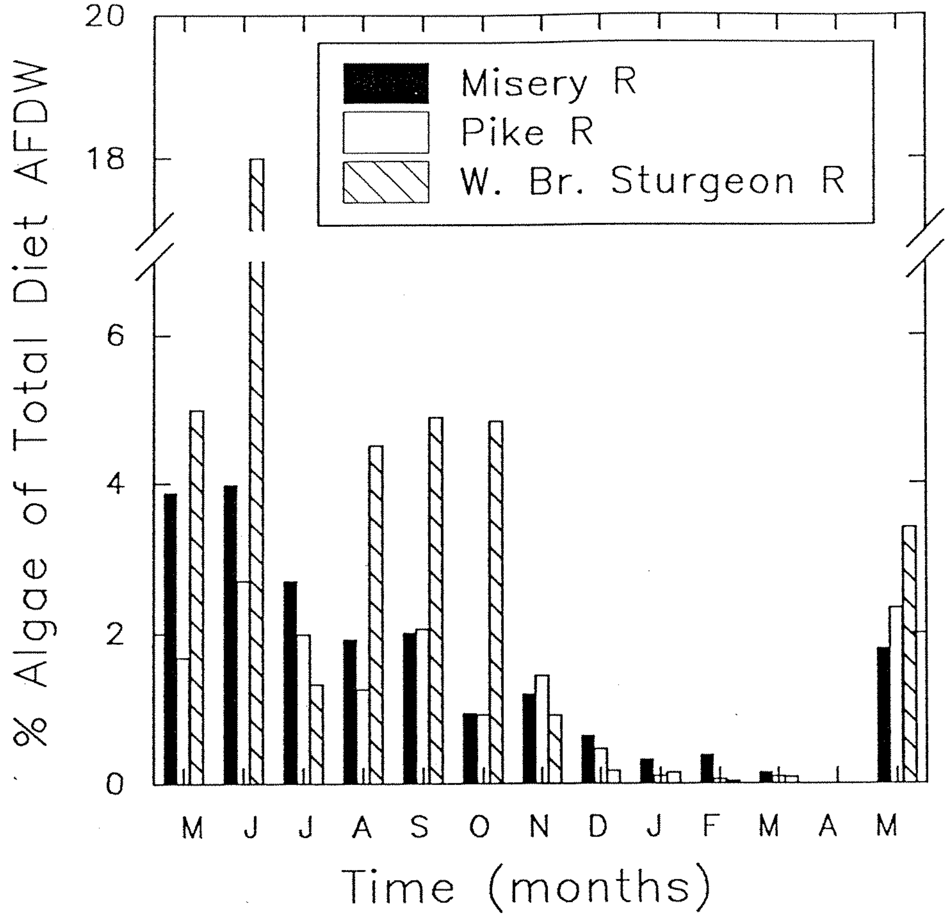

Fig. 3. Seasonal variation in the contribution of algae ingested in ammocoete diets as a percentage of total diet AFDW from May 1992 through May 1993. Values for each month and stream are means from five individual ammocoetes (for standard errors, see Appendix 1). Contribution of diatoms, green algae, and blue-green algae to total diet AFDW were determined individually for each month but pooled together in this figure. Ammocoetes collected from the Misery River were sea lampreys while those from both the Pike and West Branch - Sturgeon Rivers were northern brook lampreys. Note the break in the data during April as ammocoetes could not be collected as a result of heavy flooding in all three streams.

summer months in that stream (ANOVA; $p < 0.01$; Fig 3).

During winter sampling dates (November-March), abundance of algae in the diet declined in all streams (Fig. 3). Algae comprised 0.54, 0.43, and 0.26% in the Misery, Pike, and Sturgeon Rivers, respectively, during this period (two-factor ANOVA; both $p > 0.15$). Winter months (November-March) differed significantly from warmer sampling periods (May-October) in all three streams (t-test; $p < 0.001$). As flooding in April scoured and/or buried all soft sediment areas, ammocoetes were probably not feeding at that time. After streams resumed more typical flows in May, algal abundance in the diet, as a percentage of total AFDW, increased as stream temperatures warmed and light levels increased (Fig. 3).

Bacteria contributed < 0.5% of diet AFDW in all seasons and all streams and also showed a seasonal cycle (two-factor ANOVA; both $p > 0.25$). Bacterial abundance peaked in July and October before declining throughout the remainder of the year (Fig. 4). In the Pike River, the second peak in bacterial abundance did not occur until December (Fig. 4). Winter samples (November-March) contained a significantly lower bacterial biomass than warmer sampling periods (May-October) in all three streams (t-test; $p < 0.001$).

In all streams in all months, amorphous organic detritus (*sensu* Bowen 1984) was the principal component of the diet. Detritus averaged 98.26, 98.68, and 96.22% of diet AFDW in the Misery, Pike, and Sturgeon Rivers, respectively, from May 1992 through May 1993 (two-factor ANOVA; both $p = 0.15$; Table 1). For the Keweenaw sites together, detritus comprised 97.75%, with algae making up 2.15% and bacteria limited to 0.10%. The algal component consisted primarily of diatoms (1.94%), with green (0.21%) and blue-green algae (0.00004%) comprising the remainder. The diets of sea lamprey and northern brook lamprey ammocoetes are made up of algae, bacteria, and detritus in proportions that are not significantly different (ANOVA; $p > 0.25$). This is to be expected as ammocoetes of different lamprey species are quite similar, both morphologically and physiologically (Hardisty and Potter 1971).

Great Lakes Basin. - Ammocoetes sampled throughout the Great Lakes basin showed similar diet composition to ammocoetes sampled at Keweenaw sites (ANOVA; $0.15 < p < 0.20$; Table 2). Whether riparian canopy was categorized as open or closed was determined by field personnel of the Canadian Department of Fisheries and Oceans - Sea Lamprey Control Centre. The amount of algal AFDW in the diet was typically higher for those streams with open canopies (Fig 1, sites 1d, 2, 3, 4, 5; Table 2). Algal abundance in open canopy streams was, on average, 3.98% of total diet AFDW, whereas closed canopy streams had an algal abundance averaging only 1.27% (t-test; $p < 0.02$). Four sites had completely open canopies but other physical factors are likely to have influenced algal abundances. Two sites were deepwater, lentic environments (Fig. 1, sites 6 and 7) whereas the other two sites were large, deepwater river systems (Fig. 1, sites 9 and 12). Both habitat types have low light penetration to bottom substrate that impede the development of algae but provide a suitable environment for ammocoetes (Wagner and Stauffer 1962).

Throughout the other Great Lakes basin sites, detritus was similarly the principal component of the diet. The contribution of detritus to diet AFDW was, on average, 97.88% for all streams sampled over all months of the year. Algae contributed 2.12% (1.79% diatoms) of diet AFDW. The bacterial component was not determined as it comprised so little of total diet AFDW in other samples.

Assimilation Efficiency (%AE)

In July 1992, individual assimilation efficiencies were estimated from nine large 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%). Typically, individual ammocoetes collected were too small to provide adequate gut samples to determine individual %AE. Since there was little variation among ammocoetes collected at the same time within a stream, pooling of samples would give precise results.

Seasonal Comparisons in Upper Peninsula Streams. - %AE was greatest from July through October, peaking in July or August for all three streams (Fig. 5). Flooding in the Sturgeon River in July caused a change in diet composition

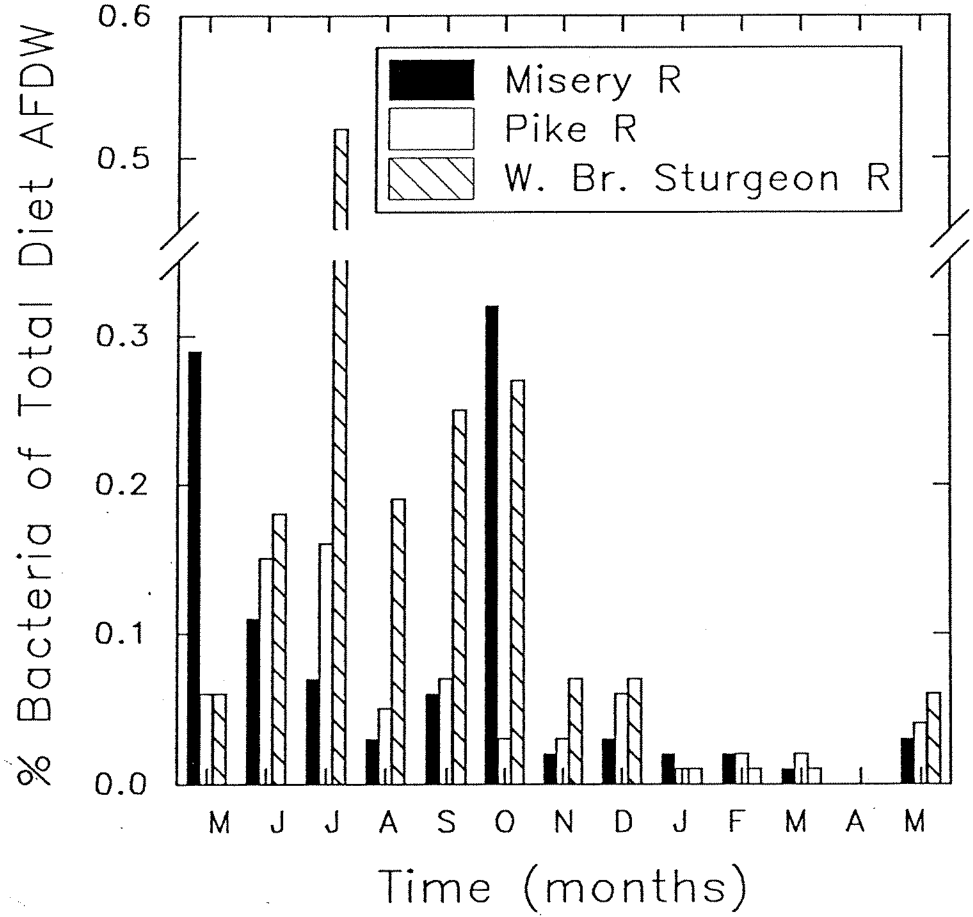

Fig. 4. Seasonal variation in the contribution of bacteria ingested in ammocoete diets as a precentage of total diet AFDW from May 1992 through May 1993. Values for each month and stream are means from five individual ammocoetes (for standard errors, see Appendix 1). Note the break in the data during April as ammocoetes could not be collected due to heavy flooding in all three streams.

Table 1. Means (standard error) for the percent contribution of detritus to total diet AFDW for lamprey ammocoetes sampled monthly in the Misery, Pike, and Sturgeon Rivers.

Month	Misery R	Pike R	West Branch Sturgeon R
May	95.83 (1.55)	98.26 (0.24)	94.83 (0.96)
June	95.91 (0.97)	97.15 (0.26)	81.82 (2.71)
July	97.23 (1.77)	97.84 (0.87)	98.15 (0.24)
August	98.04 (1.06)	98.69 (0.95)	95.30 (1.19)
September	97.94 (0.89)	97.83 (1.01)	94.55 (1.67)
October	98.74 (0.39)	99.05 (0.33)	94.90 (0.97)
November	98.78 (0.34)	98.53 (0.84)	99.01 (0.40)
December	99.31 (0.42)	99.48 (0.17)	99.76 (0.06)
January	99.66 (0.16)	99.89 (0.04)	99.85 (0.10)
February	99.61 (0.12)	99.92 (0.03)	99.96 (0.01)
March	99.84 (0.04)	99.89 (0.01)	99.91 (0.02)
April	----	----	----
May	98.17 (0.50)	97.63 (0.50)	96.54 (1.01)
MEAN	98.26 (0.39)	98.68 (0.28)	96.22 (5.04)

Table 2. Means (standard error) for percent AFDW in the diet, percent contribution of algae and detritus to diet AFDW, assimilation efficiency of AFDW, and gut fullness of AFDW for sea lamprey ammocoetes sampled throughout the Great Lakes basin.

Stream	Date	AFDW	Algae	Detritus	Assimilation Efficiency	Gut Fullness
Black Sturgeon R	08-13-92	54.42 (3.72)	0.64 (0.16)	99.36 (0.16)	86.44	0.31 (0.06)
Chocolay R	09-06-91	61.76 (5.19)	2.15 (0.38)	97.85 (0.38)	----	----
Chocolay R	09-12-91	44.20 (9.96)	7.83 (1.07)	92.24 (1.05)	----	----
Fish Cr	09-17-92	65.32 (6.93)	0.81 (0.10)	99.19 (0.10)	63.57	0.44 (0.08)
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)
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)
Nottawasaga R	09-09-92	68.04 (1.29)	1.90 (0.57)	98.10 (0.57)	49.06	0.34 (0.06)
Platte R	03-23-92	85.20 (4.91)	0.82 (0.07)	99.18 (0.07)	66.44	----
Platte R	04-29-92	62.35 (7.61)	2.87 (0.34)	97.13 (0.34)	77.92	----
Platte R	06-23-92	62.23 (3.40)	1.49 (0.23)	98.51 (0.23)	76.26	0.14 (0.01)
Rapid R	10-24-91	73.83 (7.34)	1.66 (0.59)	98.34 (0.59)	----	----
Rifle R	07-21-92	57.66 (6.59)	4.23 (1.27)	95.77 (1.27)	79.11	----
Salem Cr	09-19-92	74.43 (5.57)	1.80 (0.45)	98.20 (0.45)	62.33	0.27 (0.03)
Salmon Cr	09-11-92	59.93 (6.00)	1.97 (0.72)	98.03 (0.72)	70.69	0.41 (0.12)
St. Clair R	07-27-92	61.39 (7.29)	1.13 (0.46)	98.79 (0.54)	81.36	0.37 (0.10)
St. Marys R	08-27-92	76.61 (3.61)	0.20 (0.07)	99.80 (0.07)	85.58	0.21 (0.14)
Sturgeon R	08-20-91	46.72 (9.44)	2.49 (0.55)	97.52 (0.54)	----	----
Sturgeon R	08-31-91	44.35 (5.16)	5.53 (1.74)	94.50 (1.75)	----	----
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)

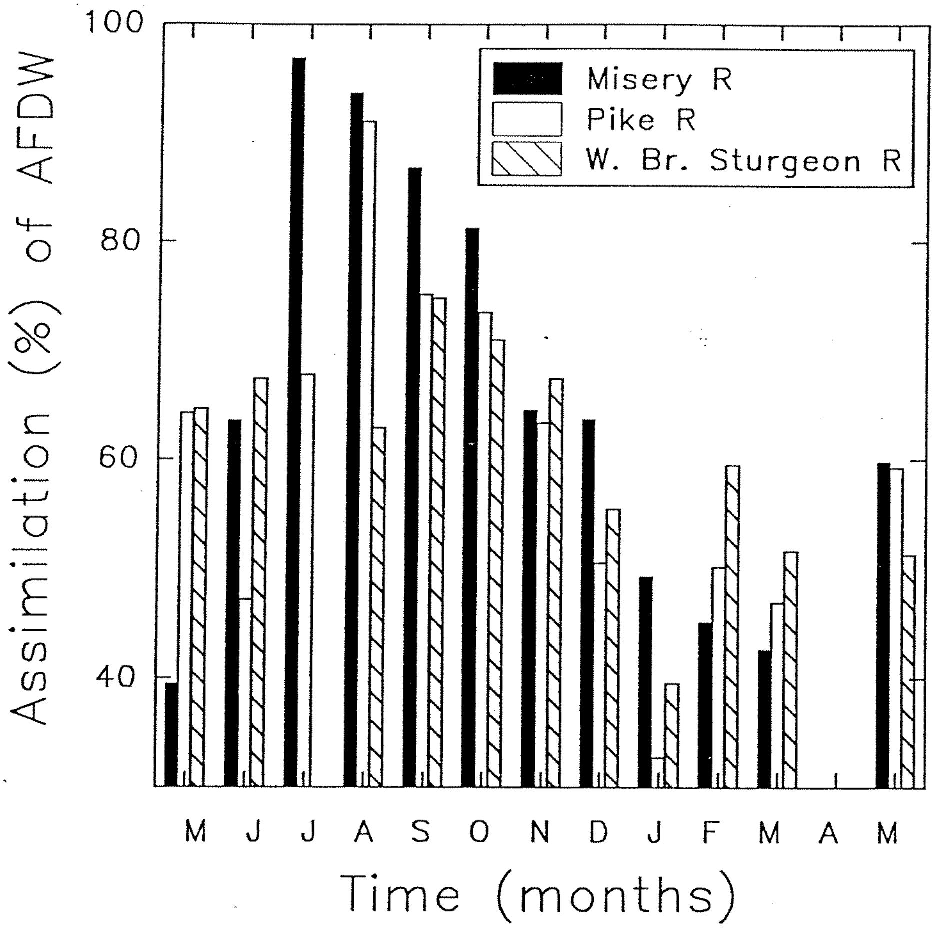

Fig. 5. Seasonal variation in the assimilation of organic matter (AFDW) ingested in ammocoete diets from May 1992 through May 1993. Estimates for each month and stream consist of five pooled ammocoetes. Note the break in the data during the month of April as ammocoetes could not be collected as a result of heavy flooding in all three streams. Due to heavy bedload movement, it would be expected that ammocoetes would be ingesting a disproportionate amount of inorganic material and therefore would not be assimilating any material. A similar observation was made in the West Branch - Sturgeon River during July as a result of heavy spate activity.

resulting in no assimilation of ingested material (Fig. 5). Typically, ammocoete diets contained only 37% mineral matter. However, in the Sturgeon River in July, ammocoete diets contained 75% mineral matter. This increase is probably due to the washing of sand downstream with heavy streamflow. %AE continued to decline as stream temperatures became colder, reaching a low in January (Fig. 5). A slight correlation existed between %AE and stream temperature for all three streams ($R^2 = 0.60$; $p < 0.001$). A significant difference did exist between warmer (May-October; mean = 72%) and colder sampling periods (November-March; mean = 53%) (t-test; $p < 0.05$). There was no significant difference in %AE between Keweenaw sites throughout the year (Tukey's Test for Non-Additivity; $p > 0.50$).

Great Lakes Basin. - No discernable pattern was evident between stream types (ie. open vs. closed canopy) or lake basin. Also, deepwater sites did not have %AE that differed from more typical ammocoete streams. As most ammocoetes throughout the Great Lakes basin were collected during August and September, %AE was relatively high (mean = 70.4%). These estimates for the Great Lakes basin sites fall within the range of values found for ammocoetes sampled during late summer at Keweenaw sites.

DISCUSSION

Diet Composition as Inferred from Gut Contents. - Organic detritus was the most quantitatively significant component of the diet for ammocoetes of both sea lamprey and northern brook lamprey in all streams and seasons sampled throughout the Great Lakes basin, accounting for 81.82 to 99.96% of total diet AFDW. Detritus was also the most abundant component in the diet throughout the day. As algal and bacterial biomass contributed so little to total diet AFDW, it would appear that organic detritus is the primary source of nutrition in ammocoete diets. However, the importance of algae and bacteria to the diet cannot be discounted, as the biofilm they produce appears to be the source of organic detritus upon which ammocoetes feed.

Variation in the contribution of organic detritus to ammocoete diets appears to be related to the annual cycle of algal production in north temperate streams (Hynes 1970). Algal abundance in ammocoete diets peaked in late spring and early autumn when light availability and stream temperatures were optimal for diatom production (Chapman and Demory 1963; Hynes 1970). A similar cycle of algal abundance in ammocoete diets has been reported in other studies (Moore 1972; Moore and Beamish 1973). Bacterial abundance in the diet also followed a seasonal cycle, lagging about a month behind peaks in algal abundance. This may be due to the time required for algal cells to develop a biofilm layer suitable for colonization by bacteria (Rounick and Winterbourn 1983). As the oral cirri of the ammocoete filtration apparatus only allows selection based on particle size (5-340 μm) (Manion 1967; Moore and Beamish 1973; Moore and Mallatt 1980), algae and bacteria are probably ingested incidentally with detritus. Thus, the variation in algae and bacteria in ammocoete diets reflects their availability as determined by the annual stream cycle.

The Seasonal Pattern of Digestibility and the Source of Detritus. - Assimilation efficiency also shows a seasonal pattern correlated with, but lagging behind, the abundance of algae and bacteria in the diet. Peak %AE occurred in July and August, whereas algal and bacterial abundance in ammocoete diets peaked in June and July, respectively. After October, %AE and microbial abundance declined as stream temperatures cooled. %AE reached a low in January, increasing slightly in February before declining again in March (Fig. 5). This increase can probably be attributed to warmer temperatures from mid-January to early February which caused some ice melt, allowing light penetration to the stream bottom, and thereby stimulating algal production.

These patterns point to microbial biofilm (both algal and bacterial) as the source of organic detritus supporting ammocoete growth. Biofilm is the accumulation of organic extracellular polymer matrix exuded by imbedded microbial cells on submerged surfaces such as rocks, logs, and living and dead vascular plants (Winterbourn et al. 1985; Decho 1990). This exuded material is considered detritus because it is dead organic matter. Functions of the extracellular matrix are: 1) to attach microbial cells to surfaces to remain in a favorable environment, 2) to sequester and concentrate dissolved organic substances which may be taken up and metabolized by microbial cells, 3) to minimize diffusion of exchange products between a substrate and the microbial cell, and 4) to provide protection to the microbial cell from unfavorable substances and abrasion (Decho 1990).

The organic exopolymer matrix exists as a tightly-bound capsule which closely surrounds the microbial cell surface. The matrix is a highly hydrated (99%), mucilaginous material composed of many intertwined polysaccharide chains. These polymers adsorb from solution a considerable amount of nitrogeneous substances, especially amino acids, thereby increasing the nutritional value of this material. As the layer thickens with time, the matrix becomes more loosely aggregated and friable (Decho 1990). Balanced against the accumulation of biofilm is its erosion by physical processes, sloughing of senescent material (Decho 1990), and removal by invertebrate feeding and movement (Allanson 1973). Dislodged fragments of biofilm are transported downstream as part of the suspended particulate load, contributing to the dead POM pool. Hence, biofilms appear to be a very important component of detrital dynamics that must be considered in aquatic food webs.

Detritus in ammocoete diets has the same general appearance as biofilm collected from the same stream. Biofilm is amorphous, translucent, and individual particles are often < 100 μm in diameter. In contrast, vascular plant detritus, i.e. morphous particles, show remnants of previous cellular structure, are often opaque, and are generally > 100 μm (Bowen 1984). Only amorphous detritus is found in the diets of ammocoetes. Both biofilm and detritus from ammocoete diets stain with alcian blue, a stain specific for polyanionic carbohydrates such as those that make up the extracellular matrix secreted by microbial cells. In contrast, vascular plant debris does not stain with alcian blue (Lemke 1992).

During the annual cycle, the heightened discharge following spring snowmelt in April scoured away and/or buried much of the detritus and algae. During the spring diatom bloom, cells begin to lay down layer upon layer of extracellular polymer matrix, gradually accumulating biofilm. The lag between peak diatom abundance and detritus digestibility (%AE) reflects the time required for biofilm to accumulate, be dislodged by physical erosion, sloughing, and invertebrate activity, and become a significant component of suspended POM in streams. This newly produced biofilm is less degraded, less refractory, and has a higher food value than older particulate matter (Bowen 1979). It can be hypothesized that the peak in assimilation efficiency is due to the increased availability of recently produced, more nutritious biofilm relative to other sources of detrital particles in streams.

This interpretation of the annual cycle is consistent with the effects of the July spate in 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 ammocoete diets containing a disproportionate amount of mineral matter when compared to other months of the year. 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 with the other two streams.

Although microbial biomass accounts for only a small fraction of the carbon and nitrogen necessary for ammocoete nutrition, the organic extracellular polymer matrix produced appears to be very important as the source of detritus upon which ammocoetes feed. Costerton (cited in Hobbie and Lee 1980) showed that microbial exudates often exceed microbial biomass by four to five times. In ammocoete diets, microbial biomass makes up, on average, 2.27% of total diet AFDW throughout the year. As ammocoetes assimilate an average of 61% of the AFDW in their diets, complete digestion of algae and bacteria in the diet could account for no more than 4% of the organic matter assimilated. Also, Moore and Beamish (1973) have shown that sea lamprey ammocoetes pass 45 and 90% of diatoms ingested through their digestive tract unharmed at 17.8°C and 0°C, respectively. Rogers et al. (1980) indicated that ammocoetes appear not to have a particularly effective mechanism for breaking down bacteria which enter the gut. Therefore, as microbial biomass actually contributes less than 4% of the assimilated organic material in ammocoete diets, it would appear that algal and bacterial biomass alone do not provide the energy required to support ammocoete nutrition. This points to organic detritus as the primary source of nutrition for lamprey ammocoetes and based on the seasonal relationship between digestibility and microbial abundance, biofilm appears to be the source of organic detritus. This same conclusion emerges from analyses of ammocoetes throughout the Great Lakes basin.

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