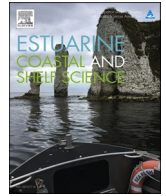




Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: <http://www.elsevier.com/locate/ecss>

Ecology, distribution and demography of erect bryozoans in Mediterranean coralligenous reefs

Edoardo Casoli^{a,*}, Luigi Piazzì^b, Luisa Nicoletti^c, Giovanna Jona-Lasinio^d, Enrico Cecchi^e, Gianluca Mancini^a, Andrea Belluscio^a, Giandomenico Ardizzone^a

^a Department of Environmental Biology, Sapienza University of Rome, Piazzale Aldo Moro, 5, 00185, Rome, Italy

^b Department of Chemistry and Pharmacy, University of Sassari, Via Piandanna 4, 07100, Sassari, Italy

^c Institute for Environmental Protection and Research (ISPRA), Via Vitaliano Brancati, 48, 00144, Rome, Italy

^d Department of Statistics, Sapienza University of Rome, Piazzale Aldo Moro, 5, 00185, Rome, Italy

^e Regional Agency of Tuscany for Environmental Protection (ARPAT), Via Marradi 114, 57126, Livorno, Italy

ABSTRACT

Coralligenous reefs are considered as one of the most important benthic ecosystems in the Mediterranean Sea in terms of biodiversity, ecosystem functioning, and aesthetic value. Bryozoans deserve special attention within the coralligenous framework fauna: they are among the most common animals, showing high diversity values and playing different functional roles. Distribution, spatial variability, and demographic features of five erect bryozoan taxa *Adeonella* sp., *Myriapora truncata*, *Pentapora fascialis*, *Reteporella* sp., and *Smittina cervicornis* were studied in the central Tyrrhenian Sea. Abundance, size, and relationship with other taxa/morphological groups of benthic organisms were studied in coralligenous reefs between 35 and 40 m depth. High density of colonies was reported especially in association to gorgonians and algae dominated assemblages. Size distributions of the five bryozoans were characterized by small colonies; only two species (*P. fascialis* and *S. cervicornis*) showed colonies larger than 50 cm². Structure of coralligenous assemblages and disturbances outlined different ecological requirements of the five studied taxa. Results provide baseline information for monitoring trajectories of change of these organisms in the coralligenous ecosystem. To date, this work represents the first study exploring ecology and distribution patterns of common erect bryozoans in the Mediterranean Sea.

1. Introduction

The comprehension of the ecological features, requirements, and distribution patterns of marine species represents one of the main goals for marine biologists and ecologists in the era of global environmental changes. The increase in frequency and impact of anthropogenic disturbances, as well as climate modifications and anomalies, threatens both composition and functions of marine communities (Harley et al., 2006; Lejeune et al., 2009). Thus, knowledge of distribution and demographic characteristics of key species is the first step for implementing effective management and conservation measures. In addition, demographic data represent valuable information to use as a baseline for assessing disturbances and trajectories of changes. This is particularly relevant for those ecosystems that show high variability, such as coralligenous reefs, an endemic Mediterranean bioconstruction with long-lived organisms that create multi-layered and structurally complex assemblages (Ingrosso et al., 2018). Coralligenous concretions are carbonate substrata, primarily produced by the accumulation of encrusting algal thalli growing at low light levels and secondarily by sessile animal

taxa; this ecosystem characterizes Mediterranean seabeds between 20 and 120 m depth (Ballesteros, 2006). It represents one of the most important marine habitats in terms of biodiversity and recreational, commercial, cultural, and aesthetic values to society (Tribot et al., 2016; Tonin, 2018; Thierry De Ville d'Avray et al., 2019). Commercial exploitation (i.e. fishing and tourism) coupled with the slow dynamics and longevity of the builder organisms make this bioconstruction one of the most vulnerable and exposed to human impacts (Teixidó et al., 2011; Piazzì et al., 2012). Nevertheless, coralligenous reefs have been classified by the European Red List of marine habitats as “data deficient” (Gubbay et al., 2016) and thorough investigations and focused monitoring plans are urgently needed.

Besides being the realm of encrusting red algae, coralligenous reefs support highly diversified communities of suspension feeders; among them, bryozoans are one of the main components of the sessile macrozoobenthos. The richest bryozoan diversity in the Mediterranean Sea is found in coralligenous habitat (219 sp.) and in marine caves (220 sp.) (Rosso and Di Martino, 2016; Rosso et al., 2019). Bryozoans play two important roles within the bioconstruction; as primary consumers, they

* Corresponding author.

E-mail address: edoardo.casoli@uniroma1.it (E. Casoli).

<https://doi.org/10.1016/j.ecss.2019.106573>

Received 2 July 2019; Received in revised form 4 November 2019; Accepted 30 December 2019

Available online 2 January 2020

0272-7714/© 2020 Elsevier Ltd. All rights reserved.

transfer particulate organic matter from the water column to benthic habitats (Gili and Coma, 1998; Belloni et al., 2019) and thus contribute to the growth of the reefs depositing carbonate (Hong, 1982; Ballesteros, 2006). Even though they have been mainly described as secondary builders, bryozoans are also able to create mono- or multi-specific bioconstructions in tropic and temperate seas (Cocito, 2004; Wood et al., 2012; Lombardi et al., 2014; Rosso et al., 2019). Several “bryo-constructions”, some of which are morphologically different, have been reported in the Mediterranean Sea: *Pentapora fascialis* (Pallas, 1766), *Cellaria salicornioides* Lamouroux, 1816, *Schizoporella errata* (Waters, 1878) and *Turbicellepora magnicostata* (Barroso, 1919), *Schizomavella* (*Schizomavella*) *cornuta* (Heller, 1867) formations, as well as multi-specific nodular concretions between semi-dark and dark cave sectors (Harmelin et al., 1985; Cocito et al., 2000; McKinney and Jaklin, 2000; Cocito and Ferdeghini, 2001; Ferdeghini et al., 2001; Nicoletti et al., 2007; Cocito et al., 2009).

Among the most common Cheilostomate bryozoans found on coralligenous reefs, *Adeonella* sp. Busk, 1884, *Myriapora truncata* (Pallas, 1766), *P. fascialis*, *Reteporella* sp. Busk, 1884 and *Smittina cervicornis* (Pallas, 1766) increase the three-dimensionality of the bioconstruction through their erect colonies (Garrabou et al., 2002; Novosel et al., 2004; Casas-Güell et al., 2015). As for growth form, *Adeonella* sp., *M. truncata*, *P. fascialis*, and *S. cervicornis* are classified as erect bilaminate colonies, composed of multiserial bilaminate branches. Conversely, *Reteporella* sp. is a unilaminate erect bryozoan, composed of closely spaced and narrow branches usually arrayed in well-developed flat or curved sheets (McKinney and Jackson, 1989). These bryozoans have fragile structures and are recognized as sensitive to both water quality and human activities (Harmelin and Capo, 2002; Rosso et al., 2010; Chimenz et al., 2014; Casoli et al., 2017a, b; Betti et al., 2019; Pagès-Escolà et al., 2020). Due to their role as bioindicators, erect bryozoans have been considered in the formulation of all the indices to assess and monitor the ecological quality, the integrity and the health and conservation status of coralligenous habitats (Deter et al., 2012; Gatti et al., 2015; Montefalcone et al., 2017; Piazzini et al., 2017a; Sartoretto et al., 2017; Ferrigno et al.,

2018a). In particular, *M. truncata* and *P. fascialis* have been also studied as model organisms to test the effect of both ocean acidification and temperature on bryozoans (Lombardi et al., 2008, 2006; 2011b, 2011a; Pagès-Escolà et al., 2018). Despite their importance, the distribution patterns, as well as the ecology and demographic processes, of erect bryozoans on coralligenous reefs have been poorly studied. Such information plays a pivotal role in the effective application of these species as bioindicators.

This study aims to provide quantitative data on the presence of the five aforementioned bryozoans on coralligenous reefs, to assess their population structures, and to explore their ecological requirements and the relationships with other sessile benthic organisms in the central Mediterranean Sea. Furthermore, human disturbances influencing the distribution and size of the taxa are considered.

2. Materials and methods

2.1. Study sites, sampling design and data collection

Fourteen localities (Fig. 1), tens to hundreds of kilometers apart from each other, were investigated to assess the spatial and ecological patterns of five erect bryozoan taxa (*Adeonella* sp., *M. truncata*, *P. fascialis*, *Reteporella* sp. and *S. cervicornis*) (Fig. 2). Within each locality three or six areas of 4 m² surface (tens of meters apart) were sampled (Table 1). In each area three replicate samples consisting of three contiguous photographs of 0.2 m² were collected. Sampling was carried out on vertical walls characterized by coralligenous concretions at a depth range of 35–40 m (Fig. 3).

Photographic sampling was carried out by scientific divers using a digital camera arranged in a PVC frame (50 × 40 cm) in order to minimize parallax errors. The camera was equipped with two electronic strobes and diffusers. Photography enabled robust identification of conspicuous erect species, based on known morphological colony features, although it also gave potential for underestimation of bryozoan colonies in cryptic micro-habitats. Despite its limitations, this non-

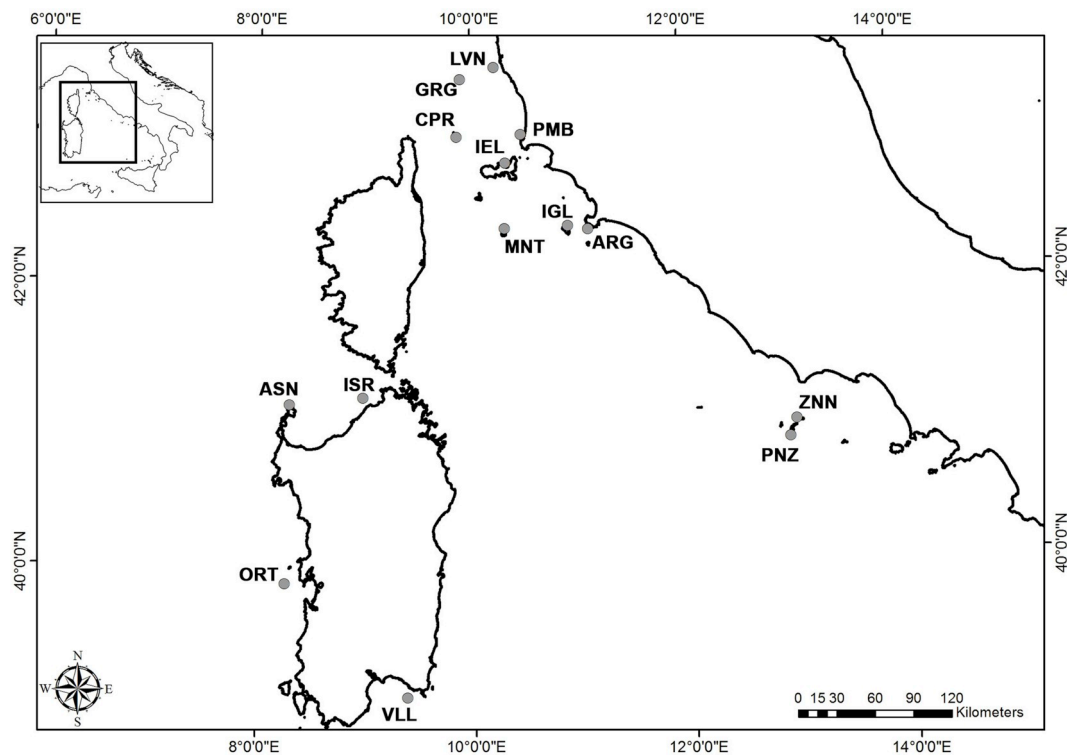


Fig. 1. Map showing the position of the thirteen localities where samplings were carried out. ARG: Argentario; ASN: Asinara; CPR: Capraia; GRG: Gorgona; IGL: Isola del Giglio; IEL: Isola d'Elba; ISR: Isola Rossa; LVN: Livorno; MNT: Montecristo; ORT: Oristano; PMB: Piombino; PNZ: Ponza; VLL: Villasimius; ZNN: Zannone.

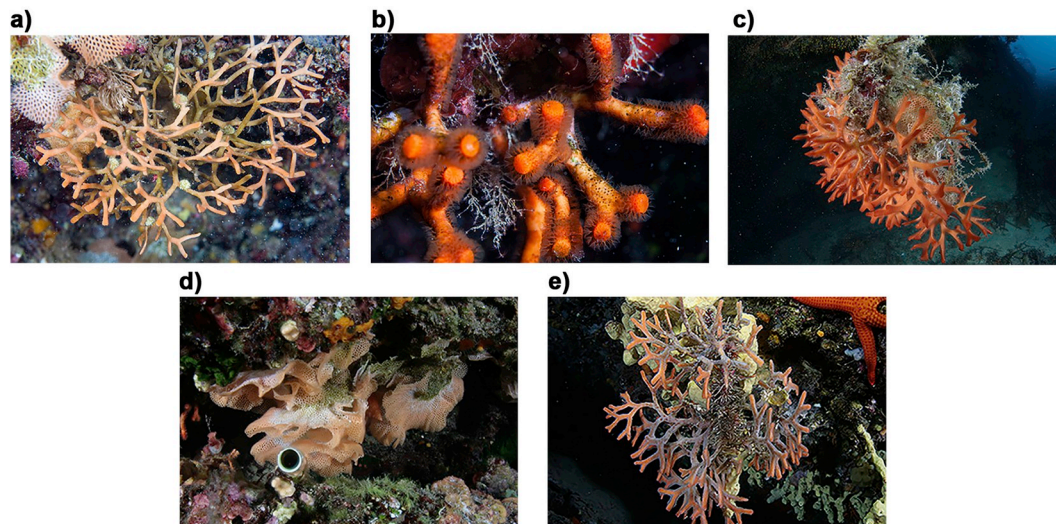


Fig. 2. Colonies of the five studied bryozoans: a) *Adeonella* sp.; b) *Myriapora truncata*; c) *Pentapora fascialis*; d) *Reteporella* sp.; e) *Smittina cervicornis*.

Table 1

Features of the sampling sites. Locality, ID refers to the locality identification code. Coordinates are reported in decimal degree; Protection indicates the level of protection of the studied sites; Disturbance takes into account proximity to commercial harbors and/or urbanized areas, levels of eutrophication, sedimentation rates, and mechanical disturbance by fishing activities.

Locality	ID	N° of areas	Longitude	Latitude	Protection	Disturbance	Type of Disturbance
Villasimius	VLL	3	9.3820	39.0741	None	Low	Diving
Oristano	ORT	3	8.2768	39.8833	None	Low	Diving
Ponza	PNZ	3	12.9405	40.8578	None	Medium	Diving, Fishing
Zannone	ZNN	3	13.0221	40.9618	None	Low	Diving
Asinara	ASN	3	8.2911	41.1340	MPA	Low	–
Isola Rossa	ISR	3	8.9587	41.1867	None	Low	Diving
Montecristo	MNT	6	10.3513	42.3086	MPA	Low	–
Isola del Giglio	IGL	6	10.9300	42.3670	None	Low	–
Argentario	ARG	6	11.0561	42.4053	None	Medium	Diving, Fishing
Isola d'Elba	IEL	6	10.3321	42.8299	None	Medium	Diving, Fishing
Capraia	CPR	6	9.8683	43.0144	MPA	Low	–
Piombino	PMB	6	10.4839	43.0289	None	High	Diving, Fishing, Urbanisation
Livorno	LVN	6	10.2893	43.4211	None	High	Diving, Fishing, Urbanisation
Gorgona	GRG	6	9.9107	43.4289	MPA	Low	–

destructive approach represented a good compromise for habitat and species conservation (Gerovasileiou et al., 2017; Dimarchopoulou et al., 2018) which was important due to the location of four study sites within Marine Protected Areas.

A total of 540 high resolution photographs of coralligenous reefs were analyzed through ImageJ analysis software (Schneider et al., 2012). From each picture, presence of the five bryozoan taxa, abundance (number of colonies/m²), colony width (i.e., the length of the longer colony's axis parallel to the substrate measured in cm), and colony coverage (i.e., the surface area of the substrate covered as a projection of the specimen measured in cm²) were estimated. Colonies were visually classified in three classes: Small, Medium, and Large according to the maximum height of the tallest colony of each species. Height classes were assigned according to the following size ranges: Small <5 cm, 5 cm < Medium <10 cm, Large >10 cm.

In addition, coralligenous assemblages were assessed with regards to the percentage cover of the main conspicuous sessile taxa and/or morphological groups (as Supplementary Materials, Table S1), following the classification given by Piazzini et al. (2017a,b). As for human pressure, three disturbance categories were here proposed (Low, Medium and High), taking into account proximity to commercial harbors and/or urbanized areas, levels of eutrophication, sedimentation rates, and mechanical disturbance by fishing activities (Montefalcone et al., 2017; Piazzini et al., 2017a; Ardizzone et al., 2019). Both composition and human pressure were considered to test their influence on

bryozoans composition and coverage.

2.2. Statistical analyses

Spatial changes in abundance of the five bryozoan species were analyzed using Linear Mixed Effect Models (MEMs). The dependent variable (number of colonies/m²) did not respect the assumptions of normality and heteroscedasticity even after log-transformation. The locality with nested area was set as random effect to solve the issue of heteroscedasticity. Hence, abundance was tested in relation to two random nested factors: Localities (13 levels) and Areas (from 3 to 6 levels). Then, to test the significance of the models, analysis of variance (ANOVA) was run on the output of the aforementioned MEMs.

The total abundance was used to test if the bryozoan species occurred together and in association with other sessile organisms. Unlike the single taxon abundance, the log-transformed (log (x+1)) total number of bryozoan colonies/m² allowed the use of a linear model to analyze its changes in relation to coralligenous assemblages and geographical location. Normality and homoscedasticity were tested through the Cochran Q and Bartlett tests, respectively. The independent variables were chosen using Akaike's criteria (AIC), an entropy-based measure of goodness of fit of statistical models; the model with the lowest AIC value was chosen (Akaike, 1974).

To investigate the relationship between coverage and width in colonies of different sizes, a linear model was fitted for each of the five

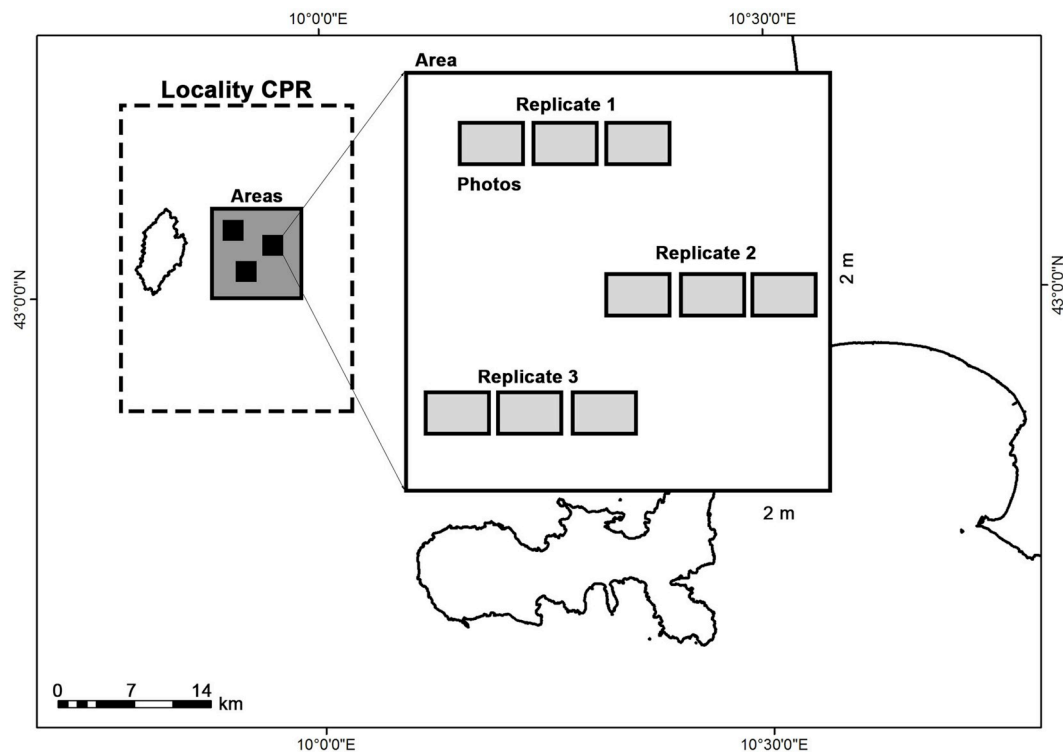


Fig. 3. Schematic diagram of the nested sampling design showing Capraia locality (ID: CPR), Areas and Replicates constituted of three contiguous Photos.

species. Both coverage and width data were log-transformed to respect the linear model assumptions.

The relationships between bryozoans mean coverage values and the composition of coralligenous assemblages were investigated using a Canonical Correspondence Analysis (CCA). The explanatory variables were the same as highlighted by Akaike's measure for the linear model. For MEMs, ANOVA and the linear models, a significance level of 0.05 (p -value < 0.05) was chosen. All the statistical analyses were performed in the R platform (version 3.5.2; R Development Core Team, 2012).

3. Results

3.1. Abundance and spatial distribution

A total of 3441 colonies were counted and measured; the five taxa showed different abundance patterns among the fourteen investigated localities (Fig. 4). *M. truncata* and *Reteporella* sp. were well represented in all localities: for both taxa higher abundances were reported at VLL, with maximum densities of 91 and 108 colonies/m², respectively. *Adeonella* sp., *P. fascialis* and *S. cervicornis* showed a scattered distribution and lower abundances when compared to the aforementioned taxa. Their maximum values were 16, 32 and 28 colonies/m², respectively. In particular, these three bryozoans were well represented at IGL and ASN. *Adeonella* sp. and *S. cervicornis* mostly differed due to the absence of the latter at CPR and IEL, although absence was registered in several replicate samples collected in the other localities as well. *P. fascialis* was absent at CPR, GRG, IEL, VLL and ISR, and occasionally found at LVN, ORT, PMB and ZNN.

All the intercepts of MEMs were deemed significant through the ANOVA; it detected significant differences in abundance in relation to the combination of locality and areas for *M. truncata*, *P. fascialis*, *Reteporella* sp. By contrast, both *Adeonella* sp. and *S. cervicornis* did not show significant variations (Table 2).

The samples characterized by higher abundances were those with all the taxa present (Fig. 5). The linear model reported the interaction between the number of colonies/m² and bryozoans richness as significant

(Table 3).

The total number of erect bryozoan colonies/m² significantly increased when the percentage cover of the following taxa and morphological groups was higher: *Peyssonellia* spp. Decaisne, 1841, *Pseudochlorodesmis furcellata* (Zanardini) Børgesen, 1925, *Flabellia petiolata* (Turra) Nizamuddin, 1987, Encrusting bryozoans, Massive sponges, the gorgonians *Paramuricea clavata* (Risso, 1826) and *Eunicella cavolini* (Koch, 1887). The total abundance also increased according to *Corallium rubrum* (Linnaeus, 1758) and Erect ascidians percentage cover, although these interactions were not reported as significant. From a spatial point of view, number of erect bryozoan colonies was inversely correlated to both latitude and longitude: this meant that total abundance increased from north to south and from east to west. Localities in the south of Tuscany, Latium and Sardinia were characterized by higher total abundances of erect bryozoans.

3.2. Colony size and population structure

Width to coverage ratio highlighted differences in colony morphology and sizes of the studied taxa (Fig. 6). Similar trends occurred for the erect bilaminar *Adeonella* sp., *M. truncata*, *P. fascialis* and *S. cervicornis*, although the latter two species reached higher width to coverage values. *Reteporella* sp. colonies showed a different pattern for width to coverage ratio. For all the bryozoans the most frequent observations were small colonies of width <5 cm and coverage <10 cm². The intercepts of the linear model fitted with coverage and width data were significant. Coverage increased with width, although magnitude differed according to taxa (Table 4).

Coverage values were used to obtain the size frequency distribution and describe the population structure of the five bryozoans (Fig. 7); log transformation was used for visual representation. A significant positive skewness clearly highlighted a prevalence of smaller colonies in all the taxa, belonging to the Small height class. *Adeonella* sp., *M. truncata* and *Reteporella* sp. showed unimodal distribution, with most frequent coverage values included in the range 0–10 cm². Colonies larger than 50 cm² were rarely found. On the other hand, *P. fascialis* and *S. cervicornis*

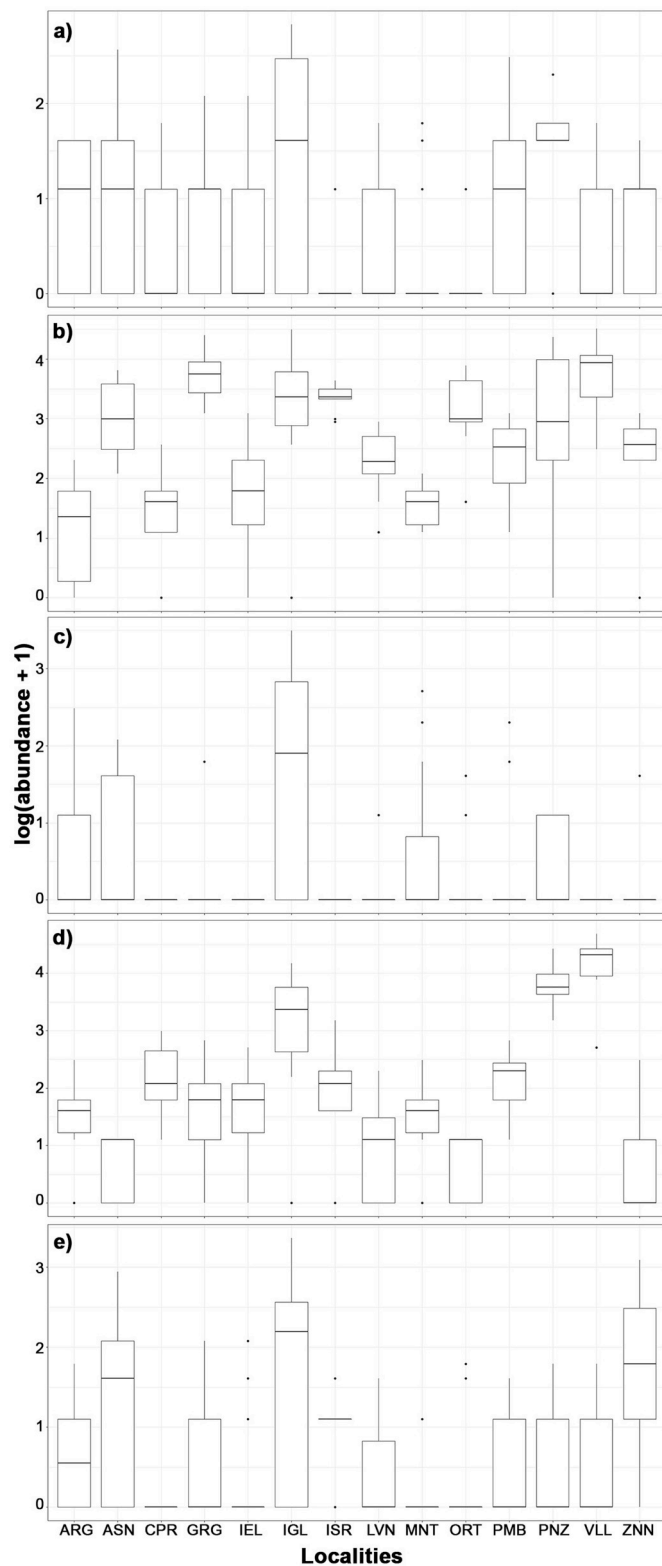


Fig. 4. Abundance (colonies/m²) per bryozoan taxa: a) *Adeonella* sp.; b) *Myriapora truncata*; c) *Pentapora fascialis*; d) *Reteporella* sp.; e) *Smittna cervicornis*. Data have been log-transformed for visual representation.

showed multimodal distribution with all the three eight classes well represented. In the former case three modes can be recognized: 5–10 cm², 30–40 cm² and 140–150 cm². The two main modes of *S. cervicornis* were in the ranges 5–10 cm² and 25–35 cm².

Table 2

Summary of ANOVA results performed on the MEMs on the five bryozoans taxa abundance.

Source of variation	num DF	den DF	F	P
<i>Adeonella</i> sp.				
intercept	1	119	22,711	<0.001
Locality*Area	65	119	1294	0.112
<i>Myriapora truncata</i>				
Intercept	1	119	3,26,754	<0.001
Locality*Area	65	119	2073	<0.001
<i>Pentapora fascialis</i>				
intercept	1	119	7521	0.007
Locality*Area	65	119	1668	0.008
<i>Reteporella</i> sp.				
intercept	1	119	1,79,245	<0.001
Locality*Area	65	119	2108	<0.001
<i>Smittna cervicornis</i>				
intercept	1	119	21,298	<0.001
Locality*Area	65	119	1330	0.089

3.3. Relationships with benthic assemblages and disturbances

The Canonical Correspondence Analysis (CCA) explained 59.7% of the total variance (40.0% axis 1 and 19.7% axis 2); the combination of the taxa/morphological groups structuring the coralligenous assemblages and the disturbances categories influenced size and composition of the erect bryozoans at the studied sites (Fig. 8). *P. fascialis* was associated with *Peyssonnelia* sp., *P. furcellata*, *P. clavata* and *E. cavolini*. Conversely, higher mean coverage values of *Reteporella* sp. were reported in sites with the green algae *F. petiolata*. Higher mean coverage of *M. truncata* was not related to any of the groups constituting the coralligenous assemblage. *Adeonella* sp. and *S. cervicornis* were both diffused in the fourth quadrant. The former was associated to the red coral *C. rubrum*, whereas the latter was related to Encrusting bryozoans and Massive sponges. As for disturbance categories, higher mean coverage of *M. truncata* was found in sites with medium and high disturbance levels, whereas *Reteporella* sp. characterized medium disturbance levels. On the other hand, *Adeonella* sp., *P. fascialis* and *S. cervicornis* colonies were associated with sites of low disturbance. From a spatial point of view, *Reteporella* sp. was the only taxon positively linked to both latitude and longitude, which characterized axis 2. The other taxa displayed higher mean coverage in southern and western samples.

4. Discussion

The present study provides pivotal information on the spatial distribution patterns, ecology, and population structure of erect bryozoans in the Mediterranean coralligenous ecosystem. The definition of the ecological and demographic features of these taxa represents a baseline knowledge, especially in the light of global change and sensitivity to stress and human disturbances that have been reported for these organisms (Montefalcone et al., 2017; Pagès-Escolà et al., 2018).

Extremely high values were reported for colony abundances, although there were differences according to taxa. *M. truncata* and *Reteporella* sp. are the more ubiquitous bryozoans, occurring in all the replicates. The former showed a higher number of colonies/m² than reported for coralligenous reefs along the coasts of Spain (Nuez-Hernández et al., 2014). Abundance of *Reteporella* sp. is comparable to that reported from healthy *Posidonia oceanica* (L.) Delile, 1813 meadows (Deudero et al., 2009), whereas no similar data are available for coralligenous reefs. The scattered distribution of the species *Adeonella* sp., *P. fascialis* and *S. cervicornis* is in accordance to Harmelin (2017a), even though large scale photographic investigations were carried out in the present study. *P. fascialis* showed higher abundance when compared to similar studies carried out with visual census (Sala et al., 1996; Cocito and Ferdeghini, 2001; Lombardi et al., 2008; Harmelin, 2017b); in the

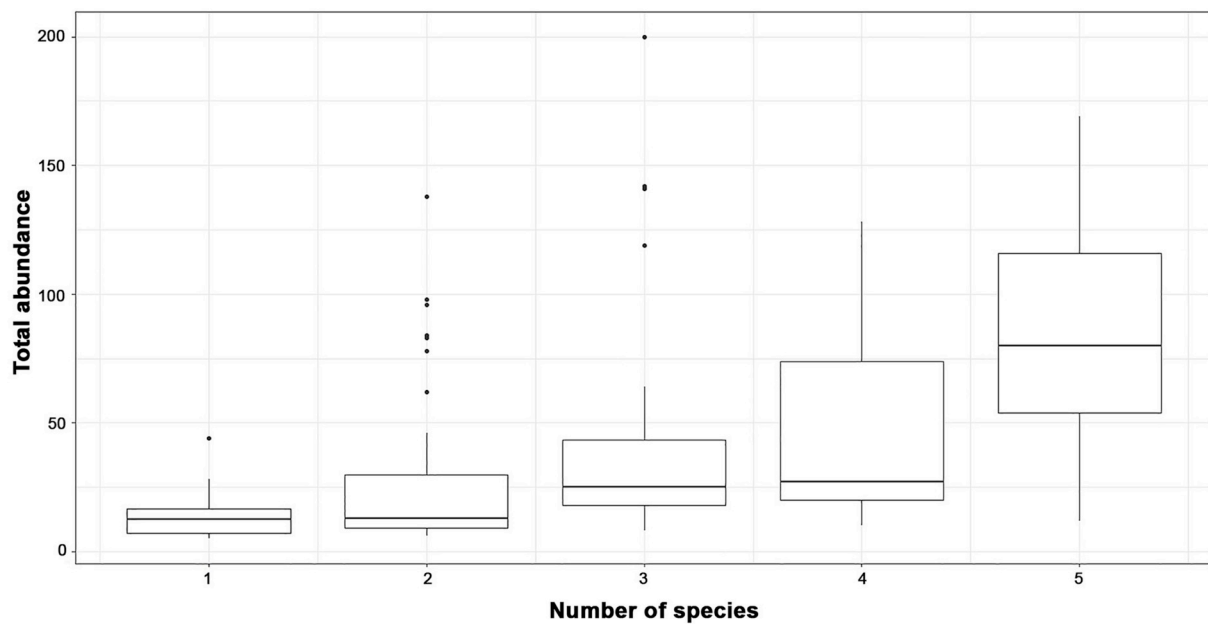


Fig. 5. Total abundance in relation to number of erect bryozoans taxa.

Table 3

Output of the linear model fitted to the total abundance of erect bryozoans. Significant values are highlighted in bold.

Coefficients	Estimates	Std. Errors	t-value	P-value
Intercept	7481	1574	4753	<0.001
Number of erect bryozoan species	0.298	0.038	7652	<0.001
<i>Peyssonnelia</i> spp.	0.011	0.001	6338	<0.001
<i>Pseudochlorodesmis furcellata</i>	0.088	0.016	5491	<0.001
<i>Flabellia petiolata</i>	0.010	0.004	2265	0.024
Encrusting bryozoans	0.143	0.056	2562	0.011
Massive sponges	0.070	0.012	5652	<0.001
<i>Paramuricea clavata</i>	0.031	0.009	3115	0.002
<i>Eunicella cavolini</i>	0.087	0.023	3735	<0.001
<i>Corallium rubrum</i>	0.042	0.028	1496	0.136
Erect ascidians	0.736	0.523	1407	0.161
Longitude	-0.114	0.044	-2583	0.010
Latitude	-0.104	0.038	-2724	0.007

Residual standard errors: 0.495 on 185 DF.

Multiple R squared: 0.656, Adjusted R squared: 0.634.

F-statistic: 29.43 on 12 and 185 DF, P-value: < 0.001.

cases of *Adeonella* sp. and *S. cervicornis*, no quantitative data are available for further comparisons. The results are consistent with previous studies in the western Mediterranean Sea, reporting erect bryozoans as one of the animal groups with highest coverage in coralligenous assemblages (Garrabou et al., 2002; Kipson et al., 2011; Casas-Güell et al., 2015; Doxa et al., 2016; Ferrigno et al., 2018b). *M. truncata*, *P. fascialis* and *S. cervicornis* have been reported to characterize the upper (between 35 and 40 m depth) coralligenous outcrops in the Southern Adriatic Sea (Corriero et al., 2019; Piazzini et al., 2019). On the contrary, erect bryozoans are lacking in the Northern Adriatic outcrops (Falace et al., 2015). Further studies are needed in order to assess and understand the variability of the structure of coralligenous assemblages over different basins of Mediterranean Sea.

Variability of abundance between areas was found for three of the five studied taxa (*M. truncata*, *P. fascialis* and *Reteporella* sp.). This pattern commonly characterizes coralligenous assemblages, where the highest variability was reported at the smallest spatial scale investigated in different regions of Mediterranean Sea (Piazzini et al., 2004; Ponti et al., 2011; Casas-Güell et al., 2015). As for other erect filter feeders, such as gorgonians (Linares et al., 2008; Sini et al., 2015), this variability can be

explained more by biological factors than physico-chemical conditions. The presence of other taxonomic groups (as underlined by linear model in Table 3) and relative interspecific interactions can influence the bryozoans reproduction, settlement, and survival success. Gorgonians (*E. cavolini* and *P. clavata*) are indicators of strong water flow, contributing to habitat heterogeneity and diversity, and enhancing associated fauna (Cerrano et al., 2010; Ponti et al., 2018). Morphology and size of gorgonians, as well as their long lifespan, contribute to create stable and long-lasting micro-habitats highly advantageous for both epizoans and bryozoan colonies settled on the basal layer of the bioconstruction (Lombardi et al., 2008; Montero-Serra et al., 2018). In algae dominated assemblages (*Peyssonnelia* sp., *P. furcellata* and *F. petiolata*) there is a high abundance of epiphytic encrusting and erect bryozoans (Hong, 1980; Harmelin, 2017a). A similar case has been reported for serpulid worms (Casoli et al., 2016). It is likely that erect bryozoans found in these assemblages benefit from both water flows and the absence of larger filter feeders (Casoli et al., 2017b). Substrate has a pivotal role influencing bryozoan settlement and growth (Amini et al., 2004): the majority of cheilostomate bryozoan larvae have the ability to select suitable substrate during the settlement phase (Harmelin, 1997; Deudero et al., 2009). Coralligenous reefs provide favorable conditions for the settlement of bryozoans due to the presence of permanent hard substrata, huge range of microhabitats, shelter, and availability of both oxygen and food (Harmelin, 1986, 2017a.; Novosel et al., 2004; Rosso and Di Martino, 2016). In particular, water movement and therefore food supply can support the co-occurrence of the five studied taxa, as well as extremely high abundance values (up to 200 colonies/m²). It is likely that shifts in some ecological aspects, as suggested by Pagès-Escolà et al. (2018) for thermal tolerance, can occur in order to reduce competition.

Width to coverage ratio reflects differences between the erect bilaminar forms (*Adeonella* sp., *M. truncata*, *P. fascialis* and *S. cervicornis*) and erect unilaminar colonies (*Reteporella* sp.). The erect bilaminar forms describe an exponential trend which increase the surface area of colonies reducing overlap between branches. Similar patterns were reported when comparing surface area with growth stage or mean path length (McKinney and Jackson, 1989). On the contrary, *Reteporella* sp. colonies appear as planar fans with folds, that increase along width axis rather than with surface area (coverage). This pattern can be linked to the plasticity of the colonies that often settle in crevices or in narrow spaces: an adaptation to spatial constraint. Plasticity in colony shape has

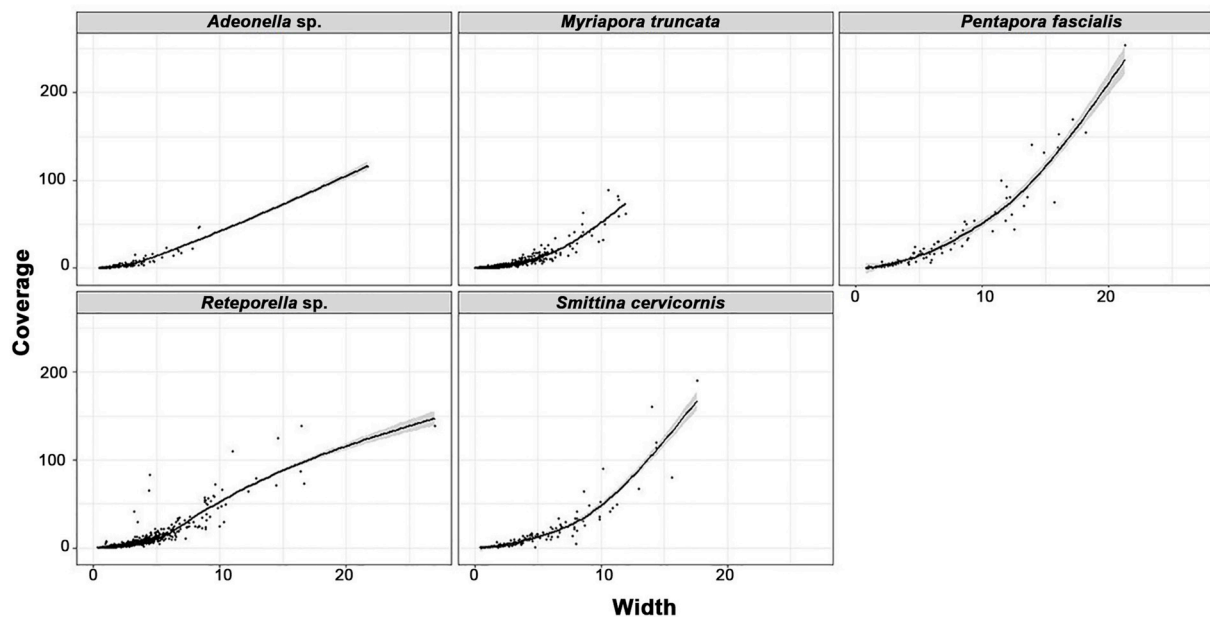


Fig. 6. Best line fits and confidence intervals describing the width to coverage ratio for each studied taxa.

Table 4

Output of the linear models for each of the five studied taxa fitted on coverage and width data. Significant values are highlighted in bold.

Coefficients	Estimates	Std. Errors	t-value	P-value
Intercept (<i>Adeonella</i> sp.)	- 0.612	0.058	-10,430	<0.001
Width	1717	0.049	34.40	<0.001
Intercept (<i>Myriapora truncata</i>)	- 0.379	0.011	- 34.23	<0.001
Width	1497	0.012	1,21,690	<0.001
Intercept (<i>Pentapora fascialis</i>)	- 0.965	0.081	- 11.89	<0.001
Width	2032	0.044	45.61	<0.001
Intercept (<i>Reteporella</i> sp.)	0.834	0.022	- 36.35	<0.001
Width	1872	0.017	105.68	<0.001
Intercept (<i>Smittina cervicornis</i>)	- 0.825	0.069	- 11.90	<0.001
Width	1902	0.044	42.60	<0.001

Residual standard errors: 0.274 on 171 DF.

Multiple R squared: 0.873, Adjusted R squared: 0.873.

F-statistic: 1184 on 1 and 171 DF, P-value: < 0.001.

Residual standard errors: 0.243 on 1819 DF.

Multiple R squared: 0.890, Adjusted R squared: 0.890.

F-statistic: <0.001 on 1 and 1819 DF, P-value: < 0.001.

Residual standard errors: 0.293 on 110 DF.

Multiple R squared: 0.949, Adjusted R squared: 0.949.

F-statistic: 2080 on 1 and 1110 DF, P-value: < 0.001.

Residual standard errors: 0.265 on 1154 DF.

Multiple R squared: 0.906, Adjusted R squared: 0.906.

F-statistic: <0.001 on 1 and 1154 DF, P-value: < 0.001.

been reported for other species of the Phidoloporidae family, such as *Schizoretopora hassi* (Harmelin et al., 2007). This allows *Reteporella* sp. to settle and use different microhabitats compared to other erect species. Furthermore, coverage can be interpreted as a proxy of width; linear models offer a mathematical relationship that can be applied in further studies.

As for demographic features, the predominance of smaller size colonies (<10 cm²) is consistent with the high abundance values. This may indicate continuous recruitment episodes or disturbed populations. *P. fascialis* and *S. cervicornis* are the only two species that represent the largest and tallest colonies (>50 cm²) well: as for *P. fascialis*, the data provided by this study are consistent with observation carried out in the North-western Mediterranean Sea (Sala et al., 1996; Pagès-Escola,

2020). Nevertheless, *P. fascialis* reaches over 1000 cm² in the northern Tyrrhenian and Adriatic Seas (Cocito and Ferdeghini, 2001; Cocito et al., 2006). The absence of these “*P. fascialis* bushes” from coralligenous reefs might be due to hydrographic features and competition phenomena with the other filter feeders. Coverage values reported for *M. truncata* are consistent with data from both MPA and no-MPA sites along the SE coast of Spain (Nuez-Hernández et al., 2014). No further comparisons can be done for the other species due to the paucity of studies.

CCA reveals ecological shifts of mean colony size between the studied species in relation to the taxa/morphological groups structuring the coralligenous assemblages and the disturbance categories. This outlines the ecological requirements or preferences of the five species. The results are in accordance to Lombardi et al. (2008) and Sala et al. (1996) reporting *P. fascialis* as common in facies characterized by gorgonians, whereas association between *Adeonella* sp., *Reteporella* sp. and *S. cervicornis* and other sessile taxa/morphological groups is here reported for the first time. *M. truncata* appears to be the most ubiquitous species, having a bathymetrical distribution and being found from shallow rocky bottoms to deep coralligenous reefs (Zabala, 1986).

Erect bryozoans have been reported as useful for the evaluation and monitoring of coralligenous reefs: the five studied taxa show different sensitivity to human disturbance. *M. truncata* is the less sensitive species: it has often been reported in highly degraded situations (Perez et al., 2002). *Reteporella* sp. reflects moderate tolerance as well, being found in sites with medium disturbance levels. Erect arborescent bryozoans (*Adeonella* sp., *P. fascialis* and *S. cervicornis*) show the highest sensitivity to anthropogenic disturbances. These results, except for *Reteporella* sp., are consistent with data reported by several authors (Garrabou et al., 1998; Gatti et al., 2015; Casoli et al., 2017a; Montefalcone et al., 2017; Piazzzi et al., 2017a).

The results confirm the importance of bryozoans within coralligenous bioconstruction, as recently reported by Franzese et al. (2017) in terms of biomass density. They play pivotal roles both as secondary builders, consolidating the framework created by calcareous algae, and by transferring energy from pelagic to secondary consumers. The abundance of suspension feeders (Gili and Coma, 1998; Casoli et al., 2019) highlight the main pathway of energy flow that sustain the high (and still largely unexplored) biodiversity of coralligenous ecosystem.

This study revealed that the structure and composition of coralligenous assemblages affects the presence and size of bryozoan

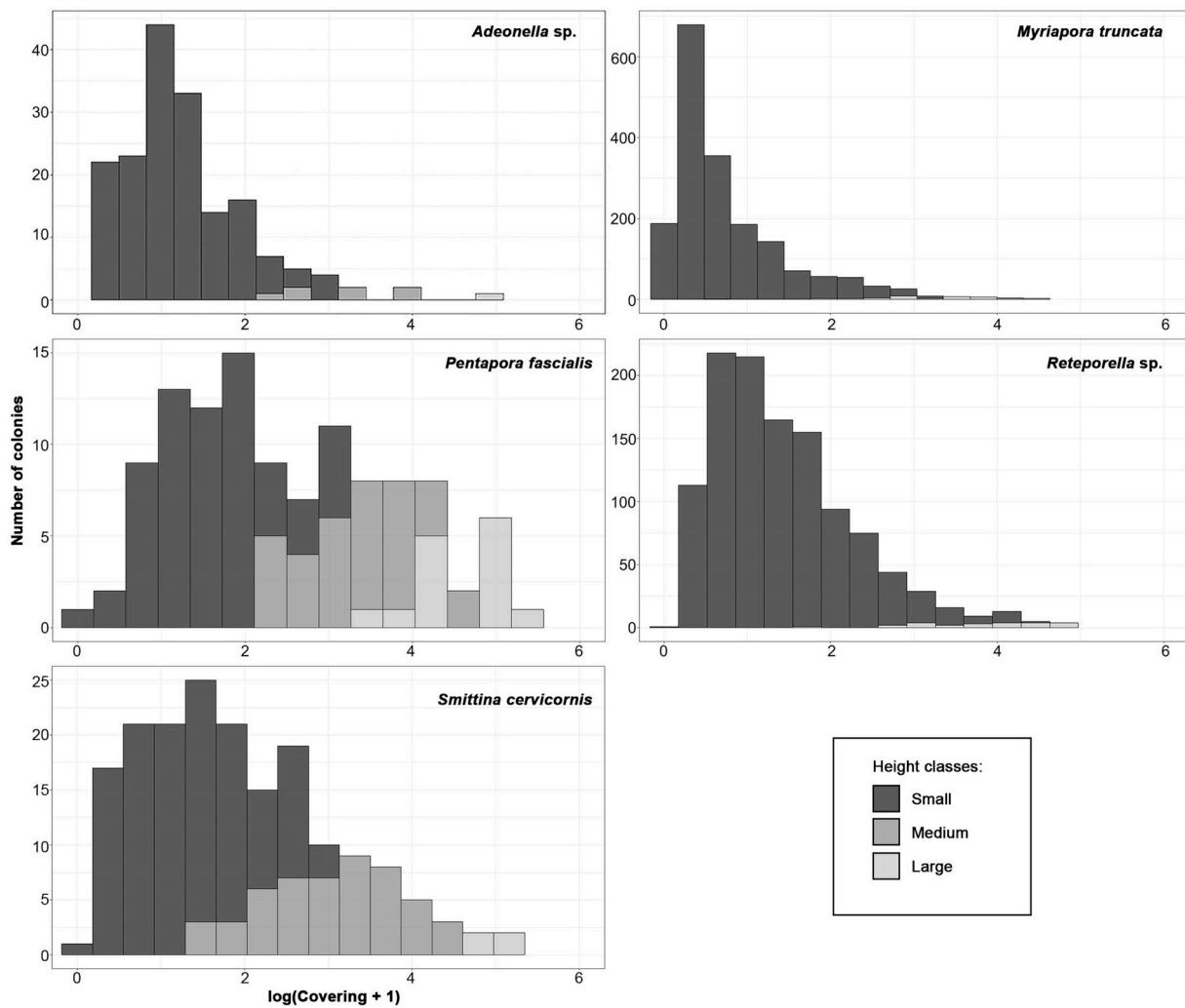


Fig. 7. Coverage distribution divided per height classes of the five investigated bryozoans.

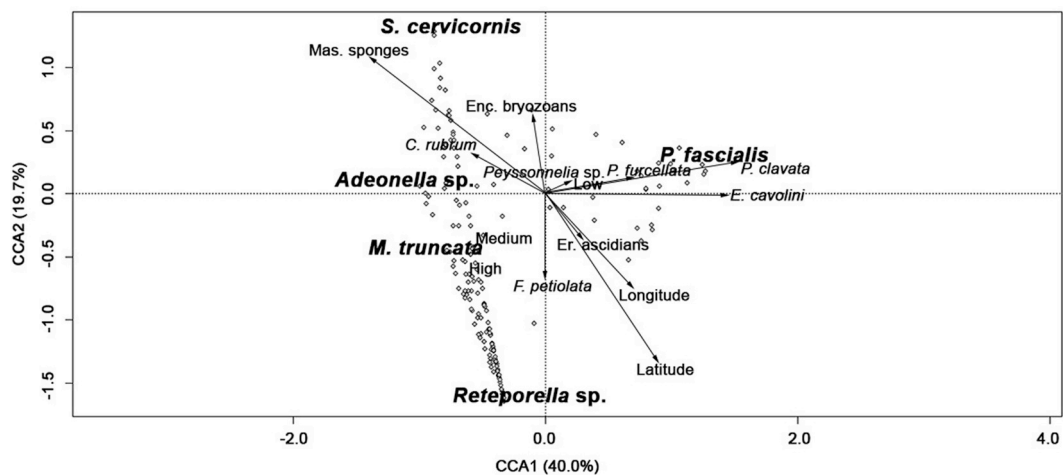


Fig. 8. Results of the Canonical Correspondence Analysis (CCA). Most diffused taxa/morphological groups composing coralligenous assemblages, disturbance levels (Low, Medium and High) and erect bryozoans are shown.

colonies. Importantly, the association with other sessile benthic groups highlights the ecological requirements of these vulnerable organisms. Coverage was found to be a good indicator for detecting human disturbance: furthermore, the different sensitivity levels reported in this

work can integrate the several indices used for coralligenous reef health assessments. Temperature rise, ocean acidification, mucilaginous blooms, alien species, and unmanaged human activities threaten the future of erect bryozoans and, due to their importance, can lead to

drastic modifications of coralligenous reefs building and trophic processes (Deudero et al., 2009; Lombardi et al., 2011a; Casoli et al., 2017a; Pagès-Escola et al., 2018; Piazzini et al., 2018). In light of their distribution, abundance and role within coralligenous ecosystem, bryozoans should be effectively monitored, and further studies should be undertaken to understand their response to the changes taking place in the Mediterranean Sea.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

We wish to thank Dr. Daniela Silvia Pace and Dr. Daniele Ventura for their help during this work. We are extremely grateful to Dr. Rebekah Susslerott and Dr. Riccardo Felici for the revision of the English language and grammar. We acknowledge the two anonymous Reviewers for their constructive comments and suggestions that improve the quality of the manuscript. This research received no external funding.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.106573>.

References

- Betti, F., Bavestrello, G., Fravega, L., Bo, M., Coppari, M., Enrichetti, F., Cappanera, V., Venturini, S., Cattaneo-Vietti, R., 2019. On the effects of recreational SCUBA diving on fragile benthic species: the Portofino MPA (NW Mediterranean Sea) case study. *Ocean Coast Manag.* 104926.
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* 19, 716–723.
- Amini, Z.Z., Adabi, M.H., Burrett, C.F., Quilty, P.G., 2004. Bryozoan distribution and growth form associations as a tool in environmental interpretation, Tasmania, Australia. *Sediment. Geol.* 167, 1–15.
- Ardizzone, G.D., Belluscio, A., Criscoli, A., 2019. Atlante degli habitat dei fondali marini del Lazio. Regione Lazio, Roma.
- Ballesteros, E., 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanogr. Mar. Biol. Annu. Rev.* 44, 123–195.
- Belloni, B., Sartoretto, S., Cresson, P., Bouchouca, M., Guillou, G., Lebreton, B., Ruitton, S., Harmelin-Vivien, M.L., 2019. Food web structure of a Mediterranean coralligenous ecosystem. In: Langar, H., Ouerghi, A. (Eds.), *Proceedings of the 3rd Symposium on the Conservation of the Coralligenous and Other Calcareous Bio-Constructions*. RAC/SPA, Antalya, Turkey, pp. 30–35. <https://doi.org/10.17882/57249>.
- Casas-Güell, E., Teixidó, N., Garrabou, J., Cebrian, E., 2015. Structure and biodiversity of coralligenous assemblages over broad spatial and temporal scales. *Mar. Biol.* 162, 901–912. <https://doi.org/10.1007/s00227-015-2635-7>.
- Casoli, E., Bonifazi, A., Ardizzone, G., Gravina, M.F., 2016. How algae influence sessile marine organisms: the tube worms case of study. *Estuar. Coast Shelf Sci.* 178 <https://doi.org/10.1016/j.ecss.2016.05.017>.
- Casoli, E., Nicoletti, L., Mastrantonio, G., Jona-Lasinio, G., Belluscio, A., Ardizzone, G.D., 2017. Scuba diving damage on coralligenous builders: bryozoan species as an indicator of stress. *Ecol. Indic.* 74 <https://doi.org/10.1016/j.ecolind.2016.12.005>.
- Casoli, E., Ventura, D., Cutroneo, L., Capello, M., Jona-Lasinio, G., Rinaldi, R., Criscoli, A., Belluscio, A., Ardizzone, G.D., 2017. Assessment of the impact of salvaging the Costa Concordia wreck on the deep coralligenous habitats. *Ecol. Indic.* 80 <https://doi.org/10.1016/j.ecolind.2017.04.058>.
- Casoli, E., Bonifazi, A., Ardizzone, G., Gravina, M.F., Russo, G.F., Sandulli, R., Donnarumma, L., 2019. Comparative analysis of mollusc assemblages from different hard bottom habitats in the central Tyrrhenian Sea. *Diversity* 11. <https://doi.org/10.3390/d11050074>.
- Cerrano, C., Danovaro, R., Gambi, M.C., Pusceddu, A., Riva, A., Schiaparelli, S., 2010. Gold coral (*Savalia savaglia*) and gorgonian forests enhance benthic biodiversity and ecosystem functioning in the mesophotic zone. *Biodivers. Conserv.* 19, 153–167. <https://doi.org/10.1007/s10531-009-9712-5>.
- Chimenz, C., Nicoletti, L., Bondanese, C., 2014. Briozoi. *Biol. Mar. Mediterr.* 20, 330.
- Cocito, S., 2004. Bioconstruction and biodiversity: their mutual influence. *Sci. Mar.* 68, 137–144. <https://doi.org/10.3989/scimar.2004.68s1137>.
- Cocito, S., 2009. Bryozoan bioconstruction. *Biologia Marina Mediterranea* 16 (1), 19–30.
- Cocito, S., Ferdeghini, F., 2001. Carbonate standing stock and carbonate production of the bryozoan *Pentapora fascialis* in the north-western Mediterranean. *Facies* 45, 25–30. <https://doi.org/10.1007/BF02668102>.
- Cocito, S., Ferdeghini, F., Morri, C., Bianchi, C.N., 2000. Patterns of bioconstruction in the cheilostome bryozoan *Schizoporella errata*: the influence of hydrodynamics and associated biota. *Mar. Ecol. Prog. Ser.* 192, 153–161. <https://doi.org/10.3354/meps192153>.
- Cocito, S., Novosel, M., Pasarić, M., Key Jr., M.M., 2006. Growth of the bryozoan *Pentapora fascialis* (Cheilostomata, Ascophora) around submarine freshwater springs in the Adriatic Sea. *Linz. Biol. Beitr.* 38, 15–24.
- Corriero, G., Pierri, C., Mercurio, M., Nonnis Marzano, C., Tarantini, S.O., Gravina, M.F., Lisco, S., Moretti, M., De Giosa, F., Valenzano, E., Giangrande, A., Mastrodonato, M., Longo, C., Cardone, F., 2019. A Mediterranean mesophotic coral reef built by non-symbiotic scleractinians. *Sci. Rep.* 9 <https://doi.org/10.1038/s41598-019-40284-4>.
- Deter, J., Descamp, P., Ballesta, L., Boissery, P., Holon, F., 2012. A preliminary study toward an index based on coralligenous assemblages for the ecological status assessment of Mediterranean French coastal waters. *Ecol. Indic.* 20, 345–352. <https://doi.org/10.1016/j.ecolind.2012.03.001>.
- Deudero, S., Blanco, A., Box, A., Mateu-Vicens, G., Cabanellas-Reboredo, M., Sureda, A., 2009. Interaction between the invasive macroalga *Lophocladia lallemandii* and the bryozoan *Reteporella grimaldii* at seagrass meadows: density and physiological responses. *Biol. Invasions* 12, 41–52. <https://doi.org/10.1007/s10530-009-9428-1>.
- Dimarchopoulou, D., Gerovasileiou, V., Voultziadou, E., 2018. Spatial variability of sessile benthos in a semi-submerged marine cave of a remote Aegean Island (eastern Mediterranean Sea). *Regional Studies in Marine Science* 17, 102–111.
- Doxa, A., Holon, F., Deter, J., Villéger, S., Boissery, P., Mouquet, N., 2016. Mapping biodiversity in three-dimensions challenges marine conservation strategies: the example of coralligenous assemblages in north-western Mediterranean Sea. *Ecol. Indic.* 61, 1042–1054. <https://doi.org/10.1016/j.ecolind.2015.10.062>.
- Falace, A., Kaleb, S., Curiel, D., Miotti, C., Galli, G., Querin, S., Ballesteros, E., Solidoro, C., Bandelj, V., 2015. Calcareous bio-Concretions in the Northern Adriatic Sea: habitat types, environmental factors that influence habitat distributions, and predictive modeling. *PLoS One* 10, 1–21. <https://doi.org/10.1371/journal.pone.0140931>.
- Ferdeghini, F., Cocito, S., Azzaro, L., Sgorbini, S., Cinelli, F., 2001. Bryozoan bioconstruction in the coralligenous formations of S. M. Leuca (Apulia, Italy). *Biol. Mar. Mediterr.* 8, 238–245.
- Ferrigno, F., Russo, G.F., Sandulli, R., 2018. Coralligenous Bioconstructions Quality Index (CBQI): a synthetic indicator to assess the status of different types of coralligenous habitats. *Ecol. Indic.* 82, 271–279.
- Ferrigno, F., Russo, G.F., Semprucci, F., Sandulli, R., 2018. Unveiling the state of some underexplored deep coralligenous banks in the Gulf of Naples (Mediterranean Sea, Italy). *Regional Studies in Marine Science* 22, 82–92.
- Franzese, P.P., Buonocore, E., Donnarumma, L., Russo, G.F., 2017. Natural capital accounting in marine protected areas: the case of the Islands of Ventotene and S. Stefano (central Italy). *Ecol. Model.* 360, 290–299. <https://doi.org/10.1016/j.ecolmodel.2017.07.015>.
- Garrabou, J., Sala, E., Zabala, M., 1998. The impact of diving on rocky sublittoral communities: a case of study of a bryozoan population. *Conserv. Biol.* 12, 302–312.
- Garrabou, J., Ballesteros, E., Zabala, M., 2002. Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. *Estuar. Coast Shelf Sci.* 55, 493–508. <https://doi.org/10.1006/ecss.2001.0920>.
- Gatti, G., Bianchi, C.N., Morri, C., Montefalcone, M., Sartoretto, S., 2015. Coralligenous reefs state along anthropized coasts: application and validation of the COARSE index, based on a rapid visual assessment (RVA) approach. *Ecol. Indic.* 52, 567–576. <https://doi.org/10.1016/j.ecolind.2014.12.026>.
- Gerovasileiou, V., Dimitriadis, C., Arvanitidis, C., Voultziadou, E., 2017. Taxonomic and functional surrogates of sessile benthic diversity in Mediterranean marine caves. *PLoS One* 12 (9), e0183707. <https://doi.org/10.1371/journal.pone.0183707>.
- Gili, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends Ecol. Evol.* 13, 316–321.
- Gubbay, S., Sanders, N., Haynes, T., Janssen, J.A.M., Rodwell, J.R., Nieto, A., Garcia Criado, M., Beal, S., Borg, J., Kennedy, M., 2016. European red list of habitats. In: *Marine Habitats*. European Union Publications Office, Luxembourg City, Luxembourg, pp. 1–46.
- Harley, C.D.G., Randall Hughes, A., Kristin, M., Miner, B.G., Cascade Sorte, J.B., Thorner, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 9, 228–241.
- Harmelin, J.G., 1985. Bryozoan dominated assemblages in Mediterranean cryptic environments. In: Nielsen, C., Larwood, G.P. (Eds.), *Bryozoan: Ordovician to Recent*. Olsen & Olsen, Fredensborg, pp. 135–143.
- Harmelin, J.G., 1986. Patterns in the distribution of bryozoans in the mediterranean marine caves. *Stygologia* 2, 10–25.
- Harmelin, J.G., 1997. Diversity of bryozoans in a Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal processes and local factors. *Mar. Ecol. Prog. Ser.* 153, 139–152. <https://doi.org/10.3354/meps153139>.
- Harmelin, J.G., 2017. Bryozoan facies in the coralligenous community: two assemblages with contrasting features at Port-Cros Archipelago (Port-Cros National Park, France, Mediterranean). *Sci. Reports Port-Cros Natl. Park* 31, 105–123.
- Harmelin, J.G., 2017. *Pentapora fascialis*, a bryozoan under stress : condition on coastal hard bottoms at Port-Cros Island. Port-Cros national Park , France ,(Mediterranean) and other sites 133, 125–133.
- Harmelin, J.G., Capo, S., 2002. Effects of sewage on bryozoan diversity in Mediterranean rocky bottoms. In: Jackson, Wyse, Butter, Jones, Spencer (Eds.), *Bryozoan Studies*. Swets & Zeitlinger, Lisse, pp. 151–158.
- Harmelin, J.G., Bitar, G., Zibrowius, H., 2007. *Schizoretopora hassi* sp. nov. (Bryozoa: Phidoloporidae) from Lebanon (eastern mediterranean) and reappraisal of *Schizotheca serratimargo* (hincks, 1886). *Cah. Biol. Mar.* 48, 179–186.
- Hong, J.S., 1980. Étude faunistique d'un fond de concrétionnement de type coralligène soumis à un gradient de pollution en Méditerranée nord-occidentale (Golfe de Fos). Université d'Aix-Marseille II.

- Hong, J., 1982. Contribution à l'étude des peuplements d'un fond de Concrétionnement Coralligène dans la région marseillaise en Méditerranée Nord-occidentale. *Bull. KORDI* 4, 27–51.
- Ingrassio, G., Abbiati, M., Badalamenti, F., Bavestrello, G., Belmonte, G., Cannas, R., Benedetti-Cecchi, L., Bertolino, M., Bevilacqua, S., Nike, C.N., Bo, M., Boscarì, E., Cardone, F., Cattaneo-Vietti, R., Cau, A., Cerrano, C., Chemello, R., Chimienti, G., Congiu, L., Corriero, G., Costantini, F., De Leo, F., Donnarumma, L., Falace, A., Fraschetti, S., Giangrande, A., Gravina, M.F., Guarnieri, G., Mastrototaro, F., Milazzo, M., Morri, C., Musco, L., Pezolesi, L., Piraino, S., Prada, F., Ponti, M., Rindi, F., Russo, G.F., Sandulli, R., Villamor, A., Zane, L., 2018. Mediterranean bioconstructions along the Italian coast. In: *Advances in Marine Biology*. Elsevier Ltd. <https://doi.org/10.1016/bs.amb.2018.05.001>.
- Kipson, S., Fourt, M., Teixidó, N., Cebrian, E., Casas, E., Ballesteros, E., Zabala, M., Garrabou, J., 2011. Rapid biodiversity assessment and monitoring method for highly diverse benthic communities: a case study of Mediterranean coralligenous outcrops. *PLoS One* 6, 11–13. <https://doi.org/10.1371/journal.pone.0027103>.
- Lejeune, C., Chevaldonne, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2009. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends Ecol. Evol.* 25, 250–260. <https://doi.org/10.1016/j.tree.2009.10.009>.
- Linares, C., Coma, R., Garrabou, J., Díaz, D., Zabala, M., 2008. Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. *J. Appl. Ecol.* 45, 688–699.
- Lombardi, C., Cocito, S., Occhipinti-Ambrogi, A., Hiscock, K., 2006. The influence of seawater temperature on zooid size and growth rate in *Pentapora fascialis* (Bryozoa: cheilostomata). *Mar. Biol.* 149, 1103–1109. <https://doi.org/10.1007/s00227-006-0295-3>.
- Lombardi, C., Cocito, S., Occhipinti-Ambrogi, A., Porter, J.S., 2008. Distribution and morphological variation of colonies of the bryozoan *Pentapora fascialis* (Bryozoa: cheilostomata) along the western coast of Italy. *J. Mar. Biol. Assoc. U. K.* 88, 711–717. <https://doi.org/10.1017/S0025315408001525>.
- Lombardi, C., Cocito, S., Gambi, M.C., Cisterna, B., Flach, F., Taylor, P.D., Keltie, K., Freer, A., Cusack, M., 2011. Effects of ocean acidification on growth, organic tissue and protein profile of the Mediterranean bryozoan *Myriapora truncata*. *Aquat. Biol.* 13, 251–262. <https://doi.org/10.3354/ab00376>.
- Lombardi, C., Gambi, M.C., Vasapollo, C., Taylor, P.D., Cocito, S., 2011. Skeletal alterations and polymorphism in a Mediterranean bryozoan at natural CO₂ vents. *Zoomorphology* 130, 135–145. <https://doi.org/10.1007/s00435-011-0127-y>.
- Lombardi, C., Taylor, P.D., Cocito, S., 2014. Bryozoan constructions in a changing Mediterranean sea. In: Goffredo, S., Dubinsky, Z. (Eds.), *The Mediterranean Sea*. Springer, Dordrecht.
- McKinney, F.K., Jackson, J.B.C., 1989. *Bryozoan Evolution*. University of Chicago Press, Chicago.
- McKinney, F.K., Jaklin, A., 2000. Spatial niche partitioning in the *Cellaria* meadow epibiotic association, northern Adriatic Sea. *Cah. Biol. Mar.* 41, 1–17.
- Montefalcone, M., Morri, C., Bianchi, C.N., Bavestrello, G., Piazzì, L., 2017. The two facets of species sensitivity: stress and disturbance on coralligenous assemblages in space and time. *Mar. Pollut. Bull.* 117, 229–238. <https://doi.org/10.1016/j.marpolbul.2017.01.072>.
- Montero-Serra, I., Linares, C., Doak, D.F., Ledoux, J.B., Garrabou, J., 2018. Strong linkages between depth, longevity and demographic stability across marine sessile species. *Proc. R. Soc. B* 285. <https://doi.org/10.1098/rspb.2017.2688>.
- Nicoletti, L., Marzaletti, S., Paganelli, D., Ardizzone, G.D., 2007. Long-term changes in a benthic assemblage associated with artificial reefs. *Hydrobiologia* 580, 233–240.
- Novosel, M., Požar-Domac, A., Pasarić, M., 2004. Diversity and distribution of the Bryozoa along underwater cliffs in the Adriatic Sea with special reference to thermal regime. *Mar. Ecol.* 25, 155–170. <https://doi.org/10.1111/j.1439-0485.2004.00022.x>.
- Nuez-Hernández, D., Valle, C., Forcada, A., Correa, J.M.G., Fernández Torquemada, Y., 2014. Assessing the erect bryozoan *Myriapora truncata* (Pallas, 1766) as indicator of recreational diving impact on coralligenous reef communities. *Ecol. Indic.* 46, 193–200. <https://doi.org/10.1016/j.ecolind.2014.05.035>.
- Pagès-Escalà, M., Hereu, B., Garrabou, J., Montero-Serra, I., Gori, A., Gómez-Gras, D., Figuerola, B., Linares, C., 2018. Divergent Responses to Warming of Two Common Co-occurring Mediterranean Bryozoans 1–9. <https://doi.org/10.1038/s41598-018-36094-9>.
- Pagès-Escalà, M., Hereu, B., La Rovira, G., Medrano, A., Aspillaga, E., Capdevila, P., Linares, C., 2020. Unravelling the population dynamics of the Mediterranean bryozoan *Pentapora fascialis* to assess its role as an indicator of recreational diving for adaptive management of marine protected areas. *Ecol. Indic.* 109, 105781. <https://doi.org/10.1016/j.ecolind.2019.105781>.
- Perez, T., Harmelin, J.G., Vacelet, J., Sartoretto, S., 2002. La bioévaluation de la qualité littorale par les peuplements de substrats durs: spongiaires, gorgonaires et bryozoaires comme indicateurs de pollution. Programme MATE, LITEAU, Rapport Final, Paris.
- Piazzì, L., Balata, D., Pertusati, M., Cinelli, F., 2004. Spatial and temporal variability of Mediterranean macroalgal coralligenous assemblages in relation to habitat and substratum inclination. *Bot. Mar.* 47, 105–115. <https://doi.org/10.1515/BOT.2004.010>.
- Piazzì, L., Gennaro, P., Balata, D., 2012. Threats to macroalgal coralligenous assemblages in the Mediterranean Sea. *Mar. Pollut. Bull.* 64, 2623–2629. <https://doi.org/10.1016/j.marpolbul.2012.07.027>.
- Piazzì, L., Gennaro, P., Cecchi, E., Serena, F., Bianchi, C.N., Morri, C., Montefalcone, M., 2017. Integration of ESCA index through the use of sessile invertebrates. *Sci. Mar.* 81 (2), 283–290. <https://doi.org/10.3989/scimar.04565.01B>.
- Piazzì, L., Bianchi, C.N., Cecchi, E., Gatti, G., Guala, I., Morri, C., Sartoretto, S., Serena, F., Montefalcone, M., 2017. What's in an index? Comparing the ecological information provided by two indices to assess the status of coralligenous reefs in the NW Mediterranean Sea. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 27 (6), 1091–1100. <https://doi.org/10.1002/aqc.2773>.
- Piazzì, L., Atzori, F., Cadoni, N., Cinti, M.F., Frau, F., Ceccherelli, G., 2018. Benthic mucilage blooms threaten coralligenous reefs. *Mar. Environ. Res.* 140, 145–151. <https://doi.org/10.1016/j.marenvres.2018.06.011>.
- Piazzì, L., Kaleb, S., Ceccherelli, G., Montefalcone, M., Falace, A., 2019. Deep coralligenous outcrops of the Apulian continental shelf: biodiversity and spatial variability of sediment-regulated assemblages. *Cont. Shelf Res.* 172, 50–56. <https://doi.org/10.1016/j.csr.2018.11.008>.
- Ponti, M., Fava, F., Abbiati, M., 2011. Spatial – temporal variability of epibenthic assemblages on subtidal biogenic reefs in the northern Adriatic Sea, 158, pp. 1447–1459. <https://doi.org/10.1007/s00227-011-1661-3>.
- Ponti, M., Abbiati, M., Turicchia, E., Ferro, F., Cerrano, C., 2018. The understory of gorgonian forests in mesophotic temperate reefs. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 28, 1153–1166. <https://doi.org/10.1002/aqc.2928>.
- R Development Core, T., 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rosso, A., Di Martino, E., 2016. Bryozoan diversity in the Mediterranean sea: an update. *Mediterr. Mar. Sci.* 17, 567–607. <https://doi.org/10.12681/mms.1474>.
- Rosso, A., Chimenz, C., Balduzzi, A., 2010. Bryozoa. *Biol. Mar. Mediterr.* 17, 589–615.
- Rosso, A., Gerovasileiou, V., Sanfilippo, R., Guido, A., 2019. Bryozoan assemblages from two submarine caves in the aegean sea (eastern mediterranean). *Mar. Biodivers.* 49 (2), 707–726. <https://doi.org/10.1007/s12526-018-0846-0>.
- Sala, E.J., Garrabou, J., Zabala, M., 1996. Effects of diver frequentation on Mediterranean sublittoral populations of the bryozoan *Pentapora fascialis*. *Mar. Biol.* 126, 451–459.
- Sartoretto, S., Schohn, T., Bianchi, C.N., Morri, C., Garrabou, J., Ballesteros, E., Ruitton, S., Verlaque, M., Daniel, B., Charbonnel, E., Blouet, S., David, R., Féral, J.P., Gatti, G., 2017. An integrated method to evaluate and monitor the conservation state of coralligenous habitats: the INDEX-COR approach. *Mar. Pollut. Bull.* 120, 222–231. <https://doi.org/10.1016/j.marpolbul.2017.05.020>.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Sini, M., Kipson, S., Linares, C., Koutsoubas, D., Garrabou, J., 2015. The yellow gorgonian *Eunicella cavolini*: demography and disturbance levels across the Mediterranean Sea. *PLoS One* 10, e0126253. <https://doi.org/10.1371/journal.pone.0126253>.
- Teixidó, N., Garrabou, J., Harmelin, J.G., 2011. Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. *PLoS One* 6. <https://doi.org/10.1371/journal.pone.0023744>.
- Thierry De Ville d'Avray, L., Ami, D., Chenail, A., David, R., Féral, J.P., 2019. Application of the ecosystem service concept at a small-scale: the cases of coralligenous habitats in the North-western Mediterranean Sea. *Mar. Pollut. Bull.* 138, 160–170. <https://doi.org/10.1016/j.marpolbul.2018.10.057>.
- Tonin, S., 2018. Economic value of marine biodiversity improvement in coralligenous habitats. *Ecol. Indic.* 85, 1121–1132.
- Tribot, A.S., Mouquet, N., Villéger, S., Raymond, M., Hoff, F., Boissery, P., Holon, F., Deter, J., 2016. Taxonomic and functional diversity increase the aesthetic value of coralligenous reefs. *Sci. Rep.* 6, 34229. <https://doi.org/10.1038/srep34229>.
- Wood, A.C.L., Probert, P.K., Rowden, A.A., Smith, A.M., 2012. Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22, 547–563. <https://doi.org/10.1002/aqc.2236>.
- Zabala, M., 1986. *Fauna Dels Brizozous Dels Països Catalans*. Institut d'Estudis Catalans, Barcelona.