

Trophic ecology of a benthic marine hydroid, *Campanularia everta*

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ABSTRACT: The diet and prey capture rate were studied in *Campanularia everta* (Hydrozoa) in the western Mediterranean Sea during both a 1 yr period and a diel period. A sample of 20 colonies was collected from the thalli of the alga *Halimeda tuna* every 2 wk, and the stomach content of 100 polyps was examined. The diet of *C. everta* consisted primarily (88%) of particulate organic matter between 30 and 80 µm in size (probably detritus). Zooplankton accounted for only 12% of the diet; the predominant prey items were crustacean eggs, larvae, and fragments, and as well as other benthic invertebrate larvae. In terms of biomass, zooplankton contributed 54% of the diet. The percentage of prey-containing polyps was rather constant at around 70% over both the annual and diel cycles. Prey capture rates were quite high overall (between 0.6 and 2.7 prey items per polyp) and likewise the number of polyps with prey is remained high throughout the year, with maximum values in autumn and minimum values in summer. Digestion time was less than 2 h. Prey capture estimates were slightly fewer than 4000 prey m⁻² d⁻¹ in summer and 800 000 prey m⁻² d⁻¹ in winter. Accordingly, *C. everta* may ingest a mean of 1925 µg C m⁻² d⁻¹ in particulate organic matter and 2260 µg C m⁻² d⁻¹ in zooplankton each year, representing a total of 1528 mg C m⁻² yr⁻¹. Each µg C of polyps (somatic biomass) ingests a mean value of 69.6 µg C of prey per year. These figures suggest that the contribution of hydroids to the transfer of energy from the plankton to the benthos in littoral systems may be much higher than that suggested by hydroid biomass values themselves.

KEY WORDS: Feeding behaviour · Prey selection · Ingestion time · Trophic ecology · Feeding cycles · Suspension feeders · Hydroids

INTRODUCTION

There is strong evidence that both benthic animal biomass and benthic food webs are trophically dependent upon plankton (Parsons et al. 1979). Food suspended in the water column is obtained by sessile benthic organisms via a variety of filtration mechanisms or advective and sedimentation processes (Smetacek 1984). A distinction is often made between those suspension feeders that capture minute particulate matter, bacteria, and phytoplankton and those that feed primarily upon zooplankton. The activity of the former group is known to have a large impact on energy flow processes between the plankton and the benthos. For example, certain molluscs have been shown to have a major role in regulating plankton production in certain areas (e.g. Dame et al. 1980,

Officer et al. 1982), and certain cnidarian species are known to be quite voracious and to have high zooplankton capture rates (Purcell 1977, Sebens & Koehl 1984, Barange & Gili 1988).

Hydroids are one group of benthic suspension feeders whose natural feeding patterns are poorly understood (Sebens 1987). Description and quantification of their dietary preferences is essential in enabling researchers to characterize the ecological niche and trophic role of hydroids in marine communities. Previous work on hydropolyps has shown that they capture a wide range of prey, including organisms commonly found in the littoral zooplankton (see Gili & Hughes in press for a review). The size of prey captured by hydroids is known to be very similar to that of the most abundant organisms in the zooplankton in the habitat (Barange 1988, Barange & Gili 1988). In addition,

periods of high rates of prey capture are related to periods of high zooplankton concentration, i.e. abundant potential prey in the habitat (Letunov & Marfenin 1980, Barange & Gili 1988). On the other hand, recent papers describe how several species of hydroids have particular food preferences as a consequence of their specific associations with other organisms (parasites, commensals or symbionts; e.g. Svoboda 1979, Piraino et al. 1992). Little information is available on the role of other types of prey, such as bacteria, detritus from vegetable matter, or particles of unspecified origin, in hydroid feeding (Simkina 1980). This is surprising, since particulate organic matter (POM) is the most abundant potential food resource in the sea and hydroids, as some of the smallest and most ephemeral species of all sessile organisms, might be expected to readily exploit it (Jørgensen 1966, Conover 1978).

Hydroids are common organisms in benthic communities in temperate seas (Riedl 1966), but their biomass is small relative to the community as a whole (Gili & Ros 1985). However, if their metabolism is as active as that expected based on the prey capture rates and growth rates observed in recent *in situ* experiments (Hughes 1983, Llobet et al. 1991a), hydroids could play a greater role in littoral food chains than suggested solely on the basis of their biomass. Support of this hypothesis requires information on (1) the actual metabolic activity of hydroids, (2) *in situ* capture rates, and (3) their spatial and temporal distributions. To this end, we studied the trophic ecology of the hydroid *Campanularia everta*, which is known to have a high growth rate (Llobet et al. 1991) and to expend a significant proportion of resources on reproduction (Coma 1994).

The objectives of our study were to (1) establish the diet of *C. everta* in both qualitative and quantitative terms, (2) determine the prey capture rate along with possible diel and seasonal variations therein, and (3) evaluate the importance of hydroids as conduits in the transfer of energy between the plankton and the benthos in marine food webs. Our hypotheses were: (1) as an opportunist, *Campanularia everta* should base its diet on the most abundant prey in the habitat at any given time; and (2) to allow high growth rates, prey capture rates should remain consistently high during the diel cycle and the entire life span.

MATERIAL AND METHODS

Morphology. *Campanularia everta* develops reptant colonies from a branching hydrorhiza that adheres to the substratum, normally an alga. The populations studied colonized the alga *Halimeda tuna*. Erect, unbranched hydrocauli bearing the polyps issue from the

hydrorhiza at irregular intervals. Each polyp is located within a hydrotheca measuring 200 to 260 μm in diameter and 400 to 500 μm in height. The polyps are 240 to 280 μm in diameter and 850 to 1000 μm in length. Around the mouth, each polyp bears a crown of 14 to 16 tentacles 1.3 mm in length and 25 μm in diameter at the base when fully extended. The minimum angle between tentacles is 10°, the maximum 75°.

Sampling. *Campanularia everta* colonies were collected randomly every 2 wk from May 1990 to May 1991 from a *Halimeda tuna* population at a depth of between 17 and 19 m off the Medes Islands (3° 13' E, 43° 2' N) (Catalonian coast, NW Mediterranean). Each sample consisted of 20 algal thalli which were immediately fixed in 10% formalin to prevent digestion in the polyps. Thalli were always collected from 09:00 to 10:00 h to avoid potential variations in stomach contents associated with circadian rhythms. In the laboratory, at least 100 polyps were randomly selected from among the colonies present on the 20 thalli. On 20 April 1992, 10 thalli were collected every 2 h for 24 h, to observe potential diel variation.

Stomach contents. A total of 50 polyps from each sample were dissected in the laboratory. The type of prey item (zooplankton and POM) and the number and size of prey items were recorded. Using these data, the percentage of prey-containing polyps, mean prey size, and mean number of prey items per polyp were calculated. POM was classified into 3 size categories: 10 to 30 μm , 30 to 80 μm , and >80 μm . The stomach contents of recently collected polyps were analyzed under an epifluorescence microscope to detect traces of chlorophyll and bacteria.

The wet weight of each zooplanktonic prey item was estimated from the volume and the specific weight (1.025 according to Hall et al. 1970). The dry weight was assumed to be 13% of the fresh weight (Beers 1966). Dry weight was converted to organic carbon by applying the general ratio for zooplankton: C:DW = 0.4 to 0.5 (Biswas & Biswas 1979). Since it was not possible to obtain enough particles from polyp gastric cavities to measure weight or organic carbon (and since published values were not considered reliable), the biomass of unidentifiable POM was estimated from the organic carbon content of particles of the same diameter collected from the sea water adjacent to the *Campanularia everta* colonies. To this end, water was collected at 5 locations next to the *Halimeda tuna* population and 3 fractions were filtered: 6 to 30, 30 to 80, and 80 to 150 μm . Five 0.5 l replicates were filtered, and the content of the filters (Whatman GF/D fiber glass) was analyzed in a C:N autoanalyzer. Particle volume and particle diameter were measured for each of the same 5 locations in 10 additional replicates of 2 ml sea water using a Coulter counter calibrated with latex balls measuring 47 μm in

Table 1. Food items captured by *Campanularia everta*. Conversion of mean biometric measurement values from μm (L: length, W: width, D: depth) to volume (V: $\text{mm}^3 \times 10^{-3}$), fresh weight (FW: μg ; specific weight 1.025 g cm^{-3}), dry weight (DW: μg , 13% fresh weight), specific weight (SW: $116 \mu\text{g C mm}^{-3}$) and organic carbon (C: μg , 50% of dry weight). The total number of food items captured in the experiments related to the diel and annual cycles are also shown

| Prey type | L | W | D | V | FW | DW | SW | C | Diel cycle | | | Annual cycle | | | |
|---------------------------------------|-----|-----|----|-------|------|-------|-----|--------|------------|-------|----|--------------|-------|----|--|
| | | | | | | | | | n | Total | % | n | Total | % | |
| Organic matter 10 to 30 μm | 15 | | | 0.002 | | | 116 | 0.0002 | 1582 | | | | 1208 | | |
| Organic matter 30 to 80 μm | 45 | | | 0.048 | | | 116 | 0.0055 | 338 | | | | 252 | | |
| Organic matter > 80 μm | 90 | | | 0.382 | | | 116 | 0.0443 | 43 | 1963 | 97 | 68 | 1527 | 88 | |
| Crustacean eggs | 78 | 78 | 78 | 0.247 | 0.25 | 0.033 | | 0.0164 | 20 | | | | 112 | | |
| Nauplii | 123 | 110 | 50 | 0.354 | 0.36 | 0.047 | | 0.0236 | 2 | | | | 26 | | |
| Crustacean fragments | 100 | 80 | 60 | 0.251 | 0.26 | 0.033 | | 0.0167 | 19 | | | | 27 | | |
| Copepodites | 337 | 105 | 65 | 1.204 | 1.23 | 0.160 | | 0.0802 | – | | | | 18 | | |
| Protozoans (Tintinnids) | 120 | 55 | 55 | 0.190 | 0.19 | 0.025 | | 0.0127 | – | | | | 4 | | |
| Invertebrate larvae | 200 | 75 | 75 | 0.589 | 0.60 | 0.078 | | 0.0392 | 4 | | | | 2 | | |
| Cladocerans | 208 | 160 | 50 | 0.871 | 0.89 | 0.116 | | 0.0580 | 1 | | | | 1 | | |
| Ostracods | 272 | 150 | 50 | 1.068 | 1.09 | 0.142 | | 0.0712 | 9 | | | | 7 | | |
| Foraminiferans | 160 | 160 | 50 | 0.670 | 0.69 | 0.089 | | 0.0447 | – | | | | 3 | | |
| Nematodes | 560 | 31 | 15 | 0.137 | 0.14 | 0.018 | | 0.0091 | 1 | 57 | 3 | 1 | 201 | 12 | |

diameter. An approximate organic carbon value was assigned to each particle size category (Table 1) by combining the number and volume of particles for each of the 3 fractions selected (chosen for feasibility of identification inside the gastric cavities of the polyps) with the total biomass.

Zooplankton density. Two zooplankton samples were collected at the same time as the *Campanularia everta* samples (every 2 wk over the annual cycle and every 4 h over the diel cycle) using plankton nets 22 cm in diameter with a mesh size of 60 μm . Nets were towed by a diver a short distance (30 to 50 cm) from the *Halimeda tuna* thalli. The volume of water filtered through the meshes during each tow was approximately 3 m^3 . Plankton samples were fixed in 5% formalin and identified in the laboratory.

Digestion time. On 1 June 1992, 70 *Halimeda tuna* thalli were sampled to determine digestion time. Ten thalli were immediately fixed in 10% formalin and 60 thalli were preserved in a container filled with filtered sea water held at the same temperature as the ambient sea water (18°C). An additional 10 thalli were fixed every 0.5 h over a period of 3 h. The colonies present on the thalli were separated in the laboratory and the stomach contents of 50 polyps analyzed for each 0.5 h period.

Prey capture rate and plankton consumption. To determine the impact of the *Campanularia everta* population on the water column, the prey capture and turnover rates were multiplied by the thallus density for the *Halimeda tuna* algal substratum and *C. everta* polyp density on each thallus (annual mean values taken from Lobet et al. 1991b). The daily prey capture rate (N_i) for each sample i was calculated using the equation:

$$N_i = \frac{24x}{d}$$

where x is the mean number of prey items and d is the digestion time (h). The total number of prey items (n_i) captured m^{-2} was calculated using the equation:

$$n_i = \sum_{i=1}^n N_i DT$$

where D is polyps m^{-2} , T is time (d) between samples (generally 15), and n is the number of samples throughout the year (24). Particles and zooplanktonic prey were considered separately when converting to units of biomass expressed as organic carbon (Table 1).

RESULTS

Stomach contents

Most of the prey items observed inside the gastric cavity of *Campanularia everta*, for both diel and annual cycles, were particles of organic matter between 10 and 80 μm in size (Tables 2 & 3). Virtually none of the particles exhibited any external morphology or texture that allowed an exact determination their origin (Fig. 1) (because of their small size and the inability to collect sufficient mass for most types of analysis). Observation of some of these particles under the epifluorescence microscope indicated that they most likely were detritus from vegetable matter.

The most abundant zooplanktonic prey items were copepod eggs, fragments of crustaceans (most probably copepods or copepodids; harpacticoids and cala-

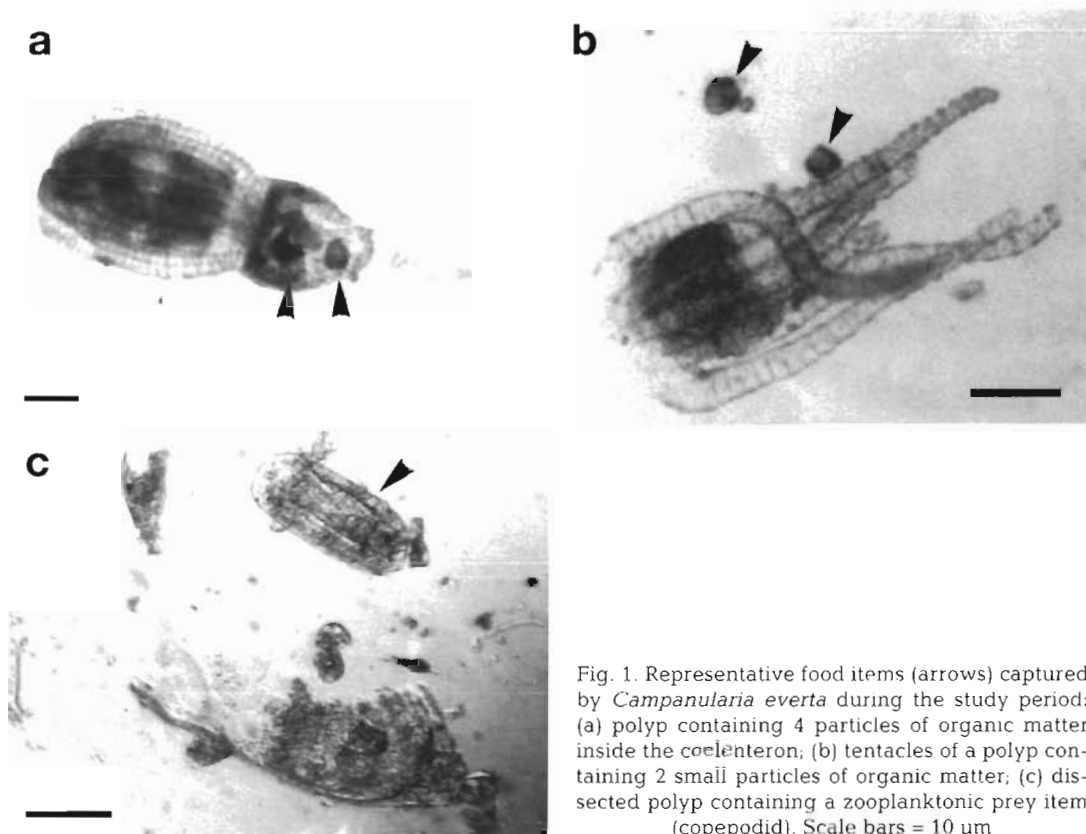


Fig. 1. Representative food items (arrows) captured by *Campanularia everta* during the study period: (a) polyp containing 4 particles of organic matter inside the coelenteron; (b) tentacles of a polyp containing 2 small particles of organic matter; (c) dissected polyp containing a zooplanktonic prey item (copepodid). Scale bars = 10 μ m

noids) and nauplii (Fig. 1). The presence of other groups was sporadic, except for the meroplanktonic larvae of benthic invertebrates, which were captured with some frequency in certain seasons of the year (spring and summer).

Diel cycle

The most noteworthy feature of the diel cycle was the scant variation in the percentage of polyps containing prey in their gastric cavities (Student's *t*-test,

Table 2. Number (n) of food items captured by *Campanularia everta* over the diel cycle. P: polyp, POM: particulate organic matter, Zoopl: zooplankton, SD: standard deviation. The number of items relative to the polyps with food (Prey/Full P) and to the total polyps studied (Prey/P) are differentiated

| Date | Time (GMT) | Full P (%) | Items (n) | POM (%) | Zoopl. (%) | Prey size (μ m) | | Prey/Full P | | Prey/P |
|---------------|------------|------------|-----------|---------|------------|----------------------|-------|-------------|------|--------|
| | | | | | | Mean | SD | Mean | SD | |
| 19 April 1992 | 14:00 | 68 | 161 | 98 | 2 | 41.92 | 45.68 | 4.21 | 4.23 | 3.22 |
| | 16:00 | 68 | 79 | 97 | 3 | 19.68 | 22.64 | 2.42 | 0.9 | 1.58 |
| | 18:00 | 72 | 267 | 100 | 0 | 24.08 | 18.88 | 7.18 | 9.65 | 5.34 |
| | 20:00 | 76 | 118 | 94 | 6 | 42.16 | 41.68 | 3.23 | 3.92 | 2.36 |
| | 22:00 | 76 | 167 | 99 | 1 | 19.68 | 15.60 | 4.71 | 2.10 | 3.34 |
| 20 April 1992 | 24:00 | 72 | 213 | 100 | 0 | 12.85 | 6.01 | 6.22 | 3.44 | 4.26 |
| | 02:00 | 74 | 153 | 97 | 3 | 30.24 | 43.76 | 3.97 | 2.09 | 3.06 |
| | 04:00 | 76 | 187 | 99 | 1 | 22.96 | 22.80 | 4.88 | 3.03 | 3.74 |
| | 06:00 | 82 | 138 | 85 | 15 | 39.36 | 41.44 | 3.43 | 2.71 | 2.76 |
| | 08:00 | 64 | 148 | 98 | 2 | 27.04 | 28.24 | 5.03 | 4.04 | 2.96 |
| | 10:00 | 66 | 119 | 95 | 5 | 27.61 | 40.69 | 3.28 | 3.91 | 2.38 |
| | 12:00 | 62 | 157 | 99 | 1 | 20.96 | 24.16 | 5.50 | 3.21 | 3.14 |
| | 14:00 | 70 | 113 | 94 | 6 | 50.64 | 51.52 | 3.47 | 3.14 | 2.26 |
| Mean | | 71 | 155 | 97 | 3 | 29.00 | | 4.40 | | 3.10 |
| SD | | 5 | 46 | 4 | 4 | 11.00 | | 1.30 | | 0.90 |

$t_{12} = 1.12 \cdot 10^{-3}$, $p > 0.05$). Nevertheless, the size and the density of the prey items within the polyps showed a significant variation (ANOVA, $F_{11,2209} = 10.25$, $p < 0.0001$; ANOVA, $F_{11,637} = 3.50$, $p < 0.0001$) (Table 2). There was a slight increase in the number of zooplanktonic prey around 06:00 h, at sunrise. During the diel cycle studied (19 to 20 April 1992) POM accounted for 97% of the total; zooplanktonic prey accounted for just 3%. In terms of organic carbon, zooplanktonic prey contributed 30% of the biomass of captured prey, though the particulate matter was the main dietary component (70%) (Fig. 2).

Annual cycle

Amorphous particles of organic matter made up 88% of the total items captured over the annual cycle, while zooplankton represented only 12%. In terms of organic carbon, the percentage values were more similar, with

particulate matter accounting for 42% and zooplankton accounting for 58% of the total biomass of material captured. The percentage of food-containing polyps was high, but varied non-significantly between months (Student's t -test, $t_{22} = 4.92 \cdot 10^{-4}$, $p > 0.05$). Lower values recorded in the summer coincide with the virtual disappearance of *Campanularia everta* from the community. In terms of number of prey items, POM accounted for the larger share, but zooplanktonic organisms contributed an important proportion of the diet in autumn and winter (up to 61% of the total prey items) and sometimes in spring (Table 3, Fig. 2). In general, crustacean (probably copepod) eggs, fragments of crustaceans (mainly copepod and copepodid carapaces) and nauplii accounted for 80% of the total number of zooplanktonic prey items. The size of prey per polyp increased in autumn/winter and showed significant seasonal differences (ANOVA, $F_{22,2073} = 7.04$, $p < 0.001$), as did the number of prey items per polyp (ANOVA, $F_{22,1065} = 5.31$, $p < 0.001$).

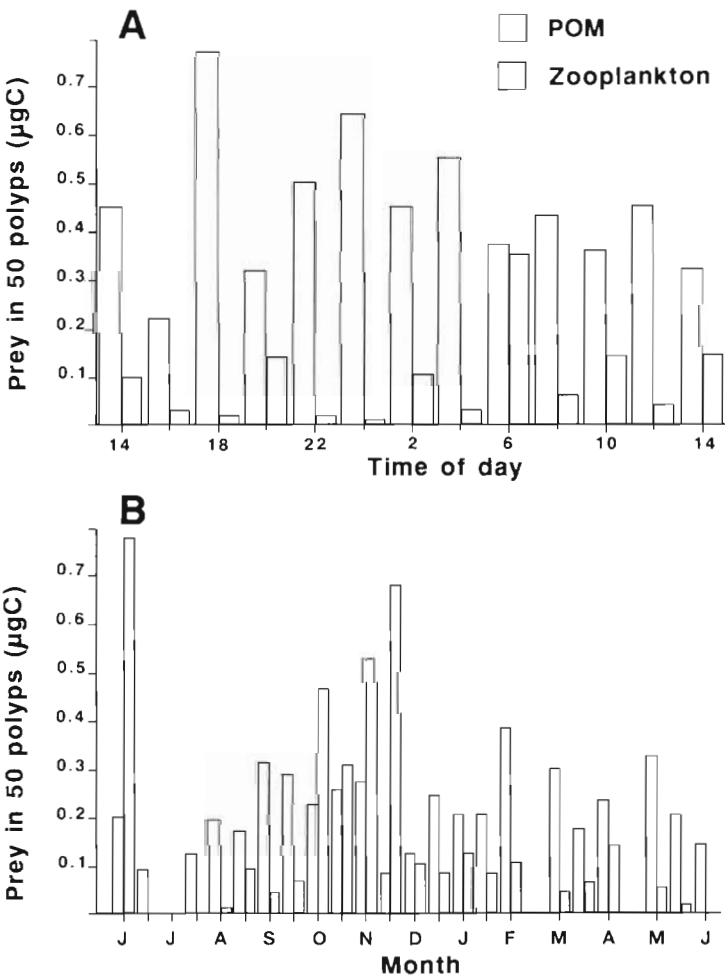


Fig. 2. Biomass ($\mu\text{g C}$) of food items captured by 50 *Campanularia everta* polyps, both particulate organic matter (POM) and zooplankton, over the diel cycle (A) (20 April 1992) and the annual cycle (B) (1990–1991)

Relationship between zooplankton dynamics and stomach contents

A comparison of the abundance of main zooplanktonic prey items in the water column and their presence in the stomach contents over the diel cycle (Fig. 3) did not yield any clear relationship between plankton density and prey capture rates. This may have been due to low abundance of such prey in the stomach contents.

One of the periods when the capture rates for zooplanktonic prey were highest was recorded for the period when zooplankton abundance in the habitat also was highest. The relationship between zooplankton concentration and number of prey in the stomach

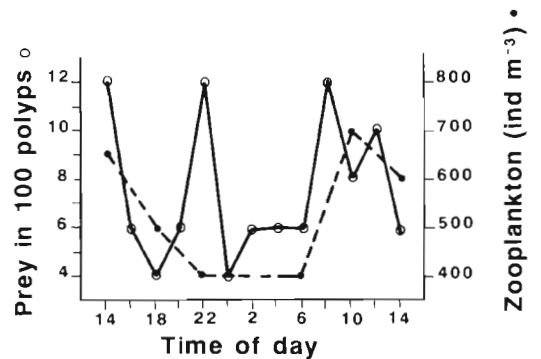


Fig. 3. Total number of zooplankton prey captured by 100 *Campanularia everta* polyps and densities for the 3 most common zooplankton prey items in the diet over the diel cycle (20 April 1992)

Table 3. Number (n) and type of food items captured by *Campanularia everta* over the annual cycle in this study. POM: particulate organic matter, P: polyp, SD: standard deviation. The number of items relative to the polyps with food (Prey/Full P) and to the total polyps studied (Prey/P) are differentiated

| Date | Full P (%) | Items (n) | POM (%) | Zoopl. (%) | Prey size (μm) | | Prey/Full P | | Prey/P |
|-------------|------------|-----------|---------|------------|-----------------------------|--------|-------------|------|--------|
| | | | | | Mean | SD | Mean | SD | |
| 29 May 1990 | 74 | 95 | 70 | 30 | 91.52 | 147.52 | 2.56 | 1.96 | 1.9 |
| 12 Jun | 52 | 45 | 100 | 0 | 22.72 | 42.72 | 2.07 | 1.21 | 1.1 |
| 28 Jun | 40 | 7 | 100 | 0 | 28.96 | 14.44 | 1.41 | 0.54 | 0.6 |
| 13 Jul | – | – | – | – | – | – | – | – | – |
| 02 Aug | 50 | 17 | 100 | 0 | 22.56 | 11.04 | 1.71 | 0.82 | 0.9 |
| 13 Aug | 55 | 28 | 100 | 0 | 18.88 | 9.76 | 2.33 | 0.65 | 1.3 |
| 04 Sep | 48 | 58 | 93 | 7 | 55.36 | 29.96 | 2.41 | 1.39 | 1.2 |
| 19 Sep | 64 | 105 | 98 | 2 | 25.76 | 17.28 | 3.29 | 1.26 | 2.1 |
| 01 Oct | 78 | 100 | 97 | 3 | 51.52 | 66.56 | 2.56 | 1.84 | 2.0 |
| 18 Oct | 78 | 96 | 77 | 23 | 74.64 | 104.64 | 2.46 | 1.42 | 1.9 |
| 31 Oct | 76 | 107 | 85 | 15 | 78.72 | 82.56 | 2.81 | 1.68 | 2.1 |
| 15 Nov | 82 | 118 | 81 | 19 | 72.32 | 76.96 | 2.89 | 1.41 | 2.4 |
| 30 Nov | 70 | 113 | 39 | 61 | 86.56 | 73.44 | 1.62 | 0.91 | 1.1 |
| 19 Dec | 50 | 51 | 90 | 10 | 32.81 | 36.32 | 2.04 | 0.88 | 1.0 |
| 31 Dec | 78 | 88 | 95 | 5 | 64.32 | 61.28 | 2.25 | 1.31 | 1.8 |
| 21 Jan 1991 | 78 | 75 | 91 | 9 | 82.88 | 67.84 | 1.92 | 1.54 | 1.5 |
| 07 Feb | 70 | 72 | 94 | 6 | 47.04 | 44.96 | 2.05 | 1.49 | 1.4 |
| 22 Feb | 84 | 134 | 96 | 4 | 45.76 | 34.08 | 3.19 | 1.76 | 2.7 |
| 21 Mar | 76 | 101 | 98 | 2 | 64.16 | 120.64 | 2.67 | 1.95 | 2.0 |
| 12 Apr | 70 | 61 | 97 | 3 | 56.81 | 56.32 | 1.75 | 0.81 | 1.2 |
| 22 Apr | 70 | 82 | 93 | 7 | 82.24 | 86.56 | 2.34 | 2.09 | 1.6 |
| 17 May | 80 | 106 | 98 | 2 | 51.52 | 78.88 | 2.66 | 1.36 | 2.1 |
| 30 May | 66 | 68 | 100 | 0 | 63.52 | 44.64 | 2.06 | 1.52 | 1.4 |
| 14 Jun | 50 | 3 | 100 | 0 | 40.16 | 11.36 | 1.51 | 0.71 | 0.8 |
| Mean | 67 | | 91 | 9 | 54.81 | | 2.29 | | 1.6 |
| SD | 13 | | 14 | 14 | 22.03 | | 0.5 | | 0.5 |

contents was particularly evident at the end of autumn/beginning of winter, coinciding with the period of greatest abundance of nauplii in the plankton (Fig. 4).

Digestion time

All food items were digested within 90 min, though there was an appreciable difference in the digestion rates for particulate matter and for zooplankton (Table 4). The abundance of the former declined rapidly, whereas

digestion of the zooplanktonic items took longer. These results indicate that under the conditions of the experiment, 1.5 to 2.0 h would be a conservative estimate of the digestion time.

Impact on the community: prey capture rate and plankton consumption

The density of *Campanularia everta* polyps ranged from a low of 500 to 1000 polyps m^{-2} in summer to a high of nearly 5×10^4 polyps m^{-2} in winter (Table 5).

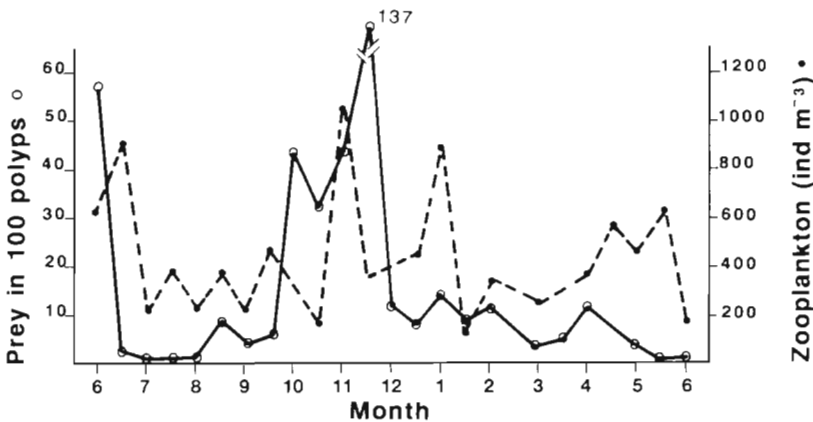


Fig. 4. Total number of zooplankton prey captured by *Campanularia everta* and densities for the main zooplankton contributors to the diet over the annual cycle (1990–1991)

decomposition and depolymerization through the action of bacteria and fungi, and this would in turn enrich protein content, thereby making detrital particles acceptable to many suspension feeders (Fenchel 1970, Mayer et al. 1993). We have observed large numbers of bacteria associated with the particles ingested by *C. everta* polyps, suggesting that such particles might be an adequate food source for this hydroid. POM was noted as a primary food source for certain species of coral and actinian during periods when the density of other prey items is scarce (Coles 1969, Van Praët 1980). In addition, it has been demonstrated that the amount of zooplankton captured by some corals does not cover their metabolic requirements, making other sources of energy necessary, such as symbioses with algae or ingestion of detritus, which may provide an essential dietary complement (Johannes et al. 1970). The present study provides the first evidence of a hydroid species whose diet is quantitatively based on POM in suspension.

Capture mechanisms

The polyps of *Campanularia everta* rhythmically expand and contract their tentacles, creating a current towards the mouth, enhancing particle capture. Similar observations have been made in other species (Boero unpubl.) which behave like active filter feeders, and whose nematocysts probably play a reduced role in taking prey. *C. everta* would thus appear to be a benthic suspension feeder that uses different methods to capture particles. Such versatility would be appropriate for species that take a wide range of food types (from particles to copepods) including species that mainly capture zooplankton (Barange 1988). On the other hand, several species of hydroids can be rather selective in their food preferences due to their specific associations. Commensal hydroids which feed on their hosts, such as bryozoans (e.g. Piraino et al. 1992) or bivalves (Piraino et al. 1994) have exceptional trophic niches within the predominantly particle-feeding hydroids.

Digestion time

The digestion time observed in *Campanularia everta*, less than 2 h, is the shortest known time for any hydroid. Certain species may take more than 24 h to digest their prey at temperatures below 10°C (Christensen 1976). Under laboratory conditions, digestion times have been observed to decrease rapidly with increasing temperature (Paffenhöfer 1968). However, the high digestion rate in *C. everta* may also be attributable to other factors. Another species in the same

region at similar temperatures (18°C), *Eudendrium racemosum*, took around 4 h to digest its prey (Barange & Gili 1988). *E. racemosum* fed exclusively on zooplankton and on generally larger prey items than did *C. everta*. The lower nutritional value of POM compared to that for zooplankton may make higher capture rate necessary, and hence indirectly a higher digestion rate, as has been reported in other marine invertebrates (Calow 1975). In any case, the amorphous nature of the particles and the lack of skeletons or other protective coverings may also facilitate rapid digestion. Suspension feeders that rely on particles of lower nutritional value have generally been reported to have higher capture, digestion, and assimilation rates as a requisite strategy to meet their metabolic energy requirements (Emlen 1973).

The digestive mechanism is another important factor in understanding the high capture rate observed in *C. everta*. The gastrodermis of hydroids has rather large digestive cells that phagocytose pieces of prey items and whole particles (Bouillon & Houvenaghel 1970). Extracellular digestion is quite rapid and intracellular digestion begins near the mouth (Bouillon in press) and, hence, by feeding on particulate matter, the polyps quickly assimilate prey. The high digestion rate is consistent with the interesting finding that polyp stomach contents exhibited little variation over the diel cycle. Rapid extracellular digestion makes it possible for the food collected by the polyps to be distributed rapidly to the rest of the colony via the stolons (Rees 1971).

Role in benthic food webs and in the plankton-benthos relationship

On average for the full range of food-particle sizes and all seasons of the year *Campanularia everta* ingests the equivalent of 19% (5 to 74%) of its weight daily. These values mean that 1 µg C of polyp biomass ingests 69.6 µg C of food yr⁻¹. The total biomass ingested by *C. everta* meets the energy demand for growth, respiration and reproduction (Coma 1994). The mass-specific ingestion rate of *C. everta* is similar to values observed in other hydroid species (e.g. 25.9% *Eudendrium racemosum*, Barange et al. 1989; 2.3 to 19% *Clava multicornis*, Paffenhöfer 1968) but is an order of magnitude greater than in anthozoan species (e.g. 0.2 to 1% *Paramuricea clavata*, Coma et al. in press; 4.5 to 6% *Aiptasia pallida*, Clayton 1986). Rates of ingestion observed in *C. everta* are similar to those recorded in other benthic filter feeders. For example, 2 species of bivalves (*Mytillus*) ingest 17% of their weight daily (Navarro & Winter 1982). Other filter feeders such as ascidians (Fiala-Medioni 1974) and

sponges (Reiswig 1981) rarely ingest more than 10% of their weight daily. The data shown could place hydroids among the most active benthic suspension feeders, though their biomass may reach less than 10% of the community (Gili & Ros 1985). In fact, though species such as *C. everta* ($95 \text{ kJ m}^{-2} \text{ yr}^{-1}$) and *E. racemosum* ($420 \text{ kJ m}^{-2} \text{ yr}^{-1}$; Barange & Gili 1988) can retain a significant amount of energy within the community through feeding activity, other filter feeders, represented by greater biomass, retain a more energy ($>50 \times 10^3 \text{ kJ m}^{-2} \text{ yr}^{-1}$ in bivalves, Griffiths & Griffiths 1987; $>20 \times 10^3$ in ascidians, Klumpp 1984).

The high, sustained prey capture rate observed for *Campanularia everta* under natural conditions, together with the high assimilation efficiencies estimated for other species (in certain cases in excess of 70 or 80%, Paffenhöfer 1968, Arndt 1984), and the high growth efficiencies (K_1 : 29%, K_2 : 48% in *C. everta*, Coma 1994; K_1 : 39 to 49% in *Clava multicornis*, Paffenhöfer 1968; K_2 : 58% in *Eudendrium racemosum*, Barange et al. 1989) appear to be consistent with the high growth rates for hydroids recorded both *in situ* and in the laboratory (Hale 1973, Llobet et al. 1991). These results together suggest that hydroids could be one of the most trophically active components of littoral benthic communities, though many other species must be studied in order to confirm this hypothesis. This study has shown that, at the community level, hydroids are capable of assimilating very large amounts of organic carbon. This source of carbon is exploited by small predators (McLeod & Valiela 1975) allowing transfer to higher trophic levels. The role of hydroids in coastal food webs be much may greater than previously believed.

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