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Diet, feeding rate, and assimilation efficiency of American brook lamprey larvae

Neal D. Mundahl, Conrad Erickson, Matthew R. Johnston, Golam A. Sayeed & Stephen Taubel
Department of Biology, Winona State University, Winona, MN 55987-5838, U.S.A. (e-mails: nmundahl@winona.edu)

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Synopsis

We examined foods ingested by American brook lamprey larvae from Minnesota streams during spring and summer seasons. The diet was dominated numerically by diatoms, but organic detritus comprised the bulk (>85%) of ingested materials. The organic contents of ingested foods did not differ among streams or between seasons, averaging approximately 70%. Feeding rates based on gut fullness were highest, but most variable, during spring. Assimilation efficiency of the organic fraction of the diet averaged >65% across streams and seasons. Larval American brook lamprey depend on organic detritus to meet most of their nutritional needs and are very efficient at digesting and assimilating these detrital foods. Survival of American brook lamprey populations may be affected by human activities that alter the production and availability of detritus within streams.

Introduction

The American brook lamprey, *Lampetra appendix* (Dekay), is distributed widely in streams and rivers across eastern North America (Page & Burr 1991), where its larvae (ammocoetes) live buried within fine sediments in stream bottoms for 5 years or more (Thomas 1962, Seagle & Nagel 1982). They feed on a mixture of algae, bacteria, and organic detritus filtered from interstitial waters within their burrows (Creaser & Hann 1929, Moore & Beamish 1973). Earlier studies emphasized the importance of the algal (especially diatoms) and bacterial components of the diets of lamprey larvae (Creaser & Hann 1929, Manion 1967), but the majority of diatoms ingested by lamprey larvae have been reported to pass through the digestive tract intact and undigested (Moore & Beamish 1973). More recent studies of the diets of lamprey larvae have implicated the importance of the detrital fraction (Moore & Potter 1976a, 1976b, Sutton & Bowen 1994). Growth of lamprey larvae apparently can be supported on a diet of organic detritus alone (Moore & Potter 1976a), with larvae under natural conditions depending on organic detritus as the source for >90% of the organic matter assimilated year round (Sutton & Bowen 1994).

There is growing concern for the continued survival of American brook lamprey populations in many regions because of the negative effects of human activities (e.g., agriculture, logging, urban development) on stream habitats, and the inadvertent killing of *L. appendix* larvae by lamprey larvicides that are targeting the parasitic sea lamprey, *Petromyzon marinus* (Vladykov 1973, Johnson 1987). The habitat requirements of *L. appendix* larvae have been quantified only recently (Beamish & Lowartz 1996), but there is no information on the extent to which American brook lamprey larvae feed on organic detritus, nor on their ability to assimilate this material. Populations of lamprey larvae can play a very significant role in the food chain of small streams, exploiting a food resource unused by other vertebrates and then serving as prey for valuable game fishes (Vladykov 1973). Consequently, the present study examined the diet of American brook lamprey larvae in several Minnesota streams and assessed their abilities to process and assimilate detrital organic matter during spring and summer.

Methods

We collected American brook lamprey larvae from six streams within three drainage basins in southeastern Minnesota. Most streams are second- and third-order coldwater streams managed for recreational trout fishing (primarily brown trout, *Salmo trutta*, and brook charr, *Salvelinus fontinalis*). Streams within this region were subjected to severe habitat degradation during a period of intensive agricultural development beginning in the late-1800s, but many have subsequently begun recovery (via natural processes and habitat improvement projects; Waters 1977, Thorn et al. 1997). In addition to American brook lamprey and trout, streams also frequently contained sculpins (slimy, *Cottus cognatus*, mottled, *Cottus bairdi*), white sucker, *Catostomus commersoni*, dace (blacknose, *Rhinichthys atratulus*, longnose, *Rhinichthys cataractae*), darters (fantail, *Etheostoma flabellare*, johnny, *Etheostoma nigrum*), brook stickleback, *Culaea inconstans*, and creek chub, *Semotilus atromaculatus*.

We conducted a quantitative examination of the diet of American brook lamprey larvae for specimens collected from three streams (West Indian Creek and Salem Creek in spring 1998, Pine Creek in summer 1996). We collected larvae by electrofishing, anesthetized them (MS-222), and either froze or fixed them in 7% formalin. We measured larvae (mm total length, TL) and dissected out the simple, straight digestive tract and measured it for length. We flushed the contents of the anterior 10% of the tract into a 1-ml Sedgwick-Rafter cell. We identified food items in each of 10 randomly selected fields and counted them under 100× magnification for each larva. We made estimates of relative areal coverage (% of all food items, to nearest 5%) for each major category of food items (diatoms, desmids, detritus) for each field. Although this method is likely to underestimate the importance of larger particles (Ahlgren & Bowen 1992), we chose to be conservative in assessing the contribution of detrital particles (expected to be much larger in size than diatoms) to diets of lamprey larvae.

During summer 1995 and 1997 and spring 1998, we collected large American brook lamprey larvae from six streams (same three streams as above for diet composition, plus North Branch Whitewater River, Ferguson Creek, Trout Valley Creek), anesthetized, sacrificed, and froze them, and used them to estimate feeding rates and assimilation efficiencies for organic matter of lamprey larvae. We weighed larvae (nearest 0.1 g wet mass) and measured (mm TL), and dissected the digestive tract out and measured it for length. We removed contents from both the anterior 10% and posterior 10% of the digestive tract (Sutton & Bowen 1994), placed them into separate containers, dried them to constant weight at 60°C, weighed, and analyzed them for organic content (ash-free dry mass, AFDM; weight loss on ignition of dried sediments at 550°C for 3 h). We used fullness of the anterior 10% of the digestive tract (mg diet AFDM g^{-1} lamprey wet weight; referred to as gut fullness) to assess feeding rate (mg AFDM g^{-1} lamprey wet weight h^{-1}), using the relationships between gut fullness, water temperature, and rate of food passage derived for lamprey larvae by Sutton & Bowen (1994). We determined assimilation efficiency (%) for organic matter by comparing the organic contents of foods from anterior and posterior digestive tract segments, with diet ash used as the unassimilated reference standard (Sutton & Bowen 1994). We estimated assimilation rate (mg AFDM g^{-1} lamprey wet weight h^{-1}) by multiplying feeding rate by assimilation efficiency (Sutton & Bowen 1994).

Results

Diet analysis

The diets of American brook lamprey larvae from three different streams were comprised of diatoms (11 genera), desmids (one genus), and detrital particles (Table 1). Although diets also likely included bacteria (Sutton & Bowen 1994), no attempt was made to quantify them. Diatoms were the most common food item in guts of larvae from

Table 1. Percentage composition (numerical abundance and relative areal coverage) of the diets of American brook lamprey larvae from three streams in southeastern Minnesota.

Stream, date, TL range	Number of food items	Percent abundance			Percent coverage		
		Diatoms[a]	Desmids[b]	Detritus	Diatoms	Desmids	Detritus
Pine Creek 2 Jul 1996 110–179 mm	2040	73.8 (18.9)	0.2 (0.2)	26.0 (19.0)	4.2 (1.9)	3.1 (2.9)	92.6 (3.8)
W. Indian Ck. 9 Apr 1998 90–97 mm	1485	60.3 (22.2)	0.1 (0.1)	39.7 (22.2)	11.2 (7.4)	0.3 (0.6)	88.4 (7.7)
Salem Creek 23 Apr 1998 136–157 mm	3318	83.5 (5.8)	0.0 (0.0)	16.5 (5.8)	14.0 (5.5)	0.0 (0.0)	86.0 (5.5)

Values are means (±SD) of three larvae from each stream. TL is larval total length.

[a] *Navicula, Synedra, Cymbella, Meridion, Tabellaria, Fragilaria, Gomphonema, Cocconeis, Amphora, Nitzschia, Gyrosigma.*

[b] *Closterium.*

all three streams, outnumbering detrital particles approximately 3:1. *Navicula, Synedra,* and *Meridion* were the most common diatoms present in larvae from all three streams. Desmids (*Closterium*) were observed in only three larvae, comprising <0.5% of the algal cells present in their digestive tracts.

Particles of detritus in digestive tracts of American brook lamprey larvae were highly variable in size and shape. However, because of their large size (areal coverage) relative to that of diatoms, detritus dominated (>85%) the diets of larvae from all three streams (Table 1). Even so, significant differences in diet composition existed among larvae collected from the three streams, both on a numerical (contingency table: $X^2 = 315.4$, $p < 0.001$) and an areal (contingency table: $X^2 = 10.7$, $p = 0.03$) basis.

Feeding rate and assimilation

Lamprey larvae collected from six streams ingested foods that averaged approximately 70% organic matter (AFDM, Table 2). AFDM of ingested foods did not differ among the four streams examined during the summer months (June–August) (Kruskal–Wallis: $H = 4.78$, $p = 0.19$) nor among the three streams examined in April (Kruskal–Wallis: $H = 3.12$, $p = 0.21$). AFDM of foods ingested by larvae also did not differ between spring and summer (Mann–Whitney: $U = 384.5$, $p > 0.10$).

Gut fullness measurements and feeding rates calculated from them displayed considerable variation among streams and seasons (Table 2). Neither differed significantly among streams in summer (Kruskal–Wallis: both $p > 0.35$), but both did in spring (Kruskal–Wallis: both $p = 0.02$). In addition, gut fullness and feeding rate in spring both were significantly higher (Mann–Whitney test: both $p < 0.05$) than they were in summer. The average lamprey larva processed 3.1 mg AFDM g^{-1} lamprey wet weight day^{-1} during spring and 1.9 mg AFDM g^{-1} lamprey wet weight day^{-1} during summer.

Assimilation efficiency of dietary AFDM averaged >65% and assimilation rates averaged >0.05 mg AFDM g^{-1} lamprey wet weight h^{-1} (Table 2). Neither assimilation efficiencies nor rates differed between seasons (Mann-Whitney: both $p > 0.10$) or among streams during spring (Kruskal–Wallis: both $p > 0.10$) or summer (Kruskal–Wallis: both $p > 0.35$).

Discussion

Diets of American brook lamprey larvae from Minnesota streams were dominated by detritus. Although these larvae also consumed diatoms and desmids similar to those reported previously in the diets of lamprey larvae (Creaser & Hann 1929, Manion 1967, Moore & Beamish 1973), the estimated contribution of these algae to the diet

Table 2. Means (±SD) for ash-free dry mass (AFDM, %) in the diet, gut fullness of AFDM (mg AFDM g^{-1} lamprey wet weight), feeding rate (mg AFDM g^{-1} lamprey wet weight h^{-1}), assimilation efficiency of AFDM (%), and assimilation rate (mg AFDM g^{-1} lamprey wet weight h^{-1}) for American brook lamprey ammocoetes from southeastern Minnesota streams during summer and spring (TL is larval total length).

Stream	Date (TL range)	Water temp.	n	AFDM	Gut fullness	Feeding rate	Assimilation. efficiencies	Assimilation rate
Summer								
Pine Creek	15 Jun 1995	17	1	33.33	0.02	0.05	22.56	0.01
	(208 mm)							
N.Br.	29 Jun 1995	19	10	70.55	0.32	0.09	70.54	0.06
Whitewater R.	(145–240 mm)			(19.61)	(0.21)	(0.06)	(24.28)	(0.04)
	30 Jul 1995	20	1	78.57	0.07	0.02	23.65	0.01
	(206 mm)							
Ferguson Creek	7 Aug 1995	16	3	78.65	0.16	0.04	74.97	0.03
	(170–185 mm)			(6.37)	(0.09)	(0.02)	(21.68)	(0.02)
Trout Valley	1 Aug 1997	17	5	86.16	0.39	0.10	67.98	0.07
Creek	(116–162 mm)			(7.83)	(0.20)	(0.05)	(27.47)	(0.05)
Summer means			20	74.21	0.29	0.08	65.82	0.05
				(18.33)	(0.20)	(0.05)	(26.57)	(0.04)
Spring								
Trout Valley	10 Apr 1998	7	17	67.12	0.89	0.16	68.10	0.12
Creek	(95–156 mm)			(23.02)	(0.59)	(0.11)	(29.52)	(0.11)
W. Indian	9 Apr 1998	8	7	57.04	0.26	0.05	66.48	0.03
Creek	(100–185 mm)			(19.44)	(0.12)	(0.02)	(32.48)	(0.02)
Salem Creek	30 Apr 1998	15	7	75.34	0.61	0.15	59.41	0.09
	(165–222 mm)			(5.78)	(0.31)	(0.08)	(23.41)	(0.07)
Spring means			31	66.70	0.69	0.13	65.76	0.09
				(20.10)	(0.52)	(0.10)	(28.25)	(0.09)

(<15% based on surface area) was minor compared to that of detritus. Because we used surface areas to quantify algae and detritus in lamprey diets, it is likely that we greatly underestimated the relative contribution of detrital particles, which were significantly larger than diatoms (Ahlgren & Bowen 1992). Consequently, the actual contribution of detritus to diets of *L. appendix* larvae may be similar to that (97% of AFDM) reported for detritus in diets of sea and northern brook lamprey, *Ichthyomyzon fossor*, larvae, where volume was used to estimate the contribution of food particles (Sutton & Bowen 1994).

Gut fullness and feeding rates estimated for *L. appendix* generally were similar to values for sea lamprey and northern brook lamprey larvae within the Great Lakes basin (Sutton & Bowen 1994), although spring values in two Minnesota streams were much (~3×) higher. In addition, spring gut fullness and feeding rates in Minnesota streams were approximately 50% higher than summer values. Higher values in spring than in summer are expected because particle filtration and food intake appear to be temperature-dependent, peaking between 9 and 15°C (Malmqvist & Bronmark 1981, Sutton & Bowen 1994), a temperature typical of southeastern Minnesota streams in April. Why *L. appendix* larvae from Minnesota streams in spring have feeding rates so much higher than those of other species is not known, although these rates are still far below those of other juvenile fishes (Brett & Groves 1979, Sutton & Bowen 1994). The higher feeding rates of *L. appendix* larvae may contribute to the larger size at metamorphosis attained by American brook lamprey compared to other species of lampreys (Page & Burr 1991).

Assimilation efficiencies of American brook lamprey larvae in Minnesota streams (65%) were similar to those reported for sea lamprey (71%) and northern brook lamprey (61%) from a wide variety of streams (Sutton & Bowen 1994). These similarities likely result from similar foods consumed by lamprey larvae (Sutton & Bowen 1994). Because *L. appendix* larvae were not examined during winter, it is not known whether the lower assimilation efficiencies found during winter for northern brook lamprey larvae (53%, Sutton & Bowen 1994) also may be typical of American brook lamprey.

Since the bulk of organic matter consumed by American brook lamprey larvae is in the form of detritus, and assimilation efficiency for total organic matter usually exceeds 60%, most of the dietary nutrients required by lamprey larvae must be supplied by detritus (Sutton & Bowen 1994). The biomass and energy content of algae and bacteria in the diet is too low to meet the dietary requirements of lamprey larvae (Sutton & Bowen 1994), but detritus alone can support growth of larvae under the proper conditions (Moore & Potter 1976a). Even though earlier studies of the diet of *L. appendix* larvae focused on diatoms as the most important food resource (Creaser & Hann 1929, Moore & Beamish 1973), large proportions (45-90%) of the diatoms ingested by lamprey larvae (including *L. appendix*) are not digested (Moore & Beamish 1973). Even though algae and bacteria in diets of larvae may supply important vitamins or supplementary digestive enzymes (Sutton & Bowen 1994), their significance in the diet apparently has been greatly overemphasized.

Most fish that consume large amounts of detritus possess various morphological adaptations of the digestive tract (e.g., intestine several times body length, digestive cecae, extensive mucosal folding of the intestine) to enhance digestion and assimilation of this often difficult-to-digest material (e.g., Bowen 1980, 1987, Mundahl & Wissing 1988). Lamprey larvae apparently have no such adaptations (digestive tract is an unspecialized, straight tube <50% of total body length; Hardisty & Potter 1971), leading to speculation that larvae accomplish high assimilation efficiency via low rates of food passage and an extraordinarily long period of digestion (Sutton & Bowen 1994). Gut clearance times for sea lamprey larvae have been reported to range from 51 to 75 h (Moore & Beamish 1973, Moore & Mallatt 1980), much slower than those observed for other fishes (Moore & Mallatt 1980). Alternatively, other detritivorous fishes have exhibited an ability to select and ingest only the more nutritious fractions of detritus (Bowen 1987, Mundahl & Wissing 1988). It is not known whether larval lamprey may have this same ability.

This study has revealed that American brook lamprey larvae rely heavily on organic detritus as a food resource during spring and summer. Although diatoms and other algae also appeared in the diet, their nutritional contribution likely is very low. Because of their dependence on detritus, populations of *L. appendix* likely are impacted by factors that affect the pathways of detritus processing in streams (Hynes 1970, Cummins 1974, Bowen 1987). Delivery of allochthonous organic matter to streams may be altered by activities (e.g., crop production, livestock grazing, timber harvest) that affect the riparian vegetation (Doppelt et al. 1993), and autochthonous production can be impacted by runoff of soils and agricultural chemicals (Hynes 1960, 1970, Doppelt et al. 1993, Waters 1995). In addition, retention of detritus can be reduced when soil erosion and the resulting stream sedimentation fills in pools and reduces stream habitat heterogeneity (Hynes 1970, Waters 1995). It is clear that, in addition to protecting the physical stream habitats needed by lampreys (Vladykov 1973), the natural stream processes involved in detritus delivery, production, and processing must be protected or restored to insure the continued survival of our native lamprey fauna in North America.

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