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Prey capture by a benthic coral reef hydrozoan

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Abstract The natural diet and prey abundance of the benthic coral reef hydrozoan *Nemalécium lighti*, a common tropical species, were studied by analysing the gastrovascular contents of polyps. Prey capture was estimated from 10 samples collected at 3-h intervals during a single diel cycle (1–2 September, 1995) in the San Blas Islands (Panamá). Prey size ranged from 5 to 550 μm , with invertebrate larvae being the main contributor to the diet of the species. Prey items were found in 56–88% of the polyps over the entire diel cycle. Gastrovascular contents varied between 0.93 and 2.13 prey items per polyp. These capture incidences are among the highest reported for cnidarian species. Such rates would allow for high production rates for *Nemalécium lighti*, consistent with reports of the species' fast growth and high reproduction rates. The observations suggest that some hydrozoans may be active heterotrophic components in coral reef ecosystems.

Introduction

Several authors have conducted a variety of studies on heterotrophic feeding in coral reef ecosystems. Prey capture incidence in the species studied have been low, ranging between 0.02 and 1.8 prey items per polyp in hexacorals and between 0.02 and 0.7 prey items per polyp in octocorals (see Table 4 in Ribes et al. 1998). Most of the studied species are among the dominant members of the community in terms of biomass. Little work has been done on small and uncommon organisms such as hydrozoans, which have been considered

as unimportant components of coral reef communities. Several recent studies on the trophic ecology of hydrozoans in temperate and polar seas have shown that hydrozoans can capture large amounts of planktonic prey (e.g. Coma et al. 1995, Gili et al. 1996a,b) and their role in reef trophodynamics is unknown.

One of the most commonly postulated causes for the low capture rates on zooplankton prey items by suspension feeders in coral reef systems was low zooplankton concentration (Johannes et al. 1970). However, the methodology used by Johannes et al. (1970) in the evaluations of zooplankton levels in coral reef systems was subsequently shown to be inappropriate for yielding reliable information on abundance, diversity, and biomass, primarily because a major portion of the epibenthic zooplankton are demersal (Alldredge and King 1977). In situ observations (Hamner and Carleton 1979) and samples collected with pumps or traps (Alldredge and King 1977) have shown that zooplankton densities are usually over $1-4 \times 10^3 \text{ ind. m}^{-3}$, with swarms of copepods hiding among the corals during the daytime and ascending to the water column at night. These high density levels, together with the depletion of microbial communities (Lindley and Koop 1986), phyto- and zoo-plankton (Glynn 1973) observed on coral reefs, suggest that the planktonic community is an important source of food for benthic organisms in coral reefs.

High diversity of hydrozoans has been reported for the Caribbean Sea, Red Sea, Indian Ocean, and Indo-West Pacific (Calder 1991; Gili and Hughes 1995; Gravier-Bonnet and Mioche 1996). Nevertheless, there have only been a few quantitative studies on hydrozoan feeding (Caribbean: Wedler 1975; Lewis 1992; Réunion Island: Gravier-Bonnet and Mioche 1996). The diet and capture rates for most tropical hydrozoans are poorly known, except for *Millepora complanata*, a species with a calcareous skeleton (Lewis 1992). Zooplankton capture rate in *M. complanata* is several times higher than the species' basal energy requirements

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(Lewis 1992) and is similar to those observed in temperate-water benthic hydrozoans (e.g. Coma et al. 1995; Gili et al. 1996b). This suggests that the importance of plankton feeders other than corals may have been underestimated on reefs. The goals of this study were to examine the natural diet and to quantify the prey capture incidence of the hydroid *Nemalécium lighti* (Hargitt), a common tropical species (Gravier-Bonnet and Mioche 1996), as well as to point out the potentially important trophic role of non-dominant sessile benthic fauna in coral reef ecosystems.

Materials and methods

Nemalécium lighti

Nemalécium lighti, a thecate species of the Family Haleciidae, is a common non-symbiotic hydroid that forms dense reptant colonies with creeping hydrorhizae from which arise erect hydrocauli up to 20 mm in height. Each hydrocaulus has between four and eight hydranths (polyps) 1.3 mm high with 25 tentacles 0.7 mm in length and microbasic mastigophores around the mouth. Several polyps on each hydrocaulus have one large nematodactyl bearing many pseudostenostels 26–29 µm in size (Calder 1991). *N. lighti* is present all year round and in some areas is one of the most abundant hydroid species (Gravier-Bonnet and Mioche 1996).

Sampling

The study was carried out at the Smithsonian Tropical Research Institute facilities in the San Blas Islands, Panamá. *Nemalécium lighti* colonies were collected at Pinnacles reef (identified as "Pico Feo 16–22" in Fig. 1 of Robertson 1987), an area of mixed sand and hardground substratum with scattered clumps of hard coral between 0.5 and 10 m depth. The population of *N. lighti* examined in this study was located on a population of the sponge *Iotrochota birotulata* (Higgin) at a depth of 4–6 m. From the surface of different sponges, a total of 5 colonies of *N. lighti* were randomly collected every 3 h during a single diel cycle. A total of 10 samples were collected from 10:00 hours on 1 September to 13:00 hours on 2 September, 1995. Hydroids were immediately placed in 10% formaldehyde solution in sea water to halt further digestion.

Nemalécium lighti colonies develop on a wide variety of substrates (Gravier-Bonnet and Mioche 1996, and personal observation). We sampled colonies growing on the sponge *Iotrochota birotulata* to minimize microhabitat heterogeneity and to reduce the possibility of sampling a different species. *N. lighti* at the study area is also present on other substrates, and we expect that substratum has no significant affect on either the diet or capture rate.

Gastrovascular contents and prey numerical abundance

The diet was established by examining 50 randomly selected polyps per sample in the laboratory (10 from each colony). The contents were isolated by dissection, identified to general taxonomic levels and counted. The maximum dimension of each prey item was recorded. From the maximum dimension, we estimated volume of each prey assuming the nearest geometrical shape. Prey biomass was estimated on the basis of biovolume using conversion factors to wet weight (1.025, Hall et al. 1970), dry weight (13% of wet weight, Murphy 1971) and carbon content (45% of dry weight, Biswas and Biswas 1979).

The assumptions of normality and homoscedasticity were tested using the Kolmogorov-Smirnov and Levene tests, respectively. Since these assumptions were not satisfied, differences in prey numerical abundance, prey size, and prey biomass among the samples were analysed using the Kruskal-Wallis test. All values have been expressed as the means \pm the standard error.

Dry weight of hydranths including the hydrocaulus (from below the hydranth to where it branched to another hydranth) was measured by drying five groups of 100 hydranths each. Colonies were maintained in filtered sea water for several hours prior to measurement. The carbon content of each replicate sample was determined using a Carbo-Erba model 1500 elemental analyser.

Results

Diet

Nemalécium lighti captured a broad spectrum of planktonic and epibenthic prey items. Prey size ranged from 5 µm (particulate organic matter) to 550 µm (appendicularians). Bivalve larvae and copepod nauplii had the largest body size among the most common prey items (Table 1). Numerically, the most frequent prey items were benthic invertebrate larvae (38%, a third of which were bivalve larvae), and diatoms (37%, Table 1). No temporal trend was observed for these prey items which were regularly present in the polyps throughout the diel cycle. Particulate organic matter (POM), which includes organic detritus but also unidentifiable prey items in an advanced stage of digestion, was also regularly found. Due to the difficulties in assigning a numerical value to particulate organic matter (i.e., they easily break during dissection), they have not been included in Fig. 1 nor in further calculations. None of the other prey items contributed more than 10% to the diet of this species, and the frequency of these prey items was less regular, with different peak times of capture for each type of prey (Table 1). In terms of carbon, invertebrate larvae made up over 60% of the prey biomass captured by *N. lighti*, with eggs (mainly copepod eggs) and nauplii making a significant but small contribution. The numerically abundant diatoms had a relatively low contribution in terms of carbon.

Capture incidences

The large amount of diatoms observed in the gastrovascular contents might be considered incidental. However, diatoms have been suggested as the main food source for this species in Réunion Island reefs (Gravier-Bonnet and Mioche 1996) where diatom digestion has been observed (N. Gravier-Bonnet, personal communication). Nevertheless, due to the relatively low contribution of diatoms in terms of carbon and because the number of prey captured would appear to be inflated if they are treated the same as the

Table 1 **A** Number and type of prey items captured over the sampling period (1 to 2 September 1995). **B** Total number and % of total, and biomass and % of total biomass of prey items observed in 500 polyps and percentage of the polyps with prey. **C** Average (\pm SE) prey size by prey category

Prey item	A Time of day (h)										B Total prey in 500 polyps				C Prey size	
	10:00	13:00	16:00	19:00	22:00	1:00	4:00	7:00	10:00	13:00	N	% of Total	Biomass (μ g C)	% of Total	Average (μ m)	SE
Bivalve larvae	9	9	19	9	19	6	20	16	7	21	135	14	8.59	44.5	110	4
Invertebrate larvae ^a	11	18	48	7	26	38	45	20	13	12	238	24	4.13	21.4	49	2
Eggs	2	5	6	5	4	17	11	9	8	10	77	8	1.32	6.8	47	4
Nauplii	7	2	11	0	4	4	2	3	0	6	39	4	1.25	6.5	143	10
Copepods	0	0	0	0	0	2	1	0	0	1	4	0.4	0.47	2.4	186	42
Tintinnids	8	7	6	1	0	7	4	8	9	18	68	7	0.45	2.3	57	4
Cysts	1	0	0	1	0	1	0	0	2	0	5	1	0.10	0.5	40	8
Crustacean fragments	1	0	2	0	0	0	0	2	0	0	5	1	0.09	0.5	91	17
Amphipods	0	0	0	0	0	0	0	0	0	1	1	0.1	0.06	0.3	65	–
Appendicularians	0	0	0	0	1	0	0	0	0	0	1	0.1	0.01	0.1	550	–
Dinoflagellates	0	2	5	1	4	1	12	6	3	5	39	4	0.001	< 0.01	36	3
Phytoplankton cells	0	0	3	0	1	1	0	0	0	0	5	1	0.001	< 0.01	21	6
Ciliates	0	0	3	0	1	0	0	0	0	0	4	0.4	0.001	< 0.01	29	5
Diatoms	8	31	41	33	61	15	30	68	42	30	359	37	2.83	14.7	54	2
Organic matter	22	46	45	28	36	54	28	18	11	11						
Polyyps with prey	N 38	44	43	30	41	40	37	37	28	38						
	% 76	88	86	60	82	80	74	74	56	76						

^aExcluding bivalve larvae

other prey items, prey abundance in Fig. 1 has been represented with and without diatoms.

Prey items were found in 56–88% of the polyps at all times during the sampling period (Table 1). Seventy four percent of the polyps with prey had more than one prey item in their gut, and 45% of the polyps with more than one prey had items in different stages of digestion. These facts suggest that polyps feed continuously and that they do not stop feeding after a prey item is captured.

Prey abundance ranged between 0.93 and 2.13 prey items per polyp (1.07 and 2.94 if diatoms are included) and there were significant differences in the number of prey items per polyp over the diel cycle (Kruskal-Wallis test, $H = 37.14$, $df = 9$, $P < 0.0001$; Fig. 1a). Prey size ranged between 43.58 and 119.87 μ m (41.88 and 87.46 if diatoms are included) and varied significantly over the study period (Kruskal-Wallis, $H = 86.15$, $df = 9$, $P < 0.0001$; Fig. 1b). Prey biomass ranged between 0.08 and 0.12 μ g C per polyp and did not vary significantly over time (Kruskal-Wallis test, $H = 12.38$, $df = 9$, $P = 0.1927$; Fig. 1c).

Discussion

Nemalécium lighti is one of the first tropical hydrozoans whose natural diet has been studied and quantified in situ. Although most species of coral capture prey mainly at night (Muscatine 1973), the presence of fresh and

partially digested prey items in all the samples of *N. lighti* suggests that this hydrozoan species captured prey over the entire diel cycle. This finding was consistent with field observations of polyp expansion both during the daytime and at night. Similar results had been reported previously for the hydrocoral *Millepora complanata* (Lewis 1992).

Although *Nemalécium lighti* captured a wide variety of prey types, the mean prey size captured by the species was small (69 μ m) in contrast to the dominance of copepods in the diet of *Millepora complanata* (Lewis 1992). A similar diversity in prey types has also been documented for temperate species (e.g., Coma et al. 1995; Gili et al. 1996b) and confirms that hydrozoans are capable of feeding on a broad range of prey types. This broad range includes, aside from zooplankton, organisms such as protozoans and phytoplankton.

In order to obtain an estimate of the daily intake rate of the species, we used our data on prey per polyp adjusted for digestion rate, using digestion time values from the literature. Digestion time has been examined for several hydrozoan species. Because digestion time is dependent on temperature and temperature is high and rather constant throughout the year at the study site (26.6–30.0°C, D'Croz and Robertson 1997), we only used values reported for relatively high temperatures ($\geq 18^\circ$ C). Polyp size and prey type are also important determinants of digestion time. Literature values of digestion time for species with a relatively similar polyp size (polyp diameter between 0.25 and 0.6 mm) and carried out with similar prey types (i.e. mainly eggs and

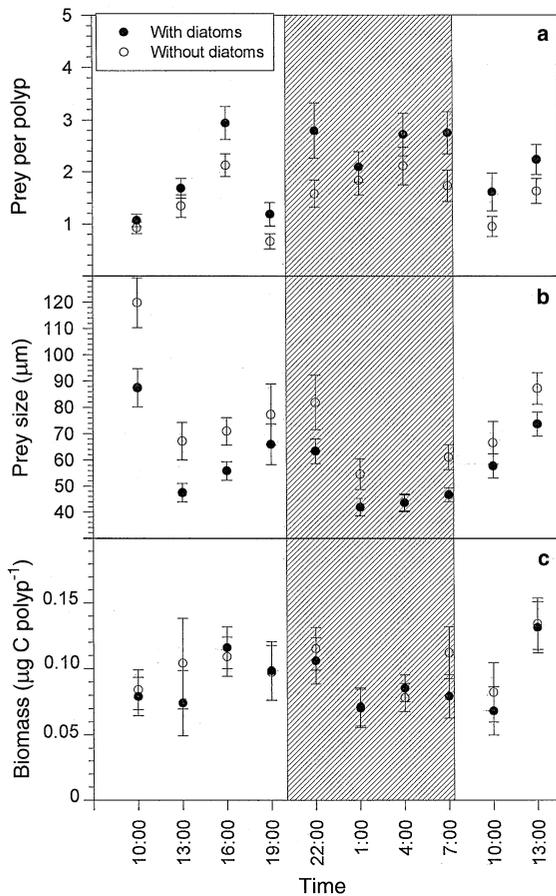


Fig. 1a–c Variation in the mean (\pm standard error) number of a prey items b prey size, and c prey biomass captured per hydranth during the sampling period (1–2 September, 1995). Stippled area shows high samples

invertebrate larvae) range from 2 h (*Campanularia everta* at 18°C) to 4 h (4 h for *Clava multicornis* at 16–20°C; 3–4 h for *Garveia franciscana* at 23–26°C; 4 h for *Eudendrium racemosum* at 20°C, see Gili and Hughes 1995). *Millepora complanata* was not considered because its diet consist largely of copepods (Lewis 1992).

Prey capture rate by single polyps were calculated using the model of Coma et al. (1994) assuming a conservative digestion time of four hours and without considering diatoms (see detailed explanation of the model in Gili et al. 1996b). The estimated range was 8.9 to 20.4 prey, or 0.40 and 0.92 $\mu\text{g C}$ per polyp per day. Dry weight values per hydranth were 1.83 μg (± 0.15), or 0.69 $\mu\text{g C}$ ($\mu\text{g C}/\mu\text{g dry weight} = 0.377 \pm 0.031$), or 0.14 $\mu\text{g N}$ ($\mu\text{g N}/\mu\text{g dry weight} = 0.075 \pm 0.009$). For a typical hydrant of 0.69 $\mu\text{g C}$, the daily amount of prey ingested amounted to 58–133% of its own weight, or a turnover time of 1.72–0.75 days. Assuming a conservative assimilation efficiency of 70% (between 70 and 80%, Zamer 1986), prey biomass assimilated daily was the equivalent of between 41 and 93% of body weight.

Feeding rates determined over short time intervals may not be representative of long-term values, and the lack of replication and lack of data on either flow speed, or prey density during the cycle make it difficult to generalise from our data. However, the relative constancy of parameters such as temperature and nutrients together with that of phytoplankton, zooplankton and flow speed at the study site (D’Croz and Robertson 1997, and unpublished data), suggest that the high frequency of prey capture estimated for *Nemalécium lighti* along the single diel cycle examined may not be unusual.

The high feeding observed in *Nemalécium lighti* appears to explain the ability of this species to sustain high production rates (i.e. growth and/or reproduction). Qualitative observations of *N. lighti* on the coral reefs off Réunion Island (Gravier-Bonnet and Mioche 1996) have shown the species to be capable of colonising all available space in crevices between the corals in just one week. These findings agree with reports by Wedler (1975) from coral reefs off Santa Marta (Colombia), where colonies of *Sertularia speciosa* grew between 3 and 6 cm in just 6 days, more or less equivalent to doubling of the species’ biomass in one week. Similar growth rates have been recorded for various species in more temperate regions, such as in the Mediterranean Sea (see Gili and Hughes 1995 for review). Reproduction rates are also high for *N. lighti*. Gravier-Bonnet and Mioche (1996) reported between two and three spawning periods per year in this species. The existence of several spawning periods contrasts with reports for hydrozoans in other regions such as the Mediterranean Sea, North Pacific, and North Atlantic (Boero and Fresi 1986; Gili and Hughes 1995; Coma et al. 1996), where a single spawning period each year is the norm. The cost of sexual reproduction in *Campanularia everta*, the only species in which reproductive effort has been quantified (Coma et al. 1996), is estimated as approximately half the total energy demand of that species (Coma et al. 1998). In conclusion, high rates of heterotrophic feeding alone can support the high rates of growth and reproduction previously reported for *Nemalécium lighti*. In this respect, *N. lighti* differs from the dominant organisms on coral reefs (i.e. hexacorals and octacorals), in which symbioses with autotrophs contribute a substantial portion of their carbon requirements. Our observations suggest that the trophic role of some hydrozoans in coral reef communities has been underestimated.

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