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S. Rossi · M. Ribes · R. Coma · J.-M. Gili

## Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study

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**Abstract** There is increasing evidence that suspension feeders play a significant role in plankton–benthos coupling. However, to date, active suspension feeders have been the main focus of research, while passive suspension feeders have received less attention. To increase our understanding of energy fluxes in temperate marine ecosystems, we have examined the temporal variability in zooplankton prey capture of the ubiquitous Mediterranean gorgonian *Leptogorgia sarmentosa*. Prey capture was assessed on the basis of gut content from colonies collected every 2 weeks over a year. The digestion time of zooplankton prey was examined over the temperature range of the species at the study site. The main prey items captured were small (80–200 µm), low-motile zooplankton (i.e. eggs and invertebrate larvae). The digestion time of zooplankton prey increased when temperature decreased (about 150% from 21°C to 13°C; 15 h at 13°C, 9 h at 17°C, and 6 h at 21°C), a pattern which has not previously been documented in anthozoans. Zooplankton capture rate (prey polyp<sup>-1</sup> h<sup>-1</sup>) varied among seasons, with the greatest rates observed in spring (0.16 ± 0.02 prey polyp<sup>-1</sup> h<sup>-1</sup>). Ingestion rate in terms of biomass (µg C polyp<sup>-1</sup> h<sup>-1</sup>) showed a similar trend, but the differences among the seasons were attenuated by seasonal differences in prey size. Therefore, ingestion rate did not significantly vary over the annual cycle and averaged 0.019 ± 0.002 µg C polyp<sup>-1</sup> h<sup>-1</sup>. At the estimated ingestion rates, the population of *L. sarmentosa* removed between 2.3 and 16.8 mg C m<sup>-2</sup> day<sup>-1</sup> from the adjacent water column.

This observation indicates that predation by macroinvertebrates on seston should be considered in energy transfer processes in littoral areas, since even species with a low abundance may have a detectable impact.

### Introduction

Quantification of energy and matter transfer processes between the various components of the ecosystem is one of the most complex aspects of marine ecology. Although energy and matter exchanges between plankton and benthos are crucial to our understanding of littoral ecosystems, the contribution of benthic suspension feeders to the rate of these exchanges has only recently been coming to light (Gili and Coma 1998). In shallow areas, active filter feeders may affect plankton communities in the water column by significantly reducing plankton abundance under certain conditions (e.g. Cloern 1982; Officer et al. 1982; Fréchette et al. 1989; Kimmerer et al. 1994; Riisgård et al. 1998). There is increasing evidence that passive suspension feeders may also play a significant role in plankton–benthos coupling (e.g. Coma et al. 1994; Gili et al. 1998). However, research has focused mainly on active suspension feeders and less attention has been devoted to the impact of passive feeders.

Studies on the effect of benthic suspension feeders on plankton abundance in littoral ecosystems have focused mainly on phytoplankton (e.g. Cloern 1982; Fréchette et al. 1989; Riisgård et al. 1998). Zooplankton is a major food source for taxa such as anthozoans and hydrozoans (e.g. Lewis 1982; Sebens and Koehl 1984; Coma et al. 1995), and also for other taxa that until recently have been regarded as microphagous filter feeders, such as bivalves and ascidians (Bingham and Walters 1989; Davenport et al. 2000). Nevertheless, fewer studies have focused on the impact of benthic suspension feeders on zooplankton than on phytoplankton.

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Knowledge of the temporal variability of prey capture rates (i.e. annual and inter-annual variation) is essential to understand ecosystem energy fluxes. In the present study we examined temporal variability over the annual cycle. In cold and temperate marine ecosystems, the high degree of environmental variability throughout the year has a major impact on biological processes. Temperature and food availability are factors that are strongly affected by this variability and are crucial in the determination of temporal variability in the prey capture of benthic suspension feeders (Graf et al. 1983; Clarke 1988; Coma et al. 2000). In temperate seas, zooplankton density usually exhibits a marked seasonal pattern (e.g. Siokou-Frangou 1996). Together with variation in hydrodynamic processes, this seasonal pattern may strongly affect the availability of resources to benthic suspension feeders (Coma and Ribes 2003). The zooplankton capture rate of benthic suspension feeders has generally been determined by means of gut content examinations over a short time period (e.g. Porter 1974; Lasker 1981; Sebens and Koehl 1984; Coma et al. 1999). In temperate seas, sampling throughout the annual cycle is a fundamental step in examining temporal variability in prey capture rates. However, because of logistical constraints, there are few studies that sample over a year.

Temperature variation throughout the annual cycle may strongly affect prey digestion time, which is a crucial element in estimating prey capture rate on the basis of gut content examinations. Some laboratory studies of prey digestion time for passive benthic suspension feeders have been conducted (Kinne and Paffenhöfer 1965; Paffenhöfer 1968), but few field approaches have yet been developed (Coffroth 1984; Coma et al. 1994). Furthermore, despite the importance of prey digestion time in estimating prey capture rate, few studies have examined the effect of temperature on prey digestion time for benthic suspension feeders (but see Kinne and Paffenhöfer 1965).

Gorgonians are conspicuous components of littoral benthic ecosystems (True 1970; Kinzie 1973; Starmans et al. 1999). The three-dimensional structure of gorgonians allow them to escape in size from the mainly two-dimensional plane of most benthic communities, thereby favoring the interaction of their capture structures with available seston. Gorgonians contribute significantly to providing habitats for epifauna composed of small species and to increasing the biomass and diversity of the community (Wendt et al. 1985; Mitchell et al. 1992). Therefore, gorgonian communities may play a significant role in the plankton–benthos trophic interaction, and hence in the matter transfer processes between the two systems in littoral ecosystems. Examination of the feeding rate of these communities is the first step in evaluating the significance of their role in matter and energy transfer processes in these ecosystems.

In this study we examined temporal variability in the zooplankton prey capture rate of the ubiquitous

Mediterranean gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), which is found in benthic communities usually dominated by boulders and organic debris (Pêrès 1967). Temporal variability in the zooplankton prey capture rate was studied by means of a field survey that examined the annual variation in prey abundance and gut contents, field experiments on prey digestion time, and laboratory analyses that estimated gut content, prey abundance and biomass of the gorgonian species. Prey digestion time was examined over the natural range of temperatures for the species at the study site. The study was conceived to estimate feeding of *L. sarmentosa* on zooplankton, to determine the effect of temperature on prey digestion time and to evaluate the consequences of this effect on estimates of ingesta over the annual cycle. In addition, by using the estimates of zooplankton feeding and prey digestion times together with data from previous feeding studies of the species on other seston fractions (Ribes et al. 2003), the study elucidates the role of passive suspension feeders in energy transfer processes in temperate littoral ecosystems.

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## Materials and methods

The *Leptogorgia sarmentosa* population studied was located at the Tascó Gran rock in the Medes Islands Marine Reserve (NW Mediterranean Sea; 42°3'N; 3°13'E). Colonies are found on small stones at a depth of about 20 m. Population density at the study site was 1.5 colonies m<sup>-2</sup>; a density within the natural range of those previously reported for the species (Weinberg 1978; Mistri 1995).

### Feeding on zooplankton

Feeding on zooplankton was assessed by means of gut content examinations of apical fragments. *L. sarmentosa* colonies were sampled at approximately 2-week intervals from 11 August 1997 to 27 August 1998. All samples were collected during the same time period (9–11 h) to preclude possible circadian influences on the annual pattern of prey capture. Each sample consisted of one apical fragment collected from five randomly selected colonies. The fragments were immediately placed in 10% formaldehyde solution in seawater to prevent further digestion. The contents of 50 polyps selected at random from each sample (ten from each apical fragment) were isolated by dissection under a binocular microscope, identified to the higher taxon level and counted. The length of all prey was measured under the microscope.

### Zooplankton density

Two zooplankton samples were collected concurrently with the collection of fragments of *L. sarmentosa* colonies for the study of annual variation of plankton. Plankton nets, 22 cm in diameter with a mesh size of 100 µm, were used. The nets were towed over a distance of 40 m by a SCUBA diver, a short distance (30–50 cm) from the gorgonian community. The zooplankton was immediately placed in 4% formaldehyde solution in seawater and was then identified to the level of main taxonomic groups and counted. Pearson's product-moment correlation (Sokal and Rohlf 1995) was used to examine the relationship between zooplankton prey capture rate and abundance of zooplankton.

### Prey digestion time

Three experiments were carried out at a range of temperatures to estimate prey digestion time. The experiments were conducted on 13 August 1999 (21°C), 26 June 1999 (17°C) and 26 February 2000 (13°C), to cover the natural temperature range of the species at the study site (12–22°C). For each experiment, one apical fragment was randomly collected (i.e. cut off) from between 40 and 55 colonies. After collection, five of the fragments were randomly selected and preserved (10% formaldehyde solution in seawater). Each of the remaining branch tips was then attached to a PVC post (1 cm in diameter, 1 cm tall) embedded in a small cement base (3 cm in diameter, 1 cm tall). Previous experiments with this technique showed that transplanted branches behave as ambient conspecifics shortly after the manipulation (Kim and Lasker 1997; Ribes et al. 1998, 1999). The transplanted branches were placed in a container with aerated, filtered (GF/F glass fiber filters) seawater at the natural seawater temperature to prevent further prey capture. The container was placed in shallow water so that ambient seawater temperature was maintained during the experiment. At 1-h intervals, five additional fragments were randomly selected and preserved. The experiment lasted 7 h at 21°C, 7 h at 17°C and 11 h at 13°C. The contents of 50 polyps selected at random from each sample (ten from each apical fragment) were examined in the same manner as the field collections.

### Prey capture rate

The zooplankton capture rate, expressed as the number of prey items captured per polyp and hour, was calculated using the following equation (Coma et al. 1994):

$$C = N \left[ \sum_{t=0}^D 1 - (t/D) \right]^{-1} \quad (1)$$

where  $C$  is the number of prey captured per polyp per hour,  $N$  is the number of prey items per polyp,  $t$  is time (in hours) and  $D$  is digestion time (in hours).

The assumptions of normality and homoscedasticity were tested using the Kolmogorov–Smirnov and the Levene's tests, respectively. The homoscedasticity assumption was satisfied, but not the former. Differences in prey per polyp, prey size, prey capture rate and prey ingestion rate throughout the year were then analyzed using the Kruskal–Wallis test.

### Biomass

Prey biomass was estimated from biovolumes (Sebens and Koehl 1984), using conversion factors for wet weight (1.025; Hall et al. 1970), dry weight (13% of wet weight, Beers 1966) and carbon content (45% of dry weight, Biswas and Biswas 1979). The biomass of *L. sarmentosa* colonies was estimated after rinsing to remove salts. Dry mass (DM) was determined by drying at 90°C for 24 h, and ash-free dry mass (AFDM), by combustion at 450°C for 5 h.

Feeding of *L. sarmentosa* colonies on nanoeukaryotes, diatoms, ciliates (i.e. live carbon < 100 µm) and on detrital particulate organic carbon (POC) (Ribes et al. 2003) has been considered to estimate the effect of the species population on seston abundance.

## Results

### Zooplankton dynamics

On the basis of abundance, zooplankton was classified in three main categories. Category 1 represented groups

that were always present and contributed significantly to the total share, such as copepods (58% of the total), nauplii (20% of the total) and eggs (10%). These were the three dominant groups throughout the annual cycle and accounted for 80% ( $\pm 8\%$ ) of the total plankton over the year. Category 2 included groups that were not always present, but were quantitatively significant at certain times of the year, such as bivalve larvae (6–19% from December to February), appendicularians (8–18% from June to August), protozoans (6–12% from October to January), polychaetes (6–9% from November to December) and tintinids (17% in August). Category 3 consisted of groups with small quantitative contributions. In all cases, the remaining groups accounted for about 5% or less of the total zooplankton catch (Table 1).

Total zooplankton abundance was highly variable within the study period, ranging between 369 and 4,015 ind. m<sup>-3</sup>, with an average of 1,624 ind. m<sup>-3</sup> ( $\pm 1,090$  SD). The highest value was recorded in July, but several peaks occurred throughout the year (Table 1). Therefore, total zooplankton abundance showed high variability, and no clear seasonal pattern was evident.

### Feeding on zooplankton

Most of the prey items observed inside the gastrovascular cavity of *Leptogorgia sarmentosa* were zooplankton (Table 2). Phytoplankton were not quantitatively studied here, since feeding on these organisms has been accurately examined with incubation chamber experiments (Ribes et al. 2003). The most abundant prey were eggs and invertebrate larvae, particularly bivalve larvae. These groups accounted for 66% of all items captured throughout the year; only on a few occasions were other groups observed (protozoans and copepods, Table 2). *L. sarmentosa* grazed on zooplankton prey that ranged in size from 80 to 340 µm, but items were particularly abundant between 80 and 200 µm (88%), and were characterized by low mobility. The mean percentage of polyps with food was 40.5% and ranged from 12% to 86% throughout the year. The mean number of prey items per polyp ranged from 0.22 to 1.74, although on a few occasions (11 of 1,250 polyps) polyps containing from 5 to 34 prey items were observed.

Although the guts of more than half the polyps were empty, ambient concentrations of all zooplankton groups combined did not contribute to explaining prey capture of the species, which has been described as percentage of polyps with food (full polyps) and as number of prey in 50 polyps (Table 3). Two observations indicate maximum efficiency of prey capture between 150 and 200 µm. Firstly, the prey size spectrum shows an almost normal distribution, with the largest share of prey between 150 and 200 µm (Fig. 1). Secondly, capture rates for specific prey correlated with ambient concentration for bivalve larvae, but not for the smallest and largest prey (Table 4). Bivalve larvae

**Table 1** Zooplankton density ( $\text{ind. m}^{-3}$ ) of the main groups of epibenthic plankton over the annual sampling period (1997–1998). Zooplankton was classified in three categories on the basis of abundance, which, respectively, from top to bottom of the table correspond to: groups always present contributing significantly to the total share (*category 1*, > 5%), groups not always present but contributing significantly at certain periods (*category 2*) and groups with a small contribution to the total share (*category 3*, < 5%)

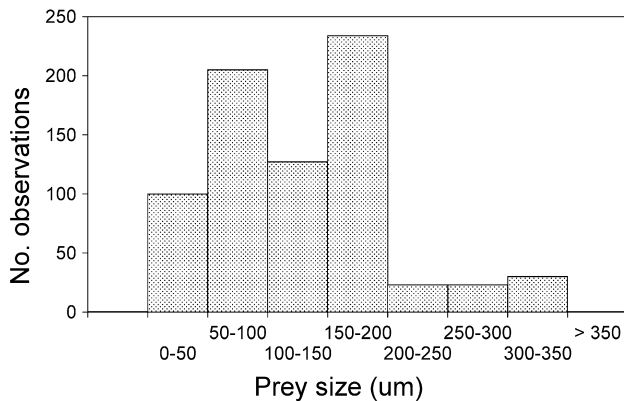
Taxon	11 Aug	29 Aug	8 Sep	23 Sep	6 Oct	12 Nov	26 Nov	12 Dec	31 Dec	14 Jan	30 Jan	27 Feb	26 Mar	9 Apr	23 Apr	29 Apr	15 May	7 Jun	13 Jun	28 Jun	15 Jul	31 Jul	19 Aug	27 Aug
<b>Category 1</b>																								
Copepoda	437	622	957	397	760	640	360	179	292	300	744	1,621	971	505	507	545	1,749	1,208	1,451	240	195	2,187	1,718	464
Nauplii	32	253	352	192	339	250	166	125	247	184	653	867	364	336	401	211	1,488	349	345	70	123	425	271	67
Eggs	4	59	13	27	0	77	23	3	1	1	4	669	251	49	63	23	219	149	92	34	1,789	657	222	120
<b>Category 2</b>																								
Appendicularia	44	26	29	75	61	21	33	9	7	25	68	147	80	57	53	17	21	248	473	32	33	315	260	32
Bivalvia larvae	7	104	19	1	0	66	19	3	161	61	51	224	11	9	8	4	59	48	89	9	24	60	120	77
Protozoa	13	7	48	79	83	79	19	4	65	85	117	43	12	31	27	8	0	45	14	18	37	9	41	40
Tintinida	124	43	56	8	3	6	1	1	41	16	73	75	3	4	4	0	21	0	0	1	21	26	3	3
Polychaeta	7	2	0	0	5	98	38	32	20	15	37	51	7	13	5	15	16	8	14	3	5	17	29	11
<b>Category 3</b>																								
Echinodermata	3	2	0	1	16	6	1	3	8	5	81	75	7	15	0	5	32	72	21	7	7	3	0	0
Cladocera	1	17	8	1	0	0	0	0	0	0	0	5	0	0	1	1	0	40	50	0	39	207	3	3
Salpae	16	10	8	13	5	0	1	0	0	0	2	3	0	3	0	4	0	13	28	7	33	43	3	5
Syphonophora	7	3	0	8	0	0	0	0	1	5	0	48	1	8	5	3	5	13	25	3	1	6	0	0
Gastropoda	4	0	8	1	5	23	1	1	12	4	0	45	8	4	4	5	11	4	4	5	4	6	12	27
Invert. larvae	0	5	3	0	0	36	9	0	3	0	37	8	0	0	0	0	5	11	18	1	11	23	18	5
Medusae	1	0	3	3	0	4	0	0	0	0	4	16	4	8	3	12	5	13	25	1	4	6	3	0
Ostracoda	7	29	5	11	3	0	0	3	3	1	0	8	3	0	1	3	11	5	21	10	12	20	9	11
Crustacea	0	3	0	0	0	0	0	4	0	3	0	19	27	3	4	7	0	11	11	4	0	0	0	3
Isopoda	1	0	8	0	5	2	3	1	1	1	11	3	0	3	0	1	0	0	0	0	0	0	0	0
Amphipoda	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Misidacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Others	1	0	0	1	5	0	1	0	1	0	2	0	0	0	0	0	5	5	4	3	7	3	0	5
<b>Total</b>	<b>709</b>	<b>1,187</b>	<b>1,517</b>	<b>819</b>	<b>1,291</b>	<b>1,310</b>	<b>675</b>	<b>369</b>	<b>864</b>	<b>708</b>	<b>1,885</b>	<b>3,925</b>	<b>1,747</b>	<b>1,048</b>	<b>1,087</b>	<b>863</b>	<b>3,643</b>	<b>2,253</b>	<b>2,684</b>	<b>449</b>	<b>2,347</b>	<b>4,015</b>	<b>2,710</b>	<b>875</b>

**Table 2** *Leptogorgia sarmentosa*. Number and type of prey items captured over the annual sampling period (1997–1998), and total number of gut contents observed in 1,250 polyps (50 per sample) (*no. of full polyps* number of polyps with prey inside; *POM* particulate organic matter; *crust.* crustacean; *invert.* invertebrate)

Prey type	11 Aug	29 Aug	8 Sep	23 Sep	6 Oct	12 Nov	26 Nov	5 Dec	12 Dec	31 Dec	6 Jan	14 Jan	30 Jan	7 Feb	27 Feb	8 Mar	26 Mar	9 Apr	23 Apr	29 Apr	15 May	7 Jun	13 Jun	28 Jun	15 Jul	31 Jul	19 Aug	27 Aug	N	%	
Invert. eggs	3	7	10	4	2	6	6	5	5	10	6	9	9	7	7	8	12	2	6	1	5	37	9	3	3	5	1	1	4	157	22
Bivalve larvae	0	10	11	1	0	2	5	3	3	31	9	9	9	13	13	12	7	4	4	1	0	13	15	1	1	1	0	0	3	151	21
POM	7	1	6	2	5	1	6	6	6	6	4	0	0	1	1	7	6	2	7	6	6	2	10	3	3	3	2	1	8	102	14
Phyto-plankton	1	1	4	8	2	0	3	9	9	9	3	3	3	1	1	10	12	3	1	7	1	1	3	2	4	0	2	1	1	90	
Copepod eggs	0	1	1	0	1	1	4	1	1	1	5	5	5	0	0	1	5	6	42	4	1	1	1	0	0	0	1	0	0	81	11
Nauplii	1	0	0	0	0	3	2	0	3	0	0	0	0	6	1	7	3	14	4	0	3	0	3	0	0	0	1	0	5	53	7
Crust.	1	4	1	1	2	0	2	1	5	1	1	0	0	2	2	9	2	2	1	0	0	2	1	1	2	1	2	2	44	6	
Fragments																															
Invert. larvae	1	3	0	1	1	1	5	0	0	1	0	0	1	1	1	1	1	2	0	1	1	3	0	0	0	1	0	0	5	29	4
Protozoans	0	1	0	1	2	3	0	2	3	0	0	0	0	1	1	3	6	1	0	0	0	0	1	1	1	1	0	0	4	30	4
Others	1	1	0	0	0	1	5	10	1	5	10	1	0	0	0	1	1	1	1	2	2	2	1	0	0	0	0	1	28	4	
Copepods	0	1	2	0	0	0	1	0	2	1	0	0	0	0	0	0	0	3	3	0	0	0	1	0	0	1	0	1	3	22	3
Unidentified	0	5	1	1	0	0	2	0	2	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	4	19	3	
Total prey	15	35	36	19	15	17	37	32	83	31	27	31	27	33	52	53	52	31	72	29	60	46	11	19	6	7	7	40	806		
No. of full polyps	9	24	20	15	14	13	27	19	43	19	17	17	17	25	25	26	26	27	22	22	20	30	26	10	16	6	7	29			
Percent	18%	48%	40%	30%	28%	26%	54%	38%	38%	86%	38%	38%	34%	50%	52%	52%	1.00	1.02	0.60	1.40	0.58	1.20	0.92	0.22	0.40	0.12	0.16	0.80	Mean = 40.5%	Mean = 0.68	SD = 0.86
Mean no. of prey polyp <sup>-1</sup>	0.30	0.72	0.72	0.38	0.32	0.34	0.74	0.66	1.74	0.62	0.62	0.58	0.70	1.00	1.02	1.02	1.22	0.81	4.82	0.86	1.48	1.32	0.46	0.64	0.33	0.42	0.86	0.86	0.86	0.86	0.86
SD	0.93	0.93	1.18	0.67	0.55	0.63	0.83	1.08	1.41	0.9	0.95	0.95	0.81	1.21	1.22	1.22	1.21	0.81	4.82	0.86	1.48	1.32	0.46	0.64	0.33	0.42	0.86	0.86	0.86	0.86	0.86

**Table 3** *Leptogorgia sarmentosa*. Pearson's product-moment correlation tests between total gut contents and total plankton densities throughout the annual cycle (\*\* $P < 0.001$ )

	Full polyps (%)	Prey in 50 polyps
Prey in 50 polyps	$r = 0.8882$ $P = 0.0001^{***}$	
Plankton density (ind. $m^{-3}$ )	$r = 0.1572$ $P = 0.4631$	$r = 0.2019$ $P = 0.3441$



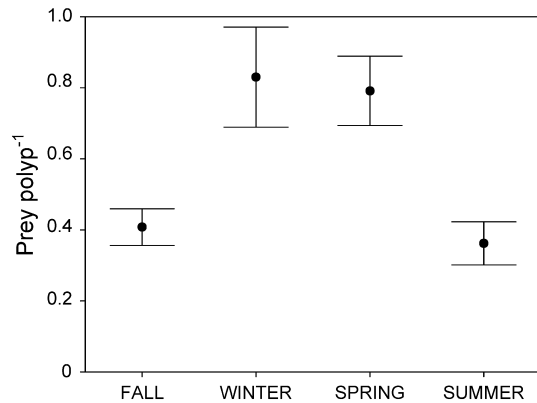
**Fig. 1** Size distribution (maximum length in  $\mu m$ ) of all prey items observed in the gut contents of *Leptogorgia sarmentosa* throughout the annual cycle (1,250 polyps);  $N = 742$

between 165 and 199  $\mu m$  accounted for 60% of prey items between 150 and 200  $\mu m$ .

The number of prey per polyp in the gastrovascular cavity of the *L. sarmentosa* polyps exhibited a marked pattern of seasonal variation (Kruskal–Wallis test,  $H = 21.13$ ,  $df = 3$ ,  $P = 0.0001$ ). During spring and winter, the number of prey was about twice that during summer and fall (Fig. 2).

#### Prey digestion time

Prey digestion time is a crucial element in estimating ingestion rates from gut contents and may be affected by

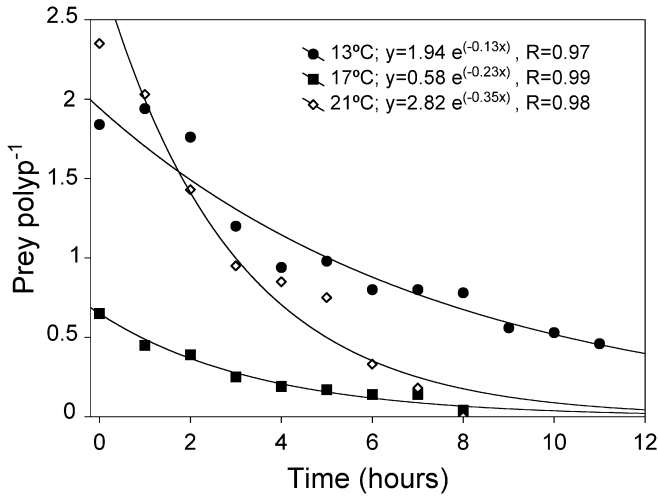


**Fig. 2** *Leptogorgia sarmentosa*. Variation in the mean ( $\pm$  standard error) number of prey items per polyp over the annual cycle

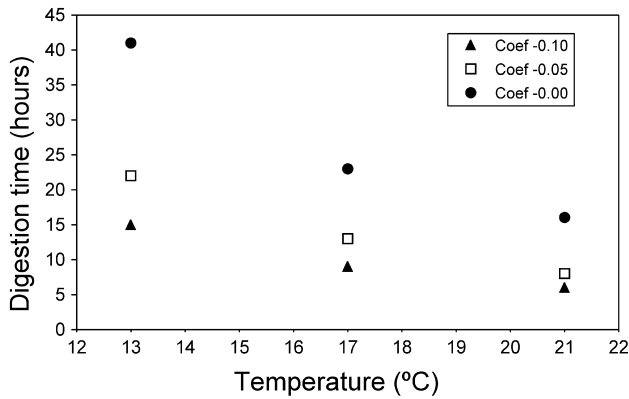
temperature. Consequently, we conducted prey digestion experiments at three temperatures that covered the annual temperature range at the study site. Clearance of the gut contents showed an exponential decrease in the number of prey items per polyp with time (Fig. 3). Digestion time was calculated from the slope of the regression lines, and it exhibited a clear pattern of decrease with temperature increase (Fig. 4). Prey digestion time increased about 150% as temperature was lowered from 21°C to 13°C (the approximate temperature range at the study site). Complete clearance of the stomach took 41 h at 13°C, 23 h at 17°C and 16 h at 21°C (Fig. 4). However, the last 10% of prey items were always copepod carapaces and a few crustacean fragments; items that are difficult to digest and that are not representative of the bulk of prey. In our view, application of the digestion time for these difficult to digest prey items to all prey would result in a substantial overestimation of digestion time. Therefore, to calculate the zooplankton prey capture rate, we used a digestion time that we considered representative of the bulk of prey (i.e. that at which 90% of the prey has been digested, corresponding to the coefficient 0.10 in Fig. 4). This coefficient is the value of the term  $e^{bx}$  from the exponential regression (Fig. 3), where  $b$  is the slope and  $x$  is the time (in hours). The coefficients 0.10, 0.05 and

**Table 4** *Leptogorgia sarmentosa*. Pearson's product-moment correlation tests between gut contents and plankton densities for specific prey items (prey in 50 polyps) throughout the annual cycle (\*\* $P < 0.001$ )

	Eggs (84–94 $\mu m$ )	Nauplii (108–123 $\mu m$ )	Bivalve larvae (165–199 $\mu m$ )	Invert. larvae (186–338 $\mu m$ )	Copepods (183–305 $\mu m$ )
Eggs	$r = 0.1658$ $P = 0.4387$				
Nauplii		$r = 0.1623$ $P = 0.4486$			
Bivalve larvae			$r = 0.539$ $P = 0.007^{***}$		
Invert. larvae				$r = 0.0658$ $P = 0.7598$	
Copepods					$r = 0.2852$ $P = 0.1768$



**Fig. 3** *Leptogorgia sarmentosa*. Prey digestion. Exponential decrease of the number of prey per polyp over time (hours) at three temperatures (13°C, 17°C and 21°C)

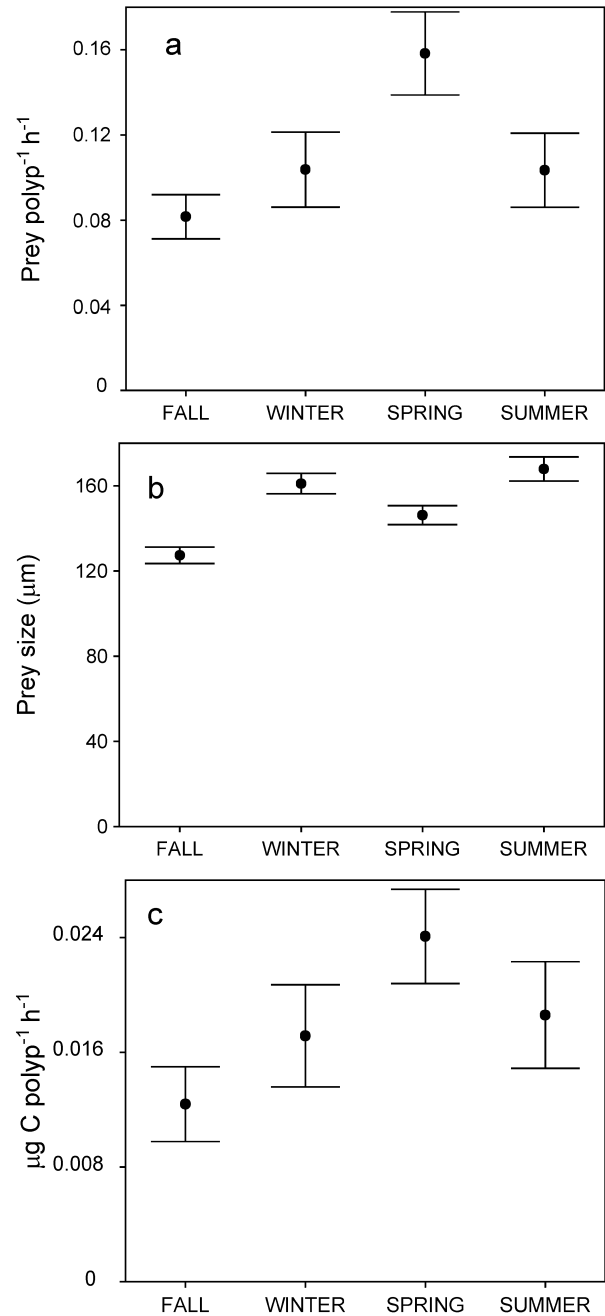


**Fig. 4** *Leptogorgia sarmentosa*. Pattern of decrease in prey digestion time (hours) with temperature increase. The coefficient is the value of the term  $e^{bx}$  from the exponential regression, where  $b$  is the slope and  $x$  is the time (in hours). The coefficients 0.10, 0.05 and 0.00 provide the time at which the number of prey per polyp is 10%, 5% and 0%, respectively, from the initial number of prey per polyp

0.00 provide the time at which the number of prey per polyp is 10%, 5% and 0%, respectively, from the initial number of prey per polyp (Fig. 4). Therefore, the time at which 90% of the prey had been digested (coefficient 0.10) was 15 h at 13°C, 9 h at 17°C and 6 h at 21°C (Fig. 4).

#### Prey capture rate

Zooplankton prey capture rate (i.e. the number of prey items captured per polyp and hour) exhibited a marked seasonal variation (Kruskal–Wallis test,  $H = 9.58$ ,  $df = 3$ ,  $P = 0.022$ ; Fig. 5a). The highest rates were observed in spring ( $0.158 \pm 0.019$  prey polyp<sup>-1</sup> h<sup>-1</sup>; mean  $\pm$  SE), while the other seasons showed similar capture rates



**Fig. 5a–c** *Leptogorgia sarmentosa*. Variation in (mean  $\pm$  standard error): **a** capture rate (prey polyp<sup>-1</sup> h<sup>-1</sup>), **b** prey size (µm) and **c** ingestion rate (µg C polyp<sup>-1</sup> h<sup>-1</sup>) of zooplankton over the annual cycle

(summer:  $0.103 \pm 0.017$ , fall:  $0.082 \pm 0.010$  and winter:  $0.104 \pm 0.018$  prey polyp<sup>-1</sup> h<sup>-1</sup>; mean  $\pm$  SE). Because of their size and abundance, invertebrate larvae were the main contributors to the bulk of zooplankton prey items in terms of biomass (53%, more than half of which were bivalve larvae). Ingestion rate in terms of biomass (µg C polyp<sup>-1</sup> h<sup>-1</sup>) showed a similar trend (Fig. 5c), but the differences among the seasons were attenuated by seasonal differences in prey size (Kruskal–Wallis test,



$H=55.46$ ,  $df=3$ ,  $P=0.0001$ ; Fig. 5b). Thus, the ingestion rate did not significantly vary over the year (Kruskal–Wallis test,  $H=6.04$ ,  $df=3$ ,  $P=0.1098$ ; Fig. 5c). The average ingestion rate over the year was  $0.019 \pm 0.002 \mu\text{g C polyp}^{-1} \text{ h}^{-1}$  (mean  $\pm$  SE), corresponding to  $136 \pm 14 \mu\text{g C g}^{-1} \text{ AFDM h}^{-1}$ . This value accounts for an average annual ingestion rate of  $3,260 \pm 340 \mu\text{g C g}^{-1} \text{ AFDM day}^{-1}$  (mean  $\pm$  SE).

## Discussion

### Zooplankton diet

The zooplankton diet of *Leptogorgia sarmentosa* was made up mainly of small (80–200  $\mu\text{m}$ ) and low-motile (i.e. eggs and larvae) prey items. Although a wide spectrum of other zooplankton was also found, including copepods up to 340  $\mu\text{m}$ , they were not quantitatively relevant. Other passive suspension feeders also feed on non-motile zooplankton of similar size (Lewis 1982; Sebens and Koehl 1984; Coma et al. 1994; Fabricius et al. 1995; Ribes et al. 1998). This behavior appears to be related to the relatively limited variety and low density of nematocysts found in octocoral (Mariscal and Bigger 1977); consequently, most prey items captured were those with little capacity to escape.

Bivalve larvae were conspicuous prey items of *L. sarmentosa* and accounted for 21% of the total (Table 2). The positive correlation between the capture rate and ambient concentration of bivalve larvae indicates that feeding on these larvae may peak during adult spawning. Little is known about the role of predation in early stages of bivalve development (Ólafsson et al. 1994; Beukema et al. 2001). Further research should be conducted to determine whether predation by octocorals and other suspension feeders could be a detectable factor that affects bivalve recruitment.

### Gut contents

Gut contents of *L. sarmentosa* exhibited an average of  $0.68 \pm 0.86$  prey polyp<sup>-1</sup>, a value similar to those previously estimated for temperate octocorals (*Alcyonium siderium*, Sebens and Koehl 1984; *Paramuricea clavata*, Coma et al. 1994), and one which differs markedly from the relatively low gut contents observed in tropical octocorals (usually below 0.3 prey polyp<sup>-1</sup>, Lewis 1982; Fabricius et al. 1995). This appears to be related to the fact that most temperate octocorals are exclusively heterotrophic (but see *Capnella gaboensis*, Farrant et al. 1987), while most tropical octocorals examined so far have symbiotic zooxanthellae (but see *Dendronephthya hemprichi*, Fabricius et al. 1998). Gut contents in temperate octocorals are associated with some of the highest values observed in reef hexacoral species, which are usually below 0.4 prey polyp<sup>-1</sup> (Porter 1974; Johnson and Sebens 1993; Sebens et al. 1996). These values are

also higher than those observed for zoanthid species, which are always below 0.12 prey polyp<sup>-1</sup> (Sebens 1977).

Gut content examination showed that the effect of temperature on prey digestion time strongly modified the pattern of seasonal variation in prey per polyp and allowed us to estimate zooplankton prey capture and ingestion rate over the annual cycle.

### Prey digestion time

Digestion time is a crucial factor in estimates of zooplankton prey capture rates, which have received relatively little attention for anthozoans (Sebens 1987). Digestion time exhibited a clear pattern of decrease with temperature increase, a pattern not previously documented in anthozoans. This result was expected because of the general tendency of chemical reaction rates to increase with temperature. The pattern observed was similar to those previously reported in hydrozoans (Kinne and Paffenhöfer 1965; Christensen 1967) and scyphomedusae (Purcell 1992). The largest temperature effect on digestion time is in the hydrozoan species *Hydractinia echinata*: digestion time was >40 h at 4°C, but only 5 h at 16°C (Christensen 1967). The estimated digestion times (6–15 h) were within the range of values reported for anthozoans (3–14 h, Boschma 1925; Yonge and Nicholls 1930; Porter 1974; Sebens and Koehl 1984; Barange and Gili 1988; Coma et al. 1994).

### Prey capture rate

Flow speed and prey concentration are crucial factors that affect the efficiency with which particles are captured in organisms like octocorals (Shimeta and Jumars 1991). In our study sampling over the annual cycle was always conducted during the same time period to avoid any potential diel cycle effect. In our study area, zooplankton exhibited a marked diel cycle in open waters (Estrada et al. 1985; Siokou-Frangou 1996), which is characteristic of many temperate areas. However, few studies have addressed the near-substratum zooplankton at such fine spatial and temporal scales. Current knowledge about the dynamics of this zooplankton comes mainly from studies of benthic suspension feeders. In general, the concentrations of various zooplankton taxa change during the diel cycle, while others stay relatively constant. However, no clear diel pattern either in size or in abundance of zooplankton has been observed (Sebens and Koehl 1984; Coma et al. 1994; Gili et al. 1996). These studies suggest that in temperate areas near-substratum zooplankton does not exhibit any clear diel pattern of size or abundance, in contrast to that in coral reef systems, where a strong pattern of upward migration at dusk and downward migration at dawn is observed (e.g. Alldredge and King 1977; Ohlhorst 1982). Therefore, the time period during which sampling was conducted (9–11 h) did not introduce any significant

bias on the estimate of the annual pattern of prey capture rates.

The results of gut content examinations integrate the effect of prey concentration and flow speed on the zooplankton prey capture rate of *L. sarmentosa*. Although there are no flow speed data available, it was surprising to observe the absence of a correlation between total ambient plankton concentration and capture rates for all but bivalve larvae. This result indicates the primary role of flow speed on prey capture rate (Dai and Lin 1993; Sebens et al. 1996; Fabricius et al. 1995). With regard to the small zooplankton taxa, the average widths of eggs (90  $\mu\text{m}$ ) and nauplii (112  $\mu\text{m}$ ) were below or to close to the size of the mesh (100  $\mu\text{m}$ ), and therefore our sampling probably underestimated the abundance of these taxa (UNESCO 1968). However, the results of the digestion experiments indicate that prey were probably captured over the previous 6–15 h, depending on the temperature. Therefore, the best estimate of prey availability to contrast with capture rates is not the zooplankton present at the time of collection, but the average of that present over several hours earlier. The higher prey capture and ingestion rates for *L. sarmentosa* in spring appear to be related to the higher values of flow speed in the area during that season (Font et al. 1995). However, in terms of ingestion rate, the higher prey capture rate observed in spring was attenuated by the differences in prey size among the seasons. Current knowledge about the dynamics of near-bottom zooplankton indicates high short-term variability in abundance, lacking any clear seasonal pattern (Coma et al. 1994; Calbet et al. 2001). The variation in prey size observed may be related to the succession of taxa that the zooplankton community displays throughout the year (Calbet et al. 2001). Therefore, despite the marked seasonal pattern in gut contents, zooplankton ingestion rates did not significantly vary over the annual cycle.

#### Ingesta of the species

To estimate total ingesta of *L. sarmentosa*, we should also consider feeding on detrital POC and live carbon (data from Rossi 2002; Ribes et al. 2003; Table 5). The coenenchyme dry mass of the *L. sarmentosa* colonies was  $56 \pm 2\%$  (mean  $\pm$  SE) of total DM, and the AFDM of the colonies was  $32 \pm 1\%$  of the dry mass. These proportions allowed us to estimate that, on average, the colonies ingested 0.5% of their total body mass daily (all seston fractions included) or 0.8% of the coenenchyme mass. This is a very low ingestion rate compared to that of other anthozoan taxa (4.5–6%) and of hydrozoan taxa [10–60%, see Table 2 in Barange et al. (1989) for a review of the literature]. To examine whether our ingesta estimates cover the metabolic expenses of the species, we used respiration rate data from a previous study. Ribes et al. (2003) estimated that the respiration rate of the species in spring (temperature ranging between 16.5°C and 18°C) was

**Table 5** *Leptogorgia sarmentosa*. Monthly capture rates of zooplankton, and live and detrital particles < 100  $\mu\text{m}$  ( $\mu\text{g C g}^{-1}$  AFDW  $\text{day}^{-1}$ ; mean  $\pm$  SE) (zoopl. zooplankton; det. POC detrital particulate organic carbon; live < 100  $\mu\text{m}$  live carbon < 100  $\mu\text{m}$ ). Data on live and detrital particles from Rossi (2002) and Ribes et al. (2003)

	Zoopl.	Det. POC	Live < 100 $\mu\text{m}$	Total
Jan	1,589 $\pm$ 354	5,079	170	6,838
Feb	2,278 $\pm$ 555	3,816	279	6,373
Mar	4,695 $\pm$ 1,047	1,024	681	6,400
Apr	3,892 $\pm$ 919	5,825	362	10,079
May	2,392 $\pm$ 1,564	5,422	816	8,630
Jun	3,737 $\pm$ 868	4,450	591	8,778
Jul	1,772 $\pm$ 499	121	35	1,928
Aug	5,003 $\pm$ 1,416	806	70	5,878
Sep	2,766 $\pm$ 1,047	187	110	3,063
Oct	1,093 $\pm$ 342	903	112	2,108
Nov	2,688 $\pm$ 836	2,181	236	5,105
Dec	4,705 $\pm$ 1,078	8,997	304	14,006

0.55  $\text{mg O}_2 \text{g}^{-1} \text{AFDM h}^{-1}$ , which is equivalent to 155  $\mu\text{g C g}^{-1} \text{AFDM h}^{-1}$ . This value would represent a maximum of 3,720  $\mu\text{g C g}^{-1} \text{AFDM day}^{-1}$  if we consider that the polyps are expanded the whole day. Average zooplankton ingesta (3,260  $\mu\text{g C g}^{-1} \text{AFDM day}^{-1}$ ) could barely account for the metabolic cost of respiration. However, several factors should be considered. First, *L. sarmentosa* does not feed on zooplankton alone, but also on detrital POC and live carbon < 100  $\mu\text{m}$ . If all seston sources are considered, the species ingested an average of 6,600  $\mu\text{g C g}^{-1} \text{AFDM day}^{-1}$ . Second, the respiration rate was estimated for expanded polyps. Therefore, the respiration rate is probably lower than the values estimated, because, on average, polyps are expanded only part of the time (Coma et al. 1994, and unpublished data) and the contraction of polyps reduces the rate of respiration between 10% and 60% (Sebens 1987; Fabricius and Klumpp 1995; Coma et al. 2002). Third, respiration was estimated in spring, one of the periods of higher investment of the species in secondary production (Rossi 2002), and, therefore, the respiration rate estimated includes the cost associated with the synthesis of new tissue (Coma et al. 2002). Fourth, the estimated values of total ingesta should be considered as conservative, because feeding on detrital POC and live carbon < 100  $\mu\text{m}$  (Ribes et al. 2003) was studied at a low flow speed (1.2  $\text{cm s}^{-1}$ ) and capture rates increase several-fold with an increase in flow speed (Fabricius et al. 1995). Thus, although this estimate may be an underestimate of the ingesta of *L. sarmentosa*, it can largely account for the respiration rate of the species.

#### Effect of octocoral predation on seston abundance

The density of *L. sarmentosa* in the study area was 1.5 colonies  $\text{m}^{-2}$ , with a mean height of 23 cm (Rossi 2002), which represents a standing stock of 1.2  $\text{g AFDM m}^{-2}$ . To estimate the effect of the octocoral

population on seston abundance, we also considered feeding of the species on detrital POC and live carbon < 100  $\mu\text{m}$  (data from Rossi 2002; Ribes et al. 2003; Table 5). At the estimated ingestion rates (1,928–14,006  $\mu\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ ) on all seston fractions (i.e. zooplankton, detrital POC and live carbon < 100  $\mu\text{m}$ ), the population of *L. sarmentosa* removed between 2.3 and 16.8  $\text{mg C m}^{-2}$   $\text{day}^{-1}$  from the adjacent water column. Higher population densities have been reported in other locations such as Banyuls-sur-Mer, France (2.4 colonies  $\text{m}^{-2}$ , Rossi 2002), and La Spezia, Italy (6.8 colonies  $\text{m}^{-2}$ , corresponding to a standing stock of 5.44  $\text{g}^{-1}$  AFDM  $\text{m}^{-2}$ , Mistri 1995). The ingestion rate of *L. sarmentosa* on all seston fractions ( $0.007 \pm 0.003$   $\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ ; mean  $\pm$  SD) is among the values reported for octocorals (*Plexaura flexuosa*:  $0.045 \times 10^{-3}$   $\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ , Ribes et al. 1998; *Dendronephthya hemprichi*:  $0.008$   $\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ , Fabricius et al. 1998; *Paramuricea clavata*:  $0.002$   $\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ , Coma et al. 1994; Ribes et al. 1999; octocoral community:  $\sim 0.010$   $\text{g C g}^{-1}$  AFDM  $\text{day}^{-1}$ , Fabricius and Dommissé 2000). Because of the relatively low density of *L. sarmentosa*, the impact of this population on the water column ( $2.3$ – $16.8$   $\text{mg C m}^{-2}$   $\text{day}^{-1}$ ) is among the lowest values reported for octocorals (*Plexaura flexuosa*:  $0.15$   $\text{mg C m}^{-2}$   $\text{day}^{-1}$ , Ribes et al. 1998; *Dendronephthya hemprichi*:  $451$   $\text{mg C m}^{-2}$   $\text{day}^{-1}$ , Fabricius et al. 1998; *Paramuricea clavata*: up to  $170$   $\text{mg C m}^{-2}$   $\text{day}^{-1}$ , Coma et al. 1994; Ribes et al. 1999; octocoral community:  $\sim 2.5$   $\text{g C m}^{-2}$   $\text{day}^{-1}$ , Fabricius and Dommissé 2000), but within the range reported for other passive suspension feeders, including most hydrozoans (between 6 and 66  $\text{mg C m}^{-2}$   $\text{day}^{-1}$ , Gili et al. 1998). These observations indicate that predation by macroinvertebrates on plankton populations and suspended detrital POC should be considered in energy transfer processes in littoral areas, since even species with a low abundance may have a detectable impact.

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