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REPORT

Natural heterotrophic feeding by a temperate octocoral with symbiotic zooxanthellae: a contribution to understanding the mechanisms of die-off events

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Abstract Octocorals are among the most emblematic and representative organisms of sublittoral communities in both tropical and temperate seas. *Eunicella singularis* is the most abundant gorgonian in shallow waters and the only gorgonian with symbiotic zooxanthellae in the Mediterranean Sea. We studied the natural diet and prey capture rate of this species over an annual cycle and characterized prey digestion time over the natural temperature regime. The species captured zooplankton prey between 40 and 920 µm. A mean content of 0.14 ± 0.02 prey polyp^{-1} was observed throughout the year. The strong pattern of decrease in digestion time with temperature increase (from 25 h at 13 °C to 8 h at 21 °C) allowed us to estimate that the prey capture rate was 0.017 ± 0.002 prey polyp^{-1} h^{-1} (mean ± SE); the ingestion rate exhibited a seasonal pattern with higher values in spring (0.007 µg C polyp^{-1} h^{-1}). Feeding on zooplankton had a low contribution to the respiratory expenses of *E. singularis* except in early spring. Then, heterotrophic nutrition in the natural environment seems unable to meet basal metabolic requirements, especially in summer and fall. This result, in conjunction with the documented collapse of photosynthetic capacity above a warm temperature threshold, indicates the occurrence of a resource acquisition limitation that may play a role in the repeated summer die-off events of the species.

Keywords Natural diet · Capture rate · Digestion time · Feeding ecology · Gorgonians · *Eunicella singularis*

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Introduction

The role of food as a constraining factor at different levels of ecological organization has been a prevalent topic in ecology. In tropical areas, special attention has been devoted to nutritional symbiosis in coral reefs due to the devastating consequences of bleaching (Muscatine and Porter 1977). These effects highlight the major ecological role that the nutritional symbiosis between scleractinian corals and zooxanthellae plays in the success of coral reef ecosystems and how the breakdown of the symbiosis can promote a transition toward an algal-dominated ecosystem (Hughes et al. 2010). However, heterotrophy has also been shown to contribute to tissue composition, photosynthesis, and skeletal growth of the corals (Houlbrèque and Ferrier-Pagès 2009; Ferrier-Pagès et al. 2011a). In temperate areas, food, as a limiting factor, is of special relevance in oligotrophic systems, and heterotrophic feeding has been documented to be a crucial determinant of the dynamics of many benthic suspension feeding taxa in the Mediterranean (Coma and Ribes 2003). Evidence of the depletion of planktonic communities by the benthic suspension feeders points to a relevant role of resource limitation in the distribution and abundance of suspension feeders, particularly in oligotrophic systems (Gili and Coma 1998).

Octocorals are among the most conspicuous organisms of rocky subtidal communities, in both tropical and temperate seas (Kinzie 1973). These ecosystem engineer species play important ecological roles in plankton–benthos coupling (Gili and Coma 1998); in addition, their tridimensional structure provides shelter to numerous other species, and therefore contributes substantially to the biomass and diversity of the benthic community (Ballesteros 2006). However, the nutrition of symbiotic octocorals has been mainly studied in tropical ecosystems. These species exhibit low rates of primary productivity and therefore depend on both autotrophy and heterotrophy to meet their metabolic needs (Sorokin 1991; Fabricius and Klumpp 1995; Ribes et al. 1998). Symbiotic octocorals in temperate ecosystems are less common than in tropical areas, and their nutrition has received less attention. This lack of knowledge may become a limiting step in understanding the factors that constrain their populations.

In the Mediterranean, gorgonians can constitute up to 40 % of the rocky sublittoral communities biomass (Ballesteros 2006). The white gorgonian *Eunicella singularis* (Esper, 1791), the only symbiotic gorgonian species in the Mediterranean, is among the most abundant and widespread species in the northwestern Mediterranean (Linares et al. 2008; Gori et al. 2011). Recently, some studies have contributed to our understanding of the resource acquisition of *E. singularis*. Cocito et al. (2013) documented that the isotopic composition of this species was close to that of zooplankton. Gori et al. (2012), by examining the isotopic and fatty acids composition of populations from another area, contributed to show the occurrence of an important variability in the main food sources of the species. Furthermore, Ezzat et al. (2013) conducted a laboratory experiment, in which they examined how warm temperature, under four nutritional regimes, affected performance of the species. However, the natural feeding rate of zooplankton and its role in the energy budget of the species remain poorly understood. This knowledge could contribute to understanding the causes of the die-off events that have been repeatedly damaging populations of this and other suspension feeder species in the NW Mediterranean during the last two decades (Coma et al. 2009; Calvo et al. 2011).

Examination of the natural diet by direct methods permits an accurate determination of the range in the type and size of prey, especially with regard to zooplankton items. In this study, we analyzed the gut content of polyps to determine the main, natural zooplankton prey types and the prey size spectra captured by the species. Temporal variability in feeding was studied by examining samples collected monthly over an annual cycle. Prey digestion time, a crucial factor to estimate capture rate (prey polyp^{-1} h^{-1}) from gut contents, is one of the least studied aspects of the feeding ecology of gorgonians and anthozoans in general (Electronic Supplementary Material, ESM, Appendix 1). Prey digestion time was examined over the natural thermal regime of the species at the study site because the amplitude of the annual temperature variation may strongly affect digestion time. In the framework of the previous studies (Gori et al. 2012; Cocito et al. 2013; Ezzat et al. 2013), this work contributes to understanding the role of the heterotrophic nutrition of the ubiquitous Mediterranean symbiotic gorgonian *E. singularis* by describing its natural diet and prey size spectra, assessing temporal variability in capture rate, and estimating its ingesta.

Materials and methods

The population of *E. singularis* studied here was located on a steep rock called "Tascó Gran" in the Medes Islands Marine Reserve (NW Mediterranean Sea; 43°2′20″N, 3°13′30″E). The population was found from 4 to 35 m depth, extending over an area of ~90,000 m^2. Using scuba gear, samples were collected from ~15 m depth where the species exhibited its highest abundance. Seawater temperature was monitored using a HOBO® Pendant Temperature Data Logger (UA-002-64, Onset Computer Corporation) placed at 15 m depth. We determined the mean daily, monthly, and annual temperatures on the basis of the data recorded hourly from October 2010 to January 2012.

Feeding on zooplankton

Feeding on zooplankton was assessed by examining the gut contents of polyps from terminal branches of *E. singularis*. To examine variation over the annual cycle, samples were collected monthly between December 2010 and December 2011. All samples were collected during the last week of each month, at the same time period of the day (9–11 h), to avoid possible circadian influences on the annual pattern of prey capture. To examine variation over the diel cycle, samples were collected every 4 h over a 24-h time period in March 1998, because this is the time period (late winter–early spring) in which plankton blooms typically occur in the NW Mediterranean (Estrada 1996). Each sample from both the annual and diel cycles consisted of one terminal branch collected from each of ten randomly selected colonies. Size of the sampled colonies was not taken into account. The fragments were immediately placed in 10 % formaldehyde solution in filtered seawater (policarbonate filters of 0.2-μm pore size) to prevent further digestion. Fifty polyps selected randomly from the samples (five from each branch) were dissected under a binocular stereomicroscope. The content of the polyps was isolated, identified

to the higher taxonomic level, and counted. The length of all prey was measured under the stereomicroscope at 50× magnification.

Prey digestion time

Three experiments were carried out to estimate the temperature effect on prey digestion time. The experiments were conducted in February (13 °C), June (17 °C), and August 2011 (21 °C), to encompass the natural range of temperature where the species live at the study site (from 12 to 23 °C). For each experiment, one terminal branch was collected by scuba divers from each of 130 randomly selected colonies. As the divers emerged, ten terminal branches were fixed with 10 % formaldehyde solution in filtered seawater (policarbonate filters of 0.2-µm pore size). The other branches were placed in aerated containers with the same filtered seawater, at the natural seawater temperature, to prevent further prey capture (Rossi et al. 2004). At hourly intervals, ten additional branches from the containers were randomly selected and fixed. Fifty polyps selected randomly from the samples (five from each branch) were dissected, and their contents were examined as described above.

Prey capture rate

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

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

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 h), and D is digestion time (in h). Prey digestion time was attributed to the gut contents from each month on the basis of the recorded mean monthly temperature.

Biomass

To facilitate comparison, prey biomass was estimated from biovolumes (Sebens and Koehl 1984) using the same conversion factors for wet mass (1.025; Hall et al. 1970), dry mass (DM) (13 % of wet mass; Beers 1966), and carbon content (45 % of dry weight; Biswas and Biswas 1979) used in previous studies (Coma et al. 1994; Rossi et al. 2004). The nitrogen content was estimated from the carbon/nitrogen ratio of each group (Gorsky et al. 1988; Faganeli et al. 1988). The DM of *E. singularis* was determined by separately drying the coenenchyme and the axis at 90 °C for 24 h from seven terminal branches (ca. 20 mm in length) from different colonies. The ash-free dry mass (AFDM) of the coenenchyme and the axis was determined by combustion at 450 °C for 5 h. For the separate determination of the carbon and nitrogen content of the coenenchyme and the axis, 14 terminal branches (ca. 10 mm in length) of non-reproductive colonies (<15 cm in height; Ribes et al. 2007) were dried and ground at 90 °C. The samples were analyzed with a C:H:N Shimatzu autoanalyzer (PerkinElmer 240). The number of polyps from each branch was counted, and the length and diameter were measured under the stereomicroscope. To examine whether ingesta cover the metabolic needs of *E. singularis*, oxygen units from the literature were converted to carbon equivalents according to Muscatine et al. (1981); respiration = µmol O_2 × RQ, where RQ is the respiratory quotient equal to 0.8 mol C:mol O_2, as used in previous studies on nutritional ecology of the species (Ferrier-Pagès et al. 2015).

Prior to analyses, the assumptions of normality and homoscedasticity of the data were examined using the Kolmogorov–Smirnov and Cochran's tests, respectively; whenever necessary, data were transformed. Differences in prey size throughout the year were analyzed using one-way ANOVA. Because transformations did not accomplish normality for the other variables examined, generalized linear models (Dobson and Barnett 2008) with a Poisson error family distribution and log link were used to analyze the variables with integer values and nonnegative predictions (i.e., prey polyp^{-1}, prey polyp^{-1} h^{-1}). The model used for the analysis of µg C polyp^{-1} h^{-1} and µg N polyp^{-1} h^{-1} followed a gamma error family distribution with identity link (to predict continuous and nonnegative values). We used the relationship between the number of prey items per polyp and time to estimate the digestion time (Rossi et al. 2004). The analyses were performed using the STATISTICA 7.0 software package.

Results

The temperature regime

Mean annual seawater temperature at 15 m depth in 2011 was 16.9 ± 0.1 °C (mean ± SE). Temperature exhibited a seasonal pattern (Fig. 1). The mean monthly temperature ranged from 22.6 °C in September to 12.6 °C in February. During the study period, the highest daily temperature was observed in September (23.5 °C), and the lowest in February (11.8 °C).

Feeding on zooplankton

Most of the prey items observed inside the gastrovascular cavity of *E. singularis* during the annual cycle were

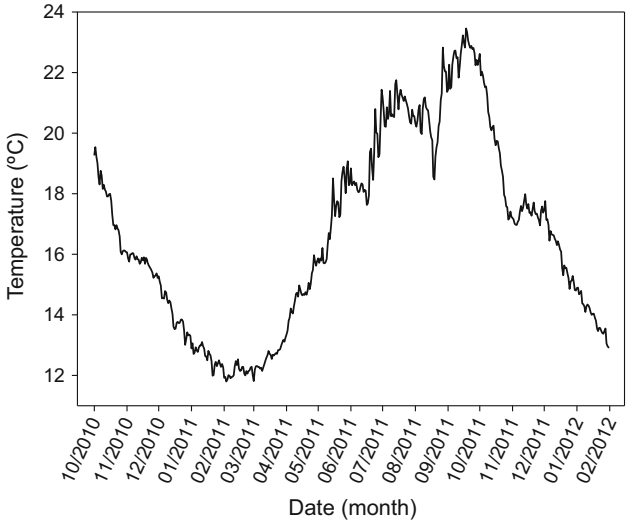

Fig. 1 Daily average seawater temperature at 15 m depth at Medes Islands (NW Mediterranean Sea) from October 2010 to January 2012

zooplankton and particulate organic matter (POM). Invertebrate eggs, larvae, crustaceans, and copepods accounted for 77 % of all items captured throughout the year (Table 1). POM was the second most abundant prey item accounting for 17 % of all items. Although the number of prey decreased with prey size, prey biomass was rather evenly distributed among the different prey size classes (Fig. 2). *Enicella singularis* captured zooplankton prey that ranged in size from 40 to 920 μm, but low mobility prey smaller than 400 μm accounted for 83 % of the prey (Fig. 2a). Despite this, 52 % of the prey biomass corresponded to prey items larger than 400 μm (Fig. 2b). The mean percentage of polyps with prey items over the annual cycle was 12 %, ranging from 4 to 34 % (Table 1).

The mean number of prey polyp^{-1} during the annual cycle was 0.14 ± 0.02 (mean ± SE), ranging from 0.04 to 0.44 prey polyp^{-1}. The mean seasonal number of prey polyp^{-1} in the gastrovascular cavity of *E. singularis* exhibited a significant pattern of higher values in spring ($\chi^2 = 13.28$, $df = 3$, $p = 0.004$; Fig. 3a).

The preys observed during the examined diel cycle were similar to those found during the annual cycle: invertebrate eggs (56 %), POM (31 %), and crustaceans (13 %; Table 2). *Enicella singularis* captured zooplankton and POM that ranged in size from 20 to 600 μm. The mean percentage of polyps with prey items over the diel cycle was 10 %, ranging from 2 to 18 % (Table 2). The number of prey per polyp was 0.11 ± 0.02 (mean ± SE) and did not exhibit significant variation over the diel cycle ($\chi^2 = 7.31$, $df = 3$, $p = 0.20$; Fig. 3b).

Prey digestion time

Digestion time was calculated from the slope of the regression lines of the data from the experiments at three different temperatures covering the annual temperature range at the study site. Because ten distinct colonies were examined at each time period of the digestion experiment, the slope of the number of prey per polyp over time was not affected by inter-colony variability. We assumed that the

Table 1 Number and type of prey items captured by *Eunicella singularis* over the annual sampling period (December 2010–December 2011), and total number of gut contents observed in the 650 examined polyps (50 per sample)

Prey type	Dec	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	*N*	%
Invertebrate eggs	1	2	0	2	1	5	7	8	2	4	1	8	1	42	47
Bivalve larvae	0	0	2	2	4	0	0	0	0	0	1	0	0	9	10
POM	6	0	2	6	1	0	0	0	0	0	0	0	0	15	17
Crustaceans	3	0	0	0	0	1	0	0	0	0	0	0	0	4	4
Crustacean larvae	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Protozoans (Tintinnida)	0	0	0	0	1	0	0	1	0	0	0	0	0	2	2
Copepods	0	0	1	12	0	0	0	0	0	0	0	0	0	13	14
Copepod eggs	0	0	0	0	1	0	0	0	0	0	0	0	1	2	2
Unidentified	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2
Total prey	11	2	5	22	8	6	7	9	2	4	2	8	4	90	100
No. of full polyps	9	2	5	17	8	5	7	9	2	4	2	8	2		
%	18	4	10	34	16	10	14	18	4	8	4	16	4		
No. of prey polyp^{-1}															
Mean	0.22	0.04	0.10	0.44	0.16	0.12	0.14	0.18	0.04	0.08	0.04	0.16	0.08		
SE	0.03	0.01	0.02	0.06	0.03	0.03	0.03	0.02	0.01	0.02	0.01	0.03	0.04		

No. of full polyps: Number of polyps with prey inside, *POM*: particulate organic matter

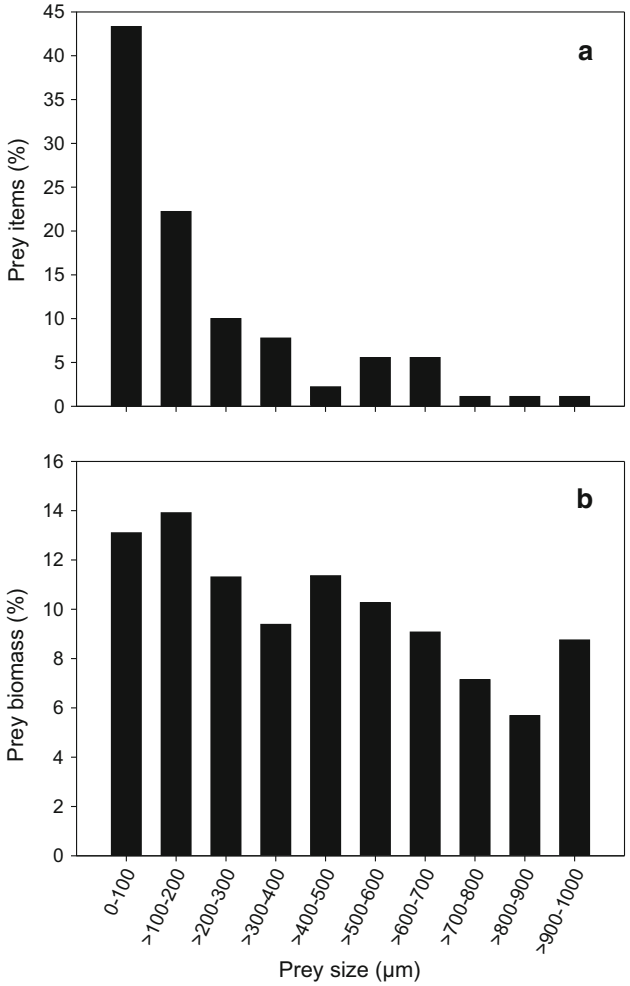

Fig. 2 Size-frequency distribution (maximum length) **a** of the number of prey items (in %) and **b** of the prey items' biomass (in %) observed in the gut contents of *Eunicella singularis* throughout the annual cycle ($n = 650$ polyps)

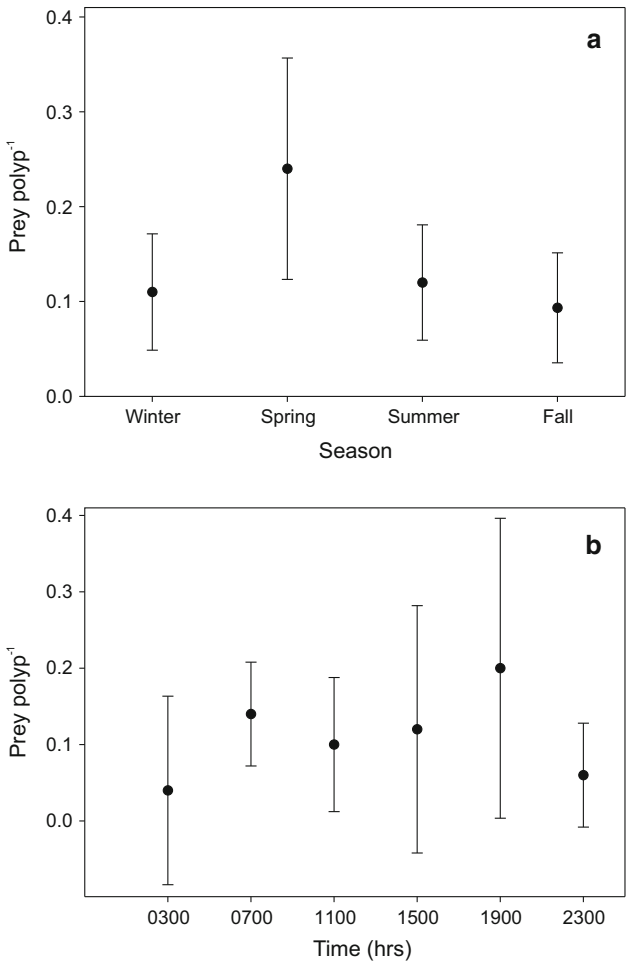

Fig. 3 *Eunicella singularis*. Variation in the mean (±95 % confidence interval) number of prey items per polyp: **a** over the annual cycle and **b** over the diel cycle

variability within the ten colonies from each time period represents the natural variability of the population. Furthermore, because the number of prey was low, often the ten colonies had different prey types. Then, our experiments provided an integrated estimate of prey digestion time but were not appropriate to examine inter-colony variability. Clearance of the gut contents showed an exponential decrease in the number of prey items per polyp with time (Fig. 4a). Complete clearance of the stomach required 57 h at 13 °C, 34 h at 17 °C, and 19 h at 21 °C; hence, digestion time exhibited a clear pattern of decrease with temperature increase. However, the last 10 % of prey items were always bivalve larvae fragments, *Tintinnida loricas*, and copepod carapaces. These items, whose digestion is difficult, are not representative of the bulk of prey, and including the additional time required to digest them would result in a substantial overestimation of digestion time. Thus, 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). Digestion times were derived from the data in Fig. 4a, using the exponential equations to estimate the time required to digest 90, 95, and 100 % of the prey items (Fig. 4b). The elapsed time at which 90 % of the prey had been digested was 25 h at 13 °C, 15 h at 17 °C, and 8 h at 21 °C. An exponential function was adjusted to the relationship between temperature and digestion time (Fig. 4b). Prey digestion times were used to calculate prey capture rate (prey polyp^{-1} h^{-1}) following Eq. (1), presented in the methods.

Prey capture rate

On the basis of the adjusted exponential function to the temperature and digestion time relationship, we used the mean monthly temperature to assign the appropriate

Table 2 Number and type of prey items captured by *Eunicella singularis* over the diel sampling cycle (March 28, 1998), and total number of gut contents observed in the 300 examined polyps (50 per sample)

Prey type	Number of prey at each time (hrs)						*N*	%
	0300	0700	1100	1500	1900	2300		
Invertebrate eggs	2	2	2	4	8	0	18	56
Bivalve larvae	0	0	0	0	0	0	0	0
POM	0	4	2	2	1	1	10	31
Crustaceans	0	1	0	0	1	1	3	9
Crustacean larvae	0	0	0	0	0	0	0	0
Protozoans (Tintinnida)	0	0	0	0	0	0	0	0
Copepods	0	0	1	0	0	0	1	3
Copepod eggs	0	0	0	0	0	0	0	0
Unidentified	0	0	0	0	0	0	0	0
Total prey	2	7	5	6	10	2	32	
No. of full polyps	1	7	5	5	9	3		
%	2	14	10	10	18	6		
No. of prey polyp^{-1}								
Mean	0.04	0.14	0.10	0.12	0.20	0.06		
SE	0.01	0.01	0.01	0.02	0.02	0.01		

No. of full polyps: Number of polyps with prey inside, *POM*: particulate organic matter

digestion time to the gut contents of each monthly sample. The zooplankton prey capture rate was 0.017 ± 0.002 prey polyp^{-1} h^{-1} (mean ± SE) and did not exhibit a significant seasonal variation ($\chi^2 = 0.27$, $df = 3$, $p = 0.96$; Fig. 5a). In contrast, the mean prey size exhibited a significant seasonal variation (one-way ANOVA, $F_{3,86} = 10.08$, $p < 0.0001$; Fig. 5b). The highest values were observed in spring (340 ± 43 µm, mean ± SE), while the other seasons showed similar prey sizes (post hoc Scheffé test). Ingestion rates were estimated on the basis of capture rate and prey size. Mean annual ingestion rate in terms of biomass was 0.003 ± 0.0005 µg C polyp^{-1} h^{-1} and 0.00056 ± 0.00012 µg N polyp^{-1} h^{-1}, but exhibited a marked seasonal pattern ($\chi^2 = 20.95$, $df = 3$, $p = 0.0001$; $\chi^2 = 23.32$, $df = 3$, $p < 0.0001$; respectively; Fig. 5c). Thus, the mean ingestion rate observed in spring (0.007 ± 0.002 µg C polyp^{-1} h^{-1}, 0.0015 ± 0.0004 µg N polyp^{-1} h^{-1}) was at least threefold higher than that observed in the other seasons (ranging between 0.001 and 0.002 µg C polyp^{-1} h^{-1}, 0.0001 and 0.0004 µg N polyp^{-1} h^{-1}; Fig. 5c), mainly due to the seasonal differences in prey size.

Ingesta of the species

The DM of the terminal branches was 18.1 ± 0.9 mg per linear cm (mean ± SE), and the AFDM was 35.8 ± 2.6 % of the overall DM (coenenchyme and axis). The coenenchyme DM was 87.0 ± 1.5 % (mean ± SE), and the axis DM was 13.0 ± 1.6 % of the overall DM. The carbon and nitrogen content of the coenenchyme was 19.5 ± 0.3 % (mean ± SE) and 3.1 ± 0.1 % of the coenenchyme DM, respectively. The carbon and nitrogen content of the axis was 45.0 ± 1.0 % (mean ± SE) and 16.2 ± 0.4 % of the axis DM, respectively. Then, the carbon and nitrogen content of the coenenchyme was 3.071 mg C cm^{-1} and 0.488 mg N cm^{-1}, respectively. The carbon and nitrogen content of the axis was 1.059 mg C cm^{-1} and 0.381 mg N cm^{-1}, respectively. The mean number of polyps per terminal cm^2 was 47.1 ± 2.3 (mean ± SE) and 31.1 ± 1.1 polyps linear cm^{-1} (branch diameter: 0.21 ± 0.01 cm). Then, on the basis of a mean annual rate of ingesta of 0.003 µg C polyp^{-1} h^{-1} and 31.1 polyps linear cm^{-1}, ingesta can be estimated as 2.239 µg C cm^{-1} d^{-1}. These values allowed us to estimate that, on average, the colonies daily ingested <0.1 % of their coenenchyme mass (2.239 µg C cm^{-1} d^{-1}/3.071 mg C cm^{-1}).

The proportion of the respiration rate that can be covered by the estimated ingesta depends on the seasonal pattern of ingesta and on the respiration of *E. singularis* (100–660 µg O_2 g AFDM^{-1} h^{-1} under the natural temperature range; Previati et al. 2010; Ezzat et al. 2013; Ferrier-Pagès et al. 2015). To examine whether the seasonally estimated ingesta can cover the metabolic expenses of the species, we used respiration rate and conversion factors from previous studies. Then, the metabolic expenses of the species were determined on the basis of the estimates of dark respiration conducted by Previati et al. (2010) between 14 and 25 °C and the monthly mean temperature at the study site. Dark respiration was interpolated between the two nearest values when mean monthly temperature fell between the temperature intervals examined by Previati et al. (2010). Dark respiration at the

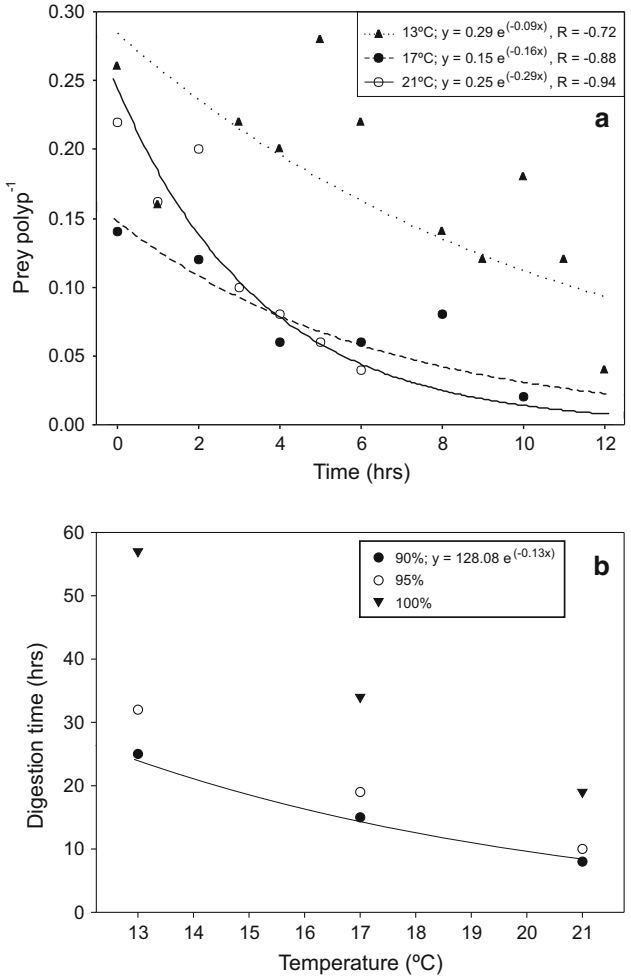

Fig. 4 *Eunicella singularis*. Prey digestion time. **a** Exponential decrease in the number of prey per polyp over time (in h) at three temperatures (13, 17, and 21 °C). The standard error of the slope was 0.03 at 13 °C, 0.04 at 17 °C, and 0.04 at 21 °C. **b** Exponential decrease in the prey digestion time (in h) with temperature increase. The proportions of prey items digested (90, 95, and 100 %) provide the time at which the number of prey per polyp is 10, 5, and 0 % from the initial number of prey per polyp, respectively

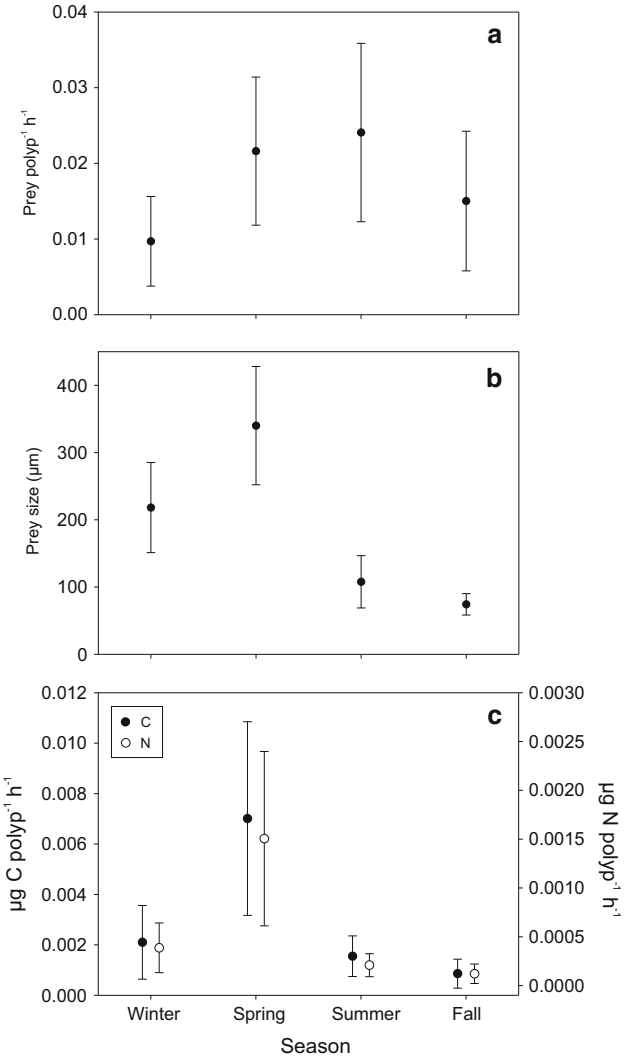

Fig. 5 *Eunicella singularis*. Variation in the mean (±95 % confidence interval): **a** capture rate (prey polyp^{-1} h^{-1}), **b** prey size (µm), and **c** ingestion rate (µg C polyp^{-1} h^{-1}, µg N polyp^{-1} h^{-1}) of zooplankton throughout the annual cycle

mean monthly temperature of 13 °C was assumed to be the same as that estimated at 14 °C. Contrasting the seasonal pattern of ingesta to the cost of dark respiration showed that ingesta can only account for the metabolic cost of respiration in early spring due to the high ingesta and low respiration at the low temperature (<14 °C; Fig. 6). In winter, despite the low temperature, ingesta accounted for ~30 % of the metabolic cost of respiration due to the low capture rate. In summer and fall, ingesta accounted for a small proportion of respiration (~6 %) due to both the low capture rate and the increase in respiration with temperature.

To determine the importance of feeding on zooplankton as a nitrogen and carbon source for colony growth, we estimated the nitrogen and carbon requirements for new production as the requirement for annual growth. New production includes growth and reproduction, but in small colonies (<15 cm in height), new production is invested only in growth. The average growth rate per branch of small *E. singularis* at the study area is 1 cm yr^{-1} (Llorente-Llurba 2011). The carbon and nitrogen content of the colony (tissue and axis, see above) was 4.130 mg C cm^{-1} and 0.869 mg N cm^{-1} of terminal branch, respectively. Therefore, a model *E. singularis* colony of 11 cm in height with five primary branches (total branch length = 33.4 cm; Llorente-Llurba 2011) would require a minimum of 20.65 mg C yr^{-1} and 4.35 mg N yr^{-1} for annual growth. Given the number of polyps per linear cm of the colony (31.1), a total number of 1039 polyps can be estimated for the model colony. On the basis of a mean annual rate of

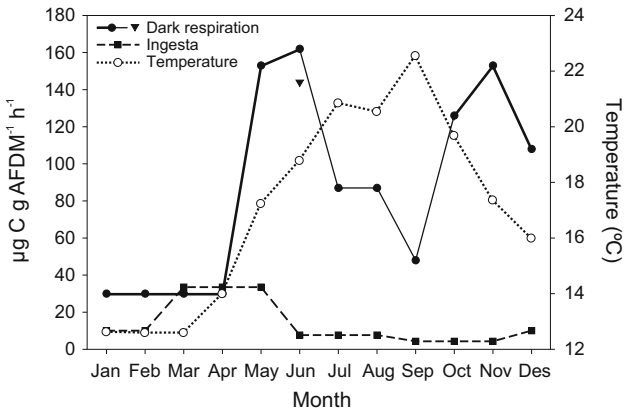

Fig. 6 *Eunicella singularis*. Monthly mean sea temperature (*empty circles*); ingesta (*full squares*, values converted to µg C g AFDM^{-1} h^{-1} based on a polyp density of 31.1 polyps linear cm^{-1} and 6.5 mg AFDM linear cm^{-1}, this study); dark respiration (*full circles*, data from Previati et al. 2010, values converted to µg C g AFDM^{-1} h^{-1} based on µmol C = µmol O_2 × RQ, RQ = 0.8 mol C:mol O_2; Muscatine et al. 1981); the *thinner part* of the *line* indicates respiration drop at ≥20 °C due to decrease in polyps activity; dark respiration (*full triangle*, data from Ferrier-Pagès et al. 2015, values converted to µg C g AFDM^{-1} h^{-1} based on 6.5 mg AFDM cm^{-1} and 47.1 polyps cm^{-2}, 31.1 polyps linear cm^{-1})

ingesta of 0.003 ± 0.0005 µg C polyp^{-1} h^{-1} (mean ± SE) and 0.00056 ± 0.00012 µg N polyp^{-1} h^{-1}, ingesta of the model colony can be estimated as 27.30 mg C yr^{-1} and 5.10 mg N yr^{-1}. Then, ingesta of the colony represented ~130 % and ~120 % of the carbon and nitrogen needs for annual growth, respectively.

Discussion

Zooplankton diet

The most abundant prey items present in the gut contents of *E. singularis* were small (40-400 µm), low-motile zooplankton (invertebrate larvae and eggs). This is in agreement with the types of prey and size spectra of diet of other octocorals observed in previous studies (ESM Appendix 1), which has been attributed to the low density of nematocysts in octocorals. However, gut contents also included larger prey up to 920 µm, which is the largest prey size reported to be captured by a gorgonian species. This is significant because, although large prey items (>400 µm) were not abundant in the gut contents (17 % of the prey), they accounted for about half of ingesta in terms of biomass. Thus, although most of the captures were small prey, the two distributions (Fig. 2) do suggest preferential uptake of larger prey and less than expected capture of the smallest items.

Gut contents

We did not observe any significant variation in the number of prey polyp^{-1} of *E. singularis* over the diel cycle. Prey concentration and flow speed are central factors affecting prey capture. Although open-water zooplankton at the study area exhibits a marked diel cycle (Siokou-Frangou 1996), near-substratum zooplankton has been less studied. Data on dynamics of near-substratum zooplankton have documented that, despite changes in composition that can occur, no clear diel pattern in either size or abundance has been observed (Sebens and Koehl 1984; Coma et al. 1994). This lack of a clear diel pattern in near-substratum zooplankton may contribute to understanding the lack of variation in gut contents of *E. singularis* over the diel cycle. But it should also be considered that near-substratum flow, a crucial factor to interpret the diel cycle, has been little studied.

The gut contents of *E. singularis* over the annual cycle exhibited an average of 0.14 prey polyp^{-1} (a mean value rather similar to that of the diel cycle, 0.11 prey polyp^{-1}), which is the lowest value observed in Mediterranean Alcyonaceas (0.14–0.68 prey polyp^{-1}) and among the lowest values observed in Alcyonacea species examined to date under natural conditions (0.01–3.3 prey polyp^{-1}; ESM Appendix 1). Nevertheless, it should be noted that *E. singularis* is zooxanthellate, and most of the previously examined gorgonian species are exclusively heterotrophic. In fact, this is the first zooxanthellate gorgonian for which the natural diet and capture rate have been examined for a long time period (i.e., an annual cycle). The gut content observed in *E. singularis* was an order of magnitude higher than those observed in the other two symbiotic gorgonians examined under natural conditions (*Plexaura flexuosa* and *Pseudoplexaura porosa:* 0.01–0.03 prey polyp^{-1}; Ribes et al. 1998). The values observed in *E. singularis* were higher than those commonly observed in Zoanthidea (0.02–0.12 prey polyp^{-1}). In general, the values of prey polyp^{-1} observed in Alcyonacea species are similar to those observed in Scleractinia (0.1–1.8 prey polyp^{-1}; ESM Appendix 1).

Prey digestion time

Prey digestion time received some attention in early studies, but, despite its importance, it has been little studied in anthozoans (ESM, Appendix 1). Factors such as prey type, prey size, and temperature can affect prey digestion time (Martinussen and Båmstedt 1999). However, our goal was to determine the effect of temperature on prey digestion time with natural gut contents. To this end, the experiments were conducted at the time of the year, in which

gorgonians were naturally acclimatized to each temperature. By conducting the experiments with natural gut contents, our results may have been affected by a variation in prey composition among the experiments. However, the proportion of the three main components of the diet (invertebrate larvae, eggs, and POM) during the experiments ranged between 75 and 84 %, which was similar to the mean value observed over the annual cycle (77 %). Therefore, we concluded that the experiments can be considered representative of the pattern of variation in digestion time of the bulk prey type of the species over the annual temperature range at the study site.

The digestion time estimated for *E. singularis* at 21 °C (8 h) is the longest reported for the octocoral species examined to date. At present, the digestion time estimates available for octocorals (4–8 h) appear longer than those for hexacorallia species (2–3 h; ESM Appendix 1). Long digestion times have also been observed in some hexacorals (8–10 h) but appear to be related to the particularly large prey items of the study (770–1000 μm in length; ESM Appendix 1).

Digestion time exhibited a strong pattern of decrease with temperature increase, a pattern that was expected because of the general tendency of chemical reaction rates to increase with temperature (Martinussen and Båmstedt 1999). The observed pattern was similar to those previously reported in hydrozoans and in several gelatinous planktonic predators (Christensen 1967; Martinussen and Båmstedt 2001). This pattern has not been examined in hexacorals, most likely because most examined species are tropical and therefore exposed to a rather narrow temperature range. Physiological processes in poikilotherms are usually governed by the ambient temperature, and a temperature effect corresponding to a Q_{10} (the variation in a rate for a 10 °C rise in temperature) between two and three seems to be the general effect; however, the Q_{10} for the digestion time of *E. singularis* (4.1) was high and higher than that previously observed in *Leptogorgia sarmentosa* (3.1; Rossi et al. 2004). The values observed in these gorgonian species are also higher than those observed in gelatinous planktonic predators (Q_{10} ranging from 1.4 to 3.0; Martinussen and Båmstedt 2001) and for the hydrozoan *Clava multicornis* (Q_{10} ranging from 1.9 to 2.3 at different salinities from 22 to 40 ‰), but lower than that observed in the hydrozoan *Hydractinia echinata* (5.6; Christensen 1967). Studies on these enzyme-catalyzed reactions are needed to increase understanding of the higher-than-expected effect of temperature on the digestion time of these gorgonian species.

Prey capture rate

The results of gut content examinations of *E. singularis* polyps integrate the effects of prey concentration and flow speed on the prey capture rate. We observed a significant seasonal variation in ingesta due to higher prey capture rate and prey size in spring. This is consistent with the recurrent annual phytoplankton bloom in late winter–early spring, the main feature affecting the planktonic community at the study area and also in other areas of the Mediterranean (Estrada 1996). However, previous studies on near-bottom zooplankton conducted in different years at the study area show that although the zooplankton community displays a succession of taxa throughout the year, total zooplankton abundance is highly variable, often lacking any clear seasonal pattern (Coma et al. 1994; Calbet et al. 2001; Rossi et al. 2004). The results of the prey digestion experiments indicate that the prey observed in the gut contents was captured over the previous 8–25 h, depending on the temperature.

Ingesta of the species

The estimated daily ingesta from the gut contents of *E. singularis*, ~0.1 % of their coenenchyme mass from zooplankton and POM, is a low ingestion rate in comparison with the values observed in other anthozoan species (0.8–6 %; Barangé et al. 1989; Ribes et al. 2003; Rossi et al. 2004). However, the contrast of the ingesta with the carbon and nitrogen needs for new production indicates that feeding can account for the carbon and nitrogen needs for annual growth. This is consistent with studies on isotopic composition of some populations from different areas, indicating that heterotrophic nutrition is a relevant contributor to the tissue signature of *E. singularis* (Gori et al. 2012; Cocito et al. 2013). Nevertheless, experiments using marked food sources are needed to assess whether heterotrophic nutrition is mainly devoted to cover basal metabolism, and/or if it is mainly addressed to new production.

The contrast between the estimated natural ingesta and dark respiration values from laboratory experiments by Previati et al. (2010; Fig. 6) indicates that ingesta appear to account for a rather small proportion of respiration (6–30 %), except in early spring (110 %). The value of dark respiration attributed to June (Fig. 6) is close to that recently obtained in field assessments (18–21 °C in June; Ferrier-Pagès et al. 2015). Field estimates of autotrophic nutrition and respiration throughout the year are needed. The drop in respiration observed at ≥20 °C by Previati et al. (2010) was attributed to the parallel decrease in polyp activity observed during the laboratory experiments because polyp contraction has been documented to produce a large reduction in respiration of other species (Fabricius and Klumpp 1995; Coma et al. 2002). Although this pattern comes from laboratory observations, a similar drop in polyp activity of *E. singularis* and *Paramurica clavata* has

been observed in the field in summer and fall (Coma et al. 1998; Rossi 2002). Overall, the proportion of respiration rate that can be covered by the ingesta observed in *E. singularis* is low, in contrast to the values observed in heterotrophic gorgonians, because feeding on zooplankton and other plankton in *L. sarmentosa* accounted for 200 % of its respiratory requirements and met the energy needs of *P. clavata* (Coma et al. 1998; Ribes et al. 1999, 2003). However, the value observed in *E. singularis* is higher than that estimated for the zooxanthellate *P. flexuosa*, in which feeding on zooplankton and other plankton accounted for 0.4 % of its respiratory requirements (Ribes et al. 1998).

These results indicate that *E. singularis* should have other sources of resource acquisition. Gut content examination has the limitation of not being able to assess the capture of prey items that do not leave remains such as pico and nanoplankton, but these plankton fractions have contributed little to the nutrition of those gorgonians examined to date (Sorokin 1991; Ribes et al. 1998, 1999, 2003; Picciano and Ferrier-Pagès 2007). Nevertheless, our present estimation may represent an underestimation of ingesta because our sampling is likely to have missed rare events of high plankton availability and capture rate (Coma et al. 1994; Rossi 2002). The occurrence of these unusual events of high capture rate and feeding on pico and nanoplankton may account for additional carbon and nitrogen inputs, but likely cannot account for the bulk energy demand of the species, especially in summer and fall when the lowest detritus availability occurs (Coma and Ribes 2003; Rossi et al. 2006). Results to date indicate that heterotrophic nutrition in the natural environment seems unable to account for the basal metabolism of *E. singularis*, except in early spring. However, the results from Gori et al. (2012) indicate that detritus and uptake of dissolved nutrients can be relevant food sources. Then, although dissolved organic matter has been shown to be quantitatively unimportant for many reef gorgonian species (Sorokin 1991), quantification of the ingesta of detritus and of the uptake of dissolved nutrients under natural conditions is lacking for *E. singularis*.

The higher $\delta^{13}C$ signature of *E. singularis*, with respect to the other azooxanthellate gorgonians studied, was attributed to the symbiosis with the zooxanthellae. This is consistent with the results from Gori et al. (2012), which point to the relevance of the translocation of lipids from the zooxanthella to the host tissue in shallow populations during the summer. This indicates that the autotrophic nutrition by means of the symbiotic zooxanthellae may represent a relevant contribution to the metabolic requirements of *E. singularis*. This is in accordance with the results of a laboratory experimental setup conducted at 18 °C that recently documented that autotrophy can supply the metabolic needs of the species in summer (Ezzat et al. 2013), the most critical time period for most passive suspension feeders in the Mediterranean (Coma et al. 2000). The amount of photosynthates obtained by *E. singularis* from its symbiosis with zooxanthellae (P:R slightly higher than 1; Ezzat et al. 2013) is lower than that commonly observed in hexacoral species (2.7–5.3; Howe and Marshall 2001) but on the order of that observed in the most common octocoral species from the Great Barrier Reef (1.0–1.3; Mergner and Svoboda 1977; Fabricius and Klumpp 1995). Furthermore, the recent results from Ferrier-Pagès et al. (2015) examining in situ photosynthetic rates during summer temperatures (18–21 °C) have shown that *E. singularis* can survive autotrophically through the period, in which our estimated ingesta represents a low contribution to metabolic expenses of the species. Although the rate of photosynthesis is expected to decrease in winter due to light and temperature decrease, the isotopic signature of *E. singularis* showed no change in the proportion of the carbon input from autotrophy between summer and winter (Cocito et al. 2013). However, the relative role of autotrophy on the Mediterranean coral *Cladocora caespitosa* was observed to increase in winter because the respiration rate is more affected by low temperature than the photosynthetic rate (Schiller 1993; Ferrier-Pagès et al. 2011b). It is unknown whether this may be the case in *E. singularis*, but its respiration rate is also highly reduced at low temperature (from 0.66 mg O_2 g $AFDM^{-1}$ h^{-1} at 18 °C to 0.10 mg O_2 g $AFDM^{-1}$ h^{-1} at 14 °C; Previati et al. 2010). The amount of photosynthates that *E. singularis* obtain from the zooxanthellae in winter is unknown and needs to be examined.

During the last two decades, *E. singularis* populations in the NW Mediterranean have been repeatedly damaged by high-temperature-related mortality events in late summer. These die-off events have been linked to the direct and indirect effects of global warming and enhanced stratification during summer and fall (Coma et al. 2009; Calvo et al. 2011), and different studies have examined the physiological response of gorgonians to warm thermal stress (Ferrier-Pagès et al. 2009; Pey et al. 2011; Linares et al. 2013; Ezzat et al. 2013). Our study on the feeding ecology of *E. singularis* may be related to these die-off events by having shown that heterotrophic nutrition cannot account for the basal metabolism of the species, especially in summer and fall. The collapse of the photosynthetic capacities of *E. singularis* above a warm temperature threshold (Ferrier-Pagès et al. 2009; Ezzat et al. 2013) points out that autotrophy can no longer supply for the metabolic needs of the species. This would be indicative of a higher heat-sensitivity of zooxanthellae than host gorgonian cells, as has been observed in some tropical octocoral species (Sammarco and Strychar 2013). Under these conditions, the heterotrophic feeding capacity of the

species could be expected to compensate for the collapse of the autotrophic capacity. However, a recent laboratory study has shown a lack of increase heterotrophic feeding of *E. singularis* upon collapse of the photosynthetic capacity (Ezzat et al. 2013). Although upregulation of heterotrophy has been documented in some coral species, not all symbiotic species can do it (Grottoli et al. 2006; Ferrier-Pagès et al. 2011a). Then, the low capture rate in summer and fall, the collapse of the photosynthetic capacity of *E. singularis* above a certain warm temperature threshold, and the lack of upregulation of heterotrophy under these conditions indicate the occurrence of a resource acquisition limitation that can contribute to understanding the causes of colony death. This does not disregard that other factors may also be simultaneously involved in causing the die-off events. Our approach suggests that die-offs may be best understood as a nested hierarchy of processes combining the fine-scale events of plankton capture rates by polyps with colony-level autotrophy, together with broader-scale events such as plankton availability and temperature regime.

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