

# Effects of gastropod predation on the reproductive output of an overexploited deep octocoral

C. Priori · F. Erra · M. Angiolillo · G. Santangelo

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**Abstract** The study presented herein is aimed at quantifying the effects of the partial predation exerted by the gastropod *Pseudosimnia carnea* on the reproductive features of the highly valuable, slow-growing, and long-lived red coral, *Corallium rubrum*. Seventy-five colonies were collected just before annual spawning from a red coral population living between 85 and 90 m deep in the NW Mediterranean; of these, 35 % were affected by *P. carnea*. Female colonies were more frequently preyed upon than males (3:1 ratio). Overall, 1,100 polyps were dissected and examined for their reproductive content. The mean number of polyps per colony and the mean fecundity of female polyps and colonies were significantly reduced by gastropod predation, which affected colonies independently of their size; in particular, colony fecundity was reduced by 81 %. The consequent reduction in population reproductive output is likely to have long-term effects on preyed-upon populations and thereby limit their resilience to intense commercial harvesting.

**Keywords** North-western Mediterranean · *Pseudosimnia carnea* · *Corallium rubrum* · Reproductive biology · Gorgonians · Mesophotic corals

## Introduction

Corals are preyed upon by a variety of macro-consumers, including polychaetes, gastropods, crabs, echinoderms, and fish (e.g., Robertson 1970; Glynn 1990; Claremont et al. 2011). Corallivory can be distinguished as “total”, when it regards whole colonies or even large extensions of coral reefs (e.g. the predation exerted by *Acanthaster planci*, the crown-of-thorns starfish; Baird et al. 2013) and “partial” when it involves only part of the prey, without causing its death. Corallivorous gastropods, in particular, can form dense aggregates that profoundly affect reef corals (Kita et al. 2005).

Gorgonians are equipped with chemical (terpenoids) and morphological (sclerites) defences against predators (e.g., Van Alstyne and Paul 1992). However, some specialised gastropods are able to overcome these defences and hence represent their main predators. As tissue loss can dramatically reduce gorgonian fecundity (Page and Lasker 2012), gastropod “grazing” could reduce population reproductive output by reducing both the number of fertile polyps per colony and the fecundity of individual polyps (Lasker 1985; Rotjan and Lewis 2008). Although several studies have been conducted on the corallivory effects exerted by gastropods on scleractinians (Hayes 1990; Turner 1994; Morton et al. 2002; Johnston and Miller 2007) and gorgonians (e.g., Burkepile and Hay 2007; Evans et al. 2013), little is known about the effects of *partial predation* (i.e. consumption of only parts of the prey; Jackson and Palumbi 1979) on the reproductive fitness of gorgonian corals. In the case of these modular organisms, it can be defined as predation that does not kill the prey, i.e. partial.

Due to the bright colour and the workability of its axial skeleton, the Mediterranean red coral, *Corallium rubrum* (L. 1758), has been harvested and traded for over

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C. Priori (✉) · F. Erra · G. Santangelo  
Department of Biology, University of Pisa, Via Volta 6,  
56126 Pisa, Italy  
e-mail: prioricristina@gmail.com; cristina.priori@for.unipi.it

M. Angiolillo  
Department of Habitat and Marine Biodiversity Protection,  
ISPRA, Via Brancati 60, 00144 Rome, Italy

2,000 years (e.g. Tsounis et al. 2010). It has been included in Annex V of the European Community Habitats Directive, which designates plant and animal species of European interest whose exploitation may be subject to conservation measures.

*Corallium rubrum* is a gonochoric internal brooder, which releases larvae annually during a limited time period in summer. It reaches sexual maturity at 3–4 yr (Santangelo et al. 2003; Gallmetzer et al. 2010) and exhibits high recruitment rates (Bramanti et al. 2007). Nevertheless, it is one of the least reproductive of the studied gorgonians (i.e. it produces the lowest number of oocytes; Cupido et al. 2012).

*Pseudosimnia carnea* (Poiret 1789, Prosobranchia, Caenogastropoda, Ovulidae) feeds exclusively on *C. rubrum* colonies, using its highly specialised mouth equipped with a tube-like proboscis to efficiently consume coral polyps. Although this gastropod is rather common on red coral colonies below 50 m depth (Abbiati and Santangelo 1989; Francour et al. 1992), no attempt has ever been made to quantify the effects of its feeding on the affected populations. Generally, such partial predation is considered to have limited effects on gorgonian mortality (Lasker et al. 1998; Burkepile and Hay 2007), though it may have a more profound impact on colony reproductive output, and hence on population dynamics.

The finding of a large number of *C. rubrum* colonies affected by *P. carnea* predation in a deep-dwelling population has provided the opportunity to quantify the effects of this predator on red coral colony reproductive parameters. This study focused on the following points: (1) determining whether *P. carnea* predation is selective towards colony sex and/or size, (2) quantifying the effects of *P. carnea* grazing on the reproductive output of female colonies, and (3) assessing whether there is any significant reduction in polyp and colony fecundity in the affected colonies.

## Materials and methods

### Sampling

During a survey carried out in early summer 2010 to study the demography of deep red coral populations (Priori et al. 2013), a total of 75 colonies were collected by rebreather SCUBA divers between 85 and 90 m deep in an area of the north-western Mediterranean, south-west of Elba Island (Tuscan Archipelago, Italy, 42°41'N, 10°01'E). Sampling was carried out in mid-July, just before the red coral annual spawning period (Santangelo et al. 2003). Several of these colonies harboured specimens of *P. carnea* (Fig. 1). Colonies were considered to be affected if they harboured the

predator snail or had more than 5 % of their surfaces covered by egg depositions and a thin layer of mucus from the predator (under the layer of gastropod eggs and mucus, polyps were empty or even swept clean for long stretches of the branches; Priori, personal observation). The presence of eggs and mucus indicates a recent predation as polyps were not regenerated yet.

Preyed-upon colonies were divided into “Class I” if up to 1/3 of their surface was covered by eggs and mucus, and “Class II” if the extent of coverage was greater; no colony had more than two-thirds of its surface covered.

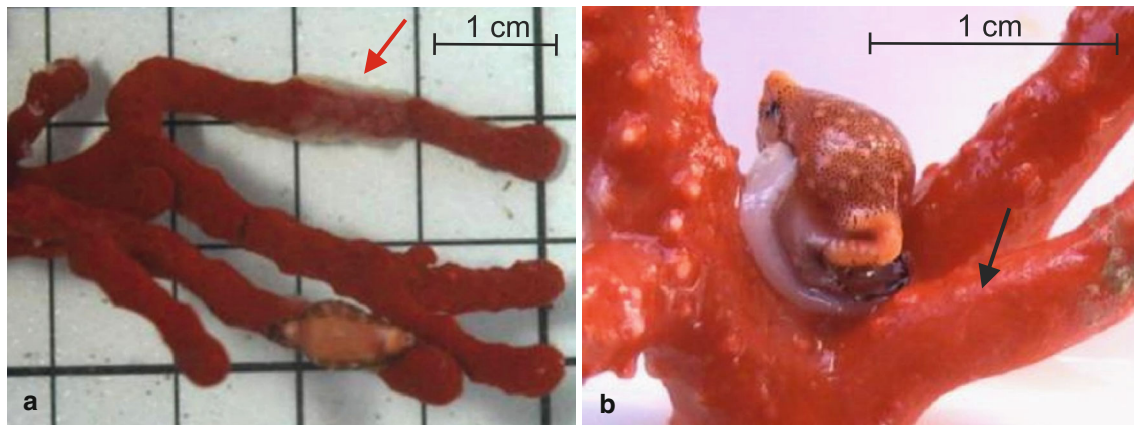
Each colony was numbered, photographed, and then fixed in 4 % formalin. Due to the sampling method and colony fragility, a portion of the colonies lost some branches during collection (*incomplete colonies*). Some parameters (female colony fecundity, number of polyps per colony, and colony weight) can only be measured on the *entire colonies*, while others (sex ratio and female polyp fecundity) can still be determined for *incomplete colonies*. Therefore, varying numbers of colonies were examined for the different parameters.

### Sex determination

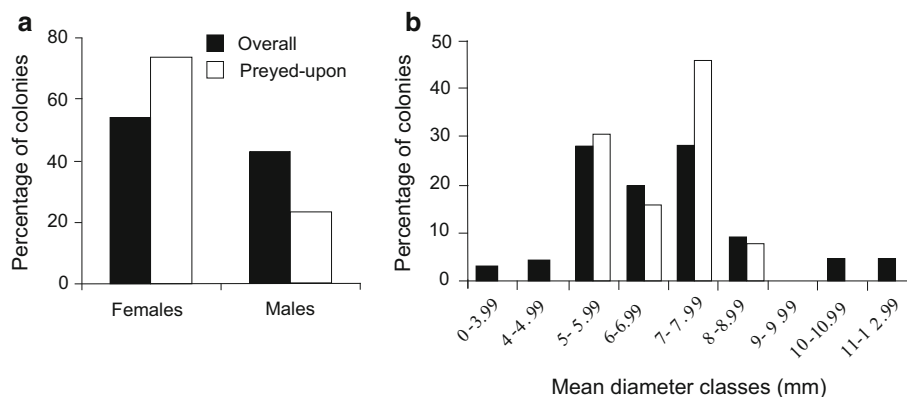
The main morphometric and reproductive parameters of fixed polyps and colonies examined were, respectively, colony weight, number of polyps per colony, sex ratio, fertility (i.e. percentage of colonies with gametes), and fecundity (i.e. mean number of oocytes or planulae per polyp and per colony). The number of polyps in each colony was determined by stereo microscope counting (6.4×). Sex and fecundity were determined by dissecting female polyps under the stereo (20–100×) and optical microscope (250–1,000×). In order to examine a representative sample, 20 polyps from smaller colonies (<400 polyps), and 5 % from polyps of larger colonies were analysed (Santangelo et al. 2003). Polyps were randomly chosen, while being sure to choose at least one on each colony branch. Once the sex of all the sampled colonies was determined, the fertility and fecundity of female polyps and colonies were also examined, and the colony reproductive output calculated on these bases.

Overall, 1,100 polyps were dissected. The sex ratios in both the whole sample and the subsample of preyed-upon colonies were then determined, and their divergence from randomness (1:1 ratio) was tested by  $\chi^2$ . The fecundity values of female polyps and colonies were then calculated. Finally, colonies were dried at room temperature for 1 week and weighed ( $\pm 0.1$  mg).

The colonies were divided into *unaffected* (i.e. not preyed upon) and *preyed upon* (partially), and examined for (1) polyp fecundity (i.e. mean number of oocytes per polyp), (2) colony fecundity-to-weight ratio, and (3)



**Fig. 1** Two colonies of *Corallium rubrum* preyed upon by *Pseudosimnia carnea*. **a** Arrow indicates a gastropod egg deposition, **b** arrow indicates a grazed area depleted of polyps



**Fig. 2** Sampling frequency data for overall colonies (*dark*) and colonies preyed upon by *P. carnea* (*light*). **a** Distribution of females and males in the overall population and in preyed-upon colonies. Although the population sex ratio was balanced, females were

significantly more frequently preyed on than males. **b** Distribution of overall and preyed-upon colonies relative to their size class. The percentage of preyed-upon colonies was proportional in each size class

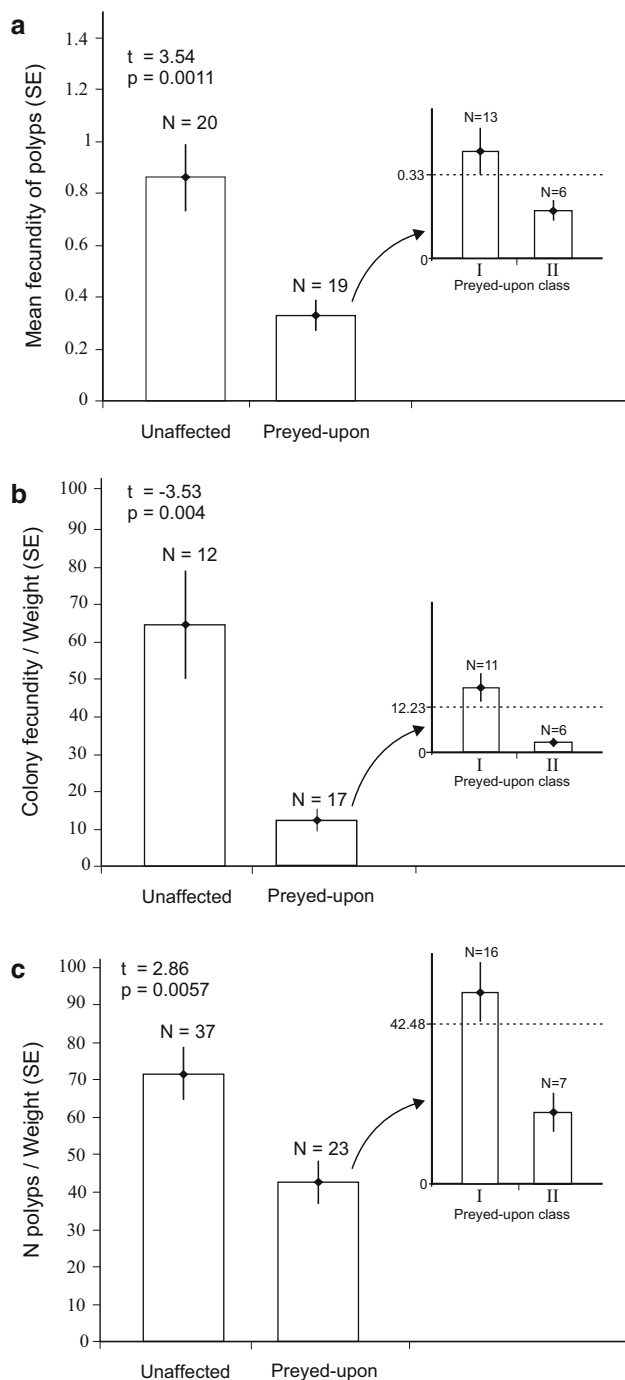
number of polyps-to-weight ratio. The latter two parameters were normalised by weight to highlight the effects of predation irrespective of colony size. Any differences in these parameters between the two colony groups were checked via Student's *t* test. The same parameters were then determined for the two subgroups of preyed-upon colonies, Class I and II separately, in order to evaluate the effect of different levels of corallivory.

## Results and discussion

During their long lifespan (which may exceed a full century), *C. rubrum* are exposed to a variety of ecto- and endoparasites (Corriero et al. 1997), as well as the species-specific partial predation of the highly specialised gastropod *P. carnea*.

A scientific cruise dedicated to the study of deep “coralligène” (Mediterranean mesophotic area) red coral populations revealed a rich fauna of sponges, polychaetes, hydroids, and molluscs living on or in the colonies. Four specimens of *P. carnea* were found, each on a different colony. No colony harboured more than one gastropod, and no one was found dead due to predation. This snail was the macro-predator most frequently associated with coral colonies, as 34.7 % (26/75) of the sampled colonies were affected by this predator (Fig. 1).

As colonies were sampled just before red coral spawning, and 96 % of them (72 out of 75) were fertile and ripe, it was possible to assess whether any differences existed between the reproductive parameters of unaffected and preyed-upon colonies. Since it was found that *P. carnea* feeds not only on polyp tissues, but also on eggs and spermaries (Priori, personal observation), it was decided to



**Fig. 3** Comparison of morphometric and reproductive descriptors of “Unaffected” and “Preyed-upon” *Corallium rubrum* colonies. N = number of colonies in each group. **a** Fecundity of polyps: mean number of oocytes/number of polyps. **b** Fecundity of colonies: mean polyp fecundity  $\times$  number of polyps (normalised by weight). **c** Number of polyps per colony (normalised by weight). Within the boxes, a further division of preyed-upon colonies into Class I and II of corallivory damage. (Dotted lines = overall mean value)

investigate whether snails exhibit any significant preference for female or male colonies. Of the 75 collected colonies, 40 were females, 32 were males, and 3 turned out

to be sterile (i.e. without gametes at sampling time). The sex ratio of the sample did not differ significantly from 1:1 ( $\chi^2 = 0.89$ ,  $p > 0.05$ ), similar to that previously determined on a larger sample of the same population (Priori et al. 2013) and as generally found in octocorals (Kahng et al. 2011; Cupido et al. 2012).

The predation frequency of female colonies was three-fold higher than that of males, significantly diverging from the expected balance in sex ratio ( $\chi^2 = 6.76$ ,  $p < 0.01$ ; Fig. 2a). This preference is likely due to the greater nutritional value of eggs in comparison with spermaries. How gastropods are able to effect such selection is unknown, though chemical gradient signals produced by female colonies (Kita et al. 2005) could possibly direct the gastropod towards them.

The number of preyed-upon colonies in the different size classes was proportional to the overall number of colonies in each of the classes ( $\chi^2 = 3.747$ ,  $p = 0.391$ ; Fig. 2b), thereby indicating no significant effect of colony size on predation frequency. The mean polyp fecundity and mean colony fecundity-to-weight ratio were 38.4 and 18.9 %, respectively, and the number of polyps-to-weight ratio in preyed-upon colonies was 58.5 % of the values found in unaffected ones (Fig. 3). All these values were significantly higher in unaffected colonies (Student’s  $t = 3.54$ ,  $p < 0.01$ ;  $t = -3.53$ ,  $p < 0.01$ ;  $t = 2.86$ ,  $p < 0.01$ , respectively). The less affected colonies (Class I) showed a drastic reduction of these parameters when contrasted with unaffected ones (47.7, 27, and 72.3 %). In the more affected colonies (Class II), these values were further reduced (20.9, 4.1, and 26.8 %).

These differences between unaffected and preyed-upon colonies highlight the effect of predation on all the studied parameters, which overall gave rise to a dramatic reduction in colony reproductive output in the affected population. This effect becomes greater in the colonies with a higher level of predation. Moreover, predation reduced not only the mean values of the three reproductive parameters reported above, but also their variability: the SE values in the preyed-upon colonies (pooled data) were 53.8, 78.9, and 8.1 % lower than in unaffected colonies. This was likely due to a levelling effect of predation on reproductive parameter variability.

The findings of this study reveal a significant effect of *P. carnea* predation on the main reproductive parameters of female red coral colonies: such predation significantly reduces their reproductive output. Any disturbance of colony fecundity could also reduce population reproductive output and thereby produce a profound, long-term, negative impact on survival and recovery (Rotjan and Lewis 2009) of overexploited populations of this long-lived, slow-growing species.



The data collected on *P. carnea* predation of a deep-dwelling red coral population has enabled us to gain a good deal of insight into its effects on the reproductive parameters of red coral colonies. Such data will undoubtedly allow us to improve the dynamic demographic models used to project population trends over time (Santangelo et al. 2007) by introducing partial predation (quantified here) as a disruptive factor in population reproductive output.

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