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Food-particle size and selection by bivalve larvae in a temperate embayment[1]

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Abstract Epifluorescence microscopy was used to analyze the stomach contents of bivalve larvae collected in the Baie des Chaleurs (western Gulf of St. Lawrence, Canada) in order to document food-particle sizes, compare feeding among taxa, and compare the diet with the in situ phytoplankton community. Stomach contents were mainly composed of small autotrophic flagellates (<5 μm) and cyanobacteria (<2 μm), reflecting the microbial food web which characterizes these waters. More than half (55%) of all veligers examined contained algal cells of 5 to 15 μm, whereas only 3% had cells of 15 to 25 μm. Differences in the size ranges of ingested algal cells among similar-sized larvae of different species suggests that veligers actively selected food particles. Among the smallest veligers (185 to 260 μm), scallops (*Placopecten magellicanus*) and mussels (*Mytilus edulis*) ingested more <5 μm and 5 to 15 μm algae than clams (*Mya arenaria*). Among larger veligers (261 to 405 μm), clams contained significantly more <5 μm cells than mussels, whereas mussels contained significantly more 5 to 15 μm algae than clams. Algal cells of 15 to 25 μm were preferentially ingested by mussel veligers. Feeding also differed between different-sized veligers within taxa, i.e. the smallest clam veligers ingested fewer of 5 to 15 μm algae than the larger size classes. Mussel veligers ingested significantly more 15 to 25 μm and fewer <5 μm cells as their size increased. The dominance of ultraplankton in the nearshore waters of Baie des Chaleurs and in the stomach contents suggests that veliger larvae may be an important export path for carbon produced by small phytoplankton.

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Introduction

Ultraplankton (<5 μm) play an important role in a wide range of aquatic environments (e.g. reviews by Joint 1986; Stockner and Antia 1986). The ubiquity of ultraplankton has been attributed to the fact that small algae are better competitors for light and nutrients than larger-sized cells (e.g. Raven 1986). Whereas large phytoplankton (>5 μm) dominate the traditional marine food web (diatoms–copepods–large metazoans), ultraplankton is associated with the microbial food web, which is known to dissipate considerble energy through respiration (Goldman 1988), thus exporting little energy to large metazoans (Cushing 1989). However, the concept of a closed microbial food web is increasingly questioned as a number of studies have suggested alternative export pathways leading to large metazoans (e.g. Riegman et al. 1993; Gallager et al. 1994; Legendre and Rassoulzadegan 1995).

To date, no other food than unicellular algae has been found to be satisfactory for cultured bivalves. Most of the algal diets used in the laboratory consist of small autotrophic cells like *Isochrysis galbana* and *Monochrisis lutheri* (Bayne 1965; Babinchak and Ukeles 1979; Pechenik et al. 1990). As autotrophic prokaryotes such as cyanobacteria are an important component of small phytoplankton (Murphy and Haugen 1985), they may be used as a food source by bivalve larvae in their natural habitat. Despite their small sizes (diameter between 0.5 and 1.5 μm for *Synechococcus* spp. in the Baie des Chaleurs, Gulf of St. Lawrence, E. Tamigneaux, Université Laval, personal communication), cyanobacteria may be ingested by bivalve larvae in the laboratory and the field (Gallager 1988; Baldwin and Newell 1991; Gallager et al. 1994; Baldwin 1995).

As algal cells are available in a wide range of taxa and sizes in nature, bivalve larvae may demonstrate a certain degree of particle selection. Active selection of phytoplankton would imply the existence of a mechanism by which particles are sorted during feeding according to their chemotactile attractiveness, size or shape. After visually observing particle manipulation of feeding veligers, Gallager (1988) proposed a sequence of events in the feeding behavior of bivalve larvae which allows food selection at three different levels: (1) rejection by the preoral cirri while transporting particles toward the mouth; (2) rejection from the esophagus by muscular contraction; (3) postingestive selection, where particles pass through the gut without digestion. The analysis of gut contents allows identification of food selection at the first two levels, but not at the third.

Size-related retention of food particles by veligers is partly related to their mouth and esophagus diameters, which gets larger as they grow. As the retention of different size food particles by veligers recorded in feeding experiments is often conducted with veligers of a particular size, the results can not be generalized for all stages of development before settlement. According to the results of Riisgard et al. (1980), mussel larvae (*Mytilus edulis*) of 5 and 13 d old (lengths: 150 and 170 μm) could not consume particles with diameters smaller than 1 μm or larger than 9 μm. The highest clearance rates were obtained with 2.5 to 3.5 μm particles. Sprung (1984) had the same results with slightly larger mussel larvae (length: 260 μm). In an additional experiment, he demonstrated that those larvae had permanently empty stomachs when fed with the larger algae *Scripsiella faeroense* (diameter: 20 to 25 μm). As mussel larvae may reach sizes of up to 400 μm before settlement, it is likely that larger algal cells become part of their diet before the end of their pelagic life. Results of incubation experiments with *Philine aperta* (Hansen 1991) suggested that the upper limit for ingestible particle size increased from 7 μm for newly hatched veligers to 18 μm for late stage veligers. To our knowledge, the widest size spectrum of particles used by bivalve veligers was reported by Baldwin and Newell (1991) for large umbo-stage oysters, which ingested particles ranging from 0.2 to 30 μm.

Another aspect of bivalve veliger feeding which has not yet been studied in the field is the possible reduction of feeding prior to settlement and metamorphosis. Young veligers feed entirely by means of ciliary currents on their velum. The velum of some species like *Mytilus edulis* (Bayne 1965) and *Crassostrea virginica* (Baker and Mann 1994) degenerate during the later stages of planktonic life. Bayne (1965) also observed a decline in the feeding rate of *M. edulis* veligers at their later stage of development. According to these observations, older, larger veligers may feed less than younger ones in a natural community.

In the present study, we documented the stomach contents of a community of veligers at the later stage of their pelagic life using epifluorescence microscopy. This technique allows detection of the presence of autotrophic plankton in the digestive tracts of the veligers by means of the natural fluorescence of chlorophyll and other photosynthetic accessory pigments (Babinchak and Ukeles 1979; Gallager et al. 1994). In parallel, the characteristics of the phytoplankton community at the sampling site (species composition and concentration) were monitored. We compared the types of fluorescence and the sizes of the algal cells which were present in the stomachs of larvae with the characteristics of those available in situ. The objectives of this study were to quantify the size spectrum of particles ingested by bivalve larvae, to evaluate the importance of small phytoplankton in their diet, and to determine if stomach content differed between similar-sized veligers of different taxa and between different-sized veligers within taxa.

Material and methods

Sampling of bivalve larvae

Sampling was conducted at Grande-Rivière in the Baie des Chaleurs (48°23.62′N; 64°27.80′W; western Gulf of St. Lawrence, Canada) in September 1991. The 20 m deep water column at the sampling station (3 km offshore) was vertically mixed from surface to bottom. Larvae were collected at 2, 4, 8 and 14 m using a high volume pump (Flygt, Model C/D-3085), every 135 min for a period of 52 h (92 samples). Bivalve larvae were then deep-frozen in liquid nitrogen. Detailed procedures of sampling and identification of veligers are given in Raby et al. (1994).

Phytoplankton

Samples for phytoplankton identification and enumeration were collected using a flexible hose. The hose was lowered to 20 m, closed by a one-way valve at its lower end, brought on board, and emptied into a single dark container. This method provided samples that were integrated over the 20-m water column. Subsamples (200 ml) were preserved with acidic Lugol's solution, for enumeration under the inverted microscope (Utermöhl 1931; Lund et al. 1958). Magnification of 400 × allowed the identification of phytoplankton ranging between ca. 1 and 200 μm. Cyanobacteria could not be detected using this technique. The mean size (length for elongated cells or diameter for spherical cells; $n = 30$) of each algal species was measured using an image analyzer. Since no cells >25 μm were observed in the digestive tracts of veligers, only cells <25 μm were considered as potential food for the larvae. In the present study, four size classes were considered: <5, 5 to 14.9, 15 to 24.9 and >25 μm.

Microscopic observation of bivalve larvae

After thawing a sample, several hundred larvae were spread on a glass slide with a drop of glycerol to avoid dessication. Only veligers that were lying on their left valves were observed, to avoid bias due to partial hiding of the stomach by the digestive gland. Randomly selected veligers (50 per sample) were identified, measured and observed under epifluorescence for stomach contents. The microscope (Zeiss, Model Axioskop-20) was equipped with two filter sets providing blue-light (No. 05) and green-light (No. 15) excitation in order to detect pigments such as chlorophyll *a* (red under green- and blue-light excitation) and phycoerythrin (yellow-orange under green-light excitation and yellow under blue-light excitation). All samples were analyzed within 12 mo of freezing, and no loss of autofluorescence with time was noted.

We were unable to count the small algal cells (<5 μm) present in the stomachs because of their high abundances. For example, veligers of *Ostrea edulis* measuring 203 μm ingest between 12 000 and 20 000 cells of *Isochrisis galbana* during 24 h (Walne 1965). Thus, veligers may have several hundreds of food cells in the stomach at the same time. In order to compare the quantity of algae <5 μm ingested by different sizes and taxa of veligers, we measured the fluorescent surface area in stomachs (μm^2) that contained no large algal cells (5 to 25 μm). The veligers without large algal cells in their digestive tracts represented between 31 and 45% of the total number of larvae observed. Because larger algal cells (5 to 25 μm) were easy to enumerate when present in the stomach (by slowly focusing from the upper to the lower surfaces of the stomach), their numbers were noted according to their diameter (5 to 15 μm and 15 to 25 μm).

The stomachs were easily delimited for most of the veligers, except for older *Mya arenaria* (>350 μm) which had thicker shells. This problem was avoided using green-light excitation which enabled to clearly discern the stomach contours because of the presence of cyanobacteria showing a bright yellow-orange fluorescence. Cyanobacteria were present in the digestive tracts of most of the veligers.

Data analysis

In order to compare the feeding of different-sized veligers, three size classes were defined: A = 185 to 260 μm, B = 261 to 330 μm and C = 331 to 405 μm. The relative importance of the three size classes of food particles (<5, 5 to 15, 15 to 25 μm) among the same size class of different species and among size classes within the same species of bivalve larvae were compared using the Welch–ANOVA nonparametric test. Differences were considered significant when $P < 0.05$.

Results

Bivalve larvae community

The veliger community was dominated by *Mya arenaria* (clams) and *Mytilus edulis* (mussels) (Table 1). Sizes of veligers differed among species (Fig. 1). Mussel veligers were the largest bivalve larvae in the samples (Size Classes B and C), most of them having already developed a foot. Even though scallop larvae (Pectinidae) were the smallest veligers in the community (99% in Size Class A), they had attained the maximum size they reach, in the region, before settlement (240 to 250 μm, Harvey et al. 1993). The present study thus corresponds to the last stage of development of bivalve veligers, just prior to settlement and metamorphosis.

Table 1 Taxonomic composition of bivalve veligers sampled at Grande-Rivière, Baie des Chaleurs

	Clams	Mussels	Scallops	Others
Counts	2904	562	222	502
% of the community	69	13	5	12

Phytoplankton community

During the entire sampling period, the phytoplankton assemblage was numerically dominated by flagellates <5 μm, such as Prasinophyceae, which represented ca. 80% of counts (Table 2). The 5 to 14.9 μm fraction (ca. 16% of the counts) included flagellates such as Crypto-, Chryso- and Euglenophyceae, dinoflagellates (e.g. *Gymnodium* sp.), and pennate diatoms (e.g. *Nitzschia closterium*). The 15 to 25 μm fraction (ca. 2.5%) contained dinoflagellates (e.g. *Dinophysis* sp. and *Gyrodinium* sp.), centric and pennate diatoms (e.g. *Nitzschia* sp. and *Skeletonema* sp.), silicoflagellates (e.g. *Distephanus* sp. and *Ebria* sp.), and coccolithophorids. The fraction >25 μm (ca. 1.5%) was represented by dinoflagellates (*Torodinium* sp. and *Goniaulax* sp.), diatoms in chains (e.g. *Chaetoceros* sp. and *Thalassiosira* sp.), and pennate diatoms (e.g. *Nitzschia longissima*). Finally, small variations were observed during the 52-h sampling period in both proportions and absolute values of counts in the four phytoplankton size fractions (Fig. 2a, b), suggesting that the phytoplankton assemblage at the anchor station was relatively similar over the sampling period.

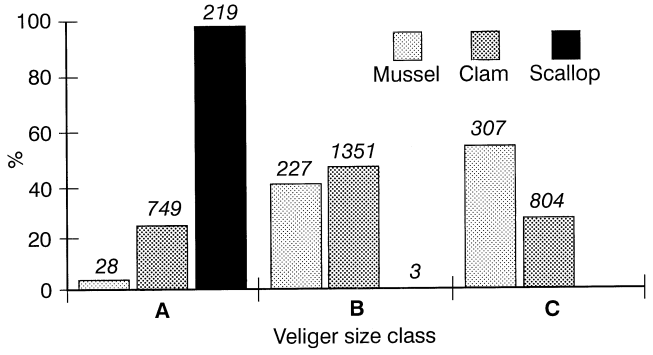

Fig. 1 Proportions of the three size classes of the three main taxa of bivalve larvae sampled in the western Gulf of St. Lawrence in 1991: A (185 to 260 μm), B (261 to 330 μm) and C (331 to 405 μm). Number of veligers observed given *above bars*

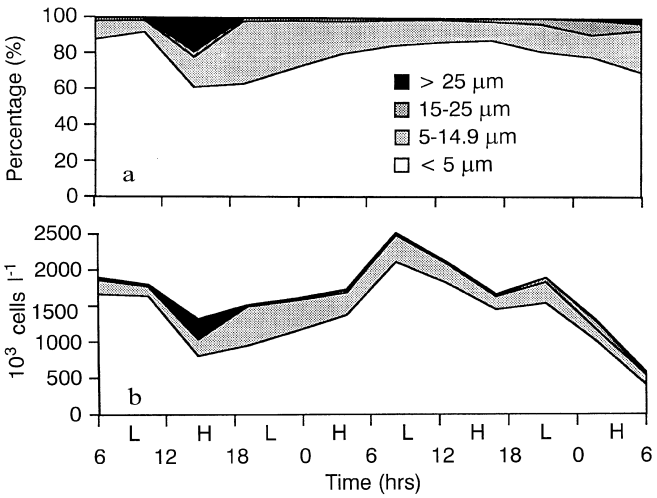

Fig. 2 Changes during the 52-h sampling period of **a** proportions (%) and **b** absolute values of cell counts in four phytoplankton size fractions (*H* high tide; *L* low tide)

Table 2 Taxonomic composition of the four phytoplankton size classes sampled in Baie-des-Chaleurs. Lengths (μm) and absolute (10^3 cells l^{-1}) and relative (%) cell counts averaged for each taxonomic group over the 52-h sampling period

Size interval	Taxonomic group	Length (μm)	10^3 cells l^{-1}	%
< 5 μm	Prasinophyceae (flagellates)	2.0	41.0	2.47
	Unidentified flagellates	3.5	1282.8	77.14
5–14.9 μm	Cryptophyceae (flagellates)	10.7	135.9	8.17
	Diatoms (pennate)	13.1	0.7	0.04
	Dinoflagellates	13.2	7.0	0.42
	Unidentified flagellates	14.5	125.3	7.54
15–25 μm	Coccolithophorids	15.0	0.3	0.02
	Diatoms (centric)	16.3	3.0	0.18
	Diatoms (pennate)	20.5	0.9	0.05
	Dinoflagellates	20.8	22.6	1.36
	Silicoflagellates	22.4	12.0	0.72
> 25 μm	Chains of diatoms (centric)	19.0	5.7	0.34
	Diatoms (pennate)	34.5	4.4	0.26
	Dinoflagellates	41.3	21.4	1.29
Total			1663.0	100

Stomach content observations

Most larvae (99%) contained a mixture of small autotrophic cells in their digestive tracts (Fig. 3) that included algae with diameters ranging from 3 to 5 μm. These cells fluoresced red under both blue- and green-light excitation indicating the presence of chlorophyll *a*. Smaller cells (<2 μm), which were also present in the digestive tracts of most larvae, were identified as cyanobacteria because of their bright yellow fluorescence under blue-light excitation, and bright yellow-orange fluorescence under green-light excitation, which is typical of phycoerythrine. High concentrations of cyanobacteria were often noted in the stomachs of scallop larvae, but systematic estimation of the numbers of cyanobacteria in stomachs was not possible.

Phytoplankton of 5 to 15 μm were present in the stomachs of 54.6% of the veligers. Larger algae (15 to 25 μm) were found in only 3.4% of the veligers (Fig. 4). Mean numbers of 5 to 15 and 15 to 25 μm algae present in the stomachs were situated between 0 and 2, but some larvae had ingested up to a dozen cells (Fig. 4).

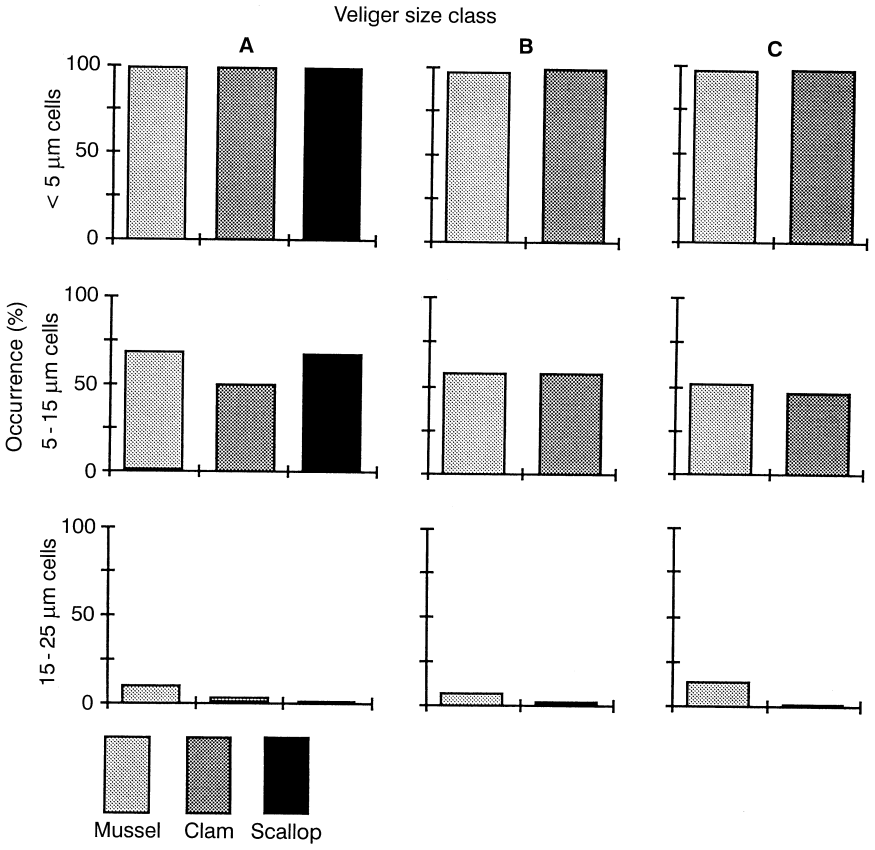

Fig. 3 Occurrence of each size class of prey in the diet of three size classes of mussel, clam and scallop

Table 3 Comparisons of stomach content between similar-sized veligers (Size Classes A, B and C) of different taxa, using Welch–ANOVA nonparametric test

Size of food cells	2 × 2 comparisons	*P*-value
Size Class A (185–260 μm)		
< 5 μm	mussels > clams	0.0467*
	mussels = scallops	0.0609
	scallops > clams	0.0000*
5–15 μm	mussels > clams	0.0340*
	mussels = scallops	0.5791
	scallops > clams	0.0000*
15–25 μ	mussels = clams	0.2510
	mussels = scallops	0.1415
	clams = scallops	0.0504
Size Class B (261–330 μm)		
< 5 μm	clams > mussels	0.0000*
5–15 μm	mussels > clams	0.0004*
15–25 μm	mussels > clams	0.0013*
Size Class C (331–405 μm)		
< 5 μm	clams > mussels	0.0000*
5–15 μm	mussels > clams	0.0007*
15–25 μm	mussels > clams	0.0000*

*Significant difference ($P < 0.05$)

Comparisons of the stomach contents of clams, mussels and scallops were made independently for each size class. Species-specific differences in the size range of ingested algal cells were observed (Table 3; Figs. 4, 5). Among the smallest veligers (Class A), the relative importance of the <5 and 5 to 15 μm algae in stomachs was significantly higher for scallops and mussels than for clams. Among larger veligers (Classes B and C), clams contained significantly more <5 μm cells than mussels, whereas mussels contained significantly more 5 to 15 μm algal cells than clams, despite similar occurrences of these cells. Larger algal cells (15 to 25 μm) were preferentially ingested (occurrence and relative importance) by mussel veliger of Size Classes B and C.

Feeding of veligers also differed among the three size classes within the same taxa. The smallest clam veligers ingested fewer 5 to 15 μm algal cells than the larger size classes (P <0.01 for comparisons between Size Classes A/B and A/C; Fig. 3). Mussel veligers ingested more 15 to 25 μm cells (P <0.01) and fewer <5 μm cells (P <0.01) as their sizes increased (Fig. 4).

Considering the total surface area occupied by autotrophic cells as an index of stomach fullness, clams of Size Classes B and C were significantly fuller than Class A clams (P <0.01, Fig. 5). Although stomach fullness of mussel larvae tended to decline as veligers increased in size, the differences were not significant (P >0.05, Fig. 5). Finally, 99% of the scallop veligers were <260 μm (Class A) so that similar comparisons were not possible.

Discussion

Small-sized phytoplankton (<5 μm) were a major component of the diet of bivalve veligers for all species and

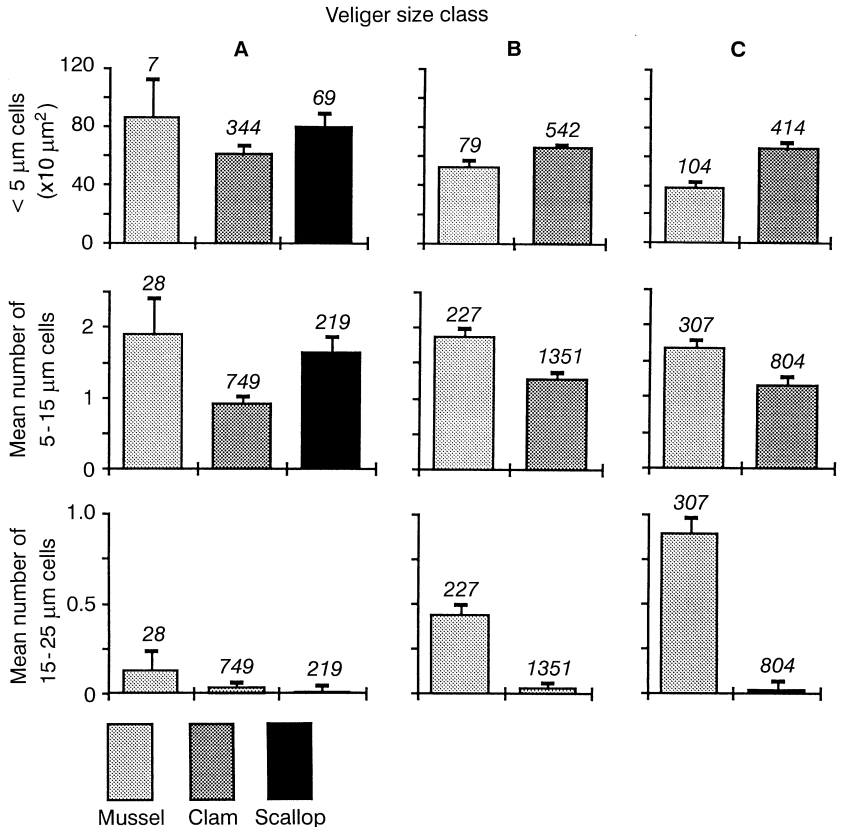

Fig. 4 Relative importance of each size class of food particles in the stomachs of three size classes of mussel, clam and scallop larvae. Relative importance was evaluated as the mean number of food particles present in the stomachs. For < 5 μm cells values are given as surface area occupied in the stomach. Number of veligers observed given *above bars*. *Error bars* = 95% confindence intervals

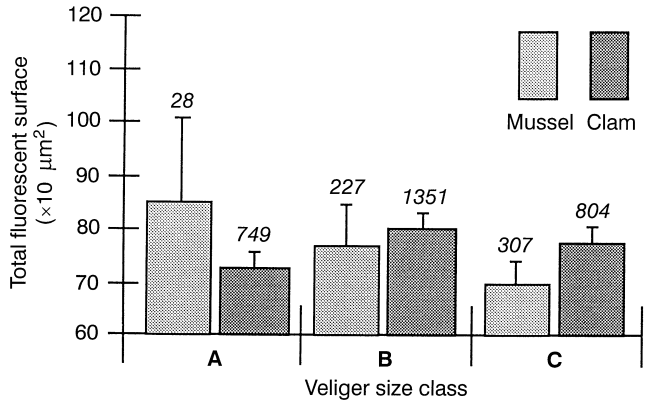

Fig. 5 Total stomach content of mussels and clams according to their size class. Fluorescent surface was measured under blue-light excitation (filter No. 05). Number of veligers observed given *above bars*. *Error bars* = 95% confidence intervals

size classes present in our samples. As 97.5% of the small phytoplankton sampled at the anchor station were flagellates, these algae constitued a major part of the veliger's diet. In addition to small flagellates, bivalve larvae also ingested cyanobacteria despite their small size (1 to 2 μm), which seemed to be part of their normal diet. These observations are consistent with those of Gallager et al. (1994) and Baldwin (1995) and indicate that larvae may use small algae to a greater extent than previous laboratory studies suggested (Riisgard et al. 1980; Bayne 1983; Sprung 1984). Riisgard et al. (1980) concluded that the clearance of particles between 1 and 2 μm represented only 20% of the maximal clearance rate, and particles <1 μm were probably not ingested. In contrast, it has been shown that bivalve larvae can feed on bacteria, and even show enhanced growth when fed with a mixture of bacteria and algae (Martin and Mengus 1977; Douillet 1993). Considering the low retention efficiency reported for small particles, the presence of cyanobacteria in the stomachs of most of the larvae observed in the present study may be explained by the availability of these cells in the natural environment. Indeed, high numbers and high biomass of small-sized phytoplankton have been reported in the nearshore waters of the Baie des Chaleurs, where the pelagic ecosystem is dominated by microbial components during summer and autumn (Mingelbier 1995; Tamigneaux et al. 1995, 1997). The dominance of small phytoplankton in stomach contents reflects the size structure of phytoplankton and organic seston in the Bay (Claereboudt et al. 1995). High concentrations of cyanobacteria (up to 9.5×10^7 cells l^{-1} during August and September; E. Tamigneaux, Université Laval, personal communication) may be an important food source for bivalve veligers. The nutritive value of cyanobacteria for bivalve larvae is probably important, as Gallager et al. (1994) recorded a retention efficiency of 55% of cell carbon with *Mercenaria mercenaria* L. veligers fed on *Synechococcus* sp. Cyanobacteria are also an important part of the diet of tintinnids (Bernard and Rassoulzadegan 1993).

Even if small cells (<5 μm) were often ingested in such high numbers that individual cells could no longer be discriminated, larger cells were also ingested, especially by the larvae of mussels and scallops. Compared to clams, the larvae of mussels and scallops ingested more 5 to 15 μm algal cells. The largest algae observed in the stomachs did not exceed 25 μm, and were almost exclusively ingested by mussel larvae.

Differences observed in the sizes of ingested cells by different species of bivalve larvae may be due to anatomical reasons such as the diameter of their mouth (passive selectivity) and/or an ability to discriminate between phytoplanktonic forms (active selectivity). To our knowledge, no comparative study has been made on mouth size for bivalve larvae. On the one hand, active selection of microalgae by veligers has been reported by Baldwin (1995) for *C. virginica*, by Gallager (1988) for *Mercenaria mercenaria*, by Loosanoff et al. (1955) for *Venus mercenaria*, by Mackie (1968) for *C.virginica*, and by Paulson and Scheltema (1968) for the gastropod *Nassarius obsoletus*. On the other hand, Ukeles and Sweeney (1969) and Fritz et al. (1984) observed that there was little or no selection of particles by *C. virginica* when food particles were in the same size range as the mouth of larvae. Our observations that similar-sized veligers fed on different sizes of prey suggests that active selection may be occurring in the natural environment, but more detailed observations in situ are required to elucidate the mechanisms of food selection.

Results of the present study showing that the sizes of ingested food particles differed between size classes for clams and mussels are most probably the result of passive selection due to increasing mouth size with body size. Larger clam larvae ingested more 5 to 15 μm cells than the small larvae, and mussel larvae ingested fewer <5 μm cells and more 15 to 25 μm cells as they became larger. From an energetics point of view, ingesting larger cells is probably more advantageous for a veliger than ingesting smaller ones, particularly as the volume of a 20 μm cell is 300 times that of a 3 μm cell. Even though protein and lipid concentration per unit volume decreases with increasing cell size due to the relatively larger vacuoles (Fogg and Thake 1987), it is likely that satiation can be achieved sooner by ingesting larger cells. The time and energy expended to catch and handle one large prey may be lower than that needed to catch hundreds of smaller prey items.

This study was conducted with veligers measuring from 175 to 405 μm. It is possible that the diets of smaller veligers also vary. Lucas and Rangel (1981) reported different ingestion capabilities between mussel larvae of 8 and 15 d old, and Davis (1953) observed that the alga *Chlorella* sp. was not ingested by young oyster larvae, but was utilized during later larval stages. Adjusting the diet of veligers in hatcheries according to their species and stage of development may help to obtain better growth rates and survival (Gruffydd and Beaumont 1972; Lubet 1978).

Another aspect of veliger feeding examined here was whether old veligers (prior to fixation) fed less than younger ones. In our results, there was no such decline for clams, but there was such a tendency for mussels. However, the low numbers of small mussels (28 for Class A) sampled compared to the two other size classes (226 and 302 for Classes B and C, respectively) did not allow us to demonstrate significant differences.

In conclusion, the stomach contents of bivalve veligers sampled in waters characterized by microbial components were dominated by cyanobacteria (<2 μm) and small autotrophic flagellates (<5 μm). Approximately 50% of all veligers examined contained cells measuring between 5 and 15 μm, whereas only 3% contained algal cells between 15 and 25 μm. Differences in the size ranges of ingested algal cells among similar-sized larvae of different species suggest that veligers actively selected food particles. The dominance of <5 μm phytoplankton in Baie des Chaleurs and in stomach contents suggests that veliger larvae may be an important export pathway for carbon produced by ultraplankton.

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