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Natural diet and grazing rate of the temperate sponge *Dysidea avara* (Demospongiae, Dendroceratida) throughout an annual cycle

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ABSTRACT: Sponges are one of the major invertebrate groups inhabiting hard-bottom communities worldwide. In this study, we measured *in situ* rates of grazing on DOC (dissolved organic carbon), POC (particulate organic carbon), and pico-, nano- and microplankton for the common temperate sponge *Dysidea avara* throughout a yearly cycle. The natural diet of the species was highly heterogeneous and included procaryotes (heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp.) and eucaryotes (protozoa, phytoplankton, and ciliates) ranging in size from 0.5 ± 0.3 (heterotrophic bacteria) to 70 ± 0.3 µm (pennate diatoms). Procaryotic cell clearance rates were higher than those for the other groups, suggesting a higher grazing efficiency upon these prey types. Specific clearance rates showed a pattern of decrease with sponge size increase, although they did not vary with prey concentration or with temperature. Overall, procaryotes contributed 74 ± 14% of the total ingested carbon, pico- and nano-eucaryotes contributed 11 ± 3%, and phytoplankton contributed 11 ± 10%. Therefore, *Dysidea avara* obtained 85% of its ingested carbon from the fraction smaller than 5 µm and 15% from the fraction larger than 5 µm. However, the partial contributions of the different groups varied seasonally, following the planktonic composition of the water column. During winter, phytoplankton was an important component of the total uptake (26%), whereas during the rest of the year it contributed less than 7% of the total uptake. The capacity of this sponge to feed on a broad size range of prey allowed it to maintain rather constant food uptake throughout the year. These results show the importance of particle type (size) for selective uptake in sponges, as well as the relevance of phytoplankton in the sponge diet. This trophic plasticity may represent an advantage for the species because it attenuates the effects of seasonal fluctuations in the planktonic community. This plasticity in trophic ecology may be one of the main factors contributing to the worldwide abundance and distribution of sponges despite large spatial and temporal variations in food sources.

KEY WORDS: Suspension feeding · Natural diet · Grazing rate · Prey selection · Sponges · *Dysidea avara* Mediterranean Sea

INTRODUCTION

Recent studies show that some benthic suspension feeders play a crucial role in energy transfer processes in coastal marine ecosystems (e.g. Cloern 1982, Officer et al. 1982, Kimmerer et al. 1994, Gili & Coma 1998). In this regard, attention should be paid to those suspension feeders responsible for the coupling of the pelagic and benthic systems. However, most of this work has been carried out on molluscan populations dwelling on soft bottoms, and little is known about dense suspension-feeder populations on hard substrates (but see Pile et al. 1997).

Sponges are one of the major invertebrate groups inhabiting hard-bottom communities worldwide. They filter large volumes of water (up to 1 l per hour and cm^3 of body volume, Reiswig 1971), with retention efficiencies between 75 and 99% (Reiswig 1971, 1975, Wilkinson 1978, Pile et al. 1996). Past and present studies have shown that grazing rates of some sponges are within the same range (29 to 1970 mg C m^{-2} d^{-1}, Reiswig 1974, 1981, Pile et al. 1996, 1997) as in certain molluscan species (9 to 3621 mg C m^{-2} d^{-1}, see Griffiths & Griffiths 1987 for review). Therefore, abundant

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sponge populations may exert an important grazing impact on their habitats. Despite the importance of sponges in a number of ecosystems, the diversity of forms, and the many different habitats they occupy, diet and grazing rates of sponge species under natural conditions are still poorly known.

Laboratory experiments, indirect measurements of particle uptake, and sampling of ambient and exhalant water samples collected *in situ* have shown that sponges can feed on a wide spectrum of food sources (Reiswig 1971, Frost 1987, Pile et al. 1996). This variety of food sources ranges from dissolved organic carbon (DOC) to phytoplankton (Schmidt 1970, Frost 1987), and in extremely food-poor environments even zooplankton can be captured (Vacelet & Boury-Esnault 1995). However, the main research effort on sponge feeding has focussed on plankton <2 µm, both in laboratory studies (van der Vyver et al. 1990, Riisgård et al. 1993, Turon et al. 1997) with artificial food and in field studies with natural diets (Reiswig 1971, 1975, Pile et al. 1996, 1997). This is due to the morphological characteristics of the filtration mechanisms, which, based on fine canals and groups of flagellate choanocytes, are able to capture particles smaller than 2 µm very efficiently (Simpson 1984). Nevertheless, as already pointed out above, sponges can feed on plankters larger than 2 µm. Pinacocytes along the extensive canal system allow sponges to ingest sestonic particles as large as the diameter of the ostia (Reiswig 1971, Frost 1981, Gaino et al. 1994). Particles larger than the diameter of the ostia can be retained and picked up by the surface epithelium (Simpson 1984, Vacelet & Boury-Esnault 1995).

Therefore, due to the observed wide range of food sources on which sponges can potentially feed, an accurate evaluation of the natural diet needs to include the entire available food spectrum. Available food in the water column is a continuum from DOC to the larger forms of particulate organic carbon, including both live carbon (bacteria, *Prochlorococcus* sp., cyanobacteria, protozoa, phytoplankton and zooplankton) and detrital organic carbon, although under normal circumstances zooplankton may be disregarded. Furthermore, because plankton communities exhibit strong temporal variability in temperate seas, feeding studies should be carried out seasonally.

In the Mediterranean Sea, seasonal variations in environmental factors such as temperature, food availability (Ribes 1998), and photoperiod (Zabala & Ballesteros 1989) can cause important shifts in resource allocation by benthic modular organisms. In this regard, a summer paucity of seasonal species such as hydroids (Boero et al. 1986, Llobet et al. 1991) and regression in the activity of perennial species such as tunicates (Turon & Becerro 1992), bryozoans (Zabala 1983), and gorgonians (Coma et al. 1998a) has been observed in the Mediterranean. The worsening of feeding conditions during the summer period due to a decline in phyto- and zooplankton abundance (Valentin 1972, Coma et al. 1994, Ribes 1998), as well as in current speed (Pasqual unpubl. data), has been suggested as the main reason for the regression or inactivity of the species at that time (Coma et al. 1998a). Knowledge of the diet of sponges and of seasonal variations in the diets could be used to test the general hypothesis that a trophic-energetic phenomenon underlies the summer regression by a sizeable number of Mediterranean species, for several reasons. Firstly, pico- and nanoplankton have been documented to be the main sources of particulate organic carbon (POC) for some sponge species (Reiswig 1971, Pile et al. 1996). Secondly, seasonal variations in these planktonic groups near the bottom have been observed to follow a rather different pattern from those of phyto- and zooplankton, with the lowest biomass during the winter period (Ribes 1998). Therefore, if the trophic-energetic phenomenon affects the abovementioned groups, and phyto- and zooplankton are not the main contributors to sponge diets, it could be postulated that sponge species should not exhibit the summer regression or inactivity.

In order to test this hypothesis we examined the trophic ecology of the Dendroceratida sponge *Dysidea avara* (Schmidt), a common and widely distributed temperate sponge species on sublittoral sciaphylous hard bottoms (Atlantic: Lombas 1982, Mediterranean: Uriz et al. 1992). *D. avara* is an epilithic species that develop between 10 and 40 m depth on a wide range of substrata, such as vertical walls, big boulders, at the entrance of caves, and between detrital debris. It grows among other sessile organisms, rarely forming monospecific patches. The rounded colonies, between 5 and 15 cm across, irregularly encrust the rocks. They can also be found as lobulated masses up to about 20 cm in height. The surface of colonies is characteristically covered with conuli and is greyish white or brownish in color. The oscula are distinct and scattered, and the skeleton is a meshwork of spongin fibres without spicules. Consumption rates for this species on the different natural food sources (DOC, pico-, nano-, and microplankton, and detritus) were studied with *in situ* incubations on a seasonal basis in order to cover the natural range of food concentration in the water column.

MATERIALS AND METHODS

This study was conducted at the Medes Islands Marine Reserve (NW Mediterranean Sea, 42° 3' N,

3° 13' E) from October 1995 to November 1996. Incubations were conducted in hemispherical UV-transparent Plexiglas chambers approximately 3 l in volume. The chambers (1 experimental, with sponge, and 1 control) were placed at 10 m depth by scuba divers. The chambers had an inlet and an outlet aperture connected to a common piece of PVC tubing, producing a closed system. An electric pump was placed at the outlet aperture which during normal operation forced water through the system at a speed of 1.2 cm s^{-1} (this flow became turbulent inside the chambers). Whole *Dysidea avara* specimens were removed together with a piece of substrate free of organisms and cleaned of any macroepibionts. Removed specimens were then transplanted back onto the substratum using an inert mastic compound (Scotch-Calk, as in Coma et al. 1996). The colonies were kept in their natural environment with conspecifics until used in the incubation experiments, which were performed *in situ*. At the beginning of each experiment, a *D. avara* colony was placed on the base of the experimental chamber and allowed to acclimatize for 1 h. During this period, the inlet and outlet apertures were not connected, so that the system worked in an open-flow mode. Three replicate water samples of 500 ml were collected from the outlets of both chambers (initial water samples) and preserved for further analysis (see below). At this point, inlet and outlet apertures were connected and the system was operated in closed-flow mode for 1 h. Several experiments were conducted to determine the most suitable combination of sponge biomass and incubation time that optimized the detection of changes in prey concentration (prey changes need to be large enough to be accurately measured for all prey types). Also, the drop in oxygen concentration during the experiment was considered not to affect the respiration rate of the species and, therefore, its feeding behavior (Ribes unpubl. data). After the incubation period, the chambers were taken to the surface and 3 replicate water samples were collected again from both chambers (final water samples). Grazing was calculated from decreases in prey concentration in the experimental chamber relative to the control chamber. The potential prey items included: heterotrophic bacteria, *Synechococcus* sp., *Prochlorococcus* sp., autotrophic pico- and nanoeucaryotes, ciliates, phytoplankton (diatoms and dinoflagellates), DOC and detrital POC. *Synechococcus* sp. and *Prochlorococcus* sp. are autotrophic procaryotes. *Prochlorococcus* sp. are difficult to quantify by methods other than flow cytometry. Water volume used for the analysis of DOC, POC, and pico- and nanoeucaryotes was filtered through a 100 µm mesh to remove larger plankters. Five experiments were carried out during each of the 4 seasons: winter (December 23, January 7, March 5, 8, and 9), spring (May 17, 21, 22, 25, and 26), summer (July 30, August 7, 8, and 10, September 5) and fall (September 30, October 8, 9, 21, and 22). Thus, a total of 20 experiments were performed over the yearly cycle.

Flow cytometry was used to quantify heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp., pico- and nanoeucaryotes. Water samples (2 ml) from the incubation chambers were preserved for flow cytometry by standard protocols (Campbell et al. 1994) and frozen in liquid nitrogen; they were then stored at −80°C or in dry ice. Samples were analyzed using a Coulter EPICS 753 flow cytometer (Coulter Electronics Corporation, Hialeah, Florida) equipped with two 5 W argon lasers and a Micro-Sampler-Delivery-System. The flow cytometer was set up for UV (220 mW) and 488 nm (1 W) colinear analysis. Hoechst 33342 (DNA-specific fluorochrome) was used to stain DNA according to Monger & Landry (1993). Five parameters were collected in list mode and analyzed with custom-designed software (CYTOPC by Daniel Vaulot): red fluorescence (from chlorophyll *a*), orange fluorescence (from phycoerythrin), blue fluorescence (from DNA stained with Hoechst 33342), and forward- and right-angle light scatter signals (FALS and RALS). For statistical purposes, sample size for analysis was chosen to provide more than 10 000 events $sample^{-1}$; 1 ml of water sample was analyzed for picoeucaryotes and nanoeucaryotes and 100 µl for heterotrophic bacteria, *Prochlorococcus* sp., and *Synechococcus* sp. Flow cytometer and epifluorescence microscopy counts were compared in a previous study to validate flow cytometer use with our samples (Ribes 1998).

Subsamples of 20 ml were stained with DAPI and retained on 0.2 µm filters to measure the cell size (length and width) of heterotrophic bacteria, *Synechococcus* sp., and pico- and nanoeucaryotes. For heterotrophic bacteria size, ≥100 cells were measured using image analysis software as described by Massana et al. (1997). For *Synechococcus* sp. and pico- and nanoeucaryotes, cell length and width were measured with an ocular micrometer. Picoeucaryotes included naked flagellates smaller than 2 µm and nanoeucaryotes included naked flagellates larger than 2 µm as well as small dinoflagellates (not discernible with an inverted microscope) and coccolithophores (uncountable with acid Lugol's) (see below). It was not possible to measure *Prochlorococcus* sp. size due to the difficulty in observing these cells with epifluorescence microscopy; a mean size of 0.7 µm calculated for the Mediterranean by Vaulot et al. (1990) was therefore used.

To quantify phytoplankton and ciliates, 350 ml water samples were preserved with acid Lugol's (1% final concentration). Subsamples of 100 ml were placed in settling chambers, and major groups of nano- and

microphytoplankton were quantified under an inverted microscope. The microscope was provided with a color CCD video camera connected to a video recorder. Images of the organisms for measurement were recorded on tape and digitized with a frame grabber. Organism size was determined by image analysis software (NIH image). In each subsample, 20 individuals of the most common groups were measured. Volumes were estimated from the length and width measurements assuming ellipsoidal or cylindrical shapes (Edler 1979).

POC was measured by filtering 60 ml water samples on pre-combusted GF/F glass fibre filters. Filters were then frozen in liquid nitrogen and kept at –80°C until analysis. Prior to analysis, filters were dried at 60°C for 24 h and exposed to chloric acid vapors for 48 h to destroy inorganic material. The filters were then dried again and analyzed with a Perkin-Elmer 240 C:H:N autoanalyser. Total particulate organic carbon measurements included both detrital and live carbon. Detrital organic carbon, hereafter detrital POC, was estimated as the difference between the total POC (C:H:N analysis) and the total live carbon estimated from cell counts and cell measurements.

For DOC, 20 ml water samples were filtered through pre-combusted GF/F glass fibre filters. The filtered water was stored in glass tubes at –20°C until analysis. Analysis was conducted by high-temperature catalytic oxidation with a Shimadzu TOC-5000 autoanalyser.

Depletion rates were calculated by assuming exponential growth and clearance of prey as described in Ribes et al. (1998). The significance of predation on each kind of prey was tested by comparing growth rates of prey in control and experimental chambers with a 2-tailed Wilcoxon test (Sokal & Rohlf 1981).

Cell biovolume was calculated from length and width by approximation to the nearest geometric shapes. Carbon content was then estimated from literature conversion factors as follows: heterotrophic bacteria 0.22 pg C μm^{-3} (Fry 1988); *Prochlorococcus* sp., 0.133 pg C μm^{-3} (Simon & Azam 1989); *Synechococcus* sp., 0.357 pg C μm^{-3} (mean value of: Bjørnsen 1986, Kana & Glibert 1987, Verity et al. 1992); pico- and nanoeucaryotes, pg C = $0.433(\mu m^3)^{0.863}$ (Verity et al. 1992); phytoplankton, pg C $cell^{-1}$ = $0.109(\mu m^3)^{0.991}$ (Montagnes et al. 1994); and ciliates, 0.19 pg C μm^{-3} (Putt & Stoecker 1989).

Scanning electron microscope (SEM) observations of sponge tissue and of the filters for both the initial and final incubation water samples were carried out in order to look for direct evidence of captured prey items. Ten tissue samples from different non-incubated sponges and the initial and final water sample filters for 5 experiments were dehydrated in graded ethanol. Afterwards, the tissue and the filters were dried by the critical point method (using CO_2 as transition fluid), mounted on aluminum stubs and coated with gold in a sputter coater. Observations were made with a Hitachi S-570 SEM.

Dysidea avara dry weight was determined by drying at 100°C for 24 h, and ash free dry weight (AFDW) was determined by combustion at 500°C for 6 h. Prior to combustion, sponges were rinsed to remove any salts and dissected to remove any associated macrofauna.

Multiple regression analysis was used to establish the percentage variance in the estimated clearance rates (*CR*) that could be explained by 3 independent factors monitored during each experiment: water temperature (°C, recorded using a WTW oxygen electrode model EOT 196), initial prey concentration (µg C l^{-1}) and sponge size (g AFDW). A backward stepwise procedure was used to exclude non-relevant variables (Sokal & Rohlf 1981). Variables were square root transformed when requirements for normality (Kolmogorov-Smirnov test) and/or heteroscedasticity (Levene's test) were not fulfilled.

Two methods were employed to examine whether or not the species was selectively grazing on any proportion of the plankton community. First, the CR_{AFDW} equations estimated for each prey type were compared using analysis of covariance (ANCOVA). Second, the percentage of carbon in the diet of sponges was compared to the percentage of carbon in the plankton component using a χ^2 test (Sokal & Rohlf 1981).

RESULTS

The total organic carbon potentially available as a food resource for *Dysidea avara* at the study site was examined. The potential food sources included DOC, detrital POC, and live carbon (i.e. recognizable cells). For all experiments overall, the growth rates calculated for the control chamber and for the experimental chamber showed that *Dysidea avara* significantly depleted all live carbon groups and exhibited a net production of DOC (mean ± SE: 0.33 ± 0.15 mg C g AFDW^{-1} h^{-1}; Fig. 1).

Ash-free dry weight specific clearance rate values (CR_{AFDW}, ml swept clear g AFDW^{-1} h^{-1}, hereafter specific clearance rate) (i.e. the volume of water that had to be filtered by the sponge to bring about the observed decrease in the number of cells, assuming 100% efficiency in particle retention) was seasonally calculated as the mean of the 5 experiments. For all experiments and prey types, the percentage decrease in prey concentration during the incubation was always less than 45% (Table 1). Oxygen concentration at the beginning of each experiment was always slightly supersaturated. The drop in oxygen concentration dur-

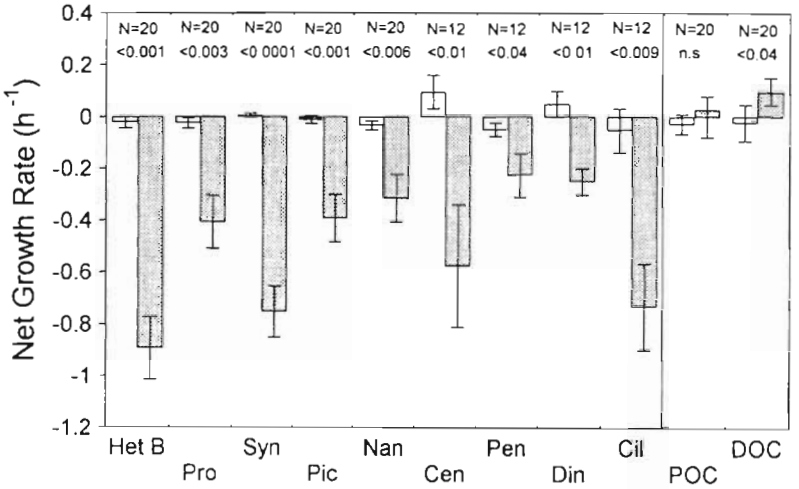

Fig. 1. Net growth rates of prey (mean ± SE) in the experimental (dotted bars) and control chambers (empty bars). Data are presented for each planktonic group: Het B: heterotrophic bacteria; Pro: *Prochlorococcus* sp.; Syn: *Synechococcus* sp.; Pic: autotrophic picoeucaryotes; Nan: autotrophic nanoeucaryotes; Cen: centric diatoms; Pen: pennate diatoms; Din: dinoflagellates; Cil: ciliates; POC: detrital particulate organic carbon; DOC: dissolved organic carbon. Number of experiments and significance levels from the 2-tailed Wilcoxon test are also shown. n.s.: not significant

ing the experiments was never above 15% of the initial oxygen concentration; such a drop is generally known not to be physiologically limiting (Crisp 1984, Ribes unpubl. data). The CR_{AFDW} for each season and prey type are shown in Fig. 2.

The experiments, carried out seasonally, encompassed the natural ranges of prey concentration (10 to 50 µg live carbon l^{-1}) and temperature (12 to 23°C; Ribes et al. 1998) at the study site throughout the year. Within these ranges, the study permitted comparison of the mean CR_{AFDW} for all prey types by sponge size (weight), prey concentration, and temperature. CR_{AFDW} did not vary with prey concentration (µg live carbon l^{-1}) or with water temperature (multiple regression analysis, n = 20, $p > 0.5$ for both variables and all prey types). For all prey types, sponge size was the only variable that explained a significant proportion of the variance in CR_{AFDW} (Table 2). The pattern of decrease in CR_{AFDW} with sponge size was best fit by a power function (Table 2). This effect was highly pronounced for sponges below about 1 g AFDW, but the pattern was less distinct for sponges above this size (Fig. 3). The effects of prey concentration and temperature were examined for sponges larger than 1 g AFDW. CR_{AFDW} did not vary within the natural ranges of prey concentration and temperature at the study site (multiple regression analysis, n = 11, $p > 0.2$ for both variables).

ANCOVA was used to examine whether or not CR_{AFDW} differed for the different prey groups, parameters '*a*' and '*b*' from the relationship between sponge size (*S*, g AFDW) and CR_{AFDW} ($CR_{AFDW} = aS^b$) were compared among the different groups (Table 3). The relationship between CR_{AFDW} and sponge size (*S*) was significantly different among some prey groups. Although not statistically different from each other, CR_{AFDW} for heterotrophic bacteria, *Prochlorococcus* sp., and *Synechococcus* sp. were significantly higher than the CR_{AFDW} for pico- and nanoeucaryotes. CR_{AFDW} for pico- and nanoeucaryotes did not differ from each other but were significantly higher than the CR_{AFDW} for diatoms, dinoflagellates, and ciliates (Table 3). Overall, the variation in CR_{AFDW} among prey types suggests an inverse relationship between prey size and CR_{AFDW}.

Ingestion rate (*I*) was calculated as a function of clearance rate (*CR*) and prey concentration (*C*) ($I = CR \times C$; see Ribes et al. 1998b for further details). Due to the dependence of clearance rate on sponge size, the amount of carbon seasonally ingested was estimated for the 2

Table 1. Seasonal prey concentration (mean ± SD; Het B, Pro, Syn, Pic, Nan: 10^3 cells ml^{-1}; Diatoms, Din, Cil: 10^3 cells l^{-1}). % change: percentage decrease in prey concentration in the final water samples with respect to the initial concentration. Prey abbreviations as in Fig. 1, except Diatoms, which includes centric and pennate diatoms

Prey	Summer		Fall		Winter		Spring	
	Concentration	% change	Concentration	% change	Concentration	% change	Concentration	% change
Het B	339 ± 88	34 ± 14	349 ± 128	41 ± 16	465 ± 139	27 ± 3	361 ± 107	42 ± 7
Pro	2.69 ± 1.94	26 ± 15	23.06 ± 15.11	24 ± 17	1.68 ± 0.36	16 ± 7	1.54 ± 0.61	36 ± 4
Syn	16.45 ± 5.73	33 ± 12	30.06 ± 18.50	31 ± 15	9.20 ± 3.54	29 ± 4	10.45 ± 6.11	42 ± 7
Pic	0.79 ± 0.51	11 ± 15	1.13 ± 0.34	29 ± 17	1.93 ± 0.81	27 ± 3	0.99 ± 0.337	33 ± 7
Nan	0.30 ± 0.25	11 ± 14	0.36 ± 0.17	21 ± 14	0.40 ± 0.17	18 ± 4	1.05 ± 0.58	37 ± 5
Diatoms	10.01 ± 0.20	14 ± 3	14.70 ± 0.46	17 ± 13	100 ± 20	16 ± 2	43.02 ± 15.70	22 ± 18
Din	1.79 ± 0.70	2 ± 1	1.78 ± 0.74	13 ± 9	2.57 ± 0.44	12 ± 9	3.51 ± 2.64	13 ± 10
Cil	0.14 ± 0.06	17 ± 14	0.22 ± 0.07	26 ± 21	0.21 ± 0.04	29 ± 2	0.27 ± 0.08	45 ± 2

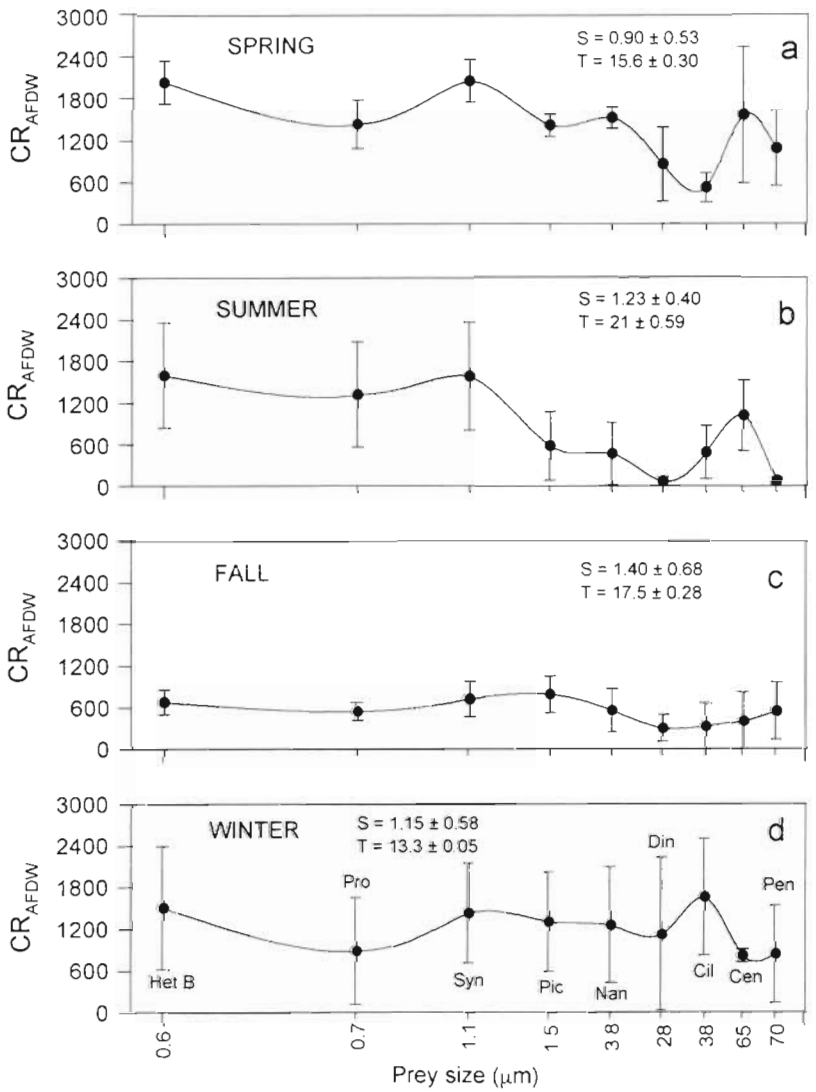

Fig. 2. *Dysidea avara*. Seasonal specific clearance rates (CR_{AFDW}; ml swept clear g AFDW^{-1} h^{-1}, mean ± SE) as a function of prey size (µm). Prey size on log scale. *S*: mean ± SD sponge size (g AFDW) used in the 5 experiments; *T*: mean ± SD water temperature (°C). Prey abbreviations as in Fig. 1

and time (10 to 12 µg C g AFDW^{-1} h^{-1}; Table 4). Overall, procaryotes (i.e. heterotrophic bacteria, *Prochlorococcus* sp., and *Synechococcus* sp.) contributed 74 ± 14% of the total ingested carbon, pico- and nanoeucaryotes contributed 11 ± 3%, and phytoplankton contributed 11 ± 10%. Thus, *Dysidea avara* obtained 85% of the ingested carbon from the fraction smaller than 5 µm and 15% from the fraction larger than 5 µm. However, partial contributions by the different groups varied throughout the year. The highest phytoplankton contribution to the carbon ingested by the sponge, mainly diatoms, was observed during the winter period (phytoplankton: 26%, procaryotes: 57%; Table 4). Overall, the heterogeneous diet of the species and its capacity to feed on a wide range of prey sizes allowed the species to maintain rather constant levels of food uptake throughout the year (Table 4).

The proportion of ingested carbon from the different prey types was statistically different from levels for the water column community (summer: χ^2 = 62.24, fall: χ^2 = 103.84, winter: χ^2 = 215, spring: χ^2 = 135.4; df = 7, $p < 0.0001$ for all seasons). These differences were due to the fact that procaryotes were captured in greater proportion than their frequency in the plankton. Furthermore, the increase in the contribution by phytoplankton to the pool of live carbon in the water column during the winter period was not ingested in the same proportion by the sponge (Table 4).

extreme sizes tested during the experiments (0.2 and 1.6 g AFDW). Seasonal carbon ingested by the species was calculated by applying the specific clearance rate for each prey type (Table 2) to the seasonal mean prey concentration values for the study area (Ribes 1998). Thus, a *Dysidea avara* colony 0.2 g AFDW in size ingested between 169 and 183 µg C g AFDW^{-1} h^{-1}, depending on the season (Table 4). A colony 1.6 g AFDW in size ingested 1 order of magnitude less carbon per unit of biomass

Table 2. *Dysidea avara*. Relationship between specific clearance rate (CR_{AFDW}; ml swept clear g AFDW^{-1} h^{-1}) and sponge size (*S*, g AFDW). n: number of cases

Prey	Power function	r	p	n
Heterotrophic bacteria	$CR_{AFDW} = 1276 \times S^{-1.04}$	0.84	<0.0001	20
Prochlorococcus sp.	$CR_{AFDW} = 1157 \times S^{-1.36}$	0.83	<0.0001	20
Synechococcus sp.	$CR_{AFDW} = 1321 \times S^{-0.95}$	0.83	<0.0001	20
Picoeucaryotes	$CR_{AFDW} = 854 \times S^{-1.15}$	0.91	<0.0001	20
Nanoeucaryotes	$CR_{AFDW} = 770 \times S^{-1.29}$	0.92	<0.0001	20
Diatoms	$CR_{AFDW} = 537 \times S^{-0.96}$	0.51	0.023	12
Dinoflagellates	$CR_{AFDW} = 176 \times S^{-2.29}$	0.73	0.012	12
Ciliates	$CR_{AFDW} = 676 \times S^{-1.03}$	0.54	0.013	12

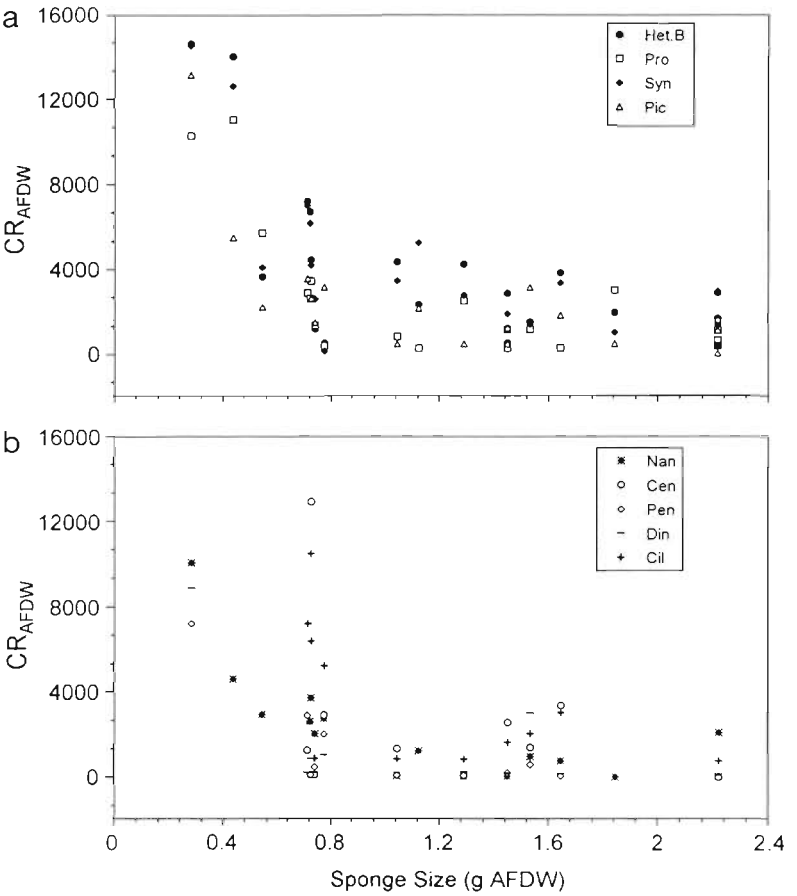

Fig. 3. *Dysidea avara*. Relationship between sponge size (g AFDW) and specific clearance rates (CR_{AFDW}; ml swept clear g AFDW^{-1} h^{-1}). (a) Heterotrophic bacteria (Het B), *Prochlorococcus* sp. (Pro), *Synechococcus* sp. (Syn), picoeucaryotes (Pic). (b) Nanoeucaryotes (Nan), centric diatoms (Cen), pennate diatoms (Pen), dinoflagellates (Din), ciliates (Cil)

SEM observations of sponge tissue showed many trapped phytoplankton in differing stages of digestion. None of the phytoplanktonic remains were larger than 30 µm. SEM observations of the filters from the final incubation water samples showed a large number of pseudopellets (between 5 and 50 µm) (Fig. 4a) in which different phytoplanktonic remains such as diatoms and coccolithophores were identified (Fig. 4b). None of the filters from the initial incubation water samples contained such pseudopellets.

DISCUSSION

The diet of *Dysidea avara* was highly heterogeneous and included heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp., pico- and nanoeucaryotes, and microplankton. This heterogeneous diet represented a broad size spectrum of food sources, from values of 0.5 ± 0.3 (heterotrophic bacteria) to 70 ± 22 µm (pennate diatoms). The ability of sponges to efficiently capture picoplankton (plankton <2 µm) has been well documented (e.g. Reiswig 1971, Pile et al. 1996), but fewer data are available on the capture of large cells such as phytoplankton (but see Reiswig 1971, Frost 1981).

Estimated clearance rates varied among some prey types, suggesting an inverse relationship between mean prey size and clearance rate. This result indicates that the smallest prey types were retained with higher efficiency, showing the ability of the species to select particles. The mean diameter of the ostia for *Dysidea avara* (30 µm, Turon et al. 1997) allows the capture of all studied prey items except diatoms. Recent laboratory experiments with *D. avara* carried out with latex beads showed that particles from 0.2 to 4 µm were retained in the choanocytes and that particles larger than 6 µm were captured by the pinacocytes; prey about 1 µm in size were captured most efficiently (Turon et al. 1997), in agreement with our study.

Pinacocytes are found in the inhalant aquiferous systems as well as on the epidermis of the sponge. Diatoms, or other cells >30 µm in size, can be phagocytosed by pinacocytes upon contact with several surfaces of the sponge (Conover 1981). As pointed out before, a portion of the differences in the ingested carbon values for the different groups and their proportions in the water

Table 3. *Dysidea avara*. Results of ANCOVA comparing specific clearance rates (CR_{AFDW}) as a function of sponge size (S, g AFDW) for the different prey groups on ln-transformed data. n: number of cases. Prey abbreviations as in Fig. 1, except Diatoms, which includes centric and pennate diatoms

	Intercept p	Slope p	Combined data $CR_{AFDW} = aS^b$ p	n	r
Het B, Pro, Syn, Pic, Nan, Diatoms, Din, Cil	0.015	[a]	<0.0001	148	0.35
Het B, Pro, Syn	0.102	0.15	0.0011	60	0.41
Pic, Nan	0.477	0.08	0.0001	40	0.59
Diatoms, Din, Cil	0.742	0.06	0.036	36	0.35

[a]The intercept for this group was significantly different (p = 0.015) so the slope could not be tested

Table 4. *Dysidea avara*. Seasonal estimated ingestion rates (µg C g AFDW^{-1} h^{-1}). Values have been estimated for the extreme sizes examined during the experiments (0.2 and 1.6 g AFDW). % diet: prey composition of the ingested carbon; % plankton: proportion of total living carbon in the water column. Prey abbreviations as in Fig. 1, except Diatoms, which includes centric and pennate diatoms

	Summer			Fall			Winter			Spring		
	Ingestion 0.2–1.6	% diet	% plankton	Ingestion 0.2–1.6	% diet	% plankton	Ingestion 0.2–1.6	% diet	% plankton	Ingestion 0.2–1.6	% diet	% plankton
Het B	76–4.30	43	32	60–3.96	33	33	59–3.90	35	19	63–3.50	35	24
Pro	2–0.10	1	1	9–0.60	5	4	1–0.04	0.4	1	1–0.02	0.2	1
Syn	74–4.20	42	25	86–5.64	47	20	37–2.42	22	4	57–3.20	32	14
Pic	2–0.10	1	4	2–0.12	1	5	3–0.22	2	9	2–0.10	1	5
Nan	11–0.60	6	28	15–0.96	8	25	20–1.32	12	14	22–1.20	12	33
Diatoms	12–0.70	7	7	7–0.48	4	7	44–2.86	26	49	11–0.60	6	18
Din	0.2–0.01	0.1	1	1–0.04	0.3	1	1–0.04	0.4	1	2–0.10	1	1
Cil	2–0.10	1	2	2–0.12	1	4	2–0.11	1	3	23–1.30	13	4
Total	176–11			183–12			169–11			180–10		

column appears to be caused by less efficient capture of phytoplanktonic cells than of the other prey groups in the water column. This is probably due to differences in the process of handling and particle incorporation by the pinacocytes, which can phagocytose large particles (Reiswig 1971). The lower efficiency on these groups may also be due to cell resistance to digestive enzymes (i.e. cellulose and siliceous walls), with these cells requiring longer exposure to digestive enzymes (Reiswig 1971).

Several previous studies have reported the ability of sponges to capture diatoms (Reiswig 1971, Frost 1981, Simpson 1984, Witte et al. 1997). However, knowledge of their importance as a food source is still limited. It has been reported that digestible particles are egested as fecal pellets while indigestible particles are egested

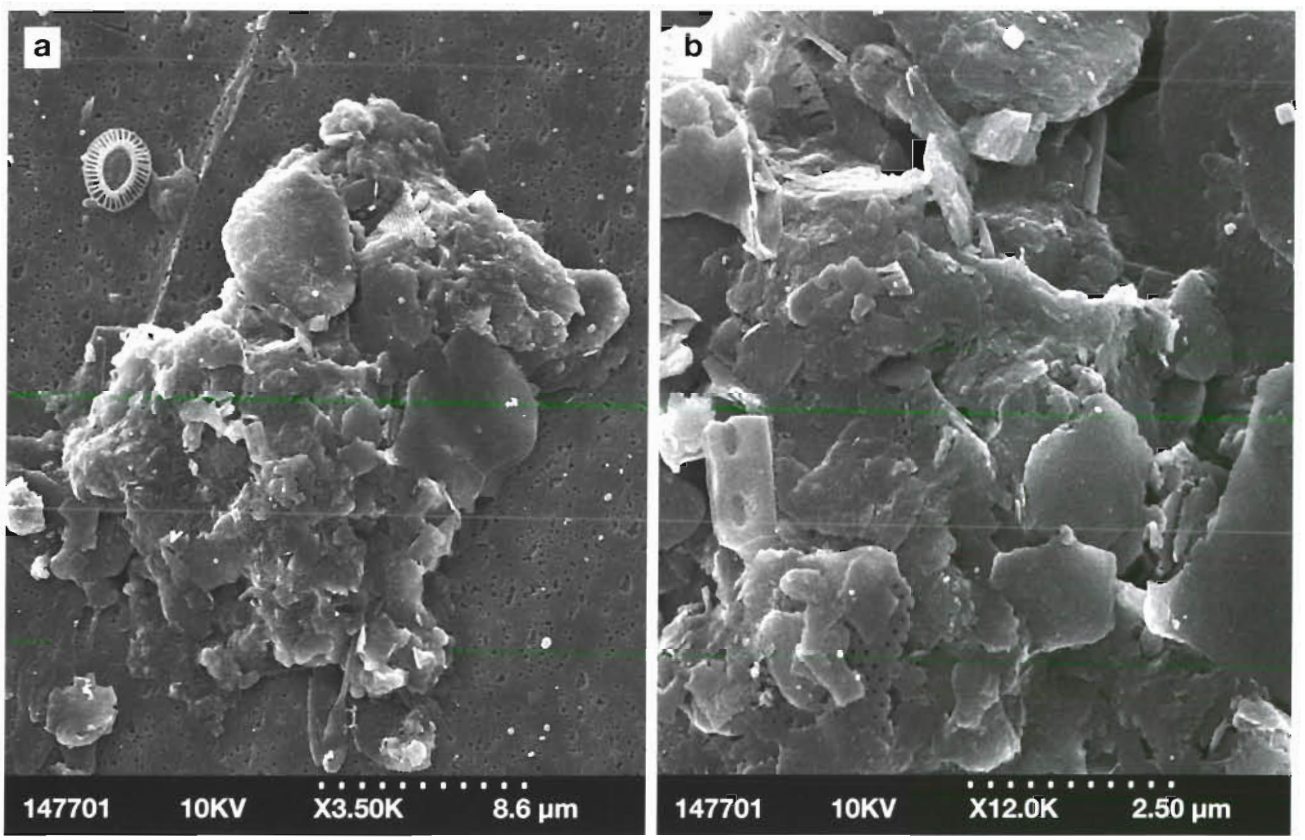

Fig. 4. SEM observations of the filters from the final incubation water samples. (a) Whole pseudopellet, ×3500, and (b) detail of a pseudopellet showing several phytoplanktonic remains, ×12 000

as single particles (Wolfrath & Barthel 1989). Therefore, the diatom remains observed inside the sponge and the large amounts of diatom and coccolithophoral fragments found in the pseudopellets suggest that the species is digesting these cells.

As a general feature of the sponge feeding system, pico- and nanoplankton are captured in the choanocytes, a particle capture system unique to sponges (Kilian 1952, Simpson 1984). Our results showed a higher clearance rate for picoplankton than for nanoplankton, suggesting higher retention efficiency for picoplankton. Selectivity in sponge feeding has some controversial points. Theoretically, the filter-pump design implies that all water being pumped runs through the collar-filter (Larsen & Riisgård 1994); hence, if all flow through the sponge has to pass through the collar-filter, it is difficult to postulate differences in retention rates. However, several studies estimating clearance rates based on the uptake of different prey sizes have observed that clearance rates varied among particle sizes, indicating differing retention efficiencies. This has been reported for tropical, temperate, and deep-sea sponges (Reiswig 1971, Pile et al. 1996, Turon et al. 1997, Witte et al. 1997), indicating that sponges are actively selecting particles, apparently during the handling process (Frost 1980, 1987).

Our experiments suggest that *Dysidea avara* does not significantly feed on POC of detrital origin or on DOC. Instead, it seems that the species was a net source of DOC. The ability to uptake DOC by sponges is evident when species have symbiotic bacteria but not so in non-symbiotic species (Frost 1987). Our results agree with this general pattern, because *D. avara* is virtually free of bacterial symbionts (Turon et al. 1997).

Specific clearance rates exhibited a pattern of decreasing values with sponge size. Low filtration rates by large sponges could be attributable to refiltration of the water in the chamber. Due to the retention efficiencies reported for sponge species (between 75 and 99%, Reiswig 1971, 1975, Wilkinson 1978, Pile et al. 1996), refiltration of water would imply practically full removal of food concentrations within the chamber. However, because the percentage decrease in prey concentration during the experiments was always less than 45% (Table 1), refiltration on its own does not explain the observed relationship between clearance rates and sponge size. Decreasing clearance rates with sponge size have previously been observed for other sponge species (Reiswig 1974, Frost 1980, Riisgård et al. 1993). Still, this general characteristic of metazoans has been accepted only cautiously for sponges (Riisgård et al. 1993). Despite differing opinions about sponges as colonial organisms (Hartman & Reiswig 1973, Simpson 1984), sponges are usually considered colonial animals (Jackson 1977, Frost et al. 1982), suggesting that their physiological capabilities should not change with size. However, sponge modules (canal system) are not clearly delimited and change continuously during the life of the sponge, and the rate of change probably depends on the species. This plasticity means that sponge shape is variable over time (Becerro et al. 1994). It has been suggested that the decrease in CR_{AFDW} with sponge size could be the result of fewer living choanocytes per unit weight in large sponges (Riisgård et al. 1993). Nevertheless, the causes underlying this effect are still not well understood.

We did not observe any significant relationship between clearance rates and temperature over the range of temperatures in this study (13 to 22°C), which corresponded very closely to the annual temperature range in the study area (12 to 23°C). This is in contrast with the results of other authors who have observed increasing clearance rates with temperature (Riisgård et al. 1993: temperature range from 6 to 12°C; Frost 1980: temperature range from 14 to 27°C). The capacity for constriction-dilation of inhalant canals and/or choanocyte chambers has been proposed as a possible regulatory mechanism (Riisgård et al. 1993 and references therein). However, how this physical factor might affect sponge filtering activity remains unclear. Most of those studies examined the effect of temperature on clearance rates under laboratory conditions and with rather fast temperature changes (i.e. hours or a few days). Our experiments represent a different approach to the effect of temperature on clearance rates, because they were carried out with specimens that were always kept in their natural environment. Consequently, specimens had a slow, natural acclimation to each temperature through the seasons. Although our experimental set-up was not designed to test for the effect of temperature (a size effect may interfere with a potential temperature effect), our results suggest that under natural circumstances of gradual temperature change, clearance rates might be only slightly affected by temperature.

Pumping activity has been shown not always to be constant for all species (Reiswig 1971, Savarese et al. 1997). Several experiments carried out throughout the year to study respiration rates in *Dysidea avara* have shown no significant differences in respiration rate over diel cycles (Ribes unpubl. data). This would suggest a rather constant level of activity, as observed in the tropical demosponge *Mycale* sp. by Reiswig (1971). However, pumping without filtering has also been observed (Wilkinson et al. 1984). Consequently, whether or not filtering was constant cannot be determined from the incubation experiments, and the estimated clearance rates have to be regarded as average values.

The mean specific clearance rate estimated in this study was within the range of values reported for

Dysidea avara with latex beads of 0.2, 0.5, and 1 µm in the laboratory (Turon et al. 1997). Comparison of clearance rate values between species is difficult due to variability within each species and the effect of sponge size. Despite this, mean clearance rate values observed for this Mediterranean species were on the same order of magnitude as those estimated for the North Sea species *Halicondria panicea*, for the Norwegian-Greenland Sea species *Therea muricata*, and for most tropical species except *Mycale* sp., though values were among the lowest (Table 5). The high clearance rate for the tropical species *Mycale* sp. appears to be related to the fact that this species does not have symbionts. Therefore, because quantities of food in tropical seas are lower than in temperate zones, to obtain their energy requirements tropical species without symbionts might need to process larger volumes of water than species living in temperate seas.

Our results showed that the composition of the ingested carbon by *Dysidea avara* mainly varied according to the availability of the different prey types in the water column. During the winter months, the low values of grazing on heterotrophic bacteria and *Synechococcus* sp. were due to a drop off in bacterial biomass during the winter period (Ribes 1998), and the high values of grazing on phytoplankton were due to the winter phytoplankton bloom (Estrada et al. 1985). However, although highest live carbon abundance occurred during the winter period (Ribes 1998), food uptake during this period was not significantly higher (Table 4). This was probably due to the fact that during that period about 50% of the live carbon was provided by phytoplanktonic cells (Ribes 1998), for which retention efficiency is lower than for the other groups. The high grazing rates on pico- and nanoeucaryotes in May-June were due to an increase in the abundance of those groups during that period as well as to the higher retention efficiency for those species compared with phytoplanktonic cells. Therefore, pico- and nanoplankton provided a stable baseline of food for the species. However, the contribution of large cells such as phytoplankton was important in the energy budget of the sponge in some periods.

Resources have usually been considered a non-limiting factor for sublittoral sponges (Reiswig 1974, Becerro et al. 1994). Sponges survive in very food-limited environments such as submarine caves and deep-sea communities, where they are also one of the dominant benthic groups (Riedl 1966, Gili et al. 1986, Gage & Tyler 1991). Nevertheless, a linkage between food availability and secondary production by sponges has been demonstrated. Seasonal inputs of POC to the water have been suggested as a trigger for sexual reproduction in deep-sea sponges (Witte 1996), and both reduced current speeds and decreased food availability produce a reduction in growth (Wilkinson & Vacelet 1979, Huysecom et al. 1988). Seasonal changes in toxicity observed in certain temperate sponges have also been related to seasonal changes in food availability (Turon et al. 1996). However, whether or not sponges are food-limited, the heterogeneous diet of *Dysidea avara* and its capacity to feed on a broad size spectrum of food sources allowed a rather constant level of food uptake to be maintained throughout the year. This feeding plasticity may represent an advantage for the species by attenuating the effects of seasonal fluctuations in planktonic communities, which have been reported to play an important role in determining the dynamics of suspension feeders in benthic communities in temperate seas (e.g. Bayne & Newell 1983, Hawkins et al. 1985, Coma et al. 1998b). The plasticity in the trophic ecology of this species may be among the factors that enable it to be one of the most widespread temperate sponges (Atlantic: Lombas 1982; Mediterranean: Uriz et al. 1992), as well as to maintain high growth rates (Uriz et al. 1996). The plasticity of sponge trophic ecology may be among the main factors contributing to the worldwide abundance and distribution

Table 5. Specific clearance rates for various marine sponge species (ranges and mean values). DW: dry weight, AFDW: ash-free dry weight

Species	Location	Clearance rate		Source
		ml g DW^{-1} h^{-1}	ml g AFDW^{-1} h^{-1}	
Dysidea avara	Mediterranean	104–2046	264–4470	This study
			1539 ± 1241 (SD)	This study
Dysidea avara	Mediterranean	1391–3806	–	Turon et al. (1997)
Halichondria panicea	North Sea	–	1700–5200	Riisgård et al. (1993)
Therea muricata	Norwegian-Greenland Sea	–	5000–9000	Witte et al. (1997)
Haliclona anonyma	South Africa	5660		Stuart & Klumpp (1984)
Mycale sp.	Tropical	–	12360	Reiswig (1974)
Tethya crypta	Tropical	–	5353	Reiswig (1973, 1974)
Verongula sp.	Tropical	–	3054	Reiswig (1974)
Verongia fistularis	Tropical	–	3150	Reiswig (1981)

of sponges despite large spatial and temporal variations in food sources. However, the role of trophic plasticity in determining the ecological success of suspension feeders is an issue requiring further study.

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