

## Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal

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### Abstract

The Alcyonacean octocoral *Alcyonium siderium* Verrill and the sea anemone *Metridium senile* (L.), the only common perennial zooplanktivores on shallow ( $\leq 16$ -m depth) subtidal rock walls in much of northern New England, USA, are of similar heights and overlap in their habitat and microhabitat distributions. The coelenteron contents of both species were sampled at four-hour intervals over a diel cycle and were compared to zooplankton available in the water at 1 to 5 cm from the rock wall, the height at which the cnidarians held their feeding tentacles. Prey in coelenterons of *A. siderium* were significantly smaller (means of 256 to 345  $\mu\text{m}$ ), and those in coelenterons of *M. senile* were equal to or slightly greater in length (means of 415 to 1006  $\mu\text{m}$ ) than the available zooplankton. The diets of *A. siderium* and *M. senile* differed significantly from each other and from the available zooplankton. *A. siderium* showed strong positive electivities for ascidian larvae and for foraminiferans, and strongly negative electivities for most crustaceans. *M. senile* had strong positive electivities for barnacle cyprids, ascidian larvae, and gammarid amphipods, and strong negative electivities for invertebrate eggs, foraminiferans, calanoid and harpacticoid copepods, and ostracods. Electivities may reflect tentacle avoidance or escape by motile prey as well as predator preference. Substratum-associated organisms (e.g. demersal crustaceans, larvae of benthic invertebrates) were the most common items in the diets of both species, suggesting a tight benthic food web, similar to the situation for coral reef anthozoans which rely on reef-generated zooplankton. *A. siderium* ate large numbers of ascidian larvae which, as benthic adults, compete for space with *A. siderium* and can overgrow small colonies. Predation on the larvae of a competing species may alleviate competition by decreasing the competitor's recruitment.

### Introduction

Despite the ubiquity and availability of both tropical and temperate anthozoans (Cnidaria), there are data on the natural diets of very few species (Porter, 1974; Koehl, 1977b; Sebens, 1977, 1981, 1982a; Purcell, 1977). Porter (1976) discussed the role of zooplanktivory in reef corals, many of which also derive energy and nutrients from photosynthesis by their symbiotic algae. The zooplankton resource on several coral reefs is primarily demersal (originating on the substratum) with a strong diel pattern of upward migration at dusk and downward migration at dawn (Emery, 1968; Glynn, 1973; Sale *et al.*, 1976; Porter and Porter, 1977; Porter *et al.*, 1977, 1978; Alldredge and King, 1977, 1980; Hobson and Chess, 1978, 1979; Rützler *et al.*, 1980; Robichaux *et al.*, 1981; Ohlhorst, 1982). Coral reef zooplanktivores capture much of their prey during these two periods of migration and at night (corals, Porter, 1974; zoanths, Sebens, 1977; some fish, Hobson and Chess, 1978, 1979). The near substratum zooplankton of temperate inshore waters (see Hobson and Chess, 1976; Hopkins and Gulliksen, 1978) and the diet of temperate benthic zooplanktivores (see Purcell, 1977; Sebens, 1981) have not been described on such fine spatial or temporal scales.

Prey selection by zooplanktivores can be studied if both the available plankton and the prey captured by the zooplanktivores during the same time period are quantified. This approach has been used successfully by Hobson and Chess (1976, 1978, 1979) for zooplanktivorous fish in the South Pacific and in Southern California, by Purcell (1977) for the sea anemone *Metridium senile* (L.) on the California coast and by Purcell (1981a, b) for planktonic siphonophores. These studies examined prey and plankton categories but did not quantify prey size. Fish may actively select certain zooplankton items but passive suspension feeders generally wait until contacted by a prey to respond. For passive feeders, success or failure in prey capture often depends on the escape ability of the prey.

Therefore, electivity (e.g. Ivlev, 1961) for passive suspension feeders (Purcell, 1981a), measures prey avoidance ability as well as predator preference.

This study compared the prey (coelenteron contents) captured by two temperate anthozoan zooplanktivores on subtidal vertical rock surfaces, the octocoral *Alcyonium siderium* and the sea anemone *Metridium senile* over a diel cycle. The prey of these species were also compared over a diel cycle with the zooplankton available in the water near the substratum where the anthozoans held their feeding tentacles. *M. senile* and *A. siderium* are the only common perennial zooplanktivores on shallow (< 16-m depth) subtidal rock walls in much of northern New England (Patterson, 1980; Sebens, 1983, in press), although hydroids become common during the summer and fall. *M. senile* and *A. siderium* overlap almost completely in their habitat and microhabitat distributions.

### Material and methods

This research was conducted at a depth of 5 m along a vertical subtidal rock wall (4 m tall) with its base in 7 m of water off Canoe Beach, Nahant, Massachusetts, USA (Lat. 45°25'N, Long. 70°64'W). Sampling was done by SCUBA divers every 4 h for 20 h beginning at 09.40 on April 22, 1979 (water temperature = 4 °C). At each sampling period one diver counted expanded and contracted individuals and colonies in a nearby marked area of the wall. At locations outside the marked area, four fully expanded colonies of *Alcyonium siderium* Verrill (approximately 4 cm tall by 2 cm wide) were collected and suction samples were taken using 100-ml syringes, from the coelenterons of three fully expanded *Metridium senile* (L.) (approximately 6 cm basal diameter by 8 cm height). Such suction samples removed coelenteron fluid and many of the mesenterial filaments that hold the prey, which were usually concentrated in one or a few mucus-wrapped boluses. Colonies of *A. siderium* were placed into small plastic bags which were then sealed.

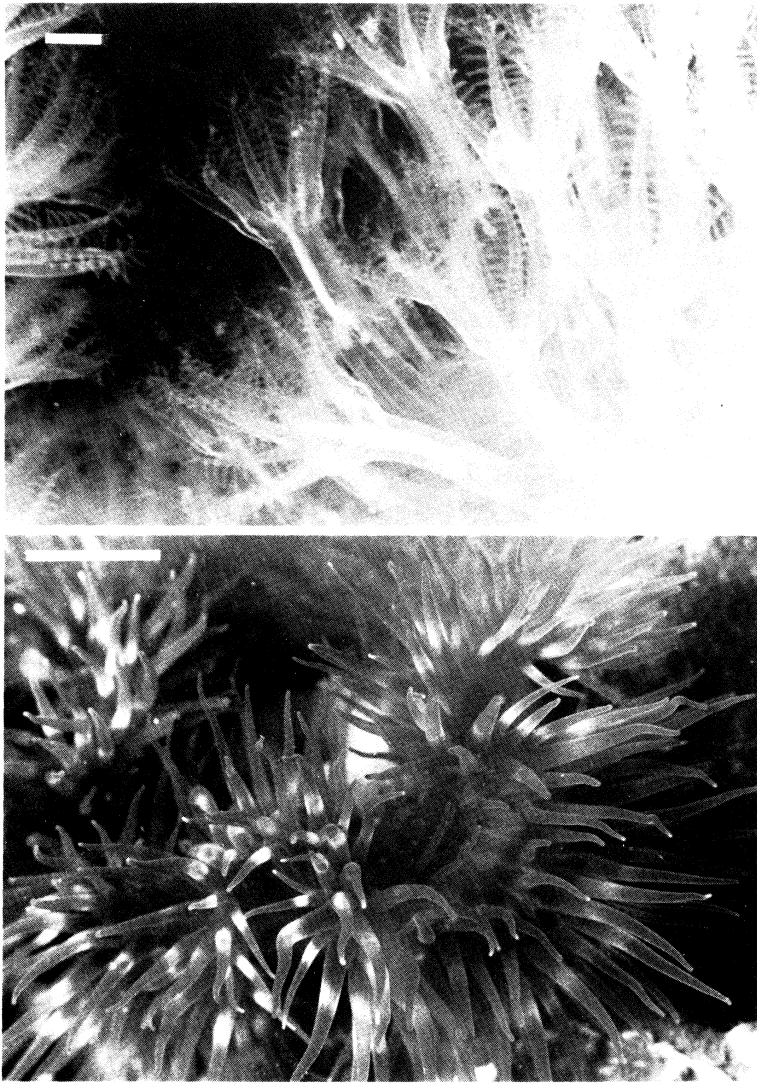
The second diver worked 3 m away at the same depth and positioned the end of a plastic hose (1-cm inside diameter) first at 70 cm, then at 5 cm, and finally at 1 cm from the rock wall surface, being careful not to touch the surface nearby. The hose, held parallel to the substratum so that its opening faced into the ambient water current, was connected to a 12-volt submersible pump (Rule Model 700) with an outlet into one of three plastic pails in a boat moored just above the site. An assistant in the boat took 10-l samples, when signaled, from each of the three positions. The diver then pushed a plankton net (23-cm mouth diameter, 60- $\mu$ m pore width) approximately 20 m at a distance of 60 to 100 cm from the rock wall. We compared the net samples with the pump samples taken at 70 cm from the substratum to assess the ability of the pump to capture various categories of zooplankton adequately. The net and the pump captured the same types of organisms, but in a few of the sampling periods the dis-

tribution among type or size categories of zooplankton sampled by the two methods differed (Koehl and Sebens, in preparation). Large, strong-swimming zooplankters may have been able to avoid both the pump and the net. Even though neither anthozoan captured prey > 3 mm frequently, this possible bias should be kept in mind when anthozoan prey is compared to available zooplankton.

All samples were immediately taken to the laboratory (Marine Sciences and Maritime Studies Center, Northeastern University) adjacent to the beach. The plankton samples in buckets were passed through a plankton net (60- $\mu$ m pore width) and the plankton was concentrated in a 50-ml vial at the base. This sample was then vacuum filtered through a 2.0- $\mu$ m millipore filter and was preserved in 3 ml of 7% buffered formalin in sea water and stored flat in a sealed plastic filter holder. *Metridium senile* coelenteron contents were also vacuum filtered directly, preserved and stored. *Alcyonium siderium* colony surfaces were brushed clean under flowing sea water and then examined with a dissecting microscope. A few millimeters of the base were cut off and then each colony was bisected parallel to its vertical axis. A filtered seawater stream from a Water-Pik was directed at the exposed inner colony surface, which consists of tubular coelenteron chambers communicating with each polyp. The force of the water stream flushed out many of the polyps' contents through their mouths, and into the vacuum filter apparatus. The filtered *A. siderium* coelenteron samples were preserved and stored as described above. Microscopic examination of washed surfaces of *A. siderium* colonies showed few adhering particles, indicating that contamination of *A. siderium* coelenteron contents with non-prey surface material was minimal.

At a later time, each of the plankton and prey samples was examined under 40, 100 or 400 $\times$  with a dissecting microscope and at 400 $\times$  with a compound microscope. Each recognizable item in the *Alcyonium siderium* or *Metridium senile* coelenteron contents (whether zooplankton or not) was recorded and measured (length and width of the primary body excluding fine appendages). Mesenterial filaments of *M. senile* were numerous and had to be picked apart to find some prey items. The plankton samples were on gridded millipore filters; counting and measuring began at a random point and continued in transects along the filter grid until 100 identifiable zooplankton items were encountered and measured. Biomass was estimated for each item by calculating the volume of an ellipsoid of the same length and diameter as the item and multiplying that by the density of sea water (assuming approximately neutral buoyancy). Parasitic copepods were obvious by their morphology and were omitted from the prey analysis. Some of the nematodes noted as prey could, however, actually have been parasites.

The time period during which the captured prey can be recognized in coelenteron contents was determined by feeding *Alcyonium siderium* and *Metridium senile* in the laboratory. After collection, the anthozoans were allowed to adjust to the running seawater tables for at least 18 h



**Fig. 1.** Prey capture structures of *Alcyonium siderium* (above, scale bar = 1 mm) and *Metridium senile* (below, scale bar = 5 mm)

**Table 1.** Prey capture structures of *Alcyonium siderium* and *Metridium senile* (means  $\pm$  one SD). Data from four *M. senile* of different sizes are presented separately. Data from four colonies of *A. siderium* 6- to 20-mm diameter are pooled because no significant differences with size were found for any of the characteristics (ANOVA). Three measures of each characteristic were taken from photographs of fully expanded individuals taken in the field (1:1 closeup lens)

	Polyp height (mm)	Polyp crown (mm)	Tentacle length (mm)	Tentacle width (middle) ( $\mu$ m)	Tentacle tip spacing (mm)	No. pinnules	Pinnule length ( $\mu$ m)	Pinnule width ( $\mu$ m)	Pinnule spacing ( $\mu$ m)
<i>Alcyonium</i> (n = 12)	7.2 $\pm$ 1.2	5.3 $\pm$ 0.8	3.0 $\pm$ 0.2	300 $\pm$ 0	1.9 $\pm$ 0.3	11 $\pm$ 1	380 $\pm$ 60	60 $\pm$ 0	230 $\pm$ 20
<i>Metridium</i> (n = 3)	20	15	6.1 $\pm$ 0.9	550 $\pm$ 80	2.2 $\pm$ 0.4	–	–	–	–
<i>Metridium</i> (n = 3)	30	40	7.7 $\pm$ 0.5	700 $\pm$ 100	2.9 $\pm$ 0.8	–	–	–	–
<i>Metridium</i> (n = 3)	60	70	9.4 $\pm$ 0.3	1 200 $\pm$ 150	3.5 $\pm$ 0.9	–	–	–	–
<i>Metridium</i> (n = 3)	80	100	9.8 $\pm$ 1.2	970 $\pm$ 200	3.2 $\pm$ 1.0	–	–	–	–

and to expand their tentacles. The colonies or individuals were then fed for 15 min with concentrated live zooplankton. After feeding, they were transferred to 5- $\mu$ m Millipore filtered sea water to prevent further prey capture and were then maintained with aeration at 7°C. Three individuals of each species were removed at 1, 2, 4 and 6 h after feeding and their coelenteron contents were sampled and examined as in the field collections.

Characteristics of prey capture structures of *Metridium senile* and *Alcyonium siderium* were measured on photographs taken of expanded individuals in the field (1:1 closeup lens, Nikonos III camera). Only polyps and tentacles aligned parallel to the plane of the photograph were selected for measurement. Three measures were taken from each of four individuals of each species.

## Results

### Morphology and feeding behavior

Polyps of *Alcyonium siderium* (Fig. 1) extend approximately 7 mm from the colony surface and bear eight tentacles 3 000  $\mu$ m long by 300  $\mu$ m diameter. Each tentacle has two rows each of 10 to 13 pinnules which are 300 to 400  $\mu$ m long and 60  $\mu$ m diameter (Table 1). The spacing between pinnules is 200 to 280  $\mu$ m and between tentacle tips it is 1 600 to 2 200  $\mu$ m. There is no significant change in any of the measured characteristics with increasing colony size (ANOVA,  $P > 0.05$ ). The polyp columns are very flexible and bend back and forth with wave surge so that water often moves across the tentacle crown from the aboral to oral side. In very slowly-moving water the upstream polyps face the current and water moves from the oral to aboral surface (Patterson, personal communication). When small prey are captured, single tentacles bend and wipe across the mouth; if a large prey item or several prey are captured, the tentacular crown closes. The mouth is approximately 400  $\mu$ m long but can probably expand during ingestion.

Colonies of *Alcyonium siderium* are ellipsoidal in cross section and are oriented so that the widest dimension of the colony is normal to the primary direction of water movement (Patterson, 1980). The smaller colonies are thin and fingerlike (e.g. 1 cm wide, 3 cm tall) while the largest are multi-lobed and wider than they are tall (to 10 by 15 cm wide, 10 cm tall). Polyps extend from very near the base to the top of the colony on all sides. The sizes attained by colonies in habitats exposed to rapid water movement from tidal currents and ocean swells are greater than those in calm water habitats.

Individual *Metridium senile* (Fig. 1) can reach 20-cm height by 14-cm basal diameter; the individuals on the rock wall examined were up to 8-cm basal diameter by 10-cm height. The tentacle crown was oriented parallel to the substratum with the lowest tentacles 1 cm or less above the substratum and the highest 10 cm away. These individuals do not extend and bend over with the aboral side

of the crown facing the current as do individuals of the large west coast *Metridium* species (Koehl, 1977a; Sebens, 1981).

The oral disk of a large *Metridium senile* bears thousands of tentacles (Sebens, 1981) each approximately 10 to 15 mm long by 1-mm diameter at their midpoint (Table 1). Tentacle lengths were significantly different for all *M. senile* sizes examined (ANOVA and Student-Newman-Keuls multiple comparisons test,  $F_{8,11} = 19.3$ ,  $P < 0.001$ ). Widths were significantly different for all but the largest and next to smallest individuals (ANOVA,  $F_{8,11} = 12.6$ ,  $P < 0.001$ ). Tentacle spacing was 1 to 2 mm at the midpoints and 2 to 5 mm at their tips, but this changes with posture and degree of expansion (Table 1). Differences between individuals of varying size were not significant (ANOVA,  $P > 0.05$ ) for tentacle spacing. Particles captured on the tentacles are passed first to an inner ring of larger tentacles surrounding the mouth and then by these tentacles to the mouth. The mouth is approximately 2 mm across on a small individual (1-cm basal diameter) to 10 mm on a large one (8-cm basal diameter), but can expand to a much larger size. Some particles are trapped in mucus strands and passed to the mouth via ciliated tracts.

### Digestion of prey items

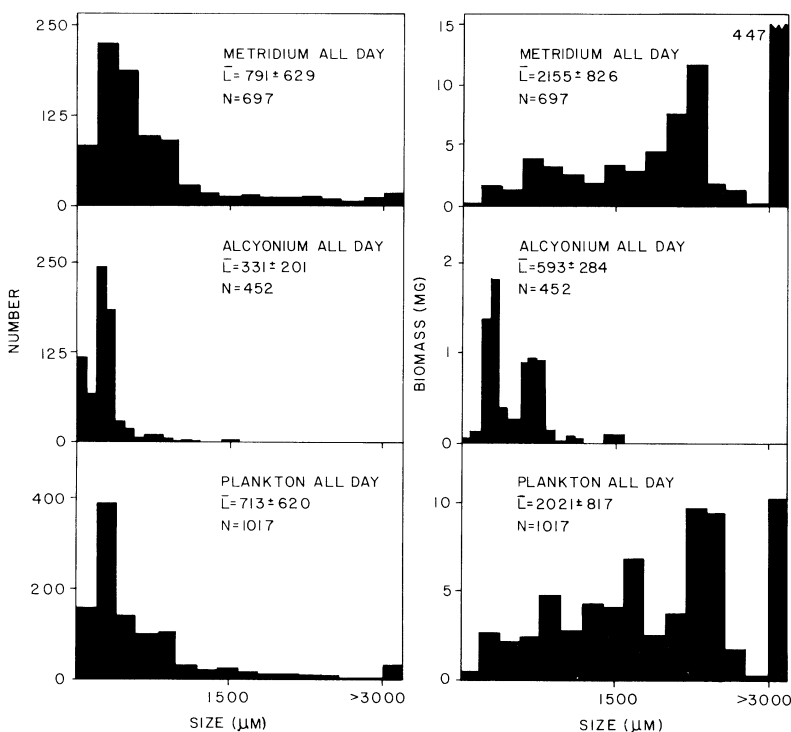
*Metridium senile* egested a mucus wrapped bolus from the mouth 2 to 4 h after feeding in the laboratory. Coelenteron contents included recognizable prey items (cladocerans, copepods, amphipods) and crustacean fragments at one and two hours but no recognizable items at 4 to 6 h after feeding. There were no whole prey items, but there were numerous prey fragments, in the two-hour sample (crustacean limbs and carapace parts); few or none could be found at 4 to 6 h. *Alcyonium siderium* did not egest a recognizable bolus of prey remains. Intact but partially digested prey could be found in the samples taken one and two hours after feeding but no items or fragments could be discerned in the 4- to 6-h samples. These results indicate that recognizable prey in field coelenteron contents of both species probably represent prey captured over the previous 0 to 2 h, with some fragments of items captured earlier. The best estimate of prey availability in the field is thus an average of the plankton available at the time of collection and that collected several hours earlier (4 h in this study). Entirely soft-bodied prey such as hydromedusae or ctenophores are probably digested very rapidly and, if captured, would be underrepresented or missed entirely in coelenteron samples.

### Zooplankton and prey sizes

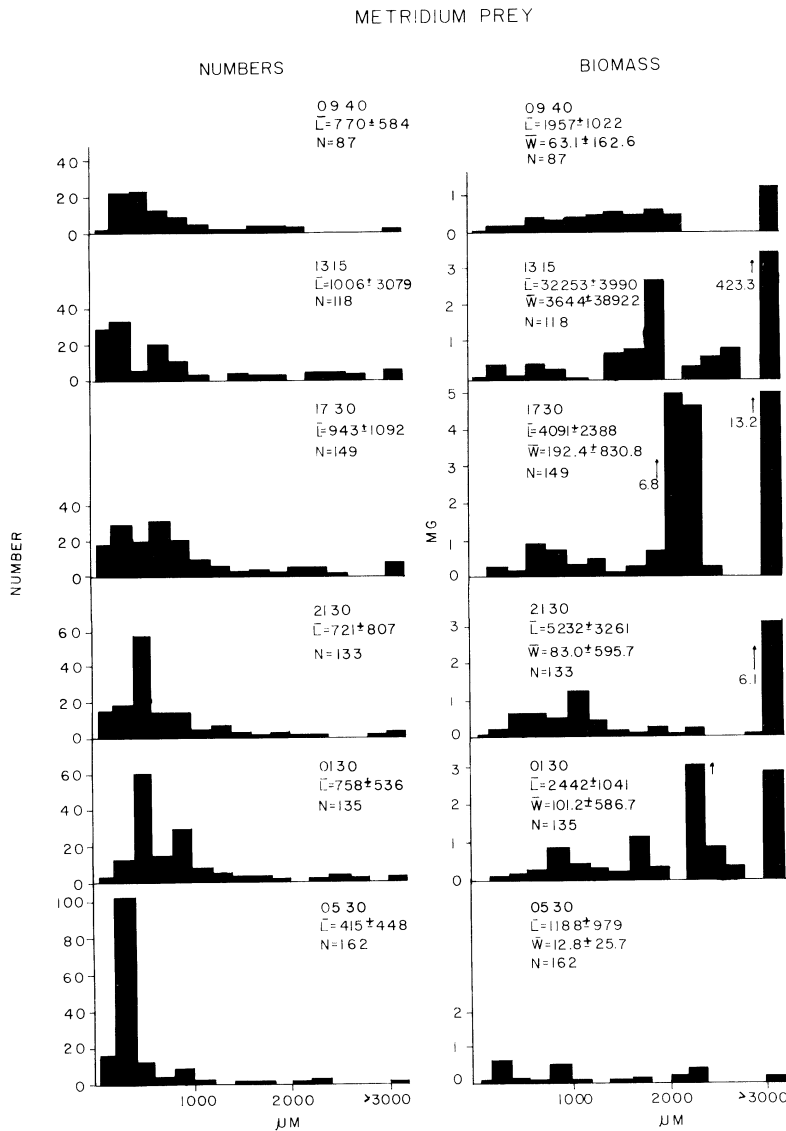
Because the food-catching tentacles of both *Metridium senile* and *Alcyonium siderium* were held  $\leq 1$  cm to 5 cm from the substratum, the zooplankton we collected at 1

**Table 2.** Zooplankton collections 1 to 5 cm from rock wall surfaces (5-m depth) at Canoe Beach, Nahant, Massachusetts, USA

	Morning (05:30, 09:40)		Afternoon (13:15, 17:30)		Night (21:30, 01:30)		Total length range ( $\mu\text{m}$ ) (min. max)
	mean length ( $\mu\text{m}$ )		mean length ( $\mu\text{m}$ )		mean length ( $\mu\text{m}$ )		
	$\pm$ one SD	<i>n</i>	$\pm$ one SD	<i>n</i>	$\pm$ one SD	<i>n</i>	
Invert. eggs or embryos	406 $\pm$ 577	36	257 $\pm$ 303	61	198 $\pm$ 98	47	48, 2 430
Foraminiferans	116 $\pm$ 40	7	193 $\pm$ 69	14	140 $\pm$ 51	4	64, 300
Ascidian larvae	289 $\pm$ 67	24	278 $\pm$ 40	103	298 $\pm$ 90	61	112, 486
Nematodes	1 565 $\pm$ 1 193	11	2 211 $\pm$ 1 932	4	721 $\pm$ 392	9	80, 4 860
Hydromedusa	880	1	—	—	—	—	880, 880
Hydroid actinula	—	—	1 440	1	—	—	1 440
Flatworm	960	1	440	1	—	—	440, 960
Harpacticoid copepods	478 $\pm$ 222	82	494 $\pm$ 183	51	556 $\pm$ 240	98	120, 1 400
Cyclopoid copepod	648	1	—	—	675 $\pm$ 121	6	486, 810
Calanoid copepods	1 337 $\pm$ 830	21	719 $\pm$ 191	12	678 $\pm$ 205	24	200, 3 726
Bivalve pediveliger	960	1	600	1	280	1	600, 960
Pteropod	560	1	—	—	200	1	200, 560
Pycnogonid	1 000	1	—	—	—	—	1 000
Nauplii	—	—	291 $\pm$ 0	2	388 $\pm$ 79	6	291, 486
Barnacle cyprids	640 $\pm$ 200	10	320	1	805 $\pm$ 116	10	280, 907
Ostracod	292 $\pm$ 153	14	460 $\pm$ 319	8	444 $\pm$ 207	8	120, 1 134
Arachnid (Mite)	528 $\pm$ 145	8	387 $\pm$ 125	7	429 $\pm$ 137	3	160, 700
Cladoceran, <i>Evadne</i>	638 $\pm$ 443	3	972	1	686 $\pm$ 299	5	259, 1 134
Cladoceran, <i>Podon</i>	733 $\pm$ 245	2	—	—	—	—	560, 907
Isopods	880 $\pm$ 452	2	4 100 $\pm$ 1 838	2	1 300 $\pm$ 141	2	640, 6 156
Gammarid amphipods	2 148 $\pm$ 1 598	57	1 389 $\pm$ 1 432	14	1 542 $\pm$ 1 195	13	240, 7 000
Caprellid amphipods	2 290 $\pm$ 912	4	1 671 $\pm$ 1 072	5	600 $\pm$ 282	2	400, 3 200
Crab zoea	680	1	240	1	1 620	1	240, 1 620
Polychaete troch.	306 $\pm$ 128	3	694 $\pm$ 520	3	462 $\pm$ 333	7	120, 1 296
Polychaete adults	817 $\pm$ 535	9	1 000	1	900 $\pm$ 430	4	300, 1 700
Juvenile mussels	1 266 $\pm$ 611	3	3 500 $\pm$ 2 687	2	—	—	600, 5 400
Crust. fragments	772 $\pm$ 851	31	1 024 $\pm$ 978	23	633 $\pm$ 734	21	40, 4 400
Bryo. fragments	2 000	1	2 160 $\pm$ 606	5	1 600	1	1 400, 3 000
Hydroid fragments	972	1	1 296	1	397 $\pm$ 253	4	160, 1 296
Sponge fragments	825 $\pm$ 607	7	1 180 $\pm$ 657	5	620 $\pm$ 141	2	120, 2 200
Ciliate protozoa	250 $\pm$ 11	4	550	1	—	—	200, 550



**Fig. 2.** Size distributions of captured prey and of available zooplankton for all sampling periods combined.  $\bar{L}$  = mean length,  $\pm$  one SD, weighted by number of items (left) and by biomass (right).  $N$  = total sample size



**Fig. 3.** *Metridium senile* coelenteron contents for each sampling period (from 09.40 hrs of the first day to 05.30 hrs of the second). Abbreviations as in Fig. 2.  $\bar{W}$  = mean biomass of items (ng)

and 5 cm (but not at 70 cm) from the wall represent prey available to these passive suspension feeders. Unless otherwise stated, "available zooplankton" refers to the animals in samples taken at 1 cm and 5 cm from the wall pooled. Details of the small-scale spatial and temporal distribution of the various types of zooplankton collected are given in Koehl and Sebens (in preparation).

There was no clear diel pattern in the size of available zooplankton (Table 2), although an abundance of ascidian larvae at 13.15 hrs decreased the mean length during that period and an abundance of gammarid amphipods and calanoid copepods (Table 2) gave the 05.30 sample a larger mean size. In general, there was a broad distribution of prey sizes (the standard deviation was as large as the mean) with a slight skew toward the smaller items (Fig. 3). Zooplankton biomass was skewed strongly to the larger items (mode  $> 3000 \mu\text{m}$ ). The items  $< 1000 \mu\text{m}$  generally accounted for less than a third of the total biomass (Fig. 2). Mean prey lengths weighted by biomass

rather than by the number of items ranged from 1580 to 5091  $\mu\text{m}$  ( $\bar{x}=2021 \mu\text{m}$ ,  $\text{SD}=817$  for all periods combined).

Mean sizes of specific categories of zooplankton over the diel cycle were compared by Analysis of Variance (Table 2), showing no change over the three periods for ascidian larvae ( $F_s=1.90$ ) or for gammarid amphipods ( $F_s=1.89$ ). The following groups did change their mean individual size between periods: invertebrate eggs ( $F_s=3.67$ ,  $P<0.05$ ), foraminiferans ( $F_s=4.19$ ,  $P<0.05$ ), harpacticoid copepods ( $F_s=3.03$ ,  $P<0.05$ ), calanoid copepods ( $F_s=9.9$ ,  $P<0.01$ ). Other groups had insufficient data for a similar analysis. In general, there appears to be a decrease in the size of plankton available over the entire sampling period rather than a day/night difference.

Prey in *Metridium senile* coelenterons had mean lengths of 415 to 1006  $\mu\text{m}$  with standard deviations approximately equal to the means (Figs. 2, 3). Size distributions were also skewed to the smaller sizes, with modes

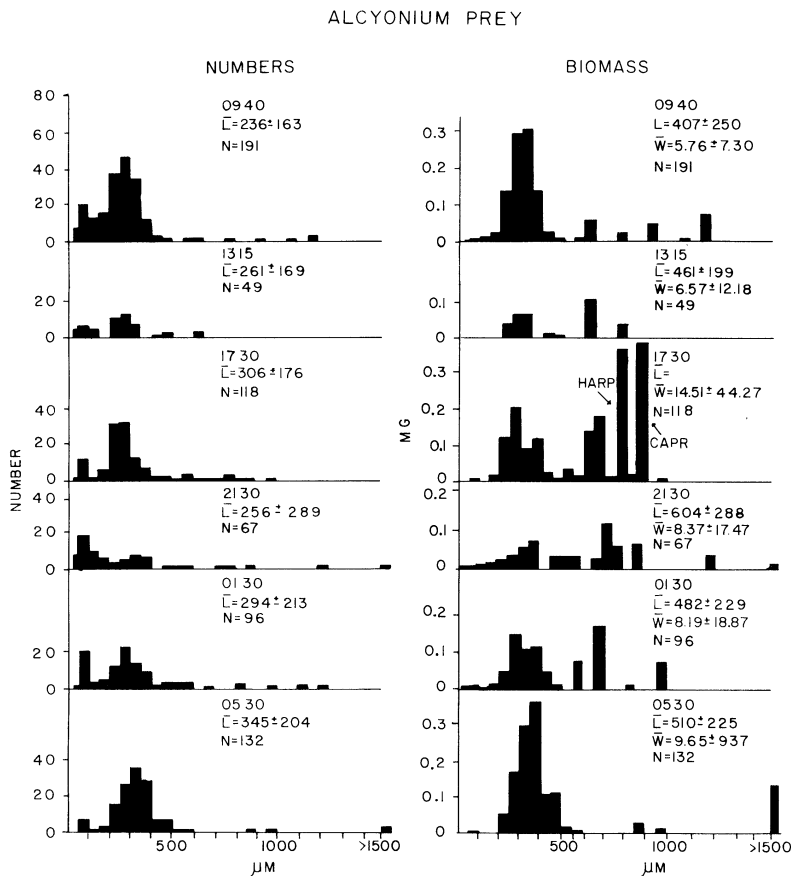


Fig. 4. *Alcyonium siderium* coelenteron contents for each sampling period from 09.40 hrs of the first day to 05.30 hrs of the second. Abbreviations as in Figs. 2 and 3

between 200 and 800  $\mu\text{m}$  as in the plankton samples. Biomass distributions were skewed strongly toward larger prey, as in the plankton samples, with modes  $>3000 \mu\text{m}$  in four of the six periods; the two lower modes were 2 200 to 2 450  $\mu\text{m}$  and 200 to 400  $\mu\text{m}$ . Mean lengths by biomass (1 188 to 5 232  $\mu\text{m}$ ) were very similar to the plankton samples, except in one period (13.15 hrs) with a mean of 32 253  $\mu\text{m}$  caused by one large caprellid amphipod (33 mm). The most important prey items for *M. senile*, by biomass, were those in the very upper tail of the plankton size distribution.

*Alcyonium siderium* prey were comparatively small, with mean lengths of 256 to 345  $\mu\text{m}$  and standard deviations less than the means (163 to 289  $\mu\text{m}$ ). The distributions of *A. siderium* prey sizes were almost normal but with tails on the large ends due to a few larger prey items (Figs. 2, 4). Modes for five of the six periods were similar (250 to 350  $\mu\text{m}$ ) but at 21.30 hrs the mode was only 50 to 100  $\mu\text{m}$ . Biomass distributions of *A. siderium* prey were also close to normal but with a few large items making a disproportionate mass contribution. A few juvenile caprellid amphipods and harpacticoid copepods at 17.30 hrs produced a biomass-weighted mean length of 700  $\mu\text{m}$  while the means for the other sampling periods were between 407 and 510  $\mu\text{m}$ , only slightly larger than the numerical mean lengths. Modes weighted by biomass varied widely between 250 and 950  $\mu\text{m}$ .

Coelenteron samples of *Alcyonium siderium* and *Metridium senile* and the plankton samples taken at 1 to 5 cm from the substratum were compared by ANOVA and by the Student Newman Keuls multiple comparisons test (Sokal and Rohlf, 1969) (Table 3, Fig. 5). For these comparisons plankton samples taken concurrently and 4 h earlier were combined. There were no significant differences in the sizes of zooplankton available at 1 and 5 cm. The lengths of prey items captured by *M. senile* were generally not different from those in the plankton samples taken at either 1 cm or 5 cm away from the rock wall (in five of the six sampling periods). Only at 17.30 hrs was *M. senile* prey significantly ( $P < 0.05$ ) larger than both plankton samples, although the *M. senile* mean prey length was usually the greatest.

In three of the six periods *Alcyonium siderium* prey was significantly smaller ( $P < 0.05$ ) than both the *Metridium senile* prey and the available plankton. In two other periods the mean length of the *A. siderium* prey was significantly smaller than that of *M. senile* prey and that of only one of the plankton samples, and in one period it was equal to the mean length of *M. senile* prey (see times in Table 3). In one of the periods when *A. siderium* prey was smaller than *M. senile* prey, the former was not distinguishable from either of the plankton samples.

Such results strongly suggest that *Alcyonium siderium* and *Metridium senile* used prey resources that differed in

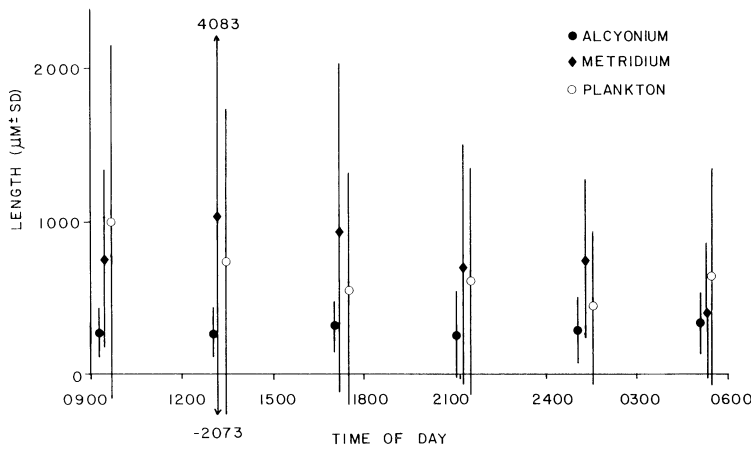


Fig. 5. Lengths of zooplankton and captured prey at each sampling period. See statistical comparison in Table 3. Error bars represent one standard deviation on either side of the mean

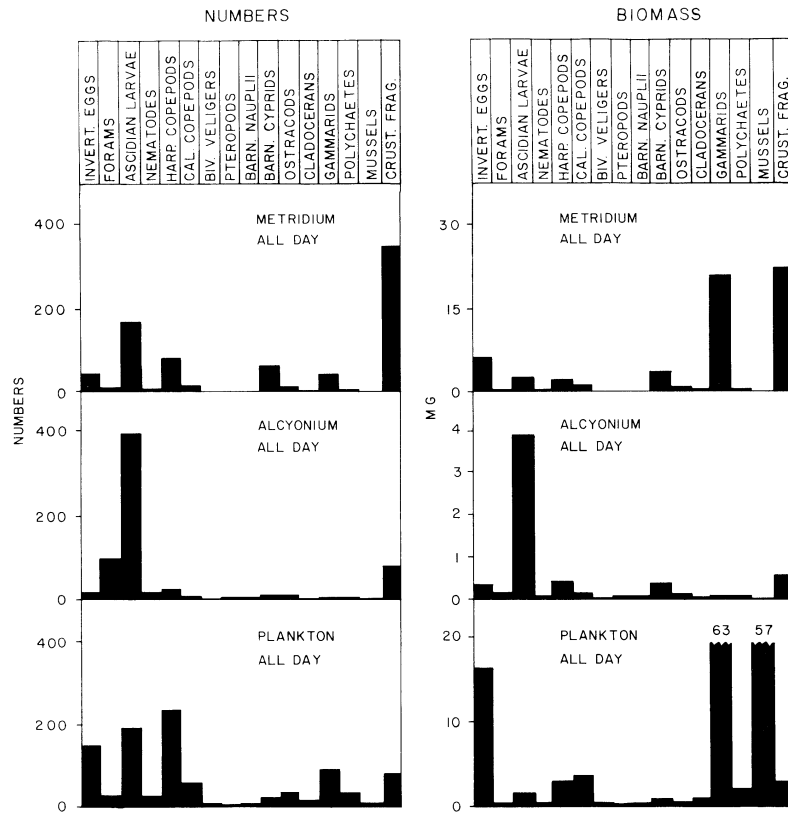


Fig. 6. Major categories of zooplankton and prey items for all sampling periods combined, by number of items (left) and biomass (right)

item length. *A. siderium* used the smaller of the available zooplankton while *M. senile* used zooplankton of approximately the length available, or only slightly larger. The most important prey for *A. siderium*, by both numbers and biomass, were those in the lower half of the zooplankton size-frequency distribution.

Zooplankton and prey composition

Certain taxa of zooplankton were always abundant near the vertical rock walls (Fig. 6, Table 2). Harpacticoid copepods were ubiquitous and often the most abundant single

group of zooplankton. Ascidian larvae were almost as common and were in fact the most abundant type of zooplankton in the afternoon samples. *Aplidium pallidum* is the most abundant ascidian at this study site (Sebens, 1982 b, in press) and most of the larvae were probably of this species. Other common items included invertebrate eggs and early embryonic stages, foraminiferans, ostracods, barnacle cyprids, and gammarid amphipods. Approximately 18 other categories of zooplankton accounted for the remaining 10% of the individuals. Biomass was concentrated in the large items, usually gammarid amphipods. Invertebrate eggs also accounted for much of the biomass in two samples. Crustacean fragments, only some of which

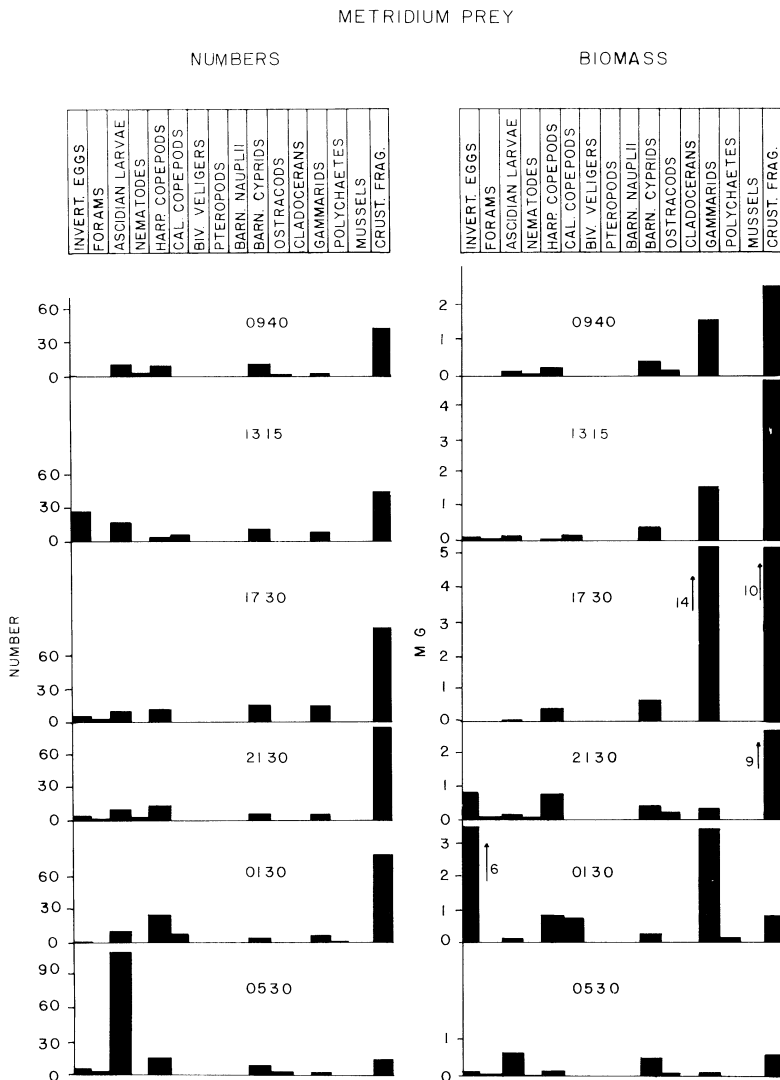


**Table 3.** Student-Newman-Keuls multiple comparisons test between mean lengths of prey items and of zooplankton. Lines connect samples not significantly different from each other at the  $P < 0.05$  level. The F statistic for the ANOVA on all four samples at each sampling period is also given. A = *Alcyonium siderium*, M = *Metridium senile*, P5 = plankton 5 cm from the wall, P1 = plankton 1 cm from the wall

	Time	Sample	F statistic
Morning (light)	05 : 30	<u>A</u> <u>M</u> <u>P5</u> <u>P1</u>	$F_s = 26.18$ (d.f. = 3 560)
	09 : 40	<u>A</u> <u>M</u> <u>P1</u> <u>P5</u>	$F_s = 27.83$ (d.f. = 3 468)
Afternoon (light)	13 : 15	<u>A</u> <u>P1</u> <u>P5</u> <u>M</u>	$F_s = 2.59$ (d.f. = 3 563)
	17 : 30	<u>A</u> <u>P1</u> <u>P5</u> <u>M</u>	$F_s = 13.77$ (d.f. = 3 593)
Night (dark)	21 : 30	<u>A</u> <u>P5</u> <u>P1</u> <u>M</u>	$F_s = 7.83$ (d.f. = 3 543)
	01 : 30	<u>A</u> <u>P5</u> <u>P1</u> <u>M</u>	$F_s = 25.70$ (d.f. = 3 504)

may have had any nutritive value, also had significant size and mass. The concentrations of various zooplankton categories changed during the diel period, while others stayed relatively constant (Table 2 and Koehl and Sebens, in preparation).

*Metridium senile* prey were primarily crustaceans, including barnacle cyprids, gammarid amphipods, harpacticoid copepods, and calanoid copepods, in descending order of abundance (Fig. 7, Table 4). Crustacean fragments were usually the most abundant items since digestion, field sampling, and storage break up partially digested prey. Of the non-crustacean prey, ascidian larvae were the most abundant. Invertebrate eggs, foraminiferans, nematodes and polychaetes were much less common. Biomass was concentrated in the large crustaceans (whole and fragments) especially gammarid amphipods, barnacle cyprids and calanoid copepods. Invertebrate eggs accounted for significant biomass in the afternoon samples.



**Fig. 7.** Major categories of prey in *Metridium senile* coelenteron contents at each sampling period, by number of items (left) and by biomass (right)

**Table 4.** *Metridium senile*. Coelenteron contents

Category	n	Total weight ( $\mu\text{g}$ )	Length ( $\mu\text{m}$ )		Individual weight ( $\mu\text{g}$ )		Length range ( $\mu\text{m}$ ) (min, max)	
			Mean	One SD	Mean	One SD		
<i>Morning</i>								
Invert. eggs or embryos	6	50	243	48	8	5	200,	320
Foraminiferans	2	358	140	56	2	2	100,	180
Ascidian larvae	119	642	265	42	5	3	100,	356
Nematodes	1	11	2 106	0	11	0	2 106,	2 106
Flatworm	1	0.3	240	0	0.3	0	240,	240
Harpacticoid copepods	25	297	541	210	12	17	300,	1 166
Barnacle cyprids	19	890	855	72	47	18	700,	960
Ostracods	5	144	548	159	29	27	320,	700
Gammarid amphipods	4	1 651	2 007	1 171	413	538	810,	3 600
Crust. fragments	56	3 181	840	609	57	112	64,	2 268
Algal fragments	26	1 049	552	406	40	51	80,	1 700
Hydroid fragments	1	107	4 000	0	107	0	4 000,	4 000
Sponge fragments	4	107	526	449	27	49	259,	1 200
Diatoms	8	23	193	30	3	1	160,	259
<i>Afternoon</i>								
Invert. eggs or embryos	31	94	120	106	3	6	32,	360
Foraminiferans	3	12	175	78	4	5	104,	259
Ascidian larvae	27	196	294	43	7	3	200,	388
Harpacticoid copepods	15	334	654	256	22	17	240,	1 134
Calanoid copepods	5	116	752	210	23	17	480,	1 000
Barnacle cyprids	27	976	762	103	36	13	400,	960
Ostracods	1	19	400	0	19	0	400,	400
Cladoceran, <i>Evadne</i>	1	54	800	0	54	0	800,	800
Gammarid amphipods	23	14 990	1 996	1 787	652	1 720	100,	6 000
Caprellid amphipods	2	422 975	19 223	19 152	211 487	298 920	5 680,	32 767
Crust. fragments	128	16 482	968	913	129	510	32,	6 000
Bryo. fragments	1	19	3 600	0	19	0	3 600,	3 600
Algal fragments	51	2 039	456	639	40	105	40,	3 000
Hydroid fragments	1	4 590	2 062	0	4 591	0	2 062,	2 062
Sponge fragments	2	5	291	137	3	3	194,	388
Dinoflagellates	3	3	56	5	1	0.9	200,	240
Diatoms	5	24	176	94	5	6	66,	300
<i>Night</i>								
Invert. eggs or embryos	5	6 129	772	937	1 226	2 730	140,	2 268
Foraminiferans	2	1	100	0	0.5	0.02	97,	100
Ascidian larvae	21	1 319	375	291	63	246	194,	3 564
Nematodes	3	46	2 160	730	15	14	1 458,	2 916
Harpacticoid copepods	39	1 349	833	217	35	38	400,	1 231
Cyclopoid copepods	1	70	810	0	70	0	810,	810
Calanoid copepods	7	741	1 036	696	106	232	648,	2 592
Barnacle cyprids	11	630	879	68	57	16	800,	1 036
Ostracod	1	170	1 231	0	170	0	1 231,	1 231
Arachnid (Mite)	1	42	615	0	42	0	615,	615
Gammarid amphipods	13	3 827	1 364	938	294	774	500,	4 212
Polychaete troch.	1	133	972	0	133	0	972,	972
Crust. fragments	162	2 459	667	725	15	62	64,	7 776
Algal fragments	75	799	301	492	11	25	80,	3 564
Hydroid fragments	1	7	1 620	0	7	0	1 620,	3 564
Diatoms	11	112	396	421	10	14	162,	1 600

In addition to the captured zooplankton, *Metridium senile* coelenterons contained significant numbers of what appeared to be macroalgal fragments of fairly small size (301 to 526  $\mu\text{m}$  mean length, Table 4), but these accounted for only a few percent of the total prey biomass. These items were usually green or colorless filaments, or red and brown sheetlike-fragments with obvious cell walls. Hydroid, sponge, and bryozoan fragments were present in

*M. senile* coelenteron contents only rarely. Diatoms and dinoflagellates made up less than 5% of the items and less than 0.1% of the calculated biomass. These few phytoplankton, and perhaps some of the detrital material, could have originated in the guts of captured crustaceans.

Ascidian larvae dominated the coelenteron contents of *Alcyonium siderium* (number and biomass, Fig. 8, Table 5). Foraminiferans and crustacean fragments were common

**Table 5.** *Alcyonium siderium*. Coelenteron contents

Category	<i>n</i>	Total weight ( $\mu\text{g}$ )	Length ( $\mu\text{m}$ )		Individual weight ( $\mu\text{g}$ )		Length range ( $\mu\text{m}$ ) (min, max)	
			Mean	One SD	Mean	One SD		
<i>Morning</i>								
Invert. eggs or embryos	7	40	174	105	6	8	64,	320
Foraminiferans	30	52	89	71	2	8	32,	440
Ascidian larvae	223	1 937	324	47	9	4	192,	486
Nematodes	4	0.02	173	9	0.005	0	162,	184
Bryozoan cyphonautes	1	27	900	0	27	0	900,	900
Harpacticoid copepods	8	142	520	216	18	25	240,	920
Nauplii	1	1	144	0	1	0	144,	144
Barnacle cyprids	1	17	800	0	2	0	800,	800
Ostracods	4	28	279	168	7	5	120,	518
Gammarid amphipods	2	3	372	22	2	0.4	144,	388
Caprellid amphipods	2	79	1 377	572	40	41	972,	1 782
Crust. fragments	33	117	311	308	4	11	40,	1 620
Algal fragments	119	251	233	317	2	7	64,	3 320
Hydroid fragments	2	5	1 120	56	2	0.4	1 080,	1 160
Sponge fragments	4	9	283	89	2	2	283,	283
Dinoflagellates	1	0.1	62	0	0.1	0	248,	248
Asteroid larvae	1	0.01	129	0	0.01	0	129,	129
Diatoms	1	0.3	80	0	0.3	0	80,	388
<i>Afternoon</i>								
Invert. eggs or embryos	2	30	291	91	15	12	226,	356
Foraminiferans	23	5	75	28	0.2	0.2	32,	144
Ascidian larvae	104	731	274	72	7	12	97,	777
Nematodes	5	1	446	122	0.3	0.5	259,	600
Harpacticoid copepods	5	112	593	132	22	27	480,	800
Calanoid copepods	2	4	500	141	2	2	64,	600
Pteropods	1	14	300	0	14	0	300,	300
Barnacle cyprids	3	63	786	61	21	11	720,	840
Ostracods	2	16	240	56	8	5	200,	280
Arachnid (Mites)	2	84	540	141	42	50	440,	640
Caprellid amphipods	5	878	808	146	176	134	640,	1 000
Crust. fragments	10	96	290	158	10	12	100,	640
Algal fragments	205	2 904	203	208	11	125	40,	2 200
Plant hairs	6	208	340	183	35	41	40,	600
Asteroid larvae	2	0.4	324	0	0.2	0	324,	324
Ciliate protozoa	1	0.05	64	0	0.05	0	64,	64
<i>Night</i>								
Invert. eggs or embryos	5	166	206	265	33	74	32,	680
Foraminiferans	39	11	90	40	0.3	0.4	32,	194
Ascidian larvae	68	531	304	55	8	5	220,	583
Nematodes	4	2	868	641	0.4	0.2	320,	1 782
Harpacticoid copepods	4	27	484	137	7	4	291,	600
Calanoid copepods	3	59	306	115	20	22	240,	440
Nauplii	1	9	259	0	9	0	259,	259
Barnacle cyprids	3	180	882	116	60	8	768,	1 000
Ostracods	1	0.4	128	0	0.4	0	128,	128
Polychaete troch.	1	0.1	96	0	0.1	0	96,	96
Crust. fragments	32	171	311	259	5	10	64,	1 231
Algal fragments	266	192	148	134	0.7	3	32,	1 231
Plant hairs	10	135	433	103	14	18	240,	583
Asteroid larvae	1	21	700	0	21	0	700,	700
Diatoms	24	15	82	48	0.6	2	32,	240
Appendicularian	1	49	580	0	49	0	580,	580

but less abundant. Invertebrate eggs, nematodes, harpacticoid copepods, ostracods, and cyprids made up most of the rest of the prey by number. After the ascidian larvae, harpacticoid copepods, barnacle cyprids, crustacean fragments and invertebrate eggs accounted for the remaining

zooplankton prey biomass. Adult caprellid amphipods (to > 30 mm length) often use the *A. siderium* colonies as feeding perches, and a few juvenile caprellid amphipods (7 individuals, 640 to 1 782  $\mu\text{m}$ ) were eaten by *A. siderium*. The pteropod (*Limacina* sp., 1 300  $\mu\text{m}$ ) was encountered

## ALCYONIUM PREY

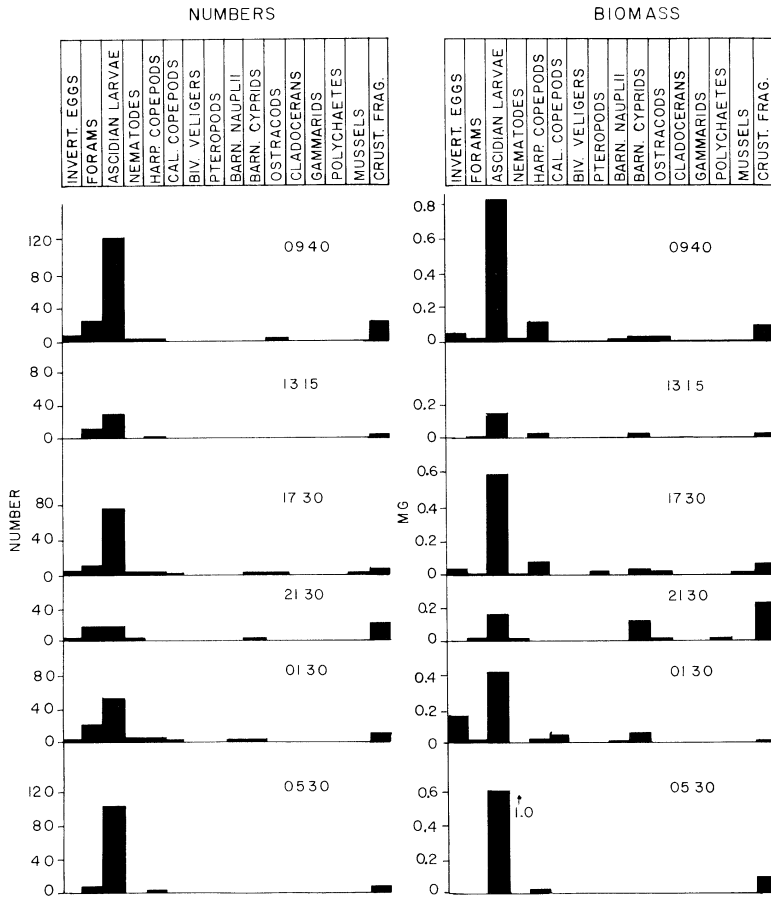


Fig. 8. Major categories of prey in *Alcyonium siderium* coelenteron contents at each sampling period, by number of items (left) and by biomass (right)

only once in this study but has occurred commonly in *A. siderium* coelenteron contents on other dates (unpublished data).

*Alcyonium siderium* coelenterons contained a larger percentage of algal fragments than did *Metridium senile* coelenterons. These fragments were similar in shape and color to those in *M. senile* but were slightly smaller (148 to 283  $\mu\text{m}$  mean length) (Table 5). The algal fragments comprised up to 57% of the items in *A. siderium*, but only up to 11% of the biomass. Sponge and hydroid fragments also appeared in *A. siderium* coelenteron contents, but accounted for less than 2% of the items in the coelenterons. Diatoms and dinoflagellates made up a maximum of only 5% of the items in the coelenterons, and less than 0.5% of the biomass. Surprising items that appeared in *A. siderium* coelenterons, but not in *M. senile*, were clusters (300 to 400  $\mu\text{m}$  diameter) of leaf hairs from a common terrestrial weed growing at Nahant (N. Riser, personal communication, possibly *Verbascum phlomoides*). A total of only 16 such clusters appeared in all 18 *A. siderium* colonies collected, although the leaf hairs were abundant in the plankton samples.

The categories of prey types captured at each time period by *Metridium senile* and by *Alcyonium siderium*

were compared with each other and with available zooplankton (1 to 5 cm from the rock wall, samples collected concurrently and 4 h earlier combined except at 09.40 hrs when no previous sample was available) (G-test of independence, Sokal and Rohlf, 1969). Because the same data were used in more than one test, the acceptance level was adjusted appropriately following the method of Lunney (1969). The coelenteron contents of the two species differed significantly at the  $P \leq 0.05$  level for each sampling period ( $G^2$  values of 40.2 to 203.0). All *A. siderium* contents differed significantly from the plankton at the  $P \leq 0.05$  level ( $G^2$  values of 24.4 to 105.8). *M. senile* contents also differed significantly from the plankton at all sampling periods ( $P \leq 0.05$ ,  $G^2 = 89.6$  to 278.4).

#### Electivities for zooplankton

Electivities (E) of *Metridium senile* and *Alcyonium siderium* for zooplankton prey items (omitting phytoplankton and detritus) were calculated, following Ivlev (1961) as  $E = (r - p)/(r + p)$ , where r is the frequency of the prey item in the diet and p is that in the environment (zooplankton sample). We also calculated Vanderploeg and

**Table 6.** Electivities of prey items >5% of either the diet or the plankton sample. Upper numbers are Ivlev's Index (E); lower ones are Vanderploeg and Scavia's Index (W); MS=*Metridium senile*; AS=*Alcyonium siderium*; %E=percent of time periods for which the electivities (E) were strongly negative or positive ( $\pm 0.20$ ); n = number of items

Time	09 : 40		13 : 15		17 : 30		21 : 30		01 : 30		05 : 30		%E MS		%E AS	
	AS	MS	AS	MS	AS	MS	AS	MS	AS	MS	AS	MS	POS	NEG	POS	NEG
Invertebrate eggs	-0.43	-1.00	-1.00	+0.37	-0.85	-0.55	-0.52	-0.45	-0.77	-0.81	-1.00	-0.62	17	83	0	100
Foraminiferans	+0.47	-1.00	+0.82	-0.34	+0.32	-0.23	+0.67	-0.29	+0.90	-1.00	-1.00	-	0	80	100	0
Ascidian larvae	+0.91	+0.77	+0.36	-0.12	+0.29	-0.40	+0.51	+0.29	+0.44	-0.18	+0.60	+0.50	50	17	100	0
Nematodes		-	-	-	-	+0.16	+0.16	-	-	-	-	-	0	0	0	0
Harpacticoid copepods	-0.86	-0.11	-0.65	-0.69	-0.75	+0.02	-1.00	+0.09	-0.67	+0.10	-0.81	-0.50	0	33	0	100
Calanoid copepods		-	-1.00	-0.47	-0.45	-1.00	-	-	-0.42	+0.19	-1.00	-1.00	0	75	0	100
Barnacle cyprids	-0.72	+0.79	+0.20	+0.81	+1.00	+1.00	+0.05	+0.56	-0.53	+0.32	-1.00	+0.37	100	0	33	50
Ostracods	-0.67	-0.25	-1.00	-1.00	-0.24	-0.28	-0.51	-0.55	-	-	-	-	0	100	0	100
Gammarid amphipods	-1.00	-0.60	-1.00	-0.24	-1.00	+0.65	-1.00	+0.28	-1.00	+0.44	-0.53	-0.78	50	50	0	100
n prey	159	35	42	72	108	60	44	48	82	53	115	142				
n plankton	135	135	316	316	263	263	197	197	256	256	267	267				

Scavia's (1979) selectivity coefficient (W), where  $W = (r_i/p_i)/\sum(r_i/p_i)$  for all prey types  $i$ . This index is not as readily interpreted as E but has the advantage that it is not affected by sample composition (p) and is thus most appropriate for comparisons between samples (Lechowicz, 1982). We combined four zooplankton samples ( $\leq 400$  items), the two collected at 1 and 5 cm above the substratum concurrently with the coelenteron samples, and the two from the sampling period four hours earlier; this sums plankton from the entire colony height range and also combines plankton that may have been captured up to 4 h earlier with that just captured. Categories of potential prey items were included only if they made up 5% or more of either the zooplankton or of the coelenteron samples thus omitting rare taxa. Electivities were calculated for each of the six time periods; however, for the 09.40 sample, we used only concurrently collected plankton for comparison since none was collected earlier. Table 6 also indicates those prey for which electivity values were high ( $E > \pm 0.20$ ). (An E of +0.20 means that the frequency of that item in the diet was 50% higher than that in the zooplankton sample.)

*Alcyonium siderium* had very clear electivities. The E's for ascidian larvae and foraminiferans were high and positive in all of the sampling periods. The electivity for barnacle cyprids was high and positive only once, but was strongly negative three times. The electivities for the

following items were strongly negative in most or all of the sampling periods: invertebrate eggs, harpacticoid copepods, calanoid copepods, ostracods and gammarid amphipods.

*Metridium senile* showed strong positive electivities (E) for barnacle cyprids and for ascidian larvae in 100% and in 50% of the sampling periods, respectively, and *M. senile* showed strong negative electivities for invertebrate eggs, foraminiferans, calanoid copepods, and ostracods in 95 to 100% of the time periods. The electivities for gammarids were strongly negative in two time periods and highly positive in three. The electivities for harpacticoid copepods were strongly negative in only two of the six periods. Nematodes were taken in frequencies similar to their abundance by both predators in the one sampling period where they were common enough to consider.

*Alcyonium siderium* had strong positive electivities for substratum-related prey (benthic or demersal animals and meroplankton), primarily foraminiferans and ascidian larvae. These were also important components of the diet by number and by biomass. True open-water plankton (holoplankton, e.g. calanoid copepods) were generally not captured, nor were other large swimming crustacea such as gammarid amphipods. *Metridium senile*'s diet was also strongly substratum-related. Although large, strong-swimming crustaceans (e.g. gammarid amphipods and barnacle cyprids) were often captured successfully, both calanoid

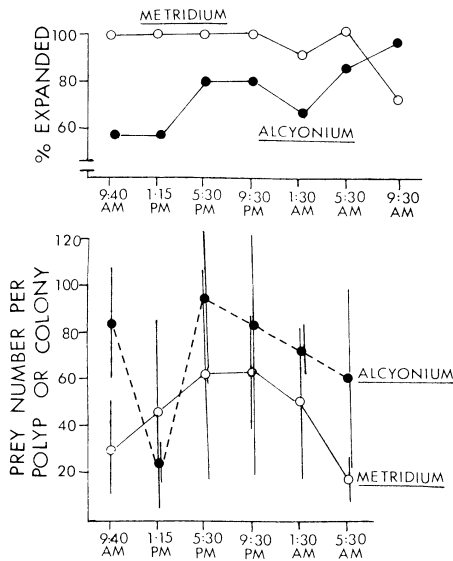


Fig. 9. (A) Expansion of *Metridium senile* and *Alcyonium siderium* over the sampling periods (percent of 20 colonies or individuals expanded), and (B) prey capture (mean  $\pm$  one SD) over the same time interval

and harpacticoid copepods were underrepresented in *M. senile* diets. Thus, although there is a clear separation between *A. siderium* and *M. senile* diets by size and by taxon composition, both appear to rely heavily on the larvae of other benthic invertebrates and on demersal crustaceans that probably live on the rock walls and occasionally swim away from the substratum.

Vanderploeg and Scavia's selectivity index (W) gave relative rankings of prey very similar to Ivlev's index in most cases (Table 6). Only a few systematic differences between the two indices appeared; for example, values of W indicate that ostracods and harpacticoid copepods were even more negatively selected by both predators than indicated by E; gammarid amphipods were also more strongly negatively selected by *A. siderium* according to index W.

Both *Alcyonium siderium* and *Metridium senile* were expanded during the entire diel cycle (Fig. 9A). The least degree of expansion was seen at 09.30 hrs for *M. senile* (70% of individuals) and at 09.40 hrs for *A. siderium* (60%). Other observations near Nahant indicate that *A. siderium* does not have the clear-cut annual cycle of winter contraction that Hartnoll (1975) described for the British species *Alcyonium digitatum* L. However, most colonies of *A. siderium* and individuals of *M. senile* were contracted on days with minimal wave action and thus with low water movement (Sebens, unpublished data). This pattern of continuous diel expansion differs from the behavior of many tropical coral reef anthozoans that expand primarily at night (Porter, 1974; Sebens, 1977; Sebens and DeRiemer, 1977; Lasker, 1976). Our data on numbers of prey captured per polyp (Fig. 9B) suggested that both *A. siderium* and *M. senile* increased their feeding success in the late afternoon and early evening, however, all data on feeding and expansion came from a single day's sampling; more

diel cycles would have to be followed to determine whether the observed patterns are repeated and are significant.

## Discussion

### Importance of substratum-related prey in diets of benthic suspension feeders

Benthic zooplanktivores have two potential prey resources: (1) zooplankton originating from the large open-water planktonic community, and (2) substratum-related prey, including the larvae of benthic invertebrates, adult benthic crustaceans that spend some time swimming (demersal zooplankton), and benthic material washed off the substratum by currents. The composition of the near-substratum plankton can change greatly within a few centimeters of the substratum (Koehl and Sebens, in preparation) due to the presence of locally dispersed larvae (e.g. ascidians) and to crustaceans that are primarily benthic (e.g. harpacticoid copepods (Hauspie and Polk, 1973), and gammarid amphipods). Furthermore, the concentration of animals in the water within a few centimeters of the substratum can be an order of magnitude greater than in the water further away (Koehl and Sebens, in preparation). Hence, the near-substratum zooplankton can be considered as a layer of greater prey availability derived largely from the benthic trophic web, and probably based partly on benthic primary productivity.

Water movement may affect the composition of the near-substratum plankton. On days with low wave action, such as the days of this study, a layer of increased zooplankton abundance develops near the substratum and moves across the rock wall with bi-directional wave-generated surge. In contrast, on days of very heavy wave action, demersal plankters might not venture off the substratum. Locally released larvae and any crustaceans that do swim would be mixed into the surrounding water, and more detritus and fragments of benthic organisms might be washed off the substratum than during calm water periods.

Both common perennial zooplanktivores at our study site, *Metridium senile* and *Alcyonium siderium*, relied heavily on substratum-associated prey (both meroplankton and demersal plankton). Furthermore, detrital material was common in the coelenterons of both species. Some of this may have been captured from the water column, but it could also have come from prey gut contents. Such detrital material has been reported from the anemone *Actinia equina* (Van Praet, 1980). The detrital material is likely to support a surface film of bacteria, which is known to be a potential food source for corals (DiSalvo, 1971; Sorokin, 1974). Although the bulk of the prey of both *Metridium senile* and *Alcyonium siderium* was substratum-associated organisms or larvae, they did consume a few holoplanktonic animals such as calanoid copepods. However, both species showed negative electivities for such prey.

There was little true phytoplankton in the coelenterons of either *Metridium senile* or *Alcyonium siderium* and the few items present could easily have come from prey gut contents or could have been ingested incidentally with zooplankton prey. Reports by Roushdy and Hansen (1961) and Roushdy (1962) of phytoplankton feeding by the British species *Alcyonium digitatum* under laboratory conditions may not reflect that species' natural diet or its normal prey selection behavior (Muscatine, 1973).

#### Morphology and the capture of prey from moving water

Both *Alcyonium siderium* and *Metridium senile* held their feeding tentacles close to the rock wall where a rich supply of near-substratum zooplankton was found. Although *M. senile* stood up to 10 cm tall, their tentacular crowns extended down to within a centimeter or two of the substratum, and colonies of *A. siderium* of all sizes had feeding polyps from base to top. The orientation of colonies of *A. siderium* with their widest axes normal to the direction of ambient water flow (Patterson, 1980) may enhance capture of zooplankton as Leversee (1976) found for gorgonian corals, although this orientation also maximizes drag forces on the colonies (Patterson, 1980; Koehl, 1982).

*Alcyonium siderium* and *Metridium senile* are passive suspension feeders, i.e. they depend on ambient currents to bring food to their tentacles. They are exposed to surge as waves pass overhead. Patterson (1980) reported that *A. siderium* at Nahant encountered water velocities from  $<0.05 \text{ m s}^{-1}$  to  $0.5 \text{ m s}^{-1}$  on a day with moderate wave action. At a later date (April, 1983) with moderate wave action (wave height around 0.6 m) similar to the day of our 1979 diel sampling, Patterson (personal communication) recorded flow velocities of  $0.1$  to  $0.2 \text{ m s}^{-1}$  with occasional peaks to  $0.4 \text{ m s}^{-1}$  within a few centimeters of the rock wall where this study was conducted.

One mechanism by which passive suspension feeders such as *Alcyonium siderium* and *Metridium senile* capture prey in the water moving across them is by sieving; all items bigger than the space between two adjacent food-catching structures (e.g. tentacles) are retained as the water flows between the structures. The spaces between the tentacles of polyps of *A. siderium* are smaller than are those between tentacles of *M. senile*. Furthermore, the inter-tentacular gaps of polyps of *A. siderium* are functionally even narrower than reported in Table 1 because the pinnules extend into the gaps. Calculated estimates of the thickness of the boundary layer of slowly-moving water surrounding individual pinnules (see Koehl, 1981) indicate that some water does flow between adjacent pinnules, even at velocities as low as  $0.015 \text{ m s}^{-1}$ . Therefore, *A. siderium*, with their feathery tentacles, have finer meshes for sieving food out of the water than do *M. senile* with their more widely-spaced smooth tentacles. More than half the particles captured by *A. siderium* were larger than the inter-pinnule spacing and thus could have been captured by sieving, whereas most prey of *M. senile* were

smaller than the intertentacular gaps. The relative importance of various physical mechanisms causing prey to contact each filter-feeder's tentacles was estimated (Rubenstein and Koehl, 1977). For most types of particles and at most flow velocities that *A. siderium* and *M. senile* encounter, direct interception is the primary mode of particle capture (i.e. particles carried by the ambient currents contact tentacles). However, inertial impaction (i.e. the momentum of dense particles causes them to deviate from the streamlines of ambient flow and to contact a suspension-feeder's tentacle as the water is deflected around it) appears to be involved in the capture of particles at the large end of the spectrum of prey for both species at peak velocities on the order of  $0.5 \text{ m s}^{-1}$ .

When the morphologies of these two cnidarian species are considered, it is not surprising that *Alcyonium siderium* feed primarily on small, non-motile or weakly-swimming prey (such as foraminiferans and ascidian larvae), whereas *Metridium senile*, whose tentacles bear larger and more numerous nematocysts (Sebens, unpublished data), capture larger and more active zooplankton. Having pinnulate tentacles may allow octocorals to specialize on relatively small prey. Lasker (1981) found that three tropical gorgonian species were unable to capture large swimming zooplankton but successfully captured *Artemia* sp. cysts ( $< 250 \mu\text{m}$  diameter).

#### Competition for food by benthic suspension-feeders

Although plankton is not usually considered a limiting resource for benthic planktivores, there is evidence that some encrusting bryozoans in still water (Buss, 1979) and arborescent bryozoans in currents (Buss, 1981; Okamura, in press) can interfere with each other's growth or food capture, and that water moving across assemblages of planktivores can become depleted of plankton (Glynn, 1973; Buss and Jackson, 1981). Both *Metridium senile* and *Alcyonium siderium* populations can be dense on subtidal rock walls (Sebens, in press), and both species rely heavily on substratum-related prey. Therefore local depletion of food in the water may be an important mechanism of intraspecific competition in this rock-wall community. For example, the poor growth of *A. siderium* juveniles that settled within two centimeters of adult colonies (Sebens, in press) might have been due to such food depletion. Although *M. senile* and *A. siderium* overlap in local microhabitat distribution, the composition of their diets is very different. Because of this "niche separation", local depletion of plankton might not be very important as a mechanism of inter-specific competition for these cnidarians (except for certain types of prey, such as ascidian larvae, that are selectively eaten by both species).

Food depletion is not the only way in which benthic organisms can affect the suspension feeding of their neighbors. The presence of large colonies or individuals may simply slow down water movement, making less zooplankton per unit time available to the smaller zooplanktivores below and behind them. The latter would

then receive less prey even if the numbers of prey per volume of water were not reduced. Koehl found that water flow was slower within beds of sea anemones (1976, 1977a) or zoanths (1977b) than outside them. Shick and Hoffmann (1980) found that intertidal *Metridium senile* in Maine grew larger in microhabitats with moderately high tidal currents than in adjacent microhabitats with less water movement and suggested that greater water flow brought more zooplankton per unit time into contact with the anemones' tentacles. The poor growth of *Alcyonium siderium* juveniles in close proximity to adults (Sebens, in press) might have been caused by slowed water flow as well as, or instead of, by the food depletion suggested above.

Changes in ambient flow velocity caused by the presence of a neighbor might well alter the composition as well as the number of prey captured. For example, *Metridium senile* and *Alcyonium siderium* polyps deform in moving water (Koehl, 1977a; Patterson, 1982) and their tentacles are thus blown closer together in fast flow. Therefore, as flow is slowed down, the sizes of intertentacular gaps increase and the ability to sieve small particles out of the water might be reduced. Conversely, if flow is slowed, the ability of a suspension-feeder to hold on to large particles might increase. In water movement slow enough that swimming organisms are not helplessly swept along in the current, the capture of animals that can avoid predators might be reduced whereas that of animals that swim about randomly might be increased. Furthermore, in slow flow, the capture of negatively buoyant particles (by gravitational sedimentation) could increase with respect to the capture of neutrally-buoyant items. The effects of benthic organisms on the diets of their suspension-feeding neighbors bears further investigation.

#### Predation by benthic animals on larvae of their competitors

Active suspension feeders and deposit feeders in soft substratum communities can be major sources of mortality for each other's larvae (Woodin, 1976). Deposit feeders disrupt the surface layers of sediments, burying or ingesting newly settled larvae while some active suspension feeders filter larvae from the water directly. The large number of ascidian larvae captured by *Alcyonium siderium* points to a similar interaction in this hard-substratum community. The tunicate *Aplidium pallidum* is often the most common invertebrate on rock walls, and can overgrow small *A. siderium* colonies (< 15 mm diameter, Sebens, 1982, in press). The predation on *A. pallidum* larvae observed in this study may reduce the recruitment rate of the ascidian and thus improve the early survivorship of juvenile *A. siderium*.

*Metridium senile* also occurs on rock walls with abundant *Aplidium pallidum*, and also feeds on the tunicate larvae. Although direct competition between *M. senile* and *A. pallidum* has not been demonstrated, one of us (K. Sebens) has observed small *M. senile* buried under the

edges of *A. pallidum* colonies in the field. Predation on ascidian larvae could thus affect competition among these species as well.

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