

## **The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example**

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Zool. Verh. Leiden 323, 31.xii.1998: 99-105, tabs 1-2.— ISSN 0024-1652/ISBN 90-73239-68-0.

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**Key words:** benthic passive suspension feeders; shallow marine ecosystems; hydroids.

Benthic suspension feeders are abundant in littoral and shallow sub-littoral ecosystems, where they feed on the plankton and on organic matter suspended in the water column. Recent studies indicate that active suspension feeders with powerful water filtration mechanisms (e.g., bivalve molluscs) may exert an important influence on the abundance and production of phytoplankton, and probably zooplankton as well. Passive suspension feeders, such as hydrozoans, have received less attention, and their effect on shallow planktonic communities is poorly understood. This paper presents evidence that hydrozoans, which make only a minor contribution to benthic community biomass, capture large amounts of zooplankton and seston, and that they may play an important role in transferring energy from pelagic to benthic ecosystems over a wide range of latitudes.

Recently, assessments of the individual components of food webs within or between different marine ecosystems have been attempted (Margalef, 1978; Paine, 1988; Goldwasser & Roughgarden, 1993). In particular, attention has focused energy transfer between the pelagic and benthic ecosystems (Bonsdorff & Blomqvist 1993). In the open ocean energy transfer flows vertically, gradually descending through the water column, with considerable reduction of surface production by the time it reaches the bottom (Smetacek, 1984). In contrast, in shallow waters benthic organisms have more immediate access to planktonic production, because of the proximity of the photic layer, and because of tidal or wind vertical mixing. Benthic suspension feeders in shallow marine ecosystems are responsible for a large proportion of the energy flow from the plankton to the benthos (Parsons et al., 1979). For example, benthic organisms that are active suspension feeders, such as bivalves, have been shown to have a major impact on the planktonic ecosystems in which they feed (Jørgensen, 1990). They capture large amounts of phytoplankton and may regulate primary production directly, and regulate secondary production indirectly (Dame et al., 1980;

Officer et al., 1982; Cohen et al., 1984). Models of energy flow have ignored passive suspension feeders such as hydrozoans and gorgonians because their impact has been assumed to be minor, on account of their negligible contribution to the biomass of benthic communities (Boero, 1984; Gili & Ros, 1985). It is clear from their diets that some passive suspension feeders, which capture small particles, zooplankters and organic matter, may also play a significant role in pelagic-benthic coupling (Sebens, 1987). Recent data on benthic hydrozoans in a number of different areas around the world have yielded capture rates for hydrozoans of over  $10^5$  prey items  $m^{-2} day^{-1}$  (Coma et al., 1995). This high level of feeding fuels the high rates of growth and reproduction shown by modular hydrozoans (Hale, 1973; Coma et al., 1996). This paper reviews the recent literature and presents the case that passive suspension feeders, even the most inconspicuous organisms such as hydrozoans, need to be taken into account when assessing energy flow into shallow benthic assemblages.

In our recent studies of the feeding of benthic hydroids samples were taken regularly, every 2 to 4 h over 24h periods. On each occasion a minimum of 50 hydranths were dissected and all the items present in the gastric cavity were identified and measured. Prey biomass was estimated and the mass-specific ingestion rate was calculated, as the percentage ratio between prey biomass ingested daily and hydranth biomass. The dry weight of hydranths was measured by drying several replicates of 100-200 hydranths to constant weight at 70° C. Daily capture rates (mean prey number hydranth<sup>-1</sup> day<sup>-1</sup>) were calculated for each species on the basis of the number of items per hydranth sampled and prey digestion times (Gili et al., 1996a). Digestion times were studied in situ using incubation chambers or were estimated from other studies. Capture rates, mean number of prey items  $m^{-2} day^{-1}$ , were estimated on the basis of the natural density of the species considered. To determine the composition and relative abundance of potential prey items, concurrent plankton samples were taken from around the hydrozoans (Coma et al., 1995).

Table 1 presents the results for all the species. The diet of most species was varied, consisting largely of algal cells (e.g. *Nemalecium lighti*) and zooplankton (e.g. *Eudendrium racemosum* or *Tubularia larynx*). In some species particulate organic matter (POM) also contributed a significant portion of the diet (e.g. *Campanularia everta* = *Orthopyxis crenata*). Benthic organisms (e.g. nematodes or small bivalves) were found only occasionally. The diet of *Silicularia rosea* was almost exclusively benthic diatoms, captured when the bottom sediment was disturbed and resuspended. The results confirm that benthic hydroids can feed on a great variety of prey. Apart from zooplankton they can feed on Bacteria, Protozoa, phytoplankton, detritus, and even on metabolites of algal origin or dissolved organic matter (see Bouillon, 1956-57; 1995).

The maximum size of the prey ingested varied between species. Hydrozoans that fed on zooplankton, e.g., *E. racemosum* and *T. larynx*, were able to capture large prey items because the mouth of the hydranths is able to expand. The mean size of *E. racemosum* hydranths was 600  $\mu m$  (table 1), but this hydrozoan was able to capture crustaceans of up to 1000  $\mu m$  in size. The prey size in hydrozoans that fed on algal cells (e.g. *S. rosea* and *N. lighti*) did not exceed 50  $\mu m$ .

The numbers of prey items per hydranth of *Obelia geniculata*, *T. larynx* and *E. racemosum* were proportional to the density of potential prey in the habitat, and consequently the capture rates were highest when zooplankton abundance in the water

Table 1. Different trophic features analysed for six species of hydroid following the same experimental methodology: for each species two diel cycles, collected every 2 or 4 h, and a minimum of 1200 polyps per species, were examined (polyp size: diameter of expanded tentacle crown).

	<i>Silicularia rosea</i> Meyen, 1834	<i>Nemalecium lighti</i> (Hargitt, 1924)	<i>Campanularia everta</i> Clarke, 1876	<i>Eudendrium racemosum</i> (Cavolini, 1785)	<i>Tubularia larinx</i> Ellis & Solander, 1786	<i>Obelia geniculata</i> (Linnaeus, 1758)
Geographic area	King George I. (South Shetland Is)	Panama (Caribbean Sea)	Catalonia (NW Mediterranean)	Catalonia (NW Mediterranean)	Scotland (NE Atlantic)	Arauco Gulf (SE Pacific)
Polyp size (mm)	0.4	0.3	0.25	0.6	1-1.2	0.3
Habitat	Tide pools	Sublittoral	Sublittoral	Sublittoral	Sublittoral	Sublittoral
Growth form	replant	replant	replant	erect	erect	replant/erect
Life cycle	no medusa	no medusa	with medusoid form	no medusa	with well developed medusa	with well developed medusa
Dominant prey (mean % of the diet)	Diatoms (95) Eggs (2)	Diatoms (32) POM (21) Invertebrate larvae (20)	POM (88) Copepod eggs (7)	Copepod eggs (28) Copepod adults (22) Invertebrate larvae (10)	Copepod eggs (28) Copepod adults (22) Cladocera (21)	Faecal pellets (48) Copepod eggs (29) Diatoms (17)
Mean prey size (in $\mu\text{m}$ ) and range	38.6 $\pm$ 0.32 (9.7-436.5)	50 (5-325)	54.8 (6-110)	350 (40-1050)	710 (520-930)	47.7 (20-420)
Observed mean prey number hydranth <sup>-1</sup> *	61.2 $\pm$ 6.7 (818)	3.5 (14)	4.4 (8)	2.5 (9)	3.4 (26)	9.3 (40)
Estimated mean prey number hydranth <sup>-1</sup> day <sup>-1</sup>	225.8	35.7	18.6	5.4	36.0 **	124.2 **
Estimated mean prey number m <sup>-2</sup> day <sup>-1</sup>	4.4 $\times$ 10 <sup>6</sup>	3.97 $\times$ 10 <sup>5</sup>	4.3 $\times$ 10 <sup>5</sup>	1.2 $\times$ 10 <sup>5</sup>	4.5 $\times$ 10 <sup>5</sup>	3.2 $\times$ 10 <sup>6</sup>
mg C removed m <sup>-2</sup> day <sup>-1</sup>	66	6	6.4	12	225	48
Prey biomass hydranth <sup>-1</sup> day <sup>-1</sup> (in $\mu\text{g}$ )	0.18	2.4	0.3	0.4	8.5	28.1
Diel mass-specific ingestion rate (in %)	12.6	136	19	39.1	89.9	113.2

\* Maximum prey number observed.

\*\* Prey capture during reproductive period

column was highest. The highest diel capture rates were recorded in *O. geniculata*, which inhabits the most productive waters of all the species studied. The large number of prey items per hydranth captured by *S. rosea* (up to 800, many more than in any other species), indicates that this hydroid is capable of taking full advantage of episodes of temporary high prey availability to feed intensely. In all the species studied the mass-specific ingestion rate was over 10 % of the hydranth biomass. In *N. lighti* and *O. geniculata* the rate was greater than 100 %, which means that the hydranths ingested more than their own weight in prey biomass daily (table 1). The high mass-specific ingestion rates in hydrozoans are similar to the estimates for some bivalves and tunicates (active suspension feeders), ranking them among the most voracious suspension feeding organisms (Klumpp, 1984; Griffiths & Griffiths 1987; table 2).

Hydrozoans account for a small fraction of total community biomass, and the amount of total energy they ingest is less than that recorded for dense populations of active suspension feeders such as bivalves. Nevertheless, the high capture rates recorded in all the species studied, and their often high densities, indicate that hydroids may play a significant role in energy transfer from the plankton to the benthos in shallow marine ecosystems. They captured up to  $10^5$  prey items  $m^{-2} d^{-1}$ . The highest capture rates recorded were very similar to the rates observed in laboratory experiments in which feeding rates were maximal as food was not limiting (Gili & Hughes, 1995). Under natural conditions, colony growth rates may be very high, with

Table 2. Ingested organic Carbon by other groups of suspension feeders.

	Species	mg C ingested $m^{-2} day^{-1}$	Reference
Sponges	<i>Mycale lingua</i>	29	Pile et al. 1996
	<i>Baikalospongia bacillifera</i>	1970	Pile et al. 1997
	several tropical species	range: 80-1800	Reiswig 1971
Ascidians	<i>Pyura stolonifera</i>	3277	Klumpp 1984
	<i>Halocynthia papillosa</i>	21	Fiala-Medioni 1974
Anthozoans	<i>Paramuricea clavata</i>	range: 12-85	Coma et al. 1994
	<i>Plexaura flexuosa</i>	1	Ribes et al. in press
Bivalves	<i>Aulacomya ater</i>	1787	Griffiths and King 1979
	<i>Chlamys islandica</i>	3621	Vahl 1981
	<i>Crassostea virginia</i>	573	Dame 1976
	<i>Geukensia demissa</i>	30	Kuenzier 1961
	<i>Mercenaria mercenaria</i>	351	Hibbert 1977
	<i>Ostrea edulis</i>	range: 9-30	Rodhouse 1979
Polychaeta	<i>Lanicea conchilega</i>	2.7	Buhr 1976

duplication of colony biomass in less than a week (Hughes, 1983; Llobet et al., 1991), in which nearly 40 % of energy consumption may be invested in growth during non-reproductive periods. In fact, hydroids are like plants. They have indeterminate growth, the rate of which is determined by energy input, and will not grow at all, but will survive indefinitely, if energy is limiting (Gili & Hughes, 1995).

Since prey capture rates varied with potential prey density, it may be that none of the species studied attained its maximum capture rate. The increase in capture rates with availability of potential prey items indicates that hydrozoans are adepagous and respond quickly to the presence of food, showing a Type 1 functional response (Valiela, 1995) typical of suspension feeders below the threshold concentration of food particles. Our results indicate that feeding in hydrozoans is opportunistic, in that they capture the most readily available prey, plant or animal, living or dead. The diet of the Antarctic hydrozoan *S. rosea*, though consisting of a single prey type, was also opportunistic, in that this species made use of the presence of potential prey in the surrounding water column brought about by resuspension of the bottom sediment (Gili et al., 1996b). Thus, *S. rosea* exploited an available resource, enabling it to complete its biological cycle in the short Austral summer before its habitat was iced over.

As a general trend reproduction coincided with the periods of high prey consumption. This indicates that feeding rates are directly important in reproduction, be it either the production of medusae (*O. dichotoma*), which may then take advantage of the high zooplankton densities, eumedusoids (*C. everta*) or actinulae (*T. larynx*). *S. rosea*, *E. racemosum* and *N. lighti*, which had the lower prey consumption rates, were not reproducing at the time of our observations (table 1). These three species, together with about 50 % of benthic hydroids lack a pelagic medusa stage (Bouillon, 1985; Boero & Bouillon, 1993; Cornelius, 1992); their planula larvae are formed in fixed gonophores. When the medusae stage is present in the life cycle our perception of food web functioning cannot be clearly understood without considering also the impact of this pelagic stage. The medusa represents matter exported to the plankton, it feeds in the plankton and produces larvae which, if successful, become part of the benthos. Thus this is another route in which energy gathered from the plankton becomes incorporated into the benthos.

Such life cycle links within food webs open wide and unexpected scenarios to the understanding of ecosystem functioning. A bloom of medusae (including those of scyphozoans for which there are not similar quantitative data), highly impacting on planktonic or nektonic production might be due to efficient incorporation of planktonic matter by benthic hydroids (or scyphistomae). The causes of patterns observed at a given moment (e.g. at the time of a jellyfish bloom) might reflect the success of the feeding by the benthic stage over the preceding months. Modular hydroids, which have a potential growth rate which approaches exponential (Gili & Hughes, 1995), and scyphistomae, which too may have very high rates of reproduction by fission, may, in the appropriate season produce many millions of medusae.

This aspect of the ecological impacts of these organisms remains to be quantified. However, in the light of the present results it is undeniable that hydroids play a considerable role in pelagic-benthic coupling, comparable to gorgonians and some sponges (tabs 1-2). Ecosystem functioning has been mainly linked to interspecific

energy fluxes (food webs) and biogeochemical cycles, whereas intraspecific fluxed life cycles have been studied within separate frameworks. Time is ripe, however, to integrate these approaches, as suggested by Boero et al. (1996), with a more complete appreciation of the processes and patterns regulating the way marine systems work.

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