Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone

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Abstract The twilight or mesophotic zone is among the less explored marine regions. In coastal areas, investigations and manipulative experiments on benthic biodiversity and ecosystem functioning at depths up to >50m have been recently made possible by the progress of SCUBA techniques. In this study, we tested the effects of the presence of a gorgonian forest characterised by a large and dense population of the gold coral *Savalia savaglia* (Bertoloni 1819) on the benthic biodiversity (nematode species richness, and meiofauna community structure and richness of taxa), trophic guilds state (molluscs) and ecosystem functioning in the surrounding sediments. The *S. savaglia* colonies create elevated and complex tertiary structures. Our results indicate that the presence of these colonies was associated with a significantly increased deposition of bioavailable substrates and enhanced biodiversity, when compared with soft bottoms at the same depth but without gold corals. The higher biodiversity and altered trophic conditions resulted in higher rates of ecosystem functioning (e.g., higher benthic biomasses). These results suggest that *S. savaglia* should be particularly protected not only for its specific rarity, endemism and vulnerability but also because has a prominent role in sustaining high levels of biodiversity and ecosystem functioning in the surrounding benthos of the twilight zone.

Key-words Ecosystem engineers, benthic biodiversity, deep corals, *Savalia savaglia* · Mediterranean Sea

Introduction

In tropical areas, mesophotic reefs or twilight zone (50-120m) are drawing ever more attention to scientists, owing to their peculiar environmental features, supporting high habitat complexity and diversity (Reed et al. 2008; Lesser et al. 2009). In the Mediterranean Sea the biodiversity of this bathymetric belt is still poorly described.

Savalia (=*Gerardia*) *savaglia* (Bertoloni 1819) is a rare and endemic Mediterranean zoanthid, belonging to the family Savaliidae (Haussermann 2003), characterized by a wide geographical distribution with a thermophilous chorology (Rossi 1958). Owing to its rarity, the species is included in the Annex II ASPIM (Barcelona Convention) and in the Annex II of the Berna Convention on the conservation of European wildlife and natural habitats.

The genus *Savalia* is characterized by a wide bathymetric distribution, ranging from 20 m to more than 600 m depth (Ocaña and Brito 2004) and by several biological peculiarities. It is the unique zoanthids able to produce a rigid and thick skeleton: the colony starts growing on the stem of a gorgonian or anthipatharian (e.g., *Paramuricea clavata*, *Eunicella* spp., and *Anthipathes* spp.). Then, after engulfing the host, this zoanthid starts to produce a hard layered proteinaceous skeleton that can reach large sizes (up to 2 m high, with a main trunk diameter up to 14 cm; Bell 1891). This skeleton is unusually rich in histidine, the only aminoacid with a side-chain that can be variably charged under normal biological conditions (Zubay 1988; Druffel et al. 1995). *S. savaglia* is the only organism known so far to produce ajugasterone-C, an ecdysterone previously known exclusively from terrestrial plants (Vallentyne 1964). The sexual reproduction of *Savalia* sp. (Waller and Baco 2007) and *S. savaglia* (Previati et al. in press) has been only recently described, whereas larval stages are still unknown as are their dispersal strategies.

Using ^{14}C, a very slow radial growth rate (14 to 45 µm yr^{-1}; Roark et al. 2006) has been calculated and the skeletons have been aged back at 2700 years. Therefore, gold corals are among the animals with the longest life span on Earth, which makes them important paleo-indicators

(Roark et al. 2006; 2009). Long-living organisms producing three-dimensional hard skeletons can play an important role as habitat-modifiers (ecosystem engineers *sensu* Jones et al. 1994). They may reduce current flow velocity, stabilize soft substrata, increase particle sedimentation and enhance local accumulation of fine particles (Bruno and Kennedy 2000).

The presence of elevated and complex tertiary substrates on deep-sea bottoms, such as the banks of the cold coral *Lophelia pertusa,* promotes benthic biodiversity and ecosystem processes (Roberts et al. 2006). The spatial heterogeneity generated by the presence of these corals is often associated with organic loads and number of niches that are higher than those in soft sediment habitats at similar depths (Kiriakoulakis et al., 2004).

In this study, we tested the null hypothesis that meiofaunal abundance, taxa richness, and the biodiversity of nematodes (the most abundant meiofaunal taxon) and molluscs do not differ significantly between sediments underneath versus far from *S. savaglia* colonies inhabiting a gorgonians' forest in the twilight zone of the Portofino Marine Protected Area (Ligurian Sea, Mediterranean Sea). We hypothesised that these colonies could have a significant impact on the benthic trophic status, on benthic assemblages structure, biodiversity and ecosystem functioning of the surrounding soft sediments.

Methods

Study area and sampling

The study area is located in the Portofino Promontory, along the eastern coast of Liguria, Italy within the Marine Protected Area (MPA) of Portofino (Fig. 1). Vertical cliffs that continue underwater down to 50 – 60m depths and diverse geo-morphological features and hydrodynamic conditions characterize the Promontory. The area is subject to the typical cyclonic circulation of the Ligurian Sea (North-Western Mediterranean Sea), with a seasonal cycle related to the seasonal variations of atmospheric forcing. Close to the coastal area of interest the circulation, indeed, runs northwest-ward with only short periods of reversal (Astraldi and Manzella 1983).

On a detrital bottom, at 67 m depth and about 50 m distant from the base of the cliff of the Portofino Promontory, we discovered a dense population of the gold coral *Savalia savaglia.* Colonies grow up from a small rocky shoal (1.5 m high and 5 m long) and are surrounded by the sea-fans *Paramuricea clavata*, *Eunicella cavolinii*, and *E. verrucosa,*. During the study period, the structure of the *S. savaglia* population was assessed in an area of about $50m^2$ by measuring the basal diameter and height of all of the colonies at each sampling date.

Sediment samples were collected by SCUBA divers in December 2006 and February 2007, by gently inserting PVC corers (20 cm high, 7 cm diameter) into the sediment. Cores went about 10 cm deep and just the top 5 cm were analyzed.

At each sampling date, sediment cores for biochemical (n=3) and faunal (n=3) analyses were collected either underneath the gold coral colonies or in soft substrates at 10-m distance from the colonies. In total six cores at each date were sampled, paying attention to avoid re-sampling the same site. Sediment grain size was compared between inside and outside of the *S. savaglia* bed considering the percentages of the coarse (> 0.63 μm) and fine (< 0.63 μm) fractions.

Considering the important role of molluscs shells in the sediment composition, two additional bulk samples (1 kg of wet weight) of superficial sediment (about 2 cm) have been collected inside and outside the *Savalia* population by using a small hand shovel, to collect

qualitative data on molluscs. The abundance of other taxa in the investigated sediments was negligible respect to molluscs and, therefore, we focused our attention towards molluscs only.

Once retrieved on board, sediment cores were immediately frozen at -20°C until analyses. Considering the limited area beneath the corals (about 2 m^2) no more replicates were performed to avoid overlap with previously sampled areas.

Quantity and biochemical composition of sediment organic matter

Chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). The pigments were extracted (12 h at 4 °C in the dark) from about 1 g of sediment using 3-5 mL of 90% acetone. The extracts were analysed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 µl 0.1 N HCl, to estimate phaeopigment concentrations. Concentrations are reported as µg g DW^{-1}. Total phytopigment concentration was defined as the sum of chlorophyll-a and phaeopigment concentrations (Pusceddu et al. 1999).

The protein, carbohydrate and lipid contents of the sediments were determined spectro-photometrically, according to Pusceddu et al. (2004), and their concentrations are expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). Protein, carbohydrate and lipid contents were converted into carbon equivalents using the conversion factors of 0.49, 0.40 and 0.75 µg $C.µg^{-1}$, respectively, and their sum defined as the biopolymeric organic carbon (Pusceddu et al. 2009).

Meiofaunal abundance and nematode biodiversity

For meiofaunal extraction, the sediment samples were sieved through a 1,000-µm mesh, and a 20-µm mesh was then used to retain the smallest organisms. The fraction remaining on the latter sieve was re-suspended and centrifuged three times with Ludox HS40 (density 1.31 g cm^{-3}), according to Heip et al. (1985). All of the meiobenthic animals were counted and classified per taxon, under a

stereomicroscope and after staining with Rose Bengal (0.5 g L^{-1}). All of the soft-body organisms from the preserved samples were mounted on slides and viewed at $1,000\times$ magnification.

Nematodes are the most abundant metazoans on Earth; in terrestrial ecosystems, they account for 80% of the abundance of multi-cellular animals, and in deep-sea sediments this proportion rises to more than 90% (Lambshead 2004). This phylum is also characterized by very high species richness (i.e., among the most diverse of marine Phyla). Altogether, these characteristics make nematodes an ideal model for investigating the effects of gold corals on the surrounding benthic biodiversity and ecosystem functioning (Danovaro et al. 2008). For the nematode biodiversity analysis, the formalin-ethanol-glycerol protocol was used to prevent dehydration (Seinhorst 1959). After the whole meiofauna extraction from the sediment samples, all of the sorted nematodes, were withdrawn and mounted on glass slides. The nematodes were identified to the species level (whenever possible), according to Platt and Warwick (1983; 1988), Warwick et al. (1998).

Nematode species diversity was expressed using the Shannon information function ((H', log-base 2; Shannon and Weaver, 1949) and evenness as J' (Pielou 1975). Species richness (SR) was calculated as the total number of species collected at each station, and the Margalef Index (D) was estimated as $D = (S-1)/\ln N$, where S is the number of species and N is the number of individuals in the sample (Margalef 1958). Moreover, at each site, the species abundance data were converted into rarefaction diversity indices (Sanders 1968, as modified by Hurlbert 1971). The expected number of species for a theoretical sample of 51 specimens, ES (51), was selected. All of the diversity indices were calculated using PRIMER v5 (Plymouth Marine Laboratory, UK; Clarke 1993).

Mollusc biodiversity

Sediment samples (cores for meiofauna and samples of sediment collected by a hand shovel) were also investigated in order to reveal possible differences in the trophic structure of mollusc assemblages. However, in the cores examined for meiofauna analyses, no living mollusc species

were obtained and the study had to be limited to the thanatocoenoses. For this reason, the whole sediment of each core was examined for dead molluscs and only shells retaining the ≥90% of the original form were taken into account, while major and minor fragments were excluded from the counts, according to Davies et al. (1989). Due to the small amount of material considered, only presence/absence data were taken into account as no taphonomic fine grain interpretation was possible to separate autochthonous from allochthonous shells or shell fragments.

On the contrary, in the two additional samples of superficial sediment which have been collected in proximity of the *Savalia* population by using a small hand shovel, and which were both sieved and sorted immediately after their collection, few specimens of living molluscs were found. These latter data have been treated from a qualitative point of view only. Trophic guilds of recognised molluscs were compiled according to the Neogene Marine Biota of Tropical America (NMITA, available at http://porites.geology.uiowa.edu/) and to personal observations. The identified shells were assigned to the following trophic categories: browsing carnivores (including 'parasites', CB), predatory carnivores (including 'scavengers', CP), herbivores (including omnivores, microalgivores, detritivores, microphages, unselective deposit feeders and herbivores on rock, rubble or algal substrates, H), and suspension feeders (SU). Herbivores were pooled into a single category due to the objective difficult to distinguish, herbivores/omnivores from microalgal feeders or detritivores, etc.

Statistical analyses

To test the null hypotheses that the quantity and biochemical composition of organic matter, abundance of meiofauna and biodiversity of nematodes do not differ significantly between sediments underneath versus far from a *S. savaglia* colony and that this applies to different periods of the year, a two-way analysis of variance (ANOVA) was applied, using sampling time and the presence of the gold coral forest as the main sources of variance. Sampling time was treated as a random factor with two levels, whereas the presence/absence of the gold coral colony was treated as

a fixed factor with 2 levels, nested in sampling time. When significant differences were observed between soft bottoms and coral-colonised substrates, a Student-Newman-Kuel test was also applied. In order to ascertain which among quantity and nutritional quality of sediment organic matter explained most of the meiofaunal abundance and the nematode diversity variances in the two investigated habitats, a non-parametric multivariate multiple regression analysis that was based on Euclidean distances was also applied, using the routine DISTLM forward (Anderson, 2003). The forward selection of the predictor variables was carried out with tests by permutation. P values were obtained using 4,999 permutations of raw data for the marginal tests (tests of individual variables), while for all of the conditional tests, the routine uses 4,999 permutations of residuals under a reduced model.

As no living molluscs were retrieved from the cores, temporal patterns were not investigated, and the trophic structure of the thanatocoenoses was studied by applying the χ^2 statistic, after having compiled the observations (i.e., the cumulative number of species belonging to different trophic guilds) into a multiple contingency table which encompassed two variables: i) presence/absence of *Savalia*, and ii) trophic guilds with levels: CB, CP, SU and H.

Results

The *Savalia* bed

The whole population counts 23 colonies with base diameters (considering the lowest part of the stalk and not the encrusting base) ranging from 0.5 to 9 cm (Fig. 2). Around the gold corals there are colonies of *Eunicella cavolinii* (about 7col/m^2), *P. clavata* (about 0,6 col/m^2) and *E. verrucosa* (about 0.2 col/m^2) and in some cases colonies partially infested by *Alcyonium coralloides* are evident. Among sponges, *Cacospongia* sp., *Axinella damicornis* overgrown by *Parazoanthus axinellae*, and *Sarcotragus* sp., are the species more represented.

Concerning sediment grain size, there were no differences between the two sampling periods, but the percentage of the fine fraction from the inside the *S. savaglia* bed site was always

higher than in the outside sampling site (35% inside and 16% outside, and 40% inside and 14% outside, in December and February, respectively).

Benthic trophic status, meiofaunal abundance and nematode biodiversity

Protein, carbohydrate, lipid and biopolymeric C concentrations (Fig. 3A-B) displayed significant differences between soft bottoms and coral-colonised sediments, but weaker differences between the two sampling periods (Table 1).

Also total meiofaunal abundance (Fig. 4A) displayed significant differences between soft bottoms and coral-colonised sediments, but no significant differences between the two sampling periods, irrespectively for the two types of sediments (Table 1).

The meiofaunal community was largely dominated by nematodes (60% of total meiofaunal abundance on average of all sediment samples) followed by copepods (34%), and exhibited clear differences between soft bottom and gold coral sediments: in both sampling periods, coral-colonised sediments were indeed characterised by increased nematode and decreased copepod abundances when compared with soft bottom sediments (Fig. 4B).

In both sampling periods, nematode species richness (Fig. 4C) displayed values in coral-colonised sediments significantly higher than those in bare sediments (Table 1).

The multiple multivariate regression analysis, testing for the variance explained by the quantity (in terms of biopolymeric C content; Pusceddu et al. 1999, Pusceddu et al. 2009) and quality (in terms of the protein to carbohydrate ratio (Pusceddu et al. 2005; Dell'Anno et al. 2008) of sediment organic matter revealed that most of the variance in meiofaunal abundance was explained by the whole amount of biopolymeric C content (Table 2). Most of the variance of all of the diversity indexes, but not equitability, was explained by the values of the protein to carbohydrate ratio and was not significantly correlated with the whole amount of biopolymeric C (Table 2). The Pielou's J index, in contrast, was not significantly correlated with the values of the protein to carbohydrate ratio, and its variance was mostly explained by the biopolymeric C content.

Mollusc biodiversity

86 species of shelled molluscs, none of which was found alive, were encountered . Bare sediment samples were characterised by higher percentages of browsing carnivores, herbivores and suspension feeders, compared to coral-colonised ones, while predatory carnivorous molluscs were more abundant only in coral sediments (Fig. 5). Although it appears appealing to suggest the hypothesis that a richer meiofaunal community could provide more preys, e.g., polychaetes and, in turn, enhance predation by highly vagile molluscs of the CP trophic guild (mainly Turridae and Buccinidae), the slight differences appreciable in Fig. 5 are not statistically significant (χ^2 = 2.43, d.f. = 5, NS). Therefore, the two thanatocoenoses cannot be separated according to their trophic guilds composition.

In comparison to the core samples, the bulk sediment samples obtained by hand shovel showed six living mollusc species: the bivalves *Astarte fusca* (Poli 1791) (two specimens), *Myrtea spinifera* (Montagu 1803) (one spec.), *Nucula nitidosa* Winckworth 1930 (one spec.), and the gastropods *Mitrella minor* (Scacchi 1836) (one spec.), *Epitonium tiberii* (de Boury 1890) (one spec.), and *Alvania cancellata* (da Costa 1778) (three spec.). All of the living species but *E. tiberii* were also present in the thanatocoenosis.

Discussion

Recent investigations have shown that processes occurring in the mesophotic zone or "Twilight Zone" (TZ, Pyle 1996), might have a global relevance (Buesseler et al. 2007), but hard bottoms habitats between 50 and 200 m depth are among the less studied marine environments. This is mainly due to the previous limitations in diving technology or difficulty in using ROV (risk of damaging the colonies, high costs related to technology and ship time). The recent improvement in the utilization of mixed-gas in diving activity has allowed the exploration of depth zones from 50-120m including deep coral reef communities (Pyle 2000). These habitats are ecologically relevant, since they may host organisms with unusual physiological adaptations, high levels of biodiversity,

and might provide resources of interest for biotechnological applications (Slattery and Gochfeld 2006; Lesser et al. 2009). To date, information available on hard bottom assemblages in the mesophotic zone of the Mediterranean Sea is very poor. Previous studies dealing with the quantity and composition of material settling along a vertical cliff carried out in the same area revealed that the detritus rolling down along the vertical cliff was largely of terrestrial origin (Bavestrello et al. 1991; Bavestrello et al. 1995). Our results on contents and composition of organic matter on soft-bottom sediments of the mesophotic zone at the cliff base at about 70 m depth, have largely the same origin. The concentrations of biopolymeric C in the soft sediments of the mesophotic zone without coral colonies were typically low, but the quantity of organic matter in sediments colonized by gold corals were high, reaching values previously reported only for highly productive sediments (Pusceddu et al. 2009). The organic enrichment reported here for coral-colonised sediments was associated with enhanced quality and food availability. In fact, sediments surrounding the gold coral colonies were characterised by significantly higher values of the protein to carbohydrate ratio than in sediments without corals (Figure 6). Sediments close to gold corals display organic matter characteristics similar to those observed in sediments receiving large inputs of N-rich organic matter (Danovaro et al. 1999, Pusceddu et al. 2009).

Sediments surrounding gold corals were characterised by a significantly higher meiofaunal abundance, which was positively correlated with the high quantity organic matter (Fig. 4C). The presence of gold coral colonies was also associated with an increase of the nematodes species richness when compared to the bare sediments (Fig. 4C).

The results of the multivariate regression analysis also revealed that, whilst the abundance of meiofauna was mostly explained by the quantity of sediment organic matter, the biodiversity of the nematode assemblages was related to the quality of organic matter (Table 2). This result points out that the availability of particulate food is a key factor controlling local benthic biodiversity. These results would suggest that the gold coral colonies could influence positively the surrounding

meiofaunal/nematode diversity by enhancing the amount of food potentially available and by diversifying the organic matter quality.

Although most of the mollusc species observed in proximity of the *S. savaglia* are typical of the deep circa-littoral environment, a few species were located at their lowest bathymetric limit or even outside their typical bathymetric range. Among these, the rissoid *Alvania cancellata,* typically encountered at shallow depths (e.g., Giribet & Peñas, 1997) was found here at much deeper depths. This species displays a planktotrophic larval stage which enables the veliger to cover even large distances as reported for the shallow seamounts off Portugal (distant hundreds of kilometres from the mainland), where this species is common (Ávila & Malaquias, 2003; Ávila et al., 2007). The presence of *Alvania cancellata* inside the gold coral forest suggests a possible process of facilitation towards the settlement and growth of this species.

On the other hand, other species typically observed in epi-bathyal sediments (such as the rissoid *Alvania punctura* Montagu 1803, and *Alvania zetlandica* Montagu 1815, and the epitoniid *Epitonium tiberii* (De Boury 1890) reached their shallower limit (Bouchet and Warén 1986; Giribet and Peñas 1997; Gofas 2007) inside the gold coral forest. Among bivalves, the record of *Limopsis minuta* (Philippi 1836) in the thanatocoenosis can be considered another example of shallower occurrence of a species which usually occurs from 300 to more than 15 m depth (Salas, 1996). These findings suggest that this habitat can be considered as a transition zone in which typically deep species are encountered together with shallower counterparts.

Any erect sessile organism with a complex three-dimensional structure, when sufficiently dense, can decrease water movements and enhance finer sediments accumulation, as observed for the *Savalia* colonies within gorgonians' forests. The accumulation of high quantities of sediment organic matter beneath the corals is most likely the result of diminished water current speeds within the gold-coral colonised forest, as also observed inside seagrass meadows (de Boer 2007), in deep cold coral reefs (Kiriakoulakis et al. 2004; Freiwald and Roberts, 2005) or inside other gorgonian forests (Scinto et al. 2009).

Although also the neighbouring gorgonian forests could have a role similar to that of the *Savalia savaglia* colonies, gold corals can be considered here of paramount importance for the surrounding biodiversity patterns. These corals, in fact, show an huge longevity (up to >2700 years) (Roark et al. 2009), and their ecological role, therefore, is likely to have effects on relevantly longer (tens of centuries) temporal scales than those (tens of years) observed for other relatively shorter-lived species such as the gorgonians structuring benthic seascapes in the meso-photic zone.

Conservation issues and conclusions

Seagrass meadows (de Boer 2007), kelp forests (Gaylord et al. 2007), coral reefs (Shashar et al. 1996), mussel and scallop beds (Cerrano et al. 2006), xenophyophore and sponge fields (Gooday et al. 1993; Beaulieu, 2001), typically modify their own habitat increasing the fitness of associated species (Bruno and Bertness 2001). These organisms are defined foundation species (Dayton 1972) or ecosystem engineers (Jones et al. 1994). The presence of foundation species can often reduce water flow velocity as demonstrated for algal canopies (Jackson and Winant 1983) and seagrass meadows (Gambi et al. 1990) and this physical effect can reduce re-suspension (Gacia and Duarte 2001) thus stabilizing the substrate, increasing the fine sediment fraction (Eckman et al. 1981) and the quantity of sediment organic matter (Pusceddu et al. 2007). As a consequence, organisms living in habitats characterised by the presence of these "engineers" can experience a sort of "buffer zone" where environmental modifications occur slower and within narrower ranges with respect to the surrounding ambient. Into a land forest several environmental factors such as light, temperature and humidity are more stable during the day and during the year respect to outside, where wind, sun and rain can rapidly change (Allen et al. 1972). In seagrass or seafan forests or among coral colonies, for example, water movement and particles transport decrease (Nepf and Ghisalberti 2008, Scinto et al, 2009). Such a process of current baffling and sand entrapment has been observed and described also in deep coral banks (Wheeler et al., 2008).

The knowledge on the effects of mesophotic coral forests on ecosystem processes is still

quite limited and information on the role of their deeper counterparts, such as deep-water cold corals, oyster beds and sponge fields, is even poorer (Byers et al. 2006).

Altogether, the results of this study point out that in the mesophotic zone the presence of engineering species as sea fans or the long-living *S. savaglia* can increase surrounding biodiversity and faunal biomass. *S. savaglia* specimens have huge life spans, and ecosystems characterised by the presence of gold corals can enhanced benthic biodiversity on the long term.

The genus *Savalia (=Gerardia)* is commercially exploited as gold coral in the Pacific Ocean (Roark et al. 2006), sold at about 500 dollars/Kg (Grigg 2002). In spite of this, gold corals do not only deserve protection because rare, endemic and endangered by human impacts, but also because they play a key ecological role in the mesophotic zone. These results highlight the need of censusing the presence and distribution of this species in the twilight zone throughout the Mediterranean Sea in order to promote effective measures of protection of this species and the surrounding habitats influenced by them.

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1 Table 1. Results of the two-way ANOVA testing for differences in sedimentary variables between

2 sampling times and types of sediment (i.e. beneath corals vs. soft bottoms). Reported are also the

3 results of the SNK post-hoc test aimed at the quantification of the differences between soft bottom

4 and coral-colonised sediments in the two sampling periods. *** = $p<0.001$; ** = $p<0.01$; * =

5 $p<0.05$; ns = not significant. DF = degrees of freedom; MS = mean square

Variable	Source	DF	MS	F	P	Student-Newman-Kuels December	February
Protein	Sampling time	1	6.571	1.27	ns	-	-
	Type of sediment (time)	2	5.157	35.49	***	Bare < Coral (**)	Bare < Coral (*)
	Residuals	8	0.145				
Carbohydrate	Sampling time	1	2.516	1.69	ns	-	-
	Type of sediment (time)	2	1.488	38.12	***	Bare < Coral (**)	ns
	Residuals	8	0.039				
Lipid	Sampling time	1	1.466	1.10	ns	-	-
	Type of sediment (time)	2	1.331	59.99	***	Bare < Coral (**)	Bare < Coral (**)
	Residuals	8	0.022				
Biopolymeric C	Sampling time	1	6.616	1.81	ns	-	-
	Type of sediment (time)	2	3.657	305.61	***	Bare < Coral (**)	Bare < Coral (**)
	Residuals	8	0.012				
Protein to carbohydrate ratio	Sampling time	1	0.086	0.17	ns	-	-
	Type of sediment (time)	2	0.509	126.07	***	Bare < Coral (**)	Bare < Coral (**)
	Residuals	8	0.004				
Meiofaunal abundance	Sampling time	1	6210.750	1.27	ns	-	-
	Type of sediment (time)	2	4897.875	21.45	***	Bare < Coral (*)	Bare < Coral (**)
	Residuals	8	228.290				
Species richness	Sampling time	1	16.333	0.08	ns	-	-
	Type of sediment (time)	2	212.833	39.91	***	Bare < Coral (**)	Bare < Coral (**)
	Residuals	8	5.333				
Evenness J	Sampling time	1	0.006	1.18	ns	-	-
	Type of sediment (time)	2	0.005	31.19	***	Bare < Coral (**)	ns
	Residuals	8	0.000				
Shannon H'	Sampling time	1	0.008	0.02	ns	-	-
	Type of sediment (time)	2	0.356	25.87	***	Bare < Coral (**)	Bare < Coral (**)
	Residuals	8	0.014				
E_{51}	Sampling time	1	0.333	0.00	ns	-	-
	Type of sediment (time)	2	67.333	12.62	***	Bare < Coral (*)	Bare < Coral (**)
	Residuals	8	5.333				

6

7

8 Table 2. Results of multiple regression analysis of organic compounds on meiofauna abundance.

9 *** = p<0.001; ** = p<0.01; ns = not significant. Prop = proportion of variance explained. SS =
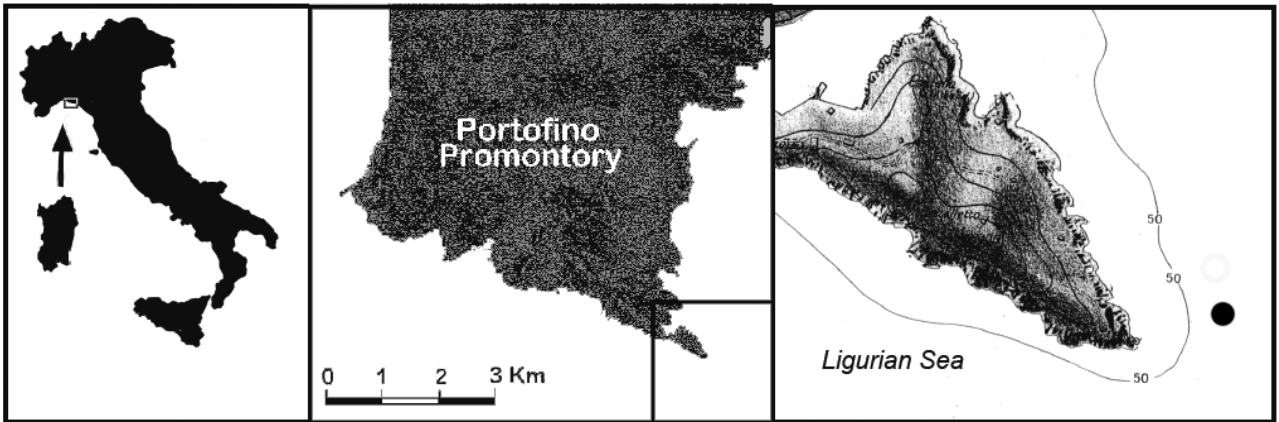
10 sum of squares.

11

Dependent Variable	Independent variable	Conditional (sequential) tests				
		SS	pseudo-F	P	Prop	cumulative
Meiofaunal abundance	Biopolymeric C	12539.6	23.690	***	0.703	0.70
	Protein to carbohydrate ratio	552.9	1.050	ns	0.031	0.73
Species richness	Protein to carbohydrate ratio	757.1	10.687	**	0.517	0.52
	Biopolymeric C	239.8	4.606	ns	0.164	0.68
Evenness J	Biopolymeric C	0.0143	39.8657	**	0.800	0.80
	Protein to carbohydrate ratio	0.0009	3.047	ns	0.051	0.85
Shannon H'	Protein to carbohydrate ratio	0.6027	26.6529	***	0.727	0.73
	Biopolymeric C	0.0013	0.05	ns	0.002	0.73
E_{51}	Protein to carbohydrate ratio	99.7792	12.8107	**	0.562	0.56
	Biopolymeric C	1.8392	0.2177	ns	0.010	0.57

12

13   Figure 1. The study area and the location of the sampling site (black circle)
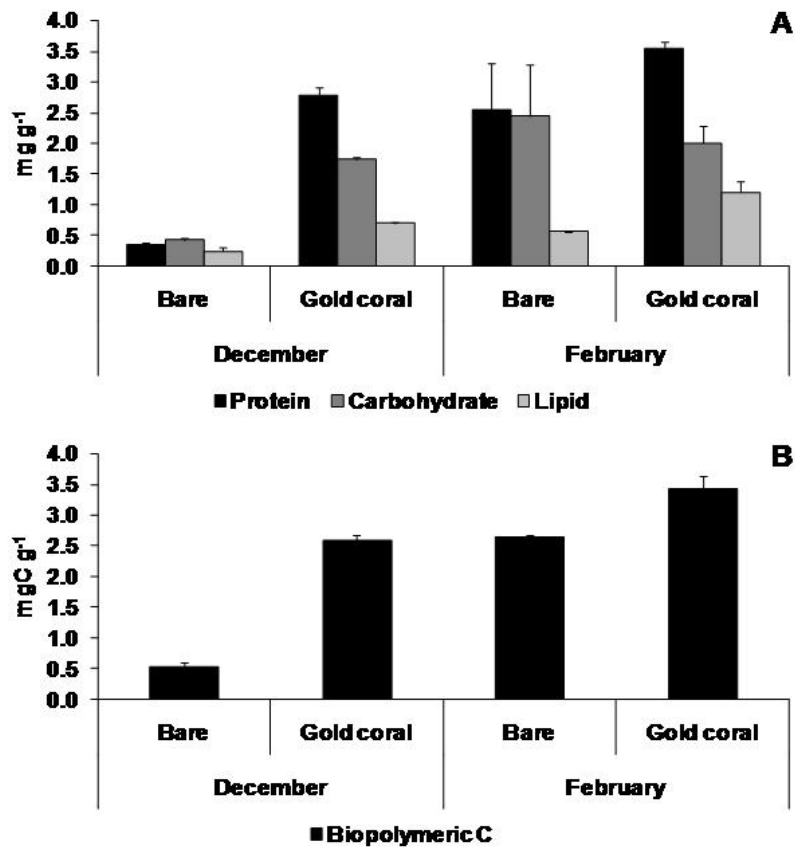
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16   Figure 2. Population structure of *Savalia savaglia* in the studied area
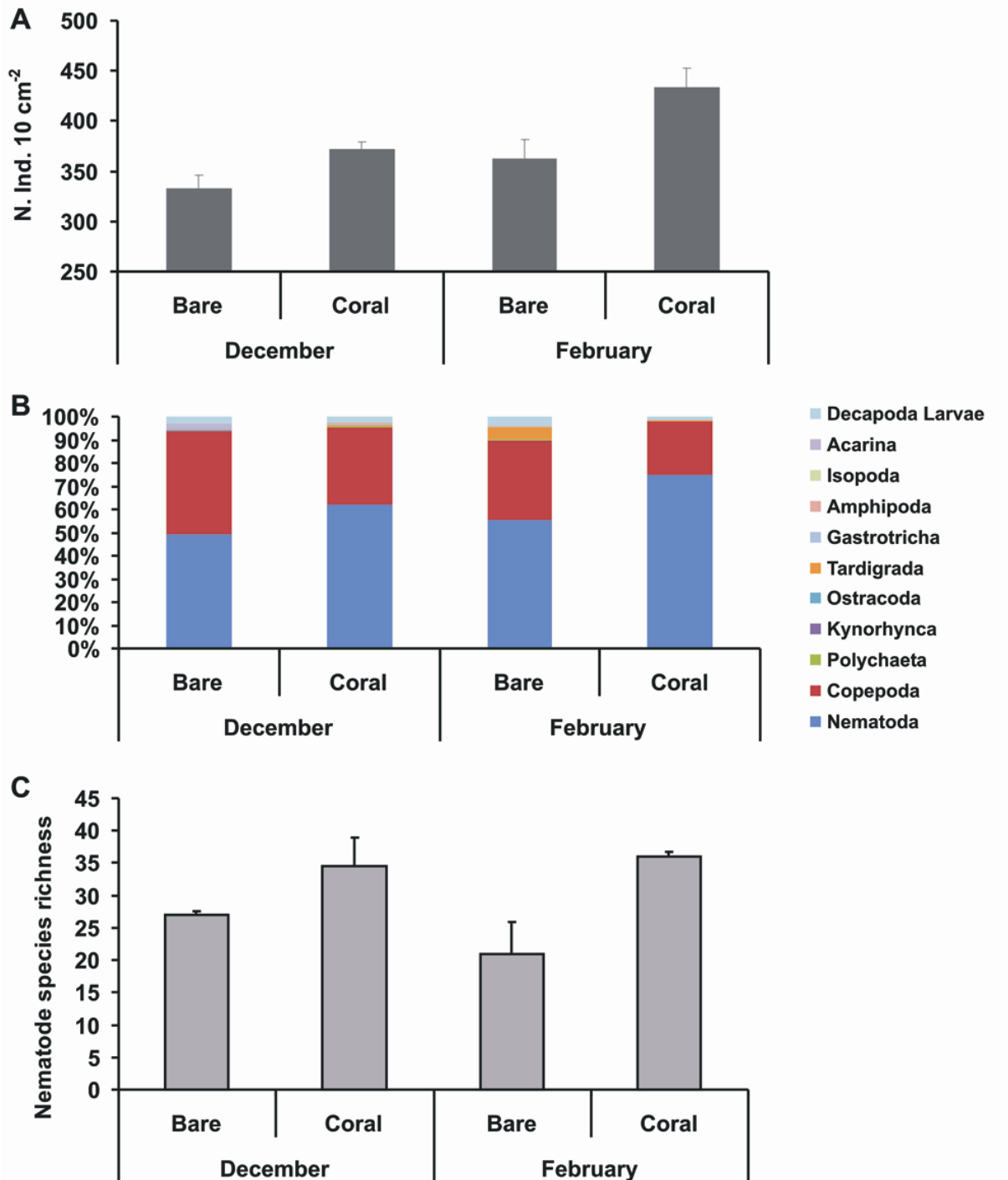
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19   Figure 3. Protein, carbohydrate, lipid (a) and biopolymeric C (b) in soft bottom and gold coral

20   colonised sediments in the two sampling periods.
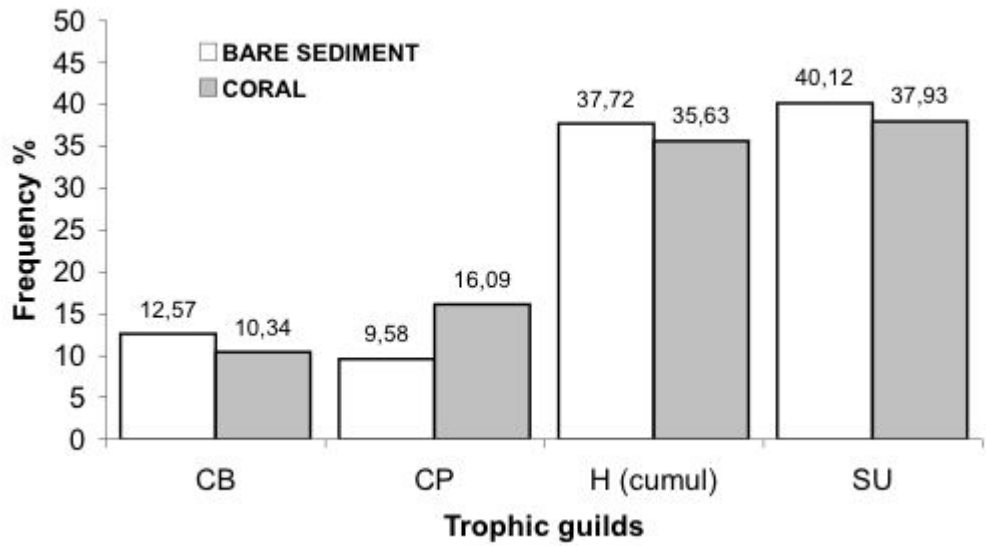
22   Figure 4. Total meiofaunal abundance (a) and community structure (b) and nematode species

23   richness (c) in gold coral and soft bottom sediments in the two sampling periods. Error bars indicate

24   standard deviations of replicate (n = 3) measurements

25

26

27   Figure 5. Trophic guilds from mollusc assembages in tanatocoenoses. CB browsing carnivores, CP

28   predatory carnivorous, H (both microalgivory and herbivores), SU suspension feeders
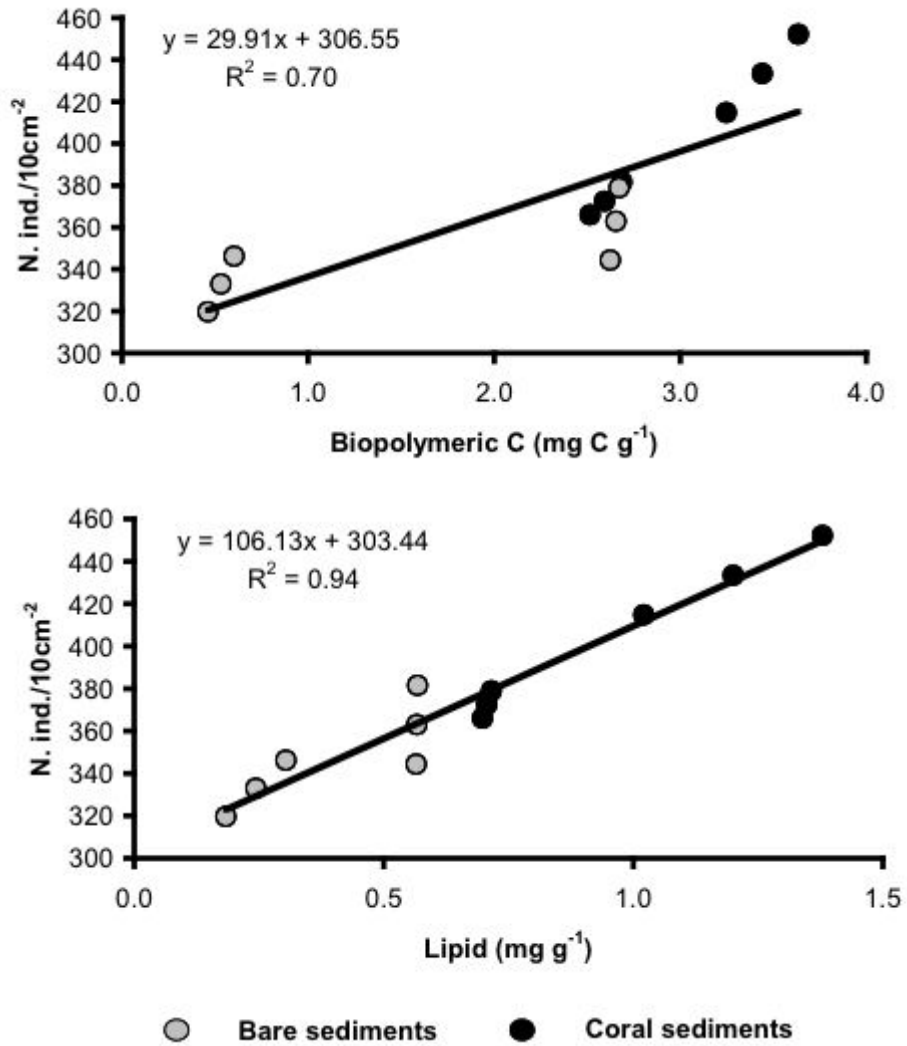
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32   Figure 6. The relationships between biopolymeric C and lipid sediment contents and the abundance

33   of meiofauna in the sediments of the Portofino Promontory

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35   ○ **Bare sediments**   ● **Coral sediments**

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