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Crowding reduces feeding rate, effectiveness of diet selection, and efficiency of digestion by Northern Brook Lamprey ammocetes (*Ichthyomyzon fossor*)

Stephen Bowen · **Maureen Rae Yap**

Abstract We studied the effect of larval density on food utilization by sediment-dwelling northern brook lamprey (*Ichthyomyzon fossor*) larvae in the Otter River, Baraga County, MI, USA using field surveys and *in situ* cage experiments. Field surveys found that food utilization was inversely proportional to density across the range of 1 to 10 larvae/m^2. Compared to 1 larvae/m^2, values at 10 larvae/m^2 were lower by an average of 36% for gut fullness, by 32% for selective ingestion of organic matter, and by 71% and 58% for assimilation of diet organic matter and diet amino acids, respectively. *In situ* cage experiments and additional field studies in other nearby rivers revealed the same relationships. We hypothesize that physical disturbance of the sediment by adjacent larvae interferes with food utilization with the frequency of disturbance proportional to density. Condition factors were not correlated with density and indicate that individual larvae minimize the effect of crowding by moving away from higher density patches. We conclude that these findings are generalizable to other lamprey species in similar environments in which lower rates of growth, maturation, and survivorship of

lamprey larvae at higher densities have been reported by other researchers.

Keywords Biofilm as food resource · Assimilation efficiency · Density dependent growth · Interference competition · Ammocete · Ammocoete

Introduction

Lamprey population dynamics are of current interest in efforts to support both the conservation of declining native populations and the efficient control of invasive populations (Docker 2015; Hansen et al. 2016). An improved understanding of the ecology of the larval (ammocete) stage is considered to be critical for both conservation and control because the larval stage makes up the majority of the life span. The duration of the larval stage ranges from three to thirteen years depending on species and habitat whereas adults typically live two years or less (Hansen et al. 2016). The density of larvae in streams (number/m^2 substrate) can play an important role in population dynamics through its effects on year class strength (Hansen et al. 2016) and the growth, maturation, and survival of individual larvae. Field surveys found reduced growth at higher densities for larvae of sea lamprey (*Petromyzon marinus*) (Manion and Smith 1978; Purvis 1979; Weise and Pajos 1998), and European brook lamprey (*Lampetra planeri*) (Malmqvist 1983). *In situ* cage studies revealed reduced growth, lower survivorship, and later maturation at higher density for sea lamprey (Morman 1987) and

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reduced growth for European brook lamprey (Malmqvist 1983). Aquarium studies found reduced growth at higher density for *sea lamprey* (Murdoch et al. 1992; Rodríguez-Muñoz et al. 2003), and Pacific lamprey (*Entosphenus tridentatus*) (Mallatt 1983a). Density of sea lamprey and least brook lamprey (*L. aepyptera*) larvae has also been linked to variation in adult sex ratio (Purvis 1979; Docker and Beamish 1994).

Although such density-dependent effects observed in other animal populations are typically interpreted as results of competition for limited space or food, the reasons for this density effect in larval lamprey populations are unclear. Larvae live in burrows in stream sediment where they feed on suspended particles (sestonic biofilm fragments) from the waters above through a small, tube-like connection to the sediment surface (Sutton and Bowen 1994; Yap and Bowen 2003; Mundahl et al. 2005). Within streams, they selectively inhabit organic sediments suitable for burrow construction and their distribution within this sediment type is patchy rather than random (Yap and Bowen 2003). Even at the highest densities observed in field studies, there is ample sediment for individual animals to establish burrows (Mallatt 1983b). In feeding, they remove such a minute fraction of the particles in suspension that they are not expected to affect food availability for other larvae (Moore and Beamish 1973; Malmqvist and Bromark 1981). Thus, it appears that lamprey larvae compete for neither space nor food, *per se*.

In earlier work, we found that several aspects of food use by northern brook lamprey (*Ichthyomyzon fossor*) larvae vary in their efficiency across habitats (Yap and Bowen 2003). Two determinants of diet quality for fishes that feed on biofilm and associated non-living organic matter are the concentration of organic matter relative to mineral matter in the diet and the level of amino acids in diet organic matter (Bowen et al. 1995). Lamprey larvae in preferred habitats selectively ingest particles that are relatively rich in these two nutrients and that are more digestible. Variation was also found in feeding rate (Sutton and Bowen 2009). In the work reported here, we tested the hypotheses that crowding affects feeding rate, diet selection, and assimilation of nutrients from the diet by northern brook lamprey larvae.

Methods

We conducted *in situ* cage experiments and field surveys with northern brook lamprey ammocetes in four rivers

affluent to Lake Superior to assess the effects of density on feeding rate, diet selection, and the efficiency with which the diet is digested and assimilated through the gut wall (assimilation efficiency). Pilgrim River (-88.517 47.101) and Pike River (-88.534 47.011) are second order streams in Houghton County, Michigan, USA that range in width from 4 – 9 m in the study reaches. The West Branch of the Sturgeon River (-88.637 46.807) and the Otter River (-88.638 46.835) are third order streams in Baraga County, USA that range in width from 10 – 14 m in the study reaches. The common riparian vegetation is tag alder (*Alnus incana*), rushes (*Juncus* spp.), spruce (*Picea mariana*), and maple (*Acer* spp.) These streams may have contained small numbers of invasive sea lamprey larvae but we did not find them in our sampling and the streams had not been treated with lampricide which would substantially alter ammocete population density, size and age characteristics, and distribution (Hansen et al. 2016). This is particularly important to the study design because density effects depend on the relationship between population size and the carrying capacity of the environment, and the time required for post-treatment populations to reach carrying capacity is unknown. The streams in this study are clear, low-productivity streams with summer high temperatures near 16 °C.

Field surveys

Previous field studies of lamprey larvae have typically distinguished three habitat types based on the stream substrate: organic sediment, sand, and stones, with larvae abundant only in organic sediment (Malmqvist 1980; Potter et al. 1986; Klar and Weise 1994; Sutton 2017). Within areas of organic sediment, the most dense aggregations of larvae are typically found immediately downstream from obstacles to flow where fine, flocculent organic matter accumulates (Yap and Bowen 2003). We collected larvae from areas of organic sediment that included these depositional areas in October, 1995, using a backpack electroshocker specially designed for capture of these animals (Model ABP-2, Instrumentation Systems Center, University of Wisconsin, Madison, WI). The Otter and Sturgeon Rivers were chosen for these surveys because northern brook lamprey larvae were abundant enough to yield multiple samples across a range of densities.

Stream reaches to be sampled were chosen arbitrarily on the basis of accessibility from a roadway and

landowner permission, and five areas of organic sediment were sampled within a 180 m reach in each stream. Because the boundaries of depositional areas are not precise, we sampled each area using a 10 by 4 grid of 0.5 m by 0.5 m quadrats with the long axis parallel to stream flow and the upstream edge adjacent to an obstacle to flow such as large stones or woody debris. This quadrat size allowed us to shock the entire quadrat area at once and to capture all the larvae that emerged from the sediment. With larger sample areas, it is sometimes difficult to capture all larvae that emerge with the result that capture efficiency declines with increasing area sampled (Steeves et al. 2003). Beginning at the downstream edge of the grid, a 0.5 m x 0.5 m plastic frame was placed on the bottom and the area within the frame (quadrat) was shocked for several seconds until no more larvae emerged. The frame was then systematically repositioned to collect ammocetes from each quadrat in the grid. In total, 40 quadrats were sampled in each of five depositional areas for a total of 200 quadrats for each of two streams. All larvae collected were euthanized with 50 mg/L tricaine methanesulfonate (MS-222; Sigma-Aldrich Corporation, St. Louis, Missouri), fixed in 4% formalin, and stored in Carosafe preservative (Carolina Biological Supply) pending laboratory analyses. Larvae from each quadrat were enumerated and all analyses were completed with 6 months of the material's collection.

In situ cage experiments

Larvae > 5 cm total length were held in cages consisting of plastic trays (35 cm x 25 cm x 8 cm) filled with organic sediment from the stream and covered with 3 mm plastic mesh to prevent their escape but allow water movement through the cage. The surface area of these cages was similar to or larger than the area occupied by groups of northern brook lamprey larvae when we found them in dense aggregations in the subject streams. Animals were introduced at 5, 10 or 15 per cage, and two replicates of each density were placed in each stream in areas of flocculent organic sediment downstream from obstacles to flow where larvae tend to aggregate (Johnson 1987; Yap and Bowen 2003). One experiment was conducted in the Pilgrim River in June and two additional experiments were conducted in the Pike and Sturgeon Rivers in September, 1994. After 1 week, the larvae were euthanized, fixed in 4% formalin, and stored in Carosafe preservative pending laboratory analyses.

Laboratory analyses

Samples of the contents of the anterior and posterior sections of the digestive tract were taken to represent the diet and feces, respectively, according to the rationale developed by Sutton and Bowen (1994). Those authors collected the contents of the anterior and posterior tenths of the digestive tract and pooled samples in order to have enough material (> 1 mg dry weight) for chemical analyses. In the present study, it was necessary to have data for individual ammocetes so the contents of the anterior and posterior quarters from individual animals were used. The diet was described in terms of the proportion of organic matter in the diet, and the proportion of total amino acids in diet organic matter (Bowen et al. 1995). Gut contents were dried at 105 °C and ash-free-dry-mass (mg AFDM/mg dry weight), an operational measure of organic matter, was determined as weight loss on ignition at 550 °C. Amino acid concentration (mg amino acid/g AFDM) was determined by alkaline hydrolysis followed by the ninhydrin assay (Allen 1981; Lemke and Bowen 1998). Gut fullness, a measure closely correlated with feeding rate, was calculated as mg food AFDM in the anterior quarter of the gut/g larvae weight (Sutton and Bowen 1994). Ammocetes selectively ingest sestonic particles high in AFDM and amino acids (Yap and Bowen 2003). The relative effectiveness of selective feeding was assessed by comparison of the levels of AFDM and amino acids in the AFDM fraction of the diets of ammocetes collected at or held at different densities (Yap and Bowen 2003). Assimilation efficiency, the proportion of material ingested that is assimilated through the gut wall, was determined by Conover's ash ratio method (Conover 1966; Gleason et al. 2016). Length and weight were measured from preserved animals. Condition factor, a ratio of weight to length that indicates nutritional status (Murdoch et al. 1992), was calculated following LeCren (1951). All analyses were completed within 6 months of the material's collection.

Data analysis

For *In situ* cage experiments, the effects of factors Density and River on gut fullness, diet composition, and diet assimilation were tested using two-way ANOVA followed by multiple comparisons using the Holm-Sidak Method. The observations were mean values for each replicate cage. For field surveys, data from four adjacent 0.25 m^2 quadrats were consolidated

to create a two cell by five cell data grid. This consolidation resulted in a range of densities from 0 to 6 larvae/m² and one or more cells with densities of 1, 2, 3, 4, or 6 larvae/m² in the Sturgeon River and a range of 0 to 10 larvae/m² and one or more cells with densities of 1, 2, 3, 4, 6, 7, 8 or 10 larvae/m² in the Otter River. Without data consolidation, >70% of cells would have been empty and most of the rest would have had a density of 1 with the result that data analyses would have been insensitive to intermediate densities. Use of larger cells in analyses also reduced the likelihood that an aggregation of ammocetes would be divided by the arbitrary location of a quadrat boundary and made the analyses sensitive to interactions of individual larvae separated by greater distances. The relationships between density and gut fullness, diet composition, and diet assimilation were tested using linear regression followed by ANOVA of regression statistics. Statistical analyses were conducted using SigmaPlot 13 (Systat Software Inc.) and comparisons were considered significantly different at $\alpha = 0.05$.

Results

Two-way ANOVA of *in situ* cage experiments revealed significant effects of density on levels of amino acid in the diet ($p=0.021$) and on assimilation efficiency for both AFDM and amino acid (both $p<0.001$; Table 1). The effect on amino acid levels in the diet did not present a pattern with respect to density with the lowest level at the intermediate density (Table 2) In contrast, assimilation efficiency for both AFDM and amino acid declined with increasing density (Fig. 1.). The decrease in assimilation of AFDM at a density of 15 compared to

Table 1 Two Way ANOVA p values for the effects of River and Density treatments and their interaction on five measures of food utilization by lamprey larvae held in cages in the Pike, Pilgrim, and Sturgeon Rivers, Michigan, USA

	River	Density	Interaction
Gut Fullness	0.002	0.278	0.145
Ash Free Dry Mass (AFDM) in Diet	0.117	0.066	0.694
Amino Acid in Diet	<0.001	0.021	0.148
Assimilation of AFDM	0.247	<0.001	0.015
Assimilation of Amino Acid	0.045	<0.001	0.015

a density of 5 was 48% for Pike, 41% for Pilgrim, and 49% for Sturgeon River. The decrease in assimilation of amino acid was 41% for Pike, 38% for Pilgrim, and 54% for Sturgeon River. Gut fullness and AFDM in the diet were not significantly affected by density. The factor River significantly affected gut fullness ($p=0.002$), levels of amino acid in the diet ($p<0.001$), and assimilation of amino acid ($p=0.045$). For each of these variables, values were higher in the Pilgrim River than in the Pike or Sturgeon Rivers. Significant interaction terms for assimilation of AFDM and amino acid reflect the different ranges for these variables in the three rivers.

Field surveys revealed a patchy distribution with no larvae collected from more than half of the 50 1m² cells per river: 26 empty cells in the Otter River and 29 empty cells in the Sturgeon River. Densities ranged from 0 to 10 larvae/m² in the Otter River (81 larvae collected) and from 0 to 6 larvae/m² in the Sturgeon River (32 larvae collected). The mean density of northern brook lamprey larvae in the field study reaches was 4.0 larvae/m² in the Otter River and 1.6 larvae/m² in the Sturgeon River. Average lengths and weights of the animals collected in the two rivers were similar: 95.0 mm (SD = 22.5, range 61 mm – 131 mm) and 1.54 g (SD = 0.95, range 0.50 g – 3.86 g) for Sturgeon River, and 99.2 mm (SD = 17.9, range 59 mm – 138 mm) and 1.67 g (SD = 0.77, range 0.77 g – 1.67 g) for Otter River.

Linear regression analyses of field survey data found that density was significantly inversely related to gut fullness in the Otter River and to diet AFDM, assimilation of AFDM, and assimilation of amino acids in both rivers (Table 3). Although significant, the relationship explained little of the variation in gut fullness (adj. $R^2 = 0.066$) and a greater but still relatively small portion of the variation in diet AFDM (adj. $R^2 = 0.210$ for Otter; adj. $R^2 = 0.228$ for Sturgeon). The relationship between density and diet assimilation explained much larger portions of the variation for both rivers (Fig. 2).

Discussion

The field survey from the Otter River provided the greatest resolution because it yielded the largest number of ammocetes (N=81) and covered the greatest range of densities (1 – 10 larvae/m²) although the survey of the Sturgeon River and cage experiments in the Pike, Pilgrim, and Sturgeon rivers produced similar results.

Table 2 Two Way ANOVA least square means for five measures of food utilization for lamprey larvae held in three rivers at three densities per cage. *Post hoc* comparisons were made using the Holm-Sidak Method for individual cell means when both factors and their interaction are significant (upper panel) and for means across a factor when only one factor was significant (lower panel). Values sharing a superscript are not significantly different

River	Density (larvae per cage)	Gut Fullness (mg dry mass $\cdot$ g^{-1} preserved mass)	AFDM in Diet (g $\cdot$ g^{-1} dry mass)	Amino Acid in Diet (mg $\cdot$ g^{-1} dry mass)	Assimilation Efficiency for AFDM	Assimilation Efficiency for Amino Acid
Pike	5	35.5	0.603	89.1	0.631	0.734
	10	52.5	0.553	62.9	0.443	0.534[a]
	15	42.2	0.544	81.0	0.331	0.435[a]
Pilgrim	5	72.6	0.621	203.5	0.617	0.708[b]
	10	73.5	0.561	159.5	0.510	0.657[b]
	15	66.0	0.453	157.1	0.373	0.481
Sturgeon	5	39.4	0.520	140.3	0.693	0.795
	10	44.7	0.485	123.6	0.367[a]	0.462[c]
	15	64.0	0.452	153.5	0.352[a]	0.363[c]
Pike	Average Across Densities	43.4[a]	0.567	77.6	0.468	0.568
Pilgrim		70.7	0.545	173.4	0.500	0.615
Sturgeon		49.4[a]	0.485	139.2	0.471	0.540
Average Across Rivers	5	49.2	0.581	144.3[b]	0.647	0.745
	10	56.9	0.533	115.4[a,b]	0.440	0.551
	15	57.4	0.483	130.6[a]	0.352	0.426

Comparison of densities in the field and in cage experiments

Ammocete densities used in cage experiments described here are comparable to densities in the wild at which crowding effects would be expected to be evident, if those effects occurred (Dawson et al. 2015). In order to compare densities reported in numerous publications, the spatial scale over which measurements were made must be considered. Ammocetes are not distributed at random but have a patchy distribution even within their preferred habitat (Yap and Bowen 2003; Sutton 2017). We have found that dense aggregations of 15 or more ammocetes in the rivers studied here typically occupy an area ≤ 0.0625 m^2 (0.25 m x 0.25 m). Thus, as sample areas are reduced from tens of m^2 to the 0.0625 m^2 area of our experimental cages, the highest density measured increases because a single sample is more likely to include just the area occupied by an aggregation.

Several authors have reported density as the number of individuals captured divided by the area surveyed for areas many m^2 in extent and these values are relatively low. Using this approach, Morman (1987) reported values of 1 - 13 larvae/m^2 for sea lamprey and Yap and Bowen (2003) reported 2.0 - 11.4 larvae/m^2 for northern brook lamprey. Sutton (2017) found $<1 - 24$ larvae/m^2 for *Lethenteron* spp. and Malmqvist (1980) found < 1 to 16 larvae/m^2 for European brook lamprey. An alternative method for quantifying density has employed sample quadrats of 0.25 to 1 m^2. Using quadrats of 0.25 m^2, Potter et al. (1986) reported values of 0 to 128 larvae/m^2 for pouched lamprey and Yap and Bowen (2003) reported values of 0 to 104 larvae/m^2 for northern brook lamprey. In the present study using 0.25 m^2 quadrats, we found values of 0 to 56 larvae/m^2. Using quadrats of 0.75 m^2, Rodríguez-Muñoz (2000) reported values of 0 to 132 larvae/m^2 for sea lamprey. Thus, higher maximum densities are found with smaller sampling areas.

Another factor affecting density estimates for wild populations is electroshocker sampling efficiency. When five or more larvae emerge from the sediment at one time, some may swim away before they can be captured. Other larvae may avoid capture by moving laterally through the sediment and yet others may be stunned while in the sediment with the result that they do not emerge and are not captured. Estimates of capture efficiency using backpack electroshockers range from
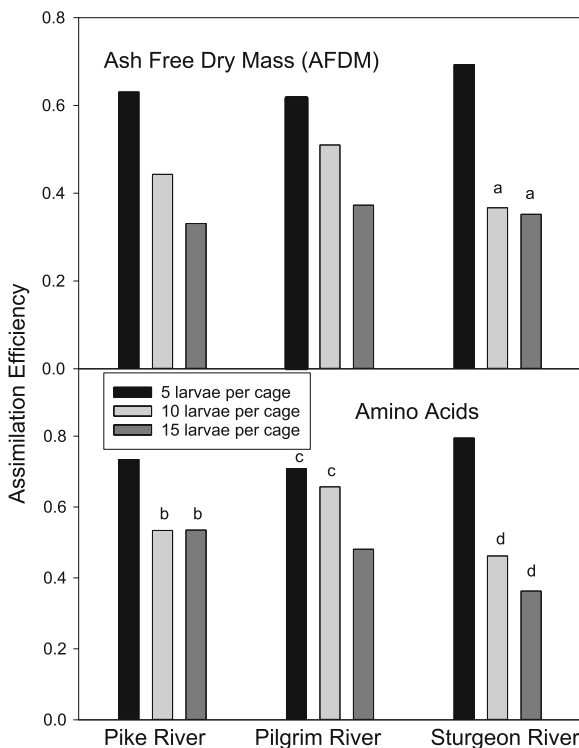
Fig. 1 Effect of larval density in 35 cm x 25 cm *in situ* cages on assimilation of total organic matter and amino acids. Bars sharing letters are not significantly different

20% (Morkert [1987]) to approximately 50% (Steeves et al. [2003]) with lower efficiencies at higher densities. In our *in situ* cage experiments, the densities of 5, 10, and 15 individuals/0.09 m^2 correspond to 57, 114, and 171 animals/m^2 and thus simulate field conditions in high density patches where crowding is most likely to affect food use. Other investigators have come to comparable conclusions and used similar densities in *in situ* cage and aquarium experiments (Malmqvist [1983];

Morman [1987]; Murdoch et al. [1991]; Murdoch et al. [1992]; Rodríguez-Muñoz et al. [2003]).

The effect of ammocete density on food utilization

Both field and *in situ* cage experiments indicated that ammocoete density affected particle selection, ingestion, and assimilation. Regression equations for dependent variables significantly correlated with density in Otter River predict that, over the range of 1 to 10 ammocetes/m^2, the concentration of AFDM in the diet will decline by 32% ($p < 0.001$), gut fullness will decline 36% ($p = 0.012$), and assimilation of AFDM and amino acids in AFDM will decline by 71% and 58%, respectively (both $p < 0.001$, Table [3]),. Regression analyses for Sturgeon River give nearly identical slopes (Fig. [2]) and the significant results of the *in situ* cage experiments generally confirm the relationships seen in the field surveys. Thus, the word "crowding" which implies a negative effect of aggregation is apt in this context.

Feeding by lamprey larvae may be particularly sensitive to disturbance. They feed continuously during the diel cycle (Sutton and Bowen [2009]) and food moves through the gut very slowly with one study finding transit times ranging from 54 - 70 h depending on temperature (Moore and Beamish [1973]). The digestive tract in lamprey larvae is a relatively undifferentiated tube made up of three parts: the esophagus, the anterior intestine, and the posterior intestine. Digestive enzymes are secreted and mixed with food in the anterior intestine whereas assimilation is the primary function of the posterior intestine (Hansen and Youson [1978]; Cake et al. [1992]). The total gut length is 0.45 times the body length. Other fishes that depend on adnate or sestonic biofilm and related sedimentary organic matter for their

Table 3 Results of significant liner regression analyses for the relationship between density (larvae • m^2) and measures food utilization by northern brook lamprey (*Ichthyomyzon fossor*) larvae in two rivers in Baraga Co., Michigan, USA

Variable	River	Intercept	Slope	p value	Adjusted R^2
Gut Fullness (mg dry mass • g^{-1} preserved mass)	Otter	0.150	0.0060	0.012	0.066
Diet AFDM (g • g^{-1} dry mass)	Otter	0.673	0.0231	<0.001	0.210
	Sturgeon	0.597	0.0406	0.004	0.228
Assimilation Efficiency for AFDM	Otter	0.850	0.0692	<0.001	0.527
	Sturgeon	0.638	0.0450	<0.001	0.387
Assimilation Efficiency for Amino Acid	Otter	0.808	0.0581	<0.001	0.443
	Sturgeon	0.672	0.0544	<0.001	0.435

Fig. 2 Effect of density on assimilation of diet organic matter (AFDM) and diet amino acids in larvae collected from Sturgeon and Otter rivers. Regression lines show estimated means and their 95% confidence intervals
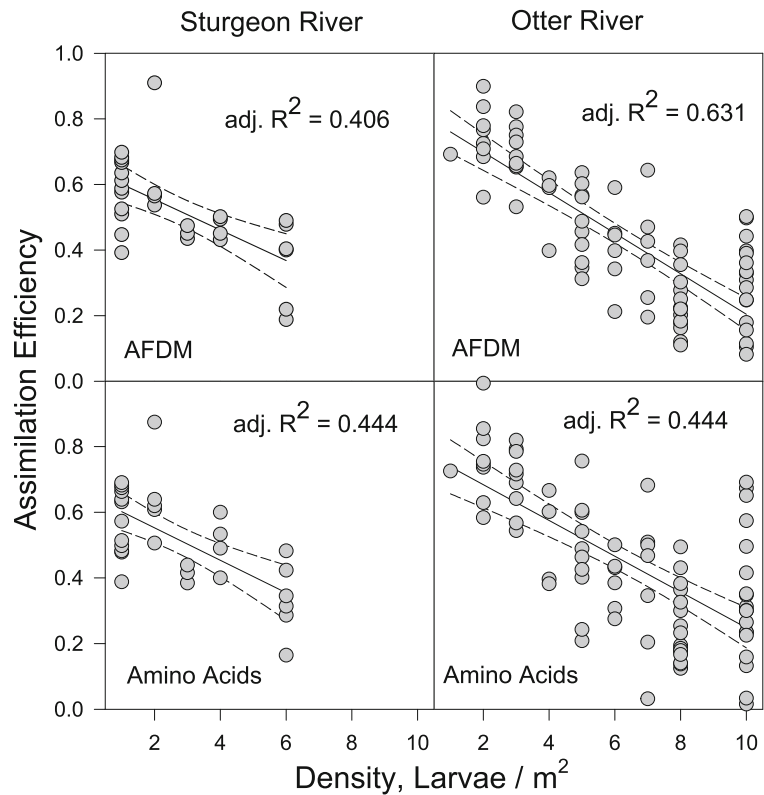
nutrition have exceptionally long intestines ranging from 3.2 to 24 times body length (Bowen et al. 2006), and demonstrate diel feeding periodicity in which the gut is largely evacuated during each diel cycle (S. Bowen, pers. obs.). It has been inferred that, absent a highly adapted gut morphology, lamprey larvae's slow rate of gut passage is required for their efficient digestion (Mundahl et al. 2005; Sutton and Bowen 2009). Rodríguez-Muñoz et al. (2003) explored the possibility that chemical substances released by conspecifics reduced the growth of sea lamprey larvae and concluded that although some influence was detected it could not account for the effect of density on growth in wild populations. Another mechanism of interaction could be disturbance caused by the movement of nearby ammocetes. If disturbance causes an ammocete to leave its burrow and move to a new site, the time spent feeding is likely to be reduced by the time required to establish a new burrow with a respiratory tube to the sediment surface. Although disturbance can inhibit secretion of gastric acid in some fish (Moriarty 1973) and others regurgitate or defecate when stressed, how disturbance affects diet selection and assimilation in lamprey larvae is not known.

Physical disturbance as a trigger to within-habitat movement

Density effects on food utilization reported here can be expected to have a significant impact on fitness and thus raise the questions of how ammocetes come to be aggregated and of the long term consequences of aggregation. Ammocetes move frequently, especially within habitat patches (Evans 2017) and they move more frequently at higher densities (Dawson et al. 2015). Their movement may result in aggregations because they move repeatedly until they find a location with desirable physical attributes and/or high quality food (Yap and Bowen 2003), or they may be attracted by conspecific pheromones or other olfactory cues (Buchinger et al. 2015; Sorensen 2015). It is not unlikely that both behaviors play roles. Whatever the behavior, the data suggest individual larvae do not spend much time in dense aggregations. Gut fullness, diet selection, and digestion are strongly affected by crowding on a scale of hours, but condition factor, a ratio of weight to length which integrates food utilization over a period of days or weeks, is not. Experience with ammocetes in aquaria indicates that one trigger for movement is disturbance of

the sediment nearby (Yap, pers. obs.). When a blunt probe is moved slowly through the sediment with within 1 cm of an ammocete, its typical response is to move rapidly through the sediment until it encounters the aquarium wall, and then to swim up into the water in what appears to be a frantic effort to escape. Disturbance of the sediment farther away may be sensed by the animal without triggering its flight. We would reasonably expect that the greater the density, the greater the probability that movement by some larvae will disturb others and cause them to move away. Thus, flight from disturbance would be a countervailing behavior that would limit time spent in dense aggregations with other larvae.

Our proposed mechanism of physical disturbance is consistent with Murdoch et al.'s (1991) findings in experiments with a pair of lamprey species that interspecific and intraspecific densities are not different in their effects on ammocete growth, survivorship, or time to maturation. Thus, we might expect the mechanism proposed here to be active both within and among in other lamprey species.

Net benefit from aggregation

Despite reduction in nutrient assimilation at higher densities, individual northern brook lamprey larvae appear to achieve a net benefit from aggregation in high-quality habitat. Within areas of organic sediment, condition factors are dramatically higher for larvae from zones where flocculent organic matter accumulates (Yap and Bowen 2003). On average and without consideration of density, diets of larvae from these depositional areas were also higher in nutrients and in digestibility. Condition factor reflects the cumulative effects of density and food use over a period of many days or weeks. Over that time period, larvae may move from areas of high to low density within a zone in which flocculent organic matter accumulates. Although most of the dense aggregations we found occurred in depositional areas, there were also many depositional areas that contained low densities of larvae. Higher density is associated with reduction in growth, maturation, and survivorship of larvae at the population level, but condition factors indicate individual larvae benefit from selectively inhabiting depositional areas where diet quality is superior. Negative effects of higher density on individuals appear to be mitigated by their movement away from other larvae but within the depositional area.

Significance for ecological theory

One of the principal projects of ecology is to develop predictive models of energy and material transfers through food webs. Early models described transfers through individual consumers (functional response) as a simple function of food availability (Holling 1966), but models have been made increasingly realistic and general by modeling additional factors including the effects of consumer density on interference competition that reduces functional response (Skalski and Gilliam 2001; Kratina et al. 2009). It has been assumed that the mechanism by which interference reduces functional response is that it distracts consumers from feeding thereby reducing feeding rate (Kratina et al. 2009). The findings reported here extend the range of mechanisms that must be considered to accurately model functional response in the context of interference competition to include the reduced effectiveness of food utilization.

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