

Population dynamics of *Eudendrium racemosum* (Cnidaria, Hydrozoa) from the North Adriatic Sea

C. G. Di Camillo · F. Betti · M. Bo ·
M. Martinelli · S. Puce · C. Vasapollo ·
G. Bavestrello

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Abstract Benthic suspension feeders in shallow waters develop in relation to the food availability and the variation of physical parameters giving rise to complex communities that act as a control factor on the plankton biomass. The aim of the work is to establish the role of the hydrozoan *Eudendrium racemosum* in the energy transfer from the plankton to the benthos in marine food chains of the North Adriatic Sea. This study highlighted that the hydroid biomass changed over time in relation to temperature and irradiance, and the highest abundance was observed during summer with about 400,000 polyps m^{-2} (about 19 g C m^{-2}). The population suffered an evident summer decrease in relation to a peak of abundance of its predator, the nudibranch *Cratena peregrina*, whose adult specimens were able to eat up to 500 polyps day^{-1} and reached an abundance of 10 individuals m^{-2} . The gut content analysis revealed that the hydroid diet was based on larvae of other benthic animals, especially bivalves and that the amount of ingested preys changed during the year with a peak in summer when it was estimated an average predation rate of 13.7 mg C $m^{-2} day^{-1}$. In July, bivalves represented over

60 % of the captured items and about 18 mg C $m^{-2} day^{-1}$. Values of biomass of *E. racemosum* are the highest ever recorded in the Mediterranean Sea, probably supported by the eutrophic conditions of the North Adriatic Sea. Moreover, our data suggest that settling bivalves provide the greater part of the energetic demand of *E. racemosum*.

Introduction

Hydroids are one of the most important components of shallow-water, hard-bottom assemblages. In temperate waters, hydroids are subjected to seasonal variations in abundance and diversity due to the synergic effect of several factors, such as sea temperature, solar radiation intensity (irradiance) and food availability (Boero and Fresi 1986; Calder 1990; Bavestrello and Arillo 1992; Genzano 1994; Gili and Hughes 1995; Genzano and Rodriguez 1998; Genzano et al. 2002). Seasonality affects also the sexual reproduction of these organisms, and generally the species show a limited fertility period (Boero 1984; Calder 1990; Zamponi and Genzano 1990; Brinckmann-Voss 1996; Bavestrello et al. 2006).

Several studies were carried out on *Eudendrium glomeratum* (Picard, 1951), one of the biggest Mediterranean hydroids. This species forms seasonal winter facies (Boero 1982; Boero et al. 1986), it is fertile from October to March–April, degenerates in May and forms resting hydrorhizae to overcome the adverse summer period. The hydroid *Eudendrium racemosum* (Cavolini, 1785), instead, is abundant in the Mediterranean Sea during the warm season, with a cycle inverse to that of *E. glomeratum* (Bavestrello and Arillo 1992). In fact, *E. racemosum* occurs on the rocky cliffs from May to December and reproduces from June to October (Boero and Fresi 1986).

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C. G. Di Camillo (✉) · F. Betti · M. Bo · M. Martinelli ·
S. Puce
Dipartimento di Scienze del Mare, Università Politecnica
delle Marche, Via Breccia Bianche, 60131 Ancona, Italy
e-mail: c.dicamillo@univpm.it

M. Martinelli · C. Vasapollo
ISMAR, CNR Ancona, Largo Fiera della Pesca,
60125 Ancona, Italy

G. Bavestrello
Dipartimento per lo Studio del Territorio e delle Sue Risorse,
Università degli Studi di Genova, Corso Europa 26, Genoa, Italy

Rossi (1964) studied the life cycle of a Ligurian population of *E. racemosum* living in a harbour and observed few small colonies in April and abundant, higher and bushy colonies in September. Azzini et al. (2003) compared Ligurian populations of *E. racemosum* living in pristine and impacted areas, pointing out that this species shows different life cycles when affected by different factors, both abiotic and biotic. The study of the feeding cycle and prey capture of this species from the Medes Islands (western Mediterranean basin) highlighted that *E. racemosum* is not a selective suspension feeder and that it may have a considerable impact on the planktonic community (Barangé 1988; Barangé and Gili 1988).

Hydroids are considered as the major regulators of zooplankton in littoral areas (Simkina 1980; Turpaeva et al. 1977); moreover, they also represent a food supply (Salvini-Plawen 1972; MacLeod and Valiela 1975) or a colonizable substrate for other organisms (Hughes 1975; Zamponi and Genzano 1992; Bavestrello et al. 2006). For these reasons, the study of hydroids' life histories, trophic ecology and the evaluation of predator effects is essential for understanding the role of hydroids in the benthic-pelagic coupling.

The North-western Adriatic Sea shows different trophic and hydrologic conditions with respect to the rest of the Mediterranean basin (Artegiani et al. 1997a, b). As already observed for several sponge and cnidarian species of this area, the life cycle of benthic communities of this basin is strongly influenced by eutrophy and low winter temperatures (Di Camillo et al. 2010, 2012, in press; Betti et al. 2012).

The aim of the work is to establish the role of the hydrozoan *Eudendrium racemosum* in the energy transfer from the plankton to the benthos in marine food chains of the North Adriatic Sea. Hence, the temporal variations of abundance and reproductive periods were determined in relation to temperature and irradiance. We have also considered the trend of prey capture rates in order to evaluate the potential impact of the hydroid on the planktonic assemblage during each season.

Materials and methods

Site description

The study was conducted at Conero Promontory, an area showing the typical characteristics of the Italian coast of the North Adriatic Sea, such as shallow waters (up to 14 m depth), high turbidity, many freshwater inputs (the most important is the Po River) and high productivity (Giordani et al. 2002). The sampling site is the 'Scoglio del Trave'

(Fig. 1), a natural rocky pier mainly colonized by mussels, sponges and cnidarians. In particular, the mussel *Mytilus galloprovincialis* Lamarck, 1819 forms a continuous belt on the rocks from 0 to 4 m depth, while below 4 m depth many massive sponges and several hydroids—among which *Eudendrium racemosum*—represent the most common organisms.

Hydroid abundance

The abundance of the colonies of *E. racemosum* was monthly determined, from November 2006 to July 2008, by means of scuba dives carried out in the study area from 4 to 6 m depth, where hydroids form a continuous facies. Each month, 75 random replicates were collected using a 20 × 20 cm frame. All colonies present in the frames were counted taking note of the fertile ones and of those lacking polyps, when present. In order to verify whether temperature and solar radiation may affect the hydroid life cycle as demonstrated for *Eudendrium glomeratum* (Bavestrello and Arillo 1992), each month, the average abundance of *E. racemosum* colonies (mean of the replicates ± SD) was calculated and put in relation with values of sea temperature and irradiance data. Average sea temperatures of the considered period were downloaded from the National Tidegauge Network website (<http://www.mareografico.it>). Data were collected by the water temperature transducer T020 TTA placed on the sea surface in the Ancona's NT station. Irradiance data were obtained from Byun and Pinardi 2007. In order to check the presence of hydrorhizae probably acting as resting stages, small pieces of substrate were detached from the rocky wall in the sampling area during winter and spring, and then, the pieces were observed under stereomicroscopy.

Colony size

From October 2008 to October 2009, 100 randomly chosen hydroid colonies were measured underwater with a calliper to establish the monthly average height variation. Ten other colonies were monthly collected to evaluate the average polyp density (number of zooids in relation to the colony surface). ImageJ software (Rasband 1997–2011) was used to measure the area of the collected colonies.

Quantitative data of colony and polyp abundances are relative to the period 2006–2009; moreover, monthly dives were conducted at the sampling site until March 2011 in order to report the presence/absence and fertility periods of *E. racemosum* colonies. Data were shown together with the trend of monthly average sea temperature of the considered period.

Fig. 1 Map of the sampling area ‘Scoglio del Trave’ located in the northern part of the Conero Promontory (North Adriatic Sea)



Gut contents

In order to obtain information about hydroid's diet and potential impact on the water column, 30 polyps were randomly detached from each of the ten collected colonies for a total of 300 polyps analysed each month. Colonies were always taken at the same time (between 11:30 and 12:30 a.m.). Polyps were dissected, and the ingested items were observed under a light microscope. For each prey type, the number of ingested items per polyp (average \pm SD) was monthly calculated in order to identify temporal variations in gut contents. For each sampling, the daily predation rate (N) and the daily predation rate m^{-2} (P) were calculated following Coma et al. (1995) and using the formulae:

$$N = n/d \times 24$$

$$P = N \times D$$

where n is the number of prey items $polyp^{-1}$, d is the digestion time (in *E. racemosum* 5 h for warmer months, from June to September; 8 h for April, May and October; and 10 h for cooler months, from November to March, Barangé and Gili 1988) and D is the number of polyps m^{-2} . Biomass of prey items (expressed as μg of C) was obtained by conversion of mean biometric volume (Biswas and Biswas 1979).

Bivalves

Pediveligers of bivalves are the main preys of *E. racemosum* in the Conero Promontory (see the following). During autumn 2008, the pediveligers settled on the hydroid branches and those present in the gastric cavity of the polyps were measured in order to estimate the maximum ingestible size.

To determine the abundance of the bivalves larvae in the water, the zooplankton was monthly collected from October 2010 to November 2011 with horizontal tows conducted parallel to the sampling site at a distance of 1–5 m from the rock and a depth of about 4 m. Each month, three tows of about 80 m were conducted using a bongo net sampler (diameter, 20 cm; length, 78 cm; mesh, 200 μm). During the horizontal tows, the boat maintained a speed of 1 Knot. The total volume of filtered water during each tow (V_T) was given doubling the cylinder volume equation:

$$V_T = \pi r^2 L$$

where L is the length of the tow and r is the diameter of the net.

The collected samples were preserved in 250 ml of 70 % ethanol. In order to determine the abundance of bivalves, each sample was re-suspended and ten subsamples of 0.1 ml were collected with a micropipette and put on slides. Each slide was analysed under a light microscope counting all pediveligers. The number of bivalves in the sample (N_c) was calculated with the formula:

$$N_c = N_{sc} \times V/v$$

where N_{sc} is the total number of bivalves in the subsample; V is the total volume of the sample (250 ml) and v is the volume of each subsamples (0.1 ml).

The abundance of bivalves, expressed as number of bivalves m^{-3} , was calculated by dividing N_c per the total volume of filtered water (V_T):

$$N_B = N_c/V_T.$$

Nudibranchs

Eolid opisthobranchs are known to actively and selectively predate hydroids (Cattaneo Vietti and Boero 1988). The most diffused species of the Conero area is *Cratena peregrina* (Gmelin, 1791), which is a predator of *Eudendrium racemosum* polyps (Martin 2003; Martin and Walther 2003).

To understand the influence of nudibranch feeding activity on *E. racemosum*, three nudibranchs *Cratena peregrina* of the same size were collected in order to determine the predation rate of the mollusc. We chose large nudibranchs (about 3 cm) to estimate the impact of adult specimens. The animals were kept in separate bowls with aerated seawater. Small portions of living *E. racemosum* colonies (each one with 50 gastrozooids counted with a stereomicroscope) were cut and used to feed the nudibranchs. The hydroid pieces were changed every hour during day and every 2 h in the night, and the number of eaten polyps was counted at each change (modified from MacLeod and Valiela 1975). Some cerata and nudibranch

faecal pellets were examined under a light microscope to observe the nematocyst types.

The number of specimens of the aeolid nudibranch *C. peregrina* found on the hydroids was monthly recorded from November 2008 to October 2009 along three horizontal transects of 10 metres each, conducted between 4 and 6 m depth in correspondence of the *E. racemosum*'s belt. Data on the size class of the specimens were also taken into account: I (less than 1.5 cm), II (between 1.5 and 2.5 cm) and III (more than 2.5 cm). Successively, the nudibranch abundance was calculated, as well as the average of the three replicates (number of nudibranch $\text{m}^{-2} \pm \text{SD}$).

Statistical analyses

To test for significativity of the zooid density variation along the considered years, a two-way nested ANOVA was performed. Since, between 2006 and 2008, samplings were not conducted in all seasons, it was decided to take a water temperature threshold of 15 °C (mean temperature of the selected period) to divide cool and warm months (factor temperature, 2 levels); then, each month was nested in the respective temperature condition (factor month, 21 levels). Cochran's C test was performed to test for variance homogeneity (Underwood 1997), and when the test was significant, data were double square root transformed. Tukey's honestly significant differences (HSD) test was performed as post hoc whenever a significant variation was shown by ANOVA. The same approach was used for estimating the variations in colony heights along the years.

A further analysis was made to assess whether the number of polyps in a colony was related to both the temperature and other features such as height and area of the colonies: an ANCOVA was performed with the number of polyps as variable, month as principal factor and height and area of the colonies as covariates. The number of polyps was square root transformed to cope with heteroscedasticity (Underwood 1997) verified by means of the Cochran's C test. A Tukey's HSD test was made as post hoc test whenever a significant variation was shown by ANCOVA.

A simple split plot randomized design (Federer and King 2007) was used to evaluate the abundance of gastrozooids, gonozooids and cnidophores for each portion of a colony. Following the Piepho et al. (2003) simple style, the experimental design model could be represented by the following equation:

$$Y = R + A + R \cdot A + B + A \cdot B + R \cdot A \cdot B$$

where R is the effect of the block (month of sampling, random effect), A is the main effect of the factor A (the single colony, random effect), B is the main effect of the

factor B (portion of the colony, fixed effect), $R \cdot A$ is the error term for the factor A , $A \cdot B$ is the error term for the factor B and $R \cdot A \cdot B$ is the overall error term. Tukey's HSD test was performed as post hoc test when significant differences were obtained by the ANOVA analysis of the split plot design.

The gut content of the polyps was analysed by means of a 2-way nested ANOVA with month as fixed factor and colony nested in month as random factor. The gut content was divided into 4 categories: bivalves (above all mussels), amphipods, tintinnids and others (comprising eggs and embryos of unidentified organisms, ascidians, diatoms, pine pollen, nematodes and unidentified parts of organisms).

Differences in the nudibranch densities along the month were tested by means of a 1-way ANOVA.

In addition, the relationship between the above variables (zooid densities, number of polyps, height and area of the colonies) and the mean water temperature and irradiance was tested by means of Spearman's rank correlations (ρ). Spearman's rank correlation was also used to test for the relationship between the presence of the nudibranch and the abundance of the *E. racemosum* polyps.

Results

In the North Adriatic Sea, adult colonies of *Eudendrium racemosum* reach the maximum size of 13 cm (average $6.4 \text{ cm} \pm 1.4 \text{ SD}$) and bear up to 3,500 hydranths per colony (annual average $539.9 \pm 574.5 \text{ SD}$; summer average $1,058.43 \pm 637 \text{ SD}$). Reproductive structure blastostyles represent up to 14 % of the total polyps.

Seasonal cycle

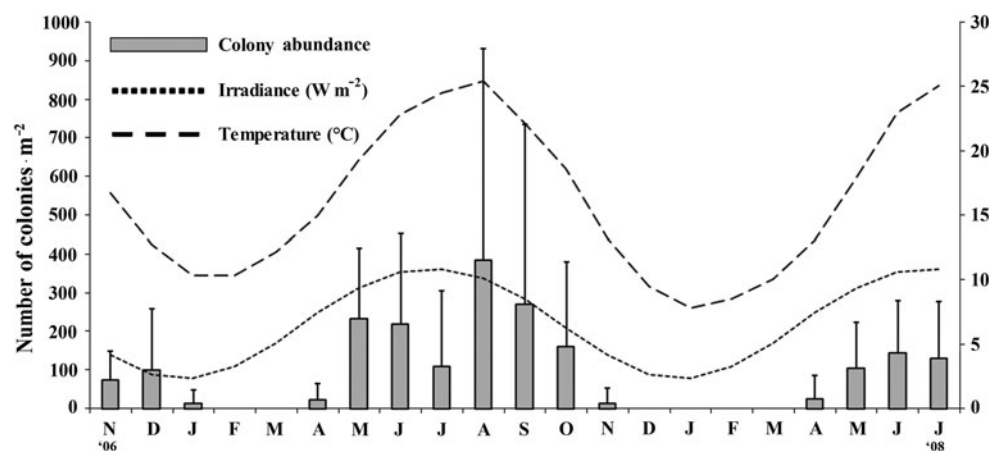
The temporal trend of *E. racemosum*'s abundance (Fig. 2) shows that in the monitored period, the number of the colonies with polyps (both unfertile and fertile ones) was

lowest during autumn ($15\text{--}160 \text{ colonies m}^{-2}$, sea temperature of $9\text{--}18 \text{ }^\circ\text{C}$, $13.8 \text{ }^\circ\text{C} \pm 4.6$ in average; irradiance $90\text{--}200 \text{ W m}^{-2}$, $146.7 \text{ W m}^{-2} \pm 60.3$ in average) while fell down to zero during winter (sea temperature of $8\text{--}10 \text{ }^\circ\text{C}$, $8.8 \text{ }^\circ\text{C} \pm 1.1$ in average and irradiance $80\text{--}170 \text{ W m}^{-2}$, $120.7 \text{ W m}^{-2} \pm 46.9$ in average). During this period, some hydrocauli lacking polyps and pieces of hydrorhizae remained attached to the rock and were covered with small mussels, detritus and other hydroids (such as *Bougainvillia muscus* (Allman, 1863) and various campanulariids). Pieces of substrate detached from the rocky wall in winter were covered with several dark hydrorhizae and short hydrocauli lacking polyps while those collected in spring showed old hydrorhizae (recognizable by their dark, sturdy perisarc) and some young hydrocauli bearing polyps. These new portions originated directly from elder stolons and were easily distinguishable for their reddish colour and thin perisarc.

The colony abundance quickly increased in spring ($22\text{--}200 \text{ colonies m}^{-2}$, sea temperature $13\text{--}23 \text{ }^\circ\text{C}$, 17.6 ± 4.4 in average; irradiance $250\text{--}350 \text{ W m}^{-2}$, $306 \text{ W m}^{-2} \pm 53.4$ in average) and reached the maximum value in August (with an average of almost $400 \text{ colonies m}^{-2}$; sea temperature $25 \text{ }^\circ\text{C}$, irradiance 340 W m^{-2}). A sharp decrease in the number of colonies with polyps was noticed in July 2007.

Densities of colonies varied significantly in the considered period (ANOVA, $p < 0.001$). Between 2006 and 2007, August 2007 showed the highest abundance value, significantly higher (Tukey's HSD, $p < 0.01$) than those obtained in the other months, except for May, June and September 2007. In July 2007, the trend showed a sharp decrease and the value was significantly lower than May, June, August and September 2007 (Tukey's HSD, $p < 0.01$). The warmer months (from May to October 2007), except for July, showed abundance values significantly higher (Tukey's HSD, $p < 0.01$) than those recorded in the cooler months (from November 2006 to April 2007).

Fig. 2 Population dynamics of *Eudendrium racemosum* from November 2006 to July 2008 (number of colonies $\text{m}^{-2} \pm \text{SD}$) in relation to sea temperature and irradiance trends. The values are referred to the colonies with polyps, including both the unfertile and fertile ones but not the colonies without polyps



The values from January to April 2007 were the lowest of the year and were significantly lower than those obtained in November and December 2006. In February and March 2007, the colonies were not observed.

Between 2007 and 2008, the highest abundance was recorded in June 2008 and its value was significantly higher than those of all the other considered months, except for July 2008 (considering the months from November 2007 to April 2008, Tukey's HSD, $p < 0.01$; considering May 2008, Tukey's HSD, $p < 0.05$). The warmer months (from May to July 2008) showed densities significantly higher than the cooler months (from November 2007 to April 2008; Tukey's HSD, $p < 0.01$). The lowest values were recorded from November 2007 to April 2008, and from December 2007 to March 2008, colonies were not found.

November and December 2006, January 2007 and May 2007, showed values significantly higher than the same months of the following year (November and December 2007 Tukey's HSD, $p < 0.001$, January 2008 Tukey's HSD, $p < 0.01$ and May 2008 Tukey's HSD, $p < 0.01$).

The trend of the colony abundance was correlated with temperature and irradiance values respectively with Spearman's $\rho = 0.89$ and $\rho = 0.74$ ($p < 0.001$). Temperature values were correlated with those of irradiance ($\rho = 0.89$, $p < 0.001$).

The histograms in Fig. 3a represent the abundance values of *E. racemosum* distinguishing between colonies with polyps (unfertile and fertile ones) and those without polyps. In July 2007, the amount of colonies without polyps (94.33 ± 105.79 SD) is similar to that of colonies with polyps (110.33 ± 195.17 SD).

In 2007, colonies were fertile from May to June (sea temperature from 16 to 23 °C), while in 2008 the fertility period was extended until July, with the highest percentage of fertile specimens recorded in June 2008 (45 %; Fig. 3a). In both years, it was observed that colonies were mainly or totally male when the temperature was not higher than 18 °C, while females started to mature when the temperature was 19–20 °C and all fertile colonies were female at a temperature of 25 °C (Fig. 3b). A few fertile colonies were found in October 2008 bearing rare female gonophores.

Table 1 resumes periods of presence/absence and fertility of *E. racemosum* from 2006 to 2011 together with temperature values. Colonies always disappeared in the coldest part of the year but the duration of the absence period may vary from one year to another. In particular, colonies were not found for 2 months in 2006–2007 (February and March) and up to 4 months during 2007–2008 and 2010–2011 (from December to March). Variations in the beginning and duration of the fertility period were also observed: for example in 2008,

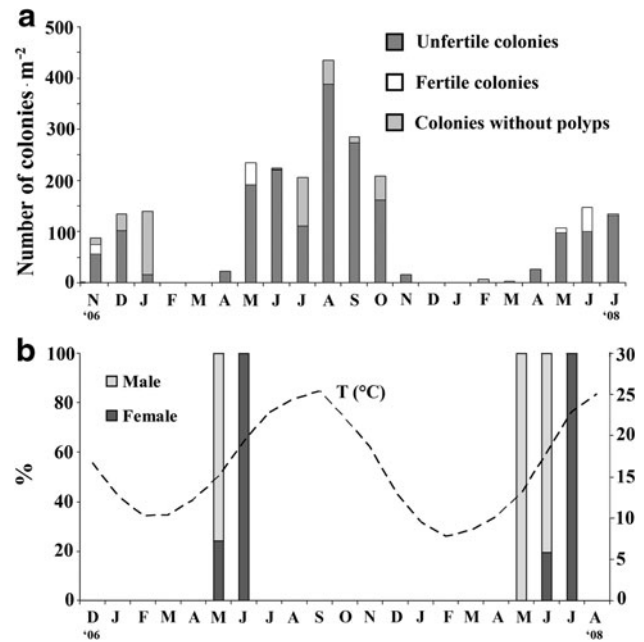


Fig. 3 Colony densities and fertility of *Eudendrium racemosum*. **a** Histogram showing densities of unfertile and fertile colonies and colonies without polyps. **b** Percentage of male and female colonies in relation to the sea temperature trend

Table 1 Monthly average sea temperatures (°C) from 2006 to 2011

	2006–2007	2007–2008	2008–2009	2009–2010	2010–2011
Nov	16.7	13.2	16.1	15.27	15.10
Dec	12.7	9.5	8	11.07	9.61
Jan	10.3	7.8	7.3	7.45	7.33
Feb	10.3	8.5	8.21	7.33	8.21
Mar	12.1	10	11.54	9.32	9.62
Apr	15	13.1	13.11	13.15	15.01
May	19.3	17.9	21.27	16.58	18.4
Jun	22.9	22.9	20.69	21.64	22.67
Jul	24.5	25.1	25.47	26.67	24.21
Aug	25.4	26.3	26.90	25.19	25.97
Sep	22.1	22.9	24.74	22.98	25.78
Oct	18.6	19.2	19.82	18.64	19.75

Grey cells represent periods of *Eudendrium racemosum* absence while the red ones correspond to fertility intervals (colour figure online)

E. racemosum produced gonophores in two different moments, from May to July and in October, while in 2009 and 2011 the gonophore production began in May and lasted until September.

Colony size

The trends of colony areas and heights from October 2008 to October 2009 (Fig. 4) show that the size reduction began

Fig. 4 Heights (cm) and areas (cm²) (means \pm SD) of *Eudendrium racemosum* colonies monthly measured from October 2008 to October 2009 and put in relation to the sea temperature trend (*Jul_a* samplings at the beginning of the month, *Jul_b* samplings at the end of the month)

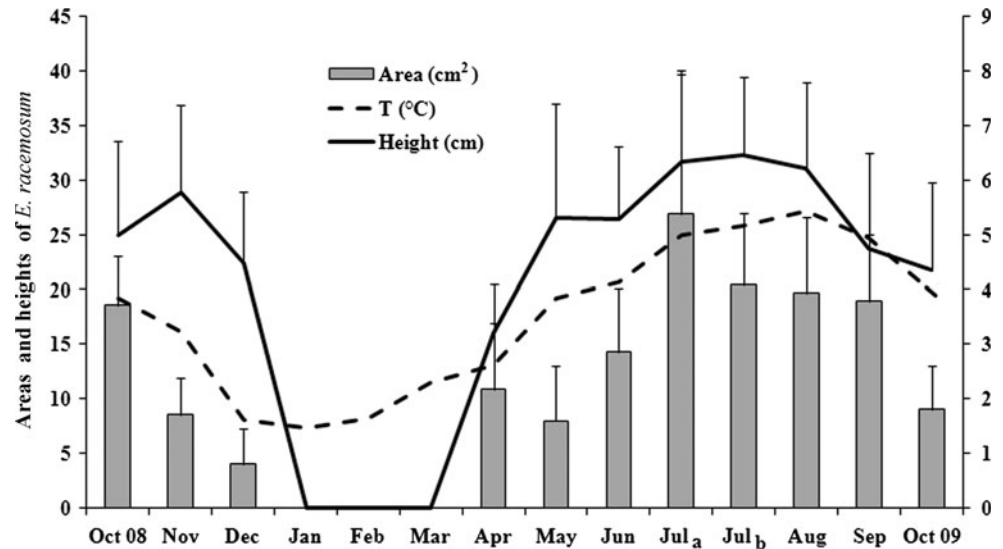
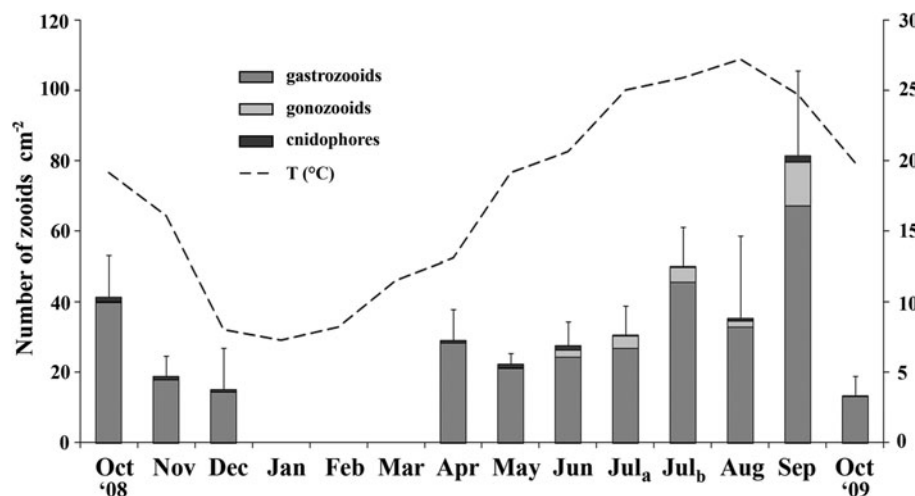


Fig. 5 Temporal variation in the abundance of *Eudendrium racemosum* polyps (number of zooids cm⁻²) from October 2008 to October 2009



in late autumn (colonies were about 5 cm high in December 2008, with a 4 cm² surface) and was followed by the complete stem degeneration in winter (from January to March 2009). New colonies reappeared in April 2009 (about 3 cm high, with a 10 cm² surface) and quickly started growing reaching the maximum values at the end of July 2009 (about 6.5 cm in height, with a 27 cm² surface).

Areas of the colonies varied significantly during the year (ANCOVA, $p < 0.001$). In particular, the average colony area in July 2009 was significantly higher than those recorded from December 2008 to March 2009 (Tukey's HSD, $p < 0.01$). Areas from June to September 2009 were significantly higher with respect to the period from January to March 2009, when the colonies were not present (Tukey's HSD, $p < 0.01$). The values of July (both Jul_a and Jul_b) and August 2009 were significantly higher than that of December 2008 (Tukey's HSD, $p < 0.01$). Data of areas resulted to be correlated with temperatures ($\rho = 0.88$; $p < 0.001$) and with irradiance ($\rho = 0.81$; $p < 0.01$).

Colony heights showed significant differences (ANCOVA, $p < 0.001$) during the year. The values of July and August 2009 were the highest of the considered period and they were significantly higher than those of June, September and October 2009 (Tukey's HSD, $p < 0.01$). In December 2008, April and October 2009, the values were the lowest of the year and were significantly lower than the others (Tukey's HSD, $p < 0.01$). Data of heights resulted to be correlated with temperature ($\rho = 0.79$; $p < 0.01$) and with irradiance ($\rho = 0.68$; $p < 0.01$).

Polyps abundance

The temporal trend of polyp abundance (number of gastrozooids, gonozooids and cnidophores cm⁻²) is showed in Fig. 5. The highest densities of gastrozooids occurred in late summer (a peak in September 2009 with up to 70 zooids cm⁻²) while the lowest values were recorded in late autumn (December 2008 and October 2009 with about 14

zooids cm^{-2}). During summer 2009, the gastrozoid abundance varied from 24 to 45 cm^{-2} while a decrease was observed in August. The gonozoid abundance varied from 2 to 12 from June to September 2009, and the production of gonozoids was continuous during this summer. The cnidophore abundance was always low, ranging from 0.2 to 1.2 cm^{-2} .

The split plot design showed that there were differences in the number of gastrozoids during the considered months (ANOVA, $p < 0.001$). September showed the highest value of gastrozoids, significantly different from all the other months (Tukey's HSD, $p < 0.01$). Following this value, August showed a steep reduction in the number of gastrozoids.

The number of gonozoids was also significantly different during the considered months (ANOVA, $p < 0.001$). Again, September showed the highest value with respect to the other months and August the lowest one (Tukey's HSD, $p < 0.01$). No gonozoids at all have been observed from October to March, probably due to the unfertile period of the species. There were differences in the position of gonozoids for each single colony (ANOVA, $p < 0.001$), and they positioned mainly at the apex of the colonies, with some polyps also in the central portion and very rarely at the basal one of the colonies (Tukey's HSD, $p < 0.01$).

The cnidophores changed along the considered months (ANOVA, $p < 0.001$), with the highest value observed in September and the lowest in October (Tukey's HSD, $p < 0.01$), while in the rest of the months the number seemed to maintain approximately constant.

Gut contents

Prey items found in *E. racemosum* polyps and their biomass are shown in Tables 2, 3 and 4. The quantity of ingested preys by *E. racemosum* varied during the year

with the highest value recorded in July 2009 (Fig. 6a). The most common preys found in *E. racemosum*'s gastric cavity were small bivalves, identified as pediveligers of *Mytilus galloprovincialis* (43.5 %). In total, we found 11 food types (Table 2) among which also pine pollen, unidentified eggs (65–70 μm in diameter), ascidian larvae (1,600 μm in length), tintinnids, foraminifers and embryos of harpacticoid copepods that usually settle on *E. racemosum* pedicels forming characteristic clusters of 3–4 embryos. The prey composition showed differences in the studied period (Fig. 6b). During early spring, the main food categories were crustaceans (mainly amphipods) and eggs, in May we observed mostly embryos of harpacticoid copepods, while in summer bivalve pediveligers and tintinnids predominated. During autumn, we found almost exclusively bivalves. Great quantities of sediment (not quantified) were occasionally found. Almost all the observed gut contents significantly varied in the considered period (ANOVA, $p < 0.001$), but in relation to the different nature of the food, different peaks are clearly evident. Moreover, not all the polyps of the colonies feed in the same way, and in fact, significant differences were put in evidence (ANOVA, $p < 0.001$), but the post hoc test did not show any alternative hypothesis; thus, no clear patterns are evident. The same conclusion is met for all the other ingested food types. Crustaceans showed a peak in April, while in the other months their presence is negligible. Tintinnids showed a longer period of presence in the gut of polyps, with a peak between July and August. Other miscellaneous food showed two main peaks in May and July, probably due to the abundance of pine pollen during the late spring and some other phytoplankton organism possibly associated with the spring-summer blooms.

Table 5 shows the monthly variation in the daily predation rate and number of prey items captured $\text{m}^{-2} \text{day}^{-1}$ in *E. racemosum*. The highest predation rate was observed

Table 2 Gut contents found in 300 *Eudendrium racemosum* polyps from October 2008 to October 2009

Prey items	Oct 2008	Nov	Dec	Apr	May	Jun	Jul	Aug	Sep	Oct 2009
Diatoms	0	0	5	31	6	0	2	0	0	0
Foraminifers	0	0	0	1	12	1	1	1	2	0
Tintinnids	0	0	0	0	0	0	534	521	0	81
Nematodes	0	0	0	2	0	6	0	0	0	0
Bivalves	31	5	48	1	6	197	1,178	38	27	4
Amphipods	0	0	0	106	21	4	15	0	8	0
Eggs	0	0	0	79	0	0	154	1	0	0
Embryos	0	0	0	0	132	68	0	0	0	0
Ascidian larvae	0	0	0	0	0	2	0	0	0	0
Pine pollen	0	0	0	13	0	0	0	0	0	0
Unidentified items	0	0	0	0	73	32	11	14	23	31

Months when the hydroid disappears are not reported

Table 3 Conversion of biometric measures of gut contents and polyps to volume (V), fresh weight (FW: μg ; specific weight, 1.025 g cm^{-3}), dry weight (DW: μg , 13 % fresh weight) and organic carbon (C : μg , 50 % of dry weight)

	L	W	D	a	b	c	$V (\text{mm}^3 \times 10^{-3})$	FW	DW	C	N	%
Eggs	70	70	70	35	35	35	0.18	0.18	0.02	0.01	234	6.63
Diatoms ^a							0.09	0.09	0.01	0.01	44	1.25
Pine pollen	90	70	70	45	35	35	0.23	0.24	0.03	0.02	13	0.37
Nematods ^a	560	31	15	280	15.5	7.5	0.14	0.14	0.02	0.01	8	0.23
Bivalves	240	93	180	120	46.5	90	2.10	2.16	0.28	0.14	1,535	43.51
Foraminifers ^a	160	160	50	80	80	25	0.67	0.69	0.09	0.04	18	0.51
Embryos	135	135	135	67.5	67.5	67.5	1.29	1.32	0.17	0.09	200	5.67
Invertebrate larvae ^a	200	75	75	100	37.5	37.5	0.59	0.60	0.08	0.04	2	0.06
U. F.	77	70	70	38.5	35	35	0.20	0.20	0.03	0.01	184	5.22
Amphipods	250	65	35	125	32.5	17.5	0.30	0.31	0.04	0.02	154	4.37
Tintinnids	88	83	83	44	41.5	41.5	0.32	0.33	0.04	0.02	1,136	32.20
Hydranths	1,600	950	950	800	475	475	755.69	774.58	100.69	50.35		
Blastostyles	1,164	1,268	1,268	582	634	634	979.42	1,003.90	130.50	65.25		

The total number of preys (N) found during the annual cycle is also shown

^a Values obtained from Coma et al. (1995) and Genzano (2005)

Table 4 Biomass of prey items ($\mu\text{g C}$) found in 300 *Eudendrium racemosum* polyps from October 2008 to October 2009

Prey items	Oct 2008	Nov	Dec	Apr	May	Jun	Jul	Aug	Sep	Oct 2009
Diatoms	0	0	0.03	0.19	0.04	0	0.01	0	0	0
Foraminifers	0	0	0	0.04	0.54	0.04	0.04	0.04	0.09	0
Tintinnids	0	0	0	0	0	0	11.29	11.01	0	1.71
Nematodes	0	0	0	0.02	0	0.05	0	0	0	0
Bivalves	4.34	0.70	6.72	0.14	0.84	27.60	165.02	5.32	3.78	0.56
Amphipods	0	0	0	2.10	0.42	0.08	0.30	0	0.16	0
Eggs	0	0	0	0.94	0	0	1.84	0.01	0	0
Embryos	0	0	0	0	11.32	5.83	0	0	0	0
Ascidian larvae	0	0	0	0	0	0.08	0	0	0	0
Pine pollen	0	0	0	0.20	0	0	0	0	0	0
Unidentified items	0	0	0	0	0.96	0.42	0.14	0.18	0.30	0.41
Total	4.34	0.70	6.75	3.64	14.11	34.11	178.64	16.58	4.33	2.68

in July and August (over 6,000 prey items captured $\text{m}^{-2} \text{ day}^{-1}$) while the lowest was recorded in November (0.2 prey items captured $\text{m}^{-2} \text{ day}^{-1}$). The annual average number of preys items captured m^{-2} was about 1,700. In terms of biomass (Table 6), the annual average of captured preys is about $5,480 \mu\text{g C m}^{-2} \text{ day}^{-1}$, with the minimum in autumn ($33.8 \mu\text{g C m}^{-2} \text{ day}^{-1}$), about $923 \mu\text{g C m}^{-2} \text{ day}^{-1}$ in spring and the highest value in summer ($13,672 \mu\text{g C m}^{-2} \text{ day}^{-1}$).

Bivalves

Bivalve pediveligers found in the gut contents were attributed to *M. galloprovincialis* that is the dominant

mollusc species present in the studied site. In November and December 2008, pediveligers of *M. galloprovincialis* were often observed crawling on *E. racemosum*'s stems, reaching the maximum length of $600 \mu\text{m}$. During autumn, up to 30 mussels were found in the examined 300 gastric cavities and the maximum shell's length recorded was $500 \mu\text{m}$, while in July we observed up to 1,178 bivalves (up to $500 \mu\text{m}$ long) in the analysed polyps.

The trend of abundance of bivalve pediveligers in the zooplankton surroundings the *E. racemosum* population from October 2010 to November 2011 showed that the values were quite similar during the year except in August with $23,482 \text{ bivalves m}^{-3} \pm 2,556$ (Fig. 7). This latter value was 10 to 1,600 times higher than the rest of the year.

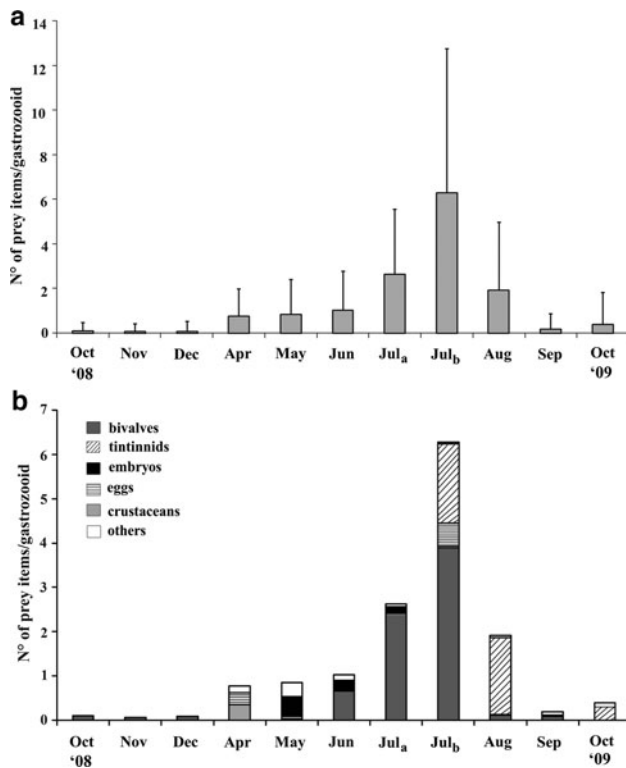


Fig. 6 *Eudendrium racemosum*'s preys. **a** Temporal variations of the most common preys (no. of prey items per gastrozoid \pm SD) from October 2008 to October 2009. **b** Prey composition in each month (the category 'others' includes occasional preys such as diatoms, pine pollen, nematodes, foraminifers, ascidian larvae and unidentified animals)

Nudibranchs

Cratena peregrina was found on *E. racemosum* especially during spring and summer (Fig. 8), when the hydroid

population was most dense. The analysis of the cnidocysts carried out on the cerata and faecal pellets of some of the collected specimens confirmed that *C. peregrina* fed on *E. racemosum*. Nudibranch abundance varied during the considered period (Fig. 8) and reached the mean maximum value of 13 individuals $m^{-2} \pm 3$, size class I, in November; the gastropod was not observed from December to April and reappeared in May, with 2.67 specimens ± 0.58 , size classes I and II. From May, the predator abundance increased and reached a mean maximum value in August (10 individual $m^{-2} \pm 1.73$). In summer and early autumn, all nudibranchs measured more than 2.5 cm (size class III) and some specimens reached 5 cm in length. The presence of nudibranchs changed significantly during the studied period (ANOVA, $p < 0.001$), with the highest values observed between June and September, while no nudibranchs at all were observed from December to March. Strong correlation was evident between the abundance of *E. racemosum* polyps and the presence of *C. peregrina* ($\rho = 0.62$, $p < 0.05$).

Concerning their feeding behaviour, specimens of *C. peregrina*, reared in experimental conditions, showed a maximum feeding rate of 65 ingested polyps $hour^{-1}$ ranging from 130 to 550 polyps in the 24 h interval.

Discussion

Population dynamics

The monitored *Eudendrium racemosum* population, reaching average maximal densities of 400 colonies m^{-2} in a 2 m wide belt for a length of 450 m, is the densest ever described for the entire Mediterranean Sea rocky coastline. Gili (1982) indicates a maximal abundance of 66 colonies

Table 5 Prey capture rates

	Oct	Nov	Apr	May	Jun	Jul	Aug	Sep
Number of polyps m^{-2} (D)	17,446.35	2,854.28	5,691.4	17,737.67	53,085.6	118,047.6	386,309	423,241.4
Number of gut contents polyp $^{-1}$ (n)	0.103	0.017	0.777	0.833	1.033	6.317	1.917	0.2
Daily predation rate ($N = n/d \times 24$)	0.00054	0.00007	0.00405	0.00434	0.00861	0.05264	0.01597	0.00167
Number of prey items captured $m^{-2} day^{-1}$ ($P = N \times D$)	9.39	0.20	23.02	76.99	457.13	6213.89	6,170.21	705.40
Percentage of bivalves	100	100	0.4	2.4	63.5	62.1	6.6	46.6
Number of bivalves captured $m^{-2} day^{-1}$	9.39	0.20	0.09	1.85	290.28	3,858.83	407.23	328.72
Number of bivalves along the transect ($900 m^2$) month $^{-1}$	261,967.8	5,351.8	2,486.4	51,550.1	7,837,425.3	107,661,314.7	11,361,830.6	8,875,371.1
Average number of prey items captured $m^{-2} day^{-1}$		1,707.03						
Number of bivalves captured in 1 year		136×10^6						

Months when the hydroid disappears are not reported

Table 6 Biomass (carbon, µg)

	Oct	Nov	Apr	May	Jun	Jul	Aug	Sep
Biomass of polyps m ⁻² (D)	878,423.7	143,713.3	286,561.9	893,091.5	2,672,860	5,943,696.7	19,450,658.2	21,310,201.9
Biomass of captured preys polyp ⁻¹ (n)	0.014	0.002	0.012	0.047	0.113	0.595	0.055	0.014
Daily predation rate (N = n/d × 24)	0.00008	0.00001	0.00006	0.00025	0.00095	0.00496	0.00046	0.00012
Preys captured m ⁻² day ⁻¹ (P = N × D)	66.23	1.40	18.09	218.82	2,532.35	29,494.70	8,956.24	2,564.74
Preys along the transect (900 m ²) per month	1,847,692.88	37,746.83	488,356.20	6,104,986.57	68,373,345.31	822,902,142.37	249,879,062.33	69,247,904.01
Percentage of bivalves	100	100	0.4	2.4	63.5	62.1	6.6	46.6
Bivalves captured m ⁻² day ⁻¹	66.23	1.40	0.072	5.25	1,608.04	18,316.21	591.11	2,564.74
Bivalves along the transect (900 m ²) per month	1,847,692.9	37,746.8	1,953.4	146,519.7	43,417,074.3	511,022,230.4	16,492,018.1	69,247,904.0
Average number of prey items captured m ⁻² day ⁻¹		5,481.57						
Number of bivalves captured in 1 year		642 × 10 ⁶						

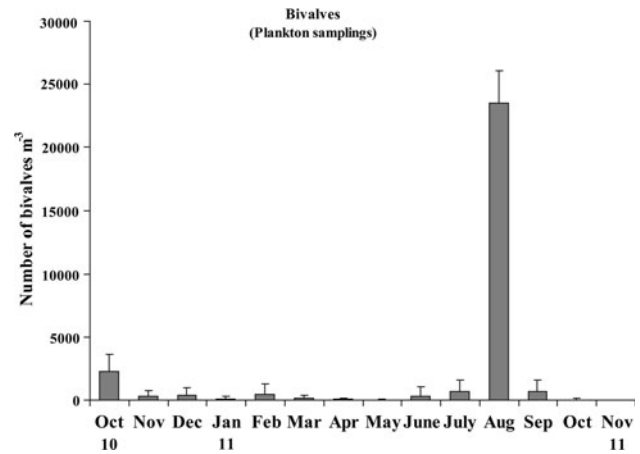


Fig. 7 Temporal variations of bivalves (number of bivalves m⁻³) in the zooplankton from October 2010 to November 2011

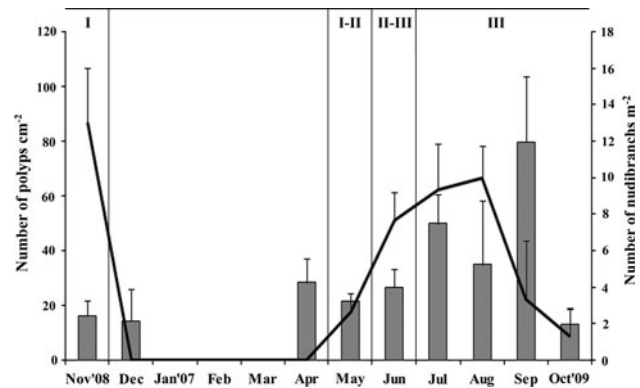


Fig. 8 *Eudendrium racemosum*'s predation. Temporal variations in the polyp abundance (number of polyps cm⁻² ± SD, grey bars) in relation to the nudibranch abundance (number of molluscs m⁻² ± SD, black line) from November 2008 to October 2009. I, II and III represent respectively the nudibranch class sizes: less than 1.5 cm, between 1.5 and 2.5 cm and more than 2.5 cm

m⁻² for this species in Medes Islands, while in other Adriatic localities such as the southern coast (Otranto) or along the eastern side (Croatian coasts), the colonies of *E. racemosum* are scattered and never form a belt (Di Camillo, personal observation). Furthermore, along the Portofino Promontory (Ligurian Sea) the most abundant winter species, *Eudendrium glomeratum*, never exceeds densities of 40 colonies m⁻² (Boero et al. 1986). The number of polyps per colony is greater in the North Adriatic Sea than in any other studied Mediterranean locality with an average of about 500 polyps per colony along the sampling site. The highest average values were recorded at the end of summer, with over 1,500 polyps per colony and 400,000 polyps m⁻², while in the Medes Islands the same species shows 250 polyps per colony (Barangé and Gili 1988) and the leptothecate *Campanularia everta* (Clarke 1876) reaches densities of 50,000 polyps m⁻² (Coma et al. 1995).

Trophic ecology

Barangé and Gili (1988) and Gili and Coma (1998) highlighted the role of benthic cnidarians in the energy transfer from the pelagic to the benthic system despite their reduced size and low abundance. In the shallow-water benthic communities of the western Mediterranean Sea, *E. racemosum* shows a feeding rate of 100,000 prey items $m^{-2} day^{-1}$, suggesting that this hydroid may have considerable effects on local plankton populations (Barangé and Gili 1988; Gili et al. 1996). During summer, *E. racemosum* from the North Adriatic Sea can eat up to 6 prey items per polyp, with a maximal estimated predation rate of over 6,000 prey items captured $m^{-2} day^{-1}$ correspondent to an average value of 13.7 mg C $m^{-2} day^{-1}$ from July to September. In this study, it was also showed that the predation rate of *E. racemosum* is variable throughout its life cycle: the maximal values occur in the end of July when the colonies reach their maximum size. Along the considered transect (about 900 m^2), the population of *E. racemosum* consumes from 37 to 800,000 mg C per month (Table 6) and a total of 1,200 g C per year.

It is intriguing that most of the preys of *E. racemosum* from the North Adriatic Sea are benthic or meroplanktonic organisms (benthic foraminifers, nematodes, larvae of bivalves, ascidians and embryos of harpacticoid copepods), while calanoid copepods and cladocerans, the main components of the plankton of the North Adriatic sector (Guglielmo et al., 2002), were very scarcely recorded.

In accordance with Barangé (1988), the gut content analysis showed that *E. racemosum* from the Adriatic Sea is not a selective feeder, but it is able to consume several food types comprising plankton, other floating elements and sediment. Smaller items, such as diatoms, sediment or pine pollen, are normally recorded in the coelenteron. Puce et al. (2002) demonstrated that *E. racemosum* is able to collect the suspended particulate matter when the water turbulence intensity is high. Larvae of mussels are the favourite preys of the studied species up to sizes not exceeding 500 μm . Colonies of *E. racemosum* represent a

primary substrate for the recruitment of *Mytilus galloprovincialis*, but when the pediveligers approach the bottom to settle, many are caught in the hydroid's tentacle trap.

The egg masses released by the adults of *M. galloprovincialis* represent a further important food source supporting the communities of *E. racemosum* in the study site. In fact, data concerning the egg diameter of *M. galloprovincialis* report for about 60 μm (Sedano et al. 1995) comparable to that of the eggs found inside the hydroid gastric cavities (65–70 μm).

Even if hydroid predation emerged as the most important factor causing mortality of planktonic larvae (Thorson 1950), there are a few studies about impact of benthic filter feeders on bivalve pediveligers. Purcell et al. (1991) observed that scyphopolyps of *Chrysaora quinquecirrha* (Desor), in experimental conditions, consumed on average 0.9 veliger $day^{-1} polyp^{-1}$ and significantly limited the settlement of the oyster *Crassostrea virginica* (Gmelin, 1791). Larviphagy was also observed in adults of *Mytilus edulis* Linnaeus, 1758 (Lehane and Davenport 2004) and *Cerastoderma edule* (Linnaeus, 1758) (André et al. 1993). The latter reduced by 33 % the settlement and recruitment of juveniles of the same species. The highest value of bivalve larvae in the plankton and the highest hydroid predation rate were observed in summer (July–August). Since in July 2009 more than 60 % of the preys were represented by mussels' pediveligers, about 3,800 mussels m^{-2} (18.3 mg C $m^{-2} day^{-1}$, Table 6) could be captured every day. The estimated total number of captured bivalves per year along the considered transect (an area of about 900 m^2) is about 136 millions (642 g C, Tables 5, 6), suggesting that the hydroid population considerably affects the bivalve settlement.

In the study area, mussel larvae were also observed in the coelenteron of other cnidarians such as the hydroids *Clava multicornis* (Forskål, 1775) and *Obelia dichotoma* (Linnaeus, 1758) (Di Camillo, personal observations), the scyphopolyps of *Aurelia aurita* (Linnaeus, 1758) (Di Camillo et al. 2010) and the stoloniferan *Cornularia cornucopiae* (Pallas, 1766) (Betti et al. 2012), suggesting that

Table 7 Percentage of carbon invested in reproduction

Date	Average number of blastostyles per colony	Average number of polyps per colony	% of blastostyles	Polyp biomass carbon (μg)	Blastostyles carbon (μg)	Total polyps carbon (μg)	%
Oct '08	2.5	747.7	0.3	Hydranths: 50.35	163.1	37,639.2	0.4
May '09	0.6	167.6	0.4	Blastostyles: 65.25	39.2	8,437	0.5
Jun '09	28.3	363.6	7.8		1,846.6	18,303.6	10.1
Jul '09	114.7	894.3	12.8		7,484.2	45,019.1	16.6
Aug '09	34.4	777.1	4.4		2,244.6	39,119.2	5.7
Sep '09	216.7	1,558.9	13.9		14,139.7	78,475	18

(1) the high biomass of these species is widely supported by a massive number of settling larvae of *M. galloprovincialis* and (2) that hydroids and other benthic cnidarians may regulate the recruitment success of bivalve larvae by predation.

Reproduction

Concerning the reproduction of *E. racemosum*, the highest percentage of blastostyles produced by colonies is up to about 14 % of the total number of polyps that in terms of invested carbon corresponds up to 18 % of the hydroid biomass (Table 7), almost twice higher than the reproductive effort of *C. everta* (Coma et al. 1998). It is likely that the high food availability, besides the satisfaction of the energetic demand for the colony growth, grants also the production of a large number of blastostyle. Both in 2007 and in 2008, we observed a temporal separation in the male and female gonad maturation with male colonies appearing in May while females in June–July and with only a short period of overlapping. A similar phenomenon was already reported by Ryland (1997) for British *Parazoanthus* spp. whose fertile colonies, when found, resulted all females or all males.

Sea temperature plays a key role in the sex determination of several cnidarian species with male gametes reaching maturity at a lower temperature with respect to female ones. For example in the dioecious species *Hydra oligactis* Pallas, 1766, only male gonophores are present when temperature is below 12 °C (Littlefield 1986). Female colonies of *Parazoanthus axinellae* (Schmidt, 1862) from the Ligurian Sea occur in shallow warmer waters while males occur in deeper cooler waters (Previati et al. 2010). The involvement of water temperature in the differential maturation of the gonads in *E. racemosum* is demonstrated by the evidence that in other Mediterranean sites (southern Adriatic Sea and Ligurian Sea), characterized by a summer thermocline, male colonies are recorded below the thermocline while the female ones above it (Di Camillo, personal observations).

Experimental studies carried out on Mediterranean colonies of *Clytia hemisphaerica* (Linnaeus, 1767) confirmed that sex determination may be strongly influenced by temperature in hydroids. In fact the medusae of this species, reared at 15 °C, developed into males while those budded and reared at 24 °C turned into females (Carré and Carré 2000). Field observations on the winter species *E. glomeratum* in the Ligurian Sea indicated that during October only male colonies were present while later, when the temperature strongly decreased, females appeared (Ariillo et al. 1989). These data support the hypothesis that an environmental determination of sex exists also in different Mediterranean *Eudendrium* species.

It is not clear the advantage of a reproductive strategy that strongly avoids the temporal overlapping of the two sexes, with the sperm release occurring when none or very few mature females are present. It is plausible that the male gametes produced in a site may drift and reach distant female colonies, thus favouring a gene flow between different populations. Nevertheless, the few data available on cnidarian sperm longevity (Yund 1990) suggest a limited dispersal ability of these gametes; for example, it has been estimated that spermatozoa of *Hydractinia echinata* (Fleming, 1828) are able to live only up to 4 h and to cover a distance of only 7 m. Alternatively, it is possible to hypothesize that *E. racemosum* spermatozoa may be able to fertilize early-developed eggs or to be retained inside the female gonophores until eggs maturation. The fertilization modality in *Eudendrium* species however is still an open question. In this context, Mergner (1975) figured out that spermatozoa may reach female gonophores through a mouth-opening of the developing female blastostyle, while Summers (1972) hypothesized that the spermatozoa are able to pierce the egg reached through a small opening, known as micropyle, forming in the ectoderm.

Conclusions

The annual trend of *E. racemosum* is similar to those observed in other Mediterranean areas such as Portofino (Boero and Fresi 1986; Azzini et al. 2002), Livorno harbour (Rossi 1964) and Medes Islands (Barangé and Gili 1988), with an increase in abundance during the warm season and a regression in winter. In the present study, quantitative data on seasonal fluctuations of the hydroid biomass are given for the first time.

It is generally stated that in the Mediterranean Sea, most of the benthic suspension feeders, like colonial cnidarians, are abundant in winter and aestivate in summer due to the plankton reduction occurring in the warm season (Coma et al. 1998). Nevertheless, the case of *E. racemosum* from the North Adriatic Sea suggests that local benthic food chains are able to support very high biomass of colonial hydrozoans also during the summer period. The gut contents peak observed in July is followed by a rapid increase in the polyp number in August and September (Fig. 9), suggesting that the remarkable growth of *E. racemosum* is due to the considerable food intake. During summer, the rich assemblages of *E. racemosum* is mainly sustained by the high abundance of planktonic larvae of bivalves. On the contrary, during winter the abundance of mussel pediveligers drastically drops, contributing to the hydroid regression. Besides *E. racemosum*, other species in the same area reach exceptional abundances or sizes, such as the sponge *Chondrosia reniformis* (Nardo, 1847) that forms specimens

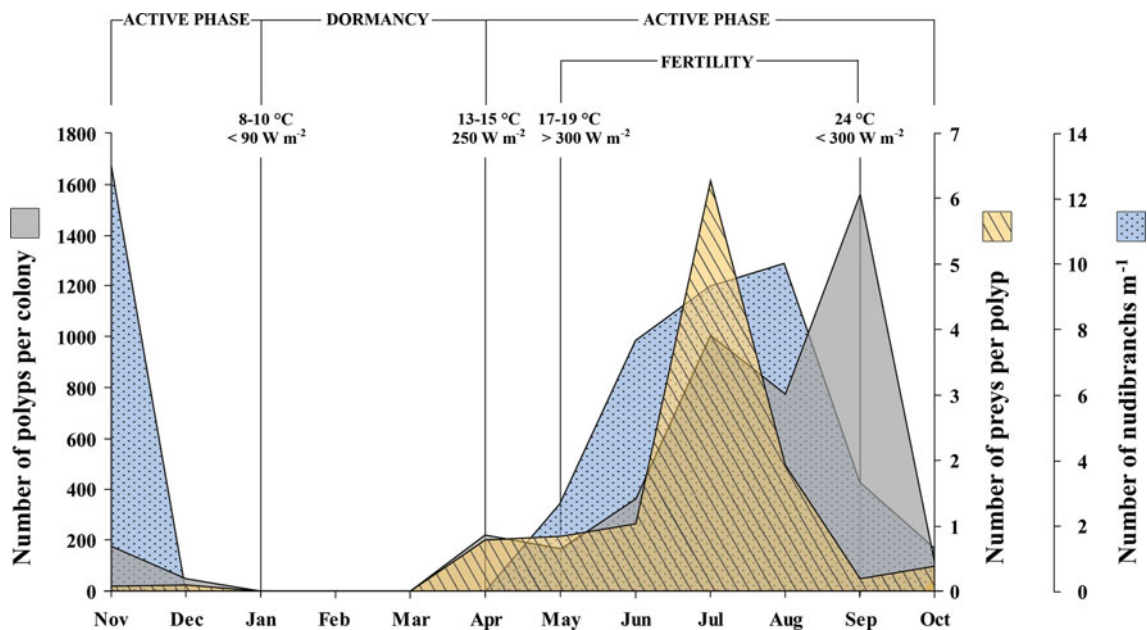


Fig. 9 *Eudendrium racemosum*'s dynamics. The graph shows the periods of activity, fertility and dormancy of the species. The growth phase (represented in grey) follows the peak of ingested preys (striped

area) and it is possible to notice the decrease in the number of polyps due to the nudibranch predation (dotted area)

larger than one metre (Di Camillo et al. 2012) or the zoanthid *Epizoanthus arenaceus* delle Chiaje, 1823 with colonies composed of an average of 3,600 polyps (Di Camillo, personal observations). This is mainly due to conspicuous river discharges causing high productivity rates all year round (Zavatarelli et al. 2000); hence, in the North Adriatic Sea the food is always available and does not represent a limiting factor even during summer (Di Camillo et al. 2012).

During the 4-year observation period, *E. racemosum* always disappeared during the cold season and reproduced in spring-summer, although variations in the blooming and reproduction time occurred in different years (Table 1). These fluctuations probably depend on the notable temperature oscillations registered from year to year, for example in May the sea temperature can range from 16 to 21 °C due to the shallowness of the water column in the area that causes quick temperature variations in relation to air temperature (Di Camillo et al. 2012).

While the exceptional polyp and colony densities of *E. racemosum* from the North Adriatic Sea are strongly related to food availability, its appearance, as well as its disappearance, is triggered by critical values of temperature. In fact, when hydrorhizae lacking polyps were collected during winter and kept in aquarium at temperature higher than 13 °C, new polyps were formed (Di Camillo, personal observations). It is plausible that irradiance, varying in relation to cloudiness and water turbidity, may

also influence *E. racemosum*'s occurrence and fertility. Bavestrello and Arillo (1992) suggested that the cyclic abundance variations of the winter species *E. glomeratum* is negatively affected by water temperature and solar irradiance. On the contrary, Rossi (1964) demonstrated, through laboratory experiments, that irradiance positively influences colony growth and polyp production in *E. racemosum*. Puce et al. (2004) elucidated the complete biochemical pathway involved in the light-induced growth of *E. racemosum*, demonstrating for the first time the role played by the phytohormone abscisic acid (ABA).

In the Mediterranean Sea, solar irradiance and water temperature trends are shifted; hence, Bavestrello and Arillo (1992) considered separately the effects of these parameters on the *E. glomeratum* population. In the North Adriatic Sea instead, the trends of these two environmental factors are strongly correlated (Fig. 4); thus, it is not possible to separate their influence on the cycle of *E. racemosum*.

During winter, the studied colonies of *E. racemosum* degenerate and the rough sea conditions induce the almost complete detachment of the stems. Parts of the hydrorhizae containing living coenosarc remain anchored on the substratum and act as resting stages allowing the colony regeneration in the following spring. *Eudendrium racemosum* starts increasing when the temperature rises above 13 °C and irradiance above 250 W m⁻², and reaches its maximum in August. The high abundance recorded in the

warm season is due both to the re-growth of over-wintering *E. racemosum* hydrorhizae and to new colonies originating from the sexual reproduction via planula settling. From late spring to summer, hydroid colonies form a *facies* stretching out all over the site.

Considering the effect of *C. peregrina* predation, sharp decreases in the polyp number were recorded in July 2007 and in August 2009 together with an increase in the abundance of the nudibranch. The polyp abundance rises again in September 2009 when the nudibranchs drop. Our laboratory experiments have indicated that a single specimen of this mollusc is able to eat more than 500 polyps day⁻¹; thus, considering that a hydroid colony has on average about 1,000 polyps in the summer season, two nudibranchs may completely eat one colony in a day. In summer, up to 10 molluscs m⁻² were found; thus, they can consume 5 hydroid colonies in 1 day and 150 in 1 month. In July 2007, about 100 colonies with polyps and about the same number without polyps were observed in a squared metre surface. The number of hydroids lacking polyps corresponds indeed to the estimated monthly nudibranch predation rate. However, the exploited colonies are able to regenerate new polyps in the following months because the molluscs do not eat branches or other parts surrounded by

perisarc, but they limit their sucking activity to the naked hydranths.

Summarizing, the population dynamics of *E. racemosum* in the North Adriatic Sea are mainly regulated by three factors (Fig. 9): first, the synergic effect of temperature and irradiance triggering hydroid appearance, dormancy and fertility; secondly, the conspicuous food intake especially occurring in summer, which allows an increase in polyp and colony abundance in summer and early autumn; thirdly, the impact of adults of *C. peregrina*, which reduces the polyp abundance in July and August but does not cause the complete hydroid regression.

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Appendix

See Tables 8, 9, 10, 11 and 12.

Table 8 ANCOVA number of polyps

	<i>df</i>	MS	<i>F</i>
Colony area (cm ²)	1	1,362.84	97.39***
Colony height (cm)	1	1.92	0.14ns
Month	12	263.60	18.84***
Error	120	13.99	

*** $p < 0.001$; ns not significant

Table 9 ANOVA colony heights

	<i>df</i>	MS	<i>F</i>
Temperature	1	3,238.04	1,940.41***
Month (temperature)	11	140.03	83.91***
Error	1,070	1.67	

*** $p < 0.001$

Table 10 Split plot—abundance of gastrozooids, gonozooids and cnidophores for each portion of a colony

	Effect	<i>df</i>	Gastrozooids		Gonozooids		Cnidophores	
			MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Month	<i>R</i>	9	7,368.9	17.16***	313.46	7.80***	7.45	3.99***
Colony	<i>R</i>	9	155.3	0.39ns	38.07	1.37ns	1.58	0.95ns
Month × colony	<i>R</i>	76	429.3	2.89***	40.19	1.23ns	1.87	1.33ns
Portion	<i>F</i>	2	12,221.9	105.65***	394.11	19.59***	2.67	2.22ns
Colony × portion	<i>R</i>	18	115.6	0.78ns	20.09	0.62ns	1.20	0.86ns
Error		170	148.8		32.64		1.40	

*** $p < 0.001$; ns not significant

Table 11 2-way nested ANOVA—gut contents

	Effect	df	Bivalves		Amphipods		Tintinnids		Others	
			MS	F	MS	F	MS	F	MS	F
Month	F	9	458.51	16.56***	3.52	6.00***	157.77	7.60***	18.65	2.22*
Colony (month)	R	82	27.78	18.43***	0.59	23.99***	20.84	21.44***	8.43	8.03***
Error		2,655	1.51		0.02		0.97		1.05	

* $p < 0.05$; *** $p < 0.001$ **Table 12** 1-way ANOVA—Nudibranchs

	df	MS	F
Month	11	67.69	24.13***
Error	24	2.80	

*** $p < 0.001$

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