University of Sassari

SPATIAL VARIABILITY AND ADAPTATION OF MEDITERRANEAN CORALLIGENOUS REEFS IN THE CURRENT AND GLOBAL WARMING SCENARIO

A Dissertation Submitted to the Department of Architecture and Environment for the
Degree of Doctor of Philosophy in Marine Ecology
(XXXIV Cycle)

Doctoral dissertation of
Federico Pinna

Supervisor
Prof.ssa Giulia Ceccherelli

Sassari
January 2022

Quel sol che pria d’amor mi scaldò ’l petto,
di bella verità m’avea scoverto,
***provando e riprovando**, il dolce aspetto*
(Paradiso, Canto III, vv. 1-3)

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisor Giulia Ceccherelli, for choosing me for this position, for the time she dedicated to me to improve my skills, and the last version of my works. She has always given me a good dose of independence which was fundamental for my temper. With her patience and passion, she pushed me to grow as a young scientist over these years. Secondly, I would like to thank Luigi Piazzi for all the support, knowledge, passion, and guidance especially in the fieldwork. I couldn't have found even a Hobo logger without his guidance!

Giulia and Luigi, your passion for science, nature, and your honesty have inspired and motivated me throughout my journey. This work would not have been possible without you both.

I would also like to thank my doctoral committee members, especially the school coordinator Vincenzo Pascucci. Vincenzo, thank you so much for your kindness and for all your support and assistance. I am incredibly grateful to you.

I would also like to acknowledge my funding sources. The research has been funded by Italian Ministry of Education and Research: PRIN 2017 (MHHWBN) “Marine Habitats restoration in a climate change-impaired Mediterranean Sea (MAHRES)”.

I am also grateful to the directors of the MPAs of Capo Carbonara, Capo Testa-Punta Falcone, Isola dell’Asinara, Capo Caccia-Isola Piana, Tavolara-Punta Coda Cavallo, Penisola del Sinis-Isola di Mal di Ventre for providing permissions and logistic assistance. I wish to thank Porto San Paolo Diving Center, Roccaruja Diving Center, Diving Center Costa Paradiso and Diving Mediterraneo for support in field activities.

I am very thankful to all my labmates, co-authors and department colleagues for their great contribution at every stage of my research. Thanks to Francesca, Giulia, Mario, Gabriella, Arianna, Alessandra, Chiara, Antonio, Daniele, Myriam and Patrizia. Dear colleagues, doing field trips with you was unforgettable! Thanks to Leonardo Casini for your availability and for your patience in listening to my questions at any time at Piandanna!

I would also like to thank what I boldly consider one of my mentors, John Bruno. Thank you, John, because even though we collaborated for a very short time, due to your authentic enthusiasm, you were able to pass me all your passion for science.

Most importantly, the biggest thanks go to my family and my love for always supporting and encouraging me. Thank you for all your patience and sacrifices. None of this would have been possible without you.

TABLE OF CONTENTS

SUMMARY

Greenhouse gas emissions are warming the atmosphere and oceans, causing disruptions to ecosystems and the services they provide to humanity. Since global warming will be the dominant driver of change in the world's oceans over the coming decades, understanding the response to warming of marine communities is crucial, because warming may affect differently the processes leading to unpredictable shifts in the structure and function of the ecosystem. Concurrent with long-term persistent warming, discrete prolonged periods of anomalously warm seawater (*i.e.,* marine heatwaves, MHWs) have increased significantly in frequency and duration since the early twentieth, with the projection to further increase due to the anthropogenic climate change. In particular, critical foundation species such as corals, seagrasses, and kelps, seem particularly vulnerable to both long-term warming and MHWs intensification.

In the Mediterranean Sea, the coralligenous reef is one of the most important benthic ecosystems, whose conservation is a major challenge for the management of coastal marine systems. Coralligenous reefs are hot spots of biodiversity being produced by carbonate deposition of encrusting coralline algae (*Lithophyllum, Lithothammnium,* and *Mesophyllum*) and by several invertebrates, mostly Cnidaria, Polychaeta, Porifera and Bryozoa. Overall, more than 1600 species can be found within coralligenous, which makes them one of the biodiversity-richest communities in the Mediterranean. However, because most of the structural species of coralligenous assemblages are long-lived and exhibit a slow population dynamic, they are also susceptible to disturbances.

Climate change is also known to affect the coralligenous reef by increasing the incidence of warming events with direct and indirect consequences on several species. In particular, mortalities of gorgonians have been recorded in recent decades and have been linked to different water heating events during water stratification seasons. Thus, considering that the Mediterranean is warming faster than the global average of the oceans (rate of 0.012° C per year), ocean warming is emerging as the most critical threat to Mediterranean coralligenous assemblages in recent decades.

Variability in temperature explains much of the spatial and temporal patterns we observe in the distribution and abundance of species worldwide. In general, to assess changes in the marine environment and quantify their magnitude, it is necessary to have a time series of crucial physicochemical parameters. Only then, by analyzing statistically the variability over time, we are able to provide evidence for the existence of changes, and we are able to make forecast models. Furthermore, experiments involving the simulation of future conditions play an essential role in testing the effects of future climate changes on marine organisms, and data, combined with today's monitoring observations, can help us chart trajectories of change.

Taking advantage of the natural differences in temperature conditions between different biogeographical regions in Sardinia (Italy) and between depths, the present Doctoral Dissertation aims to estimate the spatial variability, the vulnerability, and adaptation of an iconic habitat of the Mediterranean Sea, the coralligenous reefs, both under current conditions and into global warming scenario, focusing in particular on one of the most important bio-constructor of the coralligenous habitat, the crustose coralline algae *Lithophyllum stictiforme*.

The reasons that drove me in this research arise from the fact that, despite there are several studies on coralligenous reefs due to their extreme biodiversity and capable of also bringing economic benefit to our society through several ecosystem services, there is still a lack of knowledge about the relationships between its conservation and future scenario characterized by an increase in temperature due to anthropogenic global warming. The main questions that triggered my research hypothesis are: i) Does the structure of coralligenous assemblages change spatially in different biogeographic areas of Sardinia? ii) Is the spatial variation of the structure of coralligenous assemblages consistent through depth? iii) Is it possible to relate and thus predict differences in habitat structure based on thermal environment? iii) What is the response of one of the main builders of this habitat, the coralline algae *Lithophyllum stictiforme,* to warming? In order to answer these questions, four studies, three descriptive and one manipulative, were conducted.

In **Chapters 1 and 2,** the spatial variability of the deep coralligenous assemblages in different biogeographical areas around Sardinia and the vertical distribution of the coralligenous cliff in three different biogeographical areas of the Mediterranean Sea was evaluated, respectively. The observed variations seem largely related to biogeographic patterns rather than spatial distance and the results support the hypothesis that coralligenous assemblages, unaffected by local anthropogenic disturbance, may be relevantly different in structure and indicate that the lack of iconic species such as gorgonians and bryozoans, could merely be the result of biogeographic models probably related to the thermal environment.

In **Chapter 3,** the knowledge of the subtidal climatology has been improved to be able to identify temperature descriptors that can be useful predictors in the structure of the coralligenous community and evaluate the relationship between the subtidal temperature and the change in the community structure. With this effort, the aims were twofold: i) to evaluate if such heating descriptors can be useful predictors of the coralligenous reef community structure, ii) to identify the structure and the taxa of the community associated with the current heating events, so to provide tools to draw the trajectories of change of this community due to future warming scenarios. All the heating descriptors selected influenced several coralligenous response variables, either of the community or the main categories, so that they all might be considered useful predictors for climate change investigations on the coralligenous reef. Associations to the different types of heating descriptor have also highlighted the aspect (intensity, duration, and variability) of the heating events and the threshold for each of them responsible for the trajectories of coralligenous change.

Finally, in **Chapter 4,** manipulative experiments on *L. stictiforme* were performed for the first time in the field to examine the temperature effects in terms of survival, growth and number of conceptacles of the algae. Two experiments were done: in the first, algae were cross transplanted from a cold site to a warmer one and *vice versa* using two different depths, while in the second, transplants were done from 34 m to 15 m of depth within the same site to evaluate the influence of the thermocline, which is predicted to be increasingly deeper and persistent due to global warming.

The main goal was to understand if *L. stictiforme* is adaptable to different thermal environments and identify the changes in thallus performance due to the different temperatures. An increase in temperature positively affected the alga responses, highlighting an unexpected adaptability of this crustose coralline alga and providing useful information to forecast the effects of warming and thermocline deepening on this habitat bio-constructor and to draw up future guidelines for restoration efforts of the coralligenous habitat. Overall, my Philosophical Doctoral Dissertation results will contribute to deepening the knowledge of the coralligenous habitat and one of its main bio-constructors under the current climate condition and in the global warming scenario.

CHAPTER 1

Variations in coralligenous assemblages from local to biogeographic spatial scale

1.1 Abstract

The present study aims at contributing to the knowledge of the spatial variability of coralligenous reefs through the evaluation of patterns ranging from local to biogeographic scale around the island of Sardinia. The coralligenous reef assemblages of six areas were studied through a hierarchical sampling design: three sites per area were selected, in each site three plots were sampled and in each plot ten photographic samples were collected. The structure of coralligenous reefs across closed biogeographic regions is described, highlighting that nearly pristine assemblages, although characterized by similar high diversity, can be either dominated by animals, such as gorgonians and bryozoans, or macroalgae. The observed variations seem largely related to biogeographic patterns rather than spatial distance, supporting the need of finding specific indicators and reference conditions to assess the ecological quality of this habitat depending on the biogeographic area to be monitored.

1.2 Introduction

Biogeographic patterns result from environmental influences interacting with historic legacies and biotic characteristics (Steinbauer et al., 2016). Moreover, the emergence of biogeographic patterns is often scale dependent and, due to complex cross-scale interactions, the identification of causal processes is unobvious. However, prominent biogeographic patterns emerge particularly along strong environmental gradients, such as latitudinal gradients (De Frenne et al., 2013), or across sites which are subjected to different environmental conditions although close to each other. For example, in marine systems, upwellings bring low temperature-nutrient rich water and thus shape community structure by changing relevantly the abiotic conditions, respect to systems at similar latitudes, but unaffected by deep water rise (Adey and Steneck, 2001). Therefore, this process may change the variability ranges in physical conditions (*i.e.*, light, water movement, temperature, sedimentation, and nutrient availability), which are assumed to be the major drivers of species and trait distribution (Bustamante et al., 1997; Andrades et al., 2018) and of their variability at large spatial scale.

In marine systems, biogeographic patterns are not easy to identify as connectivity is usually higher than on land (Carr et al., 2003). However, distinct marine biogeographic regions have been described at scales ranging from regional to global (Golikov et al., 1990; Shears et al., 2008; Toonen et al., 2016; Costello et al., 2017). Biogeographic patterns are mostly related to temperature (Breeman, 1988; Blanchette et al., 2008), but other factors such as salinity and currents may determine complex patterns of spatial variability of marine assemblages (Adey and Stenbeck, 2001). For most marine areas, knowledge about the contribution of biogeographic patterns on the structure of benthic assemblages should be implemented, as their importance to conservation plans has already been recognized (Lourie and Vincent, 2004).

In the Mediterranean Sea, the coralligenous reefs are among the most important benthic ecosystems, whose conservation is a major challenge for the management of coastal marine systems (Ballesteros, 2006). Coralligenous reefs are a biodiversity hot-spot produced by carbonate deposition of encrusting coralline algae (e.g. *Lithophyllum, Lithothamnium*, and *Mesophyllum*) and several invertebrates, mostly Cnidaria, Polychaeta, Porifera and Bryozoa (Ballesteros, 2006; Martin et al., 2014). Coralligenous reefs have been included among the “special habitat types” that should be assessed and protected under the Marine Strategy Framework Directive of the European Union (EC, 2008) due to the ecological services they provide for fisheries and CO_2 balance (Thierry de Ville d’Avray et al., 2019). Therefore, due to the vulnerability of this habitat to local anthropogenic stressors, such as sediment deposition (Balata et al., 2005), eutrophication due to wastewater discharge or aquaculture (Piazzi et al., 2011, 2019a), direct habitat destruction through fishing, anchoring and coastal construction activities (Ferrigno et al., 2018; Betti et al., 2020), interest has focused on assessing coralligenous ecological status through monitoring efforts (Piazzi et al., 2021).

However, the scenario on the conservation status of coralligenous assemblages and assessment methods is even more complex due to factors acting on a wider scale such as those climate change related. For example, heat waves are known to affect the coralligenous reefs reducing habitat structure and biodiversity (Garrabou et al., 2009; Verdura et al., 2019) and widespread mortality events have involved related species (Garrabou et al., 2019). In general, a degraded coralligenous assemblage is described lacking gorgonians and with a low cover of erect bryozoans and massive sponges, but a high cover of algal turfs (Ponti et al., 2014; Verdura et al., 2019).

The spatial variability of coralligenous assemblages has been largely investigated (Piazzi et al., 2004, 2016; Virgilio et al., 2006; Ponti et al., 2011; Casas-Guell et al., 2015, 2016) and the influence of temperature on community changes has been recently evaluated (Ceccherelli et al., 2020). Moreover, differences in the structure of assemblages between distant biogeographic regions have been highlighted (Cinar et al., 2020). However, little is known about the overall influence of biogeographic patterns on the structure of coralligenous assemblages, although identification of major variations in habitat structure due to biogeography is required to evaluate the status of the assemblage in its context (Sales et al., 2012; Piazzi et al., 2018).

The present study aims at contributing to the knowledge of spatial variability of coralligenous reefs through the assessment of patterns ranging from local to biogeographic scale. To achieve this goal, a hierarchical sampling design was used to describe the structure of the coralligenous assemblage at different spatial scales in Sardinia, a unique opportunity to investigate this topic since coastal areas are generally in pristine conditions (far from urbanization) and belong to different biogeographic regions (Manca et al., 2004; Bianchi, 2007; Coll et al., 2010). In fact, due to its geographic position with respect to the circulation of Mediterranean currents (Pinardi et al., 2015), the western and northern coasts directly receive Atlantic waters through the Western Mediterranean Surface Current, while the eastern Sardinian coast is affected by the Algerian Current (Pinardi et al., 2015). At the north-western corner of Sardinia, the Atlantic flow segregates into two branches affecting the northern and western coasts of the island, respectively. The western coast is also influenced by upwelling currents that cause a decrease in sea surface temperature (Olita et al., 2013). Therefore, within a narrow range of latitudes, we could test the hypothesis that the structure of coralligenous assemblage changes spatially across different spatial scales, and that a large variability is due to the geographic position of the areas around the island of Sardinia, regardless of their distance.

1.3 Material and methods

This study was performed along the coasts of Sardinia (Mediterranean Sea, Italy) where, according to previous knowledge (Pinardi et al., 2015, Olita et al., 2013; Ceccherelli et al., 2020), six areas were selected: South-East (SE), North-East (NE), North (N), North-North-West (NNW), North-West (NW), West (W) (Figure 1.1). From July to November 2019, when water was stratified, the mean water temperature at 35 m of depth has reached 19.5°C and 20.1°C in SE and NW areas respectively, and 18.7°C in N area and 17.5°C in NW and W areas (Ceccherelli et al., 2020). In each area, three nearly pristine sites several kms apart were chosen. The sites are all exposed to high water flow and are located away from any source of anthropogenic influence (urbanization, industries, aquaculture, harbors, mining and dredging, Piazzi et al., 2021), being characterized by clear water and low sedimentation rates. At each site, three plots of about 4 m^2 where randomly selected on vertical rocky substrate at 35 m depth. In each plot, ten photographs of 0.2 m^2 areas were collected by a framed camera (Piazzi et al., 2019b). Easily identified organisms in the photographic samples were considered as taxa, while those displaying similar morphological features were assembled into morphological groups (Piazzi et al., 2017). The percentage cover of the main was assessed by manual contour technique using the ImageJ software (Cecchi et al., 2014).

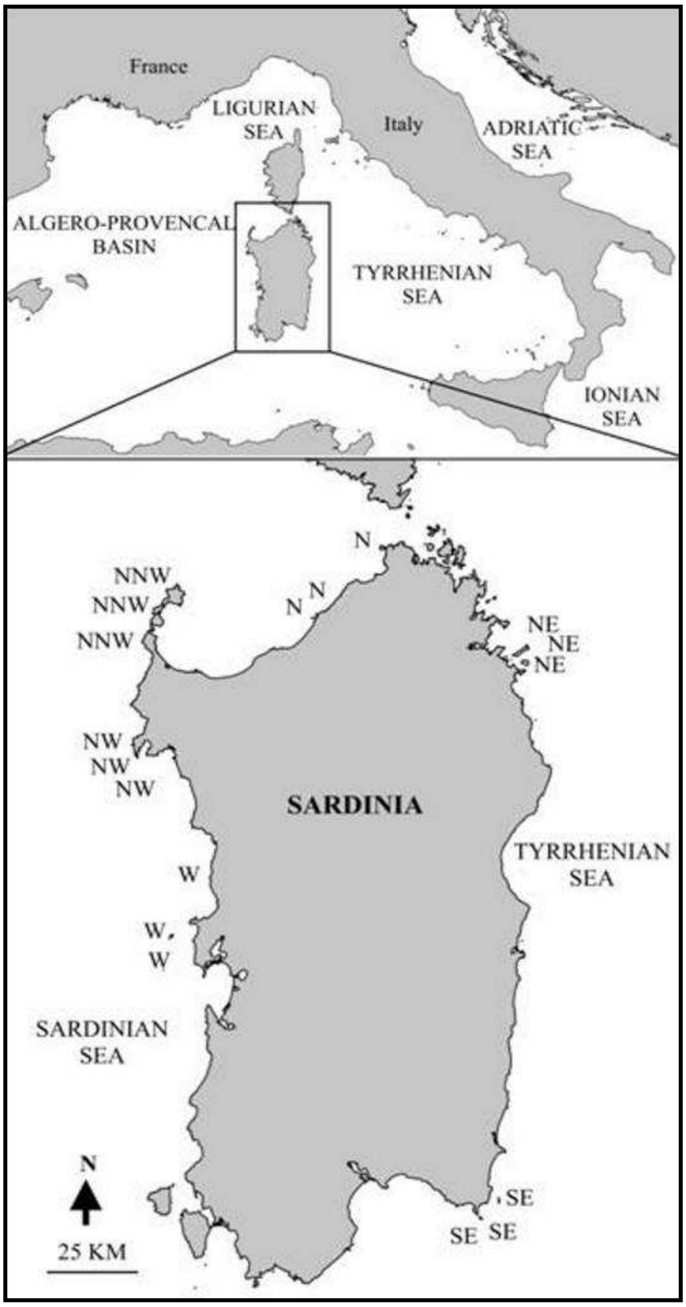


Fig. 1.1 Map of the study sites. W=west, NW=north-west, NNW=north-north-west, N=north, NE=north-east, and SE=south-east.

The diversity of assemblages was evaluated as both number taxa/morphological groups of taxa/groups per sample (alpha diversity) and mean distance from centroids (beta diversity) calculated through PERMDISP analysis (Anderson et al., 2006). The alpha diversity was analyzed through a permutational analysis of variance (Primer6 + PERMANOVA, Anderson, 2001) based on Euclidean distance. A 3-way model was used with Area as fixed factor, Site (three levels) as random factor nested in Area and Plot (three levels) as random factor nested in Site. Spatial differences in the structure of assemblages (presence and abundance of taxa/groups) were analyzed by PERMANOVA based on Bray-Curtis resemblance matrix of fourth root transformed data, using the same model of univariate analysis. The Pair-wise test was used to discriminate between levels of significant factors. Pseudo-variance components were also calculated for each spatial scale considered. A canonical analysis of principal coordinates (CAP) on fourth root transformed Bray-Curtis resemblance matrix (Anderson and Robinson, 2003) was performed in order to discriminate the main categories (i.e. taxa/morphological groups) contributing to dissimilarities among areas.

1.4 Results

A total of 34 taxa/morphological groups were identified (Table S1.1). The number of taxa/groups per sample (alpha diversity) was significantly different at small spatial scales (plot and site), but not among areas (Table 1.1, Fig. 1.2). On the contrary, the structure of the assemblage differed at all the spatial scales (plot, site and area; Table 1.2, PERMANOVA). Particularly, based on the differences among areas, alternative hypotheses were found (Pair-wise test) among all, except for the two eastern areas (SE and NE) which were found similar. The CAP analysis, based on the similarity among sites, has highlighted three main spatial groups, the eastern, the northern and the western (including W, NW and NNW), with some taxa characterizing each of them (Fig. 1.3). The E areas were characterized by bryozoans and gorgonians, the N area by *Corallium rubrum* (Linnaeus, 1758) and the western (NNW, NW and W) by encrusting sponges and erect algae (mostly Ochrophyta and Rhodophyta) (Fig. 1.3, 1.4 and 1.5). *Peyssonnelia* spp. were abundant everywhere except in the

NNW area, where encrusting sponges dominated the basal layer (Fig. 1.5), while erect algae were extraordinary abundant in the NNW rather than in the other areas. The gorgonians, *Paramuricea clavata* (Risso 1826) and *Eunicella cavolini* (Koch 1887), were much more abundant in the SE rather than in the NE and N, but were completely lacking in all the western areas, where also the bryozoans were remarkably low in cover. Estimates of pseudo-variance components showed the higher variability at large (among areas) and small scale (among samples), rather than at the intermediate spatial scales (site and plot) (Fig. 1.6).

Table 1.1 PERMANOVA results on the number of taxa/groups per sample. Significant effects (P(perm)<0.05) are in bold.

Source	***df***	***MS***	***Pseudo-F***	***P(perm)***
Area = A	5	107.9	1.402	0.299
Site(A) = S(A)	12	76.9	2.581	**0.022**
Plot(S(A))	36	29.7	6.445	**0.001**
Residual	486	4.6		

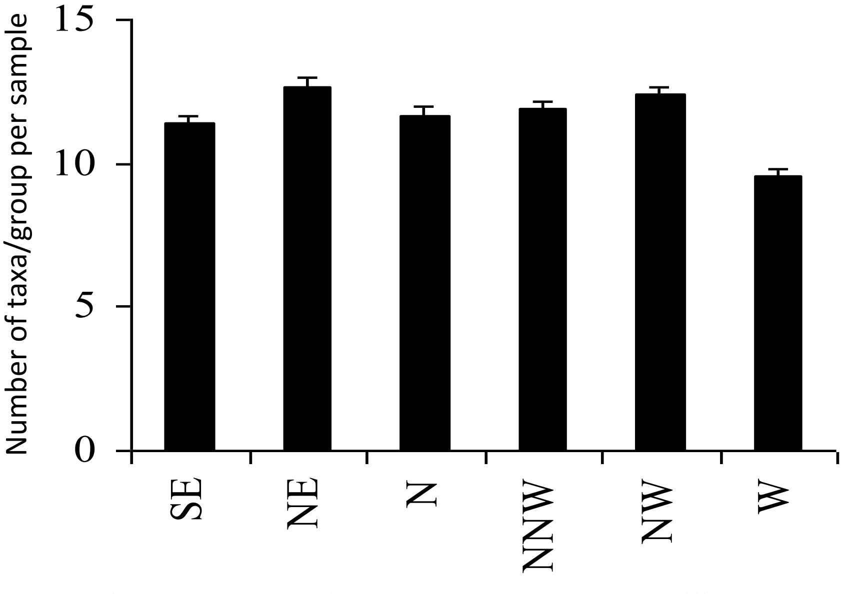


Fig. 1.2 Number of taxa/groups per sample (mean±SE, n=90) of coralligenous assemblages

Table 1.2 PERMANOVA on the structure of coralligenous assemblages. SE: South-East, NE: North-East, N: North, NNW: North-North-West, NW: North-West, W: West. Significant effects (P(perm)<0.05) are in bold.

Source	*df*	*MS*	*Pseudo-F*	*P(perm)*
Area = A	5	37321	5.252	**0.001**
Site(A) = S(A)	12	7105	2.621	**0.001**
Plot(S(A))	36	2710	5.019	**0.001**
Residual	486	539		
Pair-wise test (A):	SE=NE≠N≠NNW≠NW≠W			

1.5 Discussion

The results showed a variability in the structure of the coralligenous assemblages among several Sardinian areas, due to the different presence and abundance of taxa/morphological groups, although the diversity of assemblages was homogeneous. In particular, the observed variations in coralligenous assemblage seem largely related to biogeographic patterns rather than spatial distance, as evidenced by the high similarity between eastern areas even though they are far apart, or by the high dissimilarity between northern and western areas regardless of their proximity.

The coralligenous assemblages appear highly variable at large (among areas 10s of km apart) and small (among samples 10s of cm apart) spatial scales, rather than at intermediate one. High variability at small spatial scale is a common pattern in coralligenous assemblages generally attributed to patch distribution of organisms, mostly due to a biotic control of assemblages (Piazzi et al., 2004, 2016; Balata et al., 2005, 2006). In fact, likely due to the steady environmental conditions that characterize deep subtidal habitats, the importance of physical factors in controlling the assemblage structure decreases and species distribution is mainly driven by competitive outcomes (Ballesteros 2006; Virgilio et al. 2006).

Moreover, the complexity of biogenic substrata contributes to heterogeneous distribution patterns of sessile organisms, influencing recruitment, offering suitable refuges and creating microhabitats with different physical conditions (Cocito et al., 1997, 2002). In contrast, the high variability at large scales is not obvious, as in some cases coralligenous assemblages are similar even across large distances (Piazzi et al., 2004, 2016; Casas-Guell et al., 2015). The patterns highlighted in the present study showed deep differences among Sardinian areas supporting the presence of effects due to different biogeographic regions.

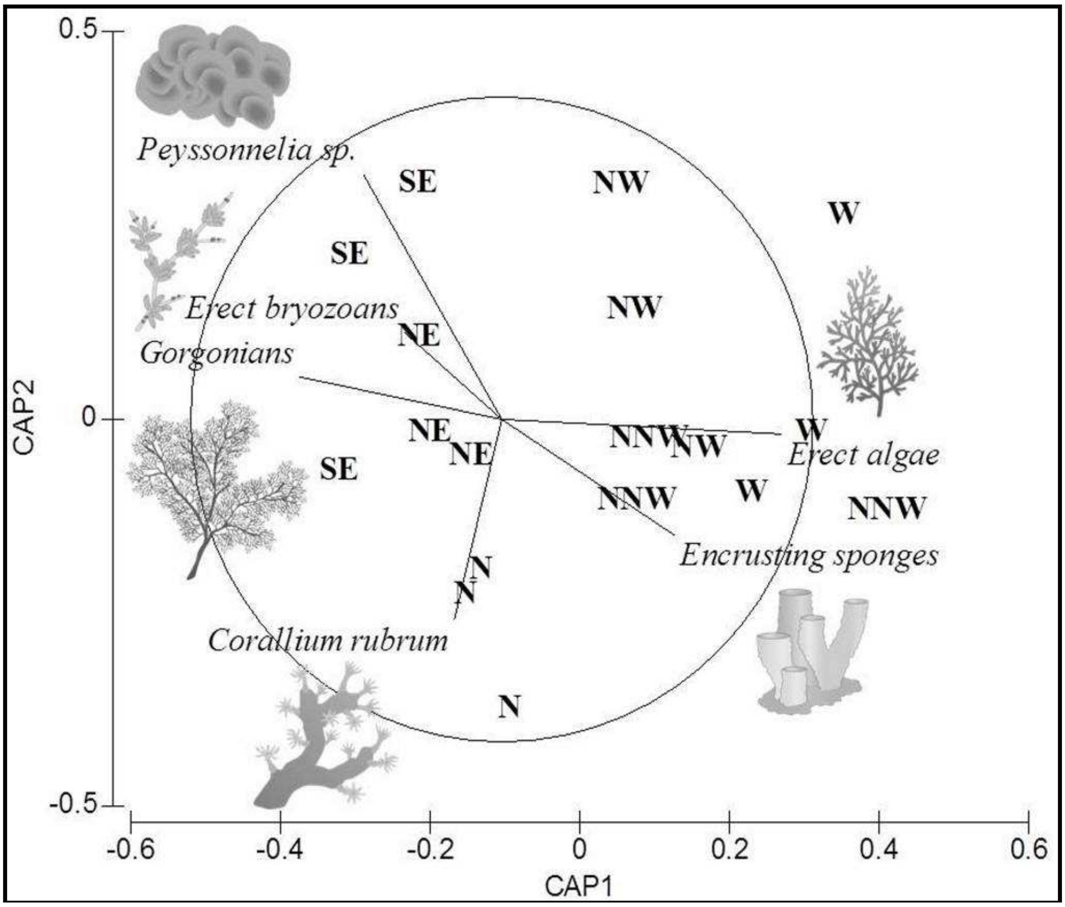


Fig. 1.3 CAP on the structure of coralligenous assemblages. SE: South-East, NE: North-East, N: North, NNW: North-North-West, NW: North-West, W: West.

Differences among areas were considerable although all the studied sites have not been affected by anthropogenic activities and are characterized by similar water clarity and sedimentation rates. On the contrary, water temperature and current circulation are known to vary among study areas (Ceccherelli et al., 2020) and can explain the segregation of different biogeographic regions. Certainly, warm southern currents along the eastern Sardinian coasts influence water temperature by driving the gradient from South to North (Ceccherelli et al., 2020), while upwelling currents affecting the western side of the island contribute to lower the water temperature in the W, NW, and NNW areas, despite the latitude (Olita et al., 2013). The differences between the assemblages of East and West sides of Sardinia could also be explained by the two different broad biogeographic regions they belong to, the Sardinian and Tyrrhenian Seas, respectively (Bianchi, 2007; Coll et al., 2010). The dissimilarity between the N area and all the others is not surprising since all geographic straits, although small in extent, are recognized as marine biogeographic regions characterized by peculiar hydrodynamic conditions (Bianchi, 2007). The areas of the western Sardinian side, despite several common features, were found to be significantly different likely for the occurrence of upwelling currents that may create local gradients in temperature and nutrient supply, pivotal in selecting species presence. This pattern is completely different from the eastern side of Sardinia where similar assemblages were found between NE and SE areas regardless the distance.

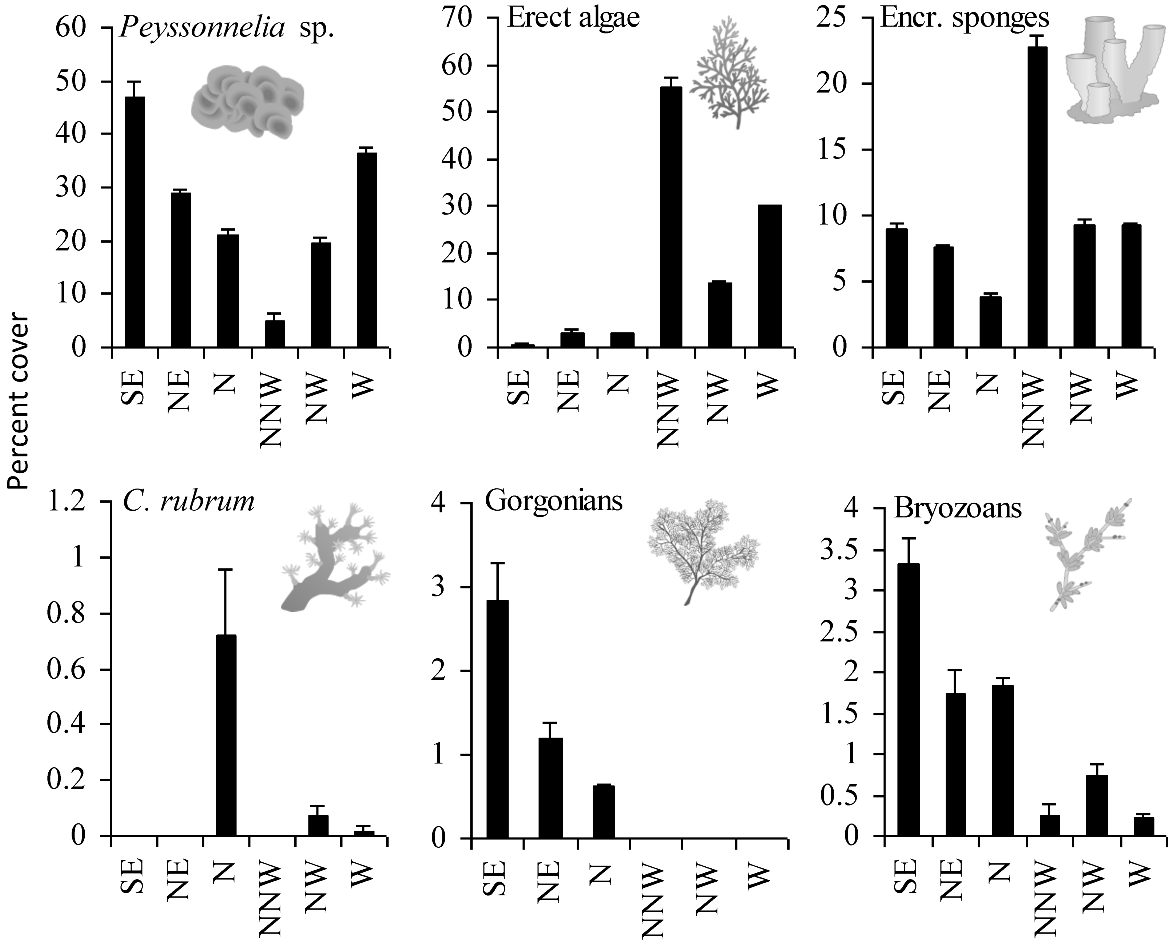


Fig. 1.4 Abundance of the main taxa/groups of coralligenous assemblages (mean±SE, n=3). SE: South-East, NE: North-East, N: North, NNW: North-North-West, NW: North-West, W: West.

Important differences in taxa composition and physical structure of assemblages were highlighted. Only the eastern coralligenous reefs were characterized by a stratified structure considered typical of coralligenous assemblages (Gatti et al., 2012, 2015), with gorgonians forming the erect layer, bryozoans the intermediate layer and *Peyssonnelia* spp. and encrusting sponges the basal layer. Thus, the Tyrrhenian side of Sardinia seems to have features typical of most of the Western Mediterranean Sea (Linares et al., 2008; Casas-Guell et al., 2015; Ponti et al., 2018; Casoli et al., 2020; Cinar et al., 2020). Conversely, the northern sites were mostly characterized by bryozoans and *Corallium rubrum*.

The latter is widely distributed in the Western Mediterranean Sea (Casas-Guell et al., 2016), but mechanisms related to spatial patterns of distribution are not fully understood (Giannini et al., 2003), as several factors, including harvest and mass mortality events, may contribute to local abundance (Garrabou et al., 2001; Montero-Serra et al., 2015). Moreover, differences in vertical zonation (depth gradient) may also be claimed, as *C. rubrum* occurs in a wide depth range (Cau et al., 2015; Casas-Guell et al., 2016) and the abundance in the northern sites could be related to a shallower distribution in the N area compared to the other ones. The western coralligenous reefs were dominated by brown erect macroalgae, organisms considered of boreal origin (Giaccone and Geraci, 1989), which probably benefit from bottom-up processes through a high nutrient availability due to the up-welling characterizing this zone. Preemption competition by brown algae due to the high nutrient availability might explain the low abundance of sessile invertebrates in this area.

The present study described the structure of coralligenous reefs across closed biogeographic regions, highlighting that nearly pristine assemblages, although characterized by similar high diversity, can be either dominated by animals, such as gorgonians and bryozoans, or macroalgae. This finding is absolutely important when considering ecological indicators for assessing the status of coralligenous assemblages. In fact, to date most of the monitoring programs for coralligenous assemblages consider the presence and abundance of gorgonians as a valuable ecological indicator (Deter et al., 2012; Gatti et al., 2015; Piazzi et al., 2019). However, despite gorgonians lack could be informative of anthropogenic stressors or heat waves effects (Linares et al., 2008; Garrabou et al., 2017; Verdura et al., 2019; Betti et al., 2020), these data provide clear evidence that nearly pristine coralligenous reefs may host assemblages without animal forests (i.e. gorgonians, Piazzi et al., 2021) and their lack does not necessary indicate a bad ecological status (Piazzi et al., 2021). Therefore, the need of qualifying the status of the coralligenous has to involve the research of accurate indicators for any kind of assemblage, both the invertebrate and the macroalgae dominated.

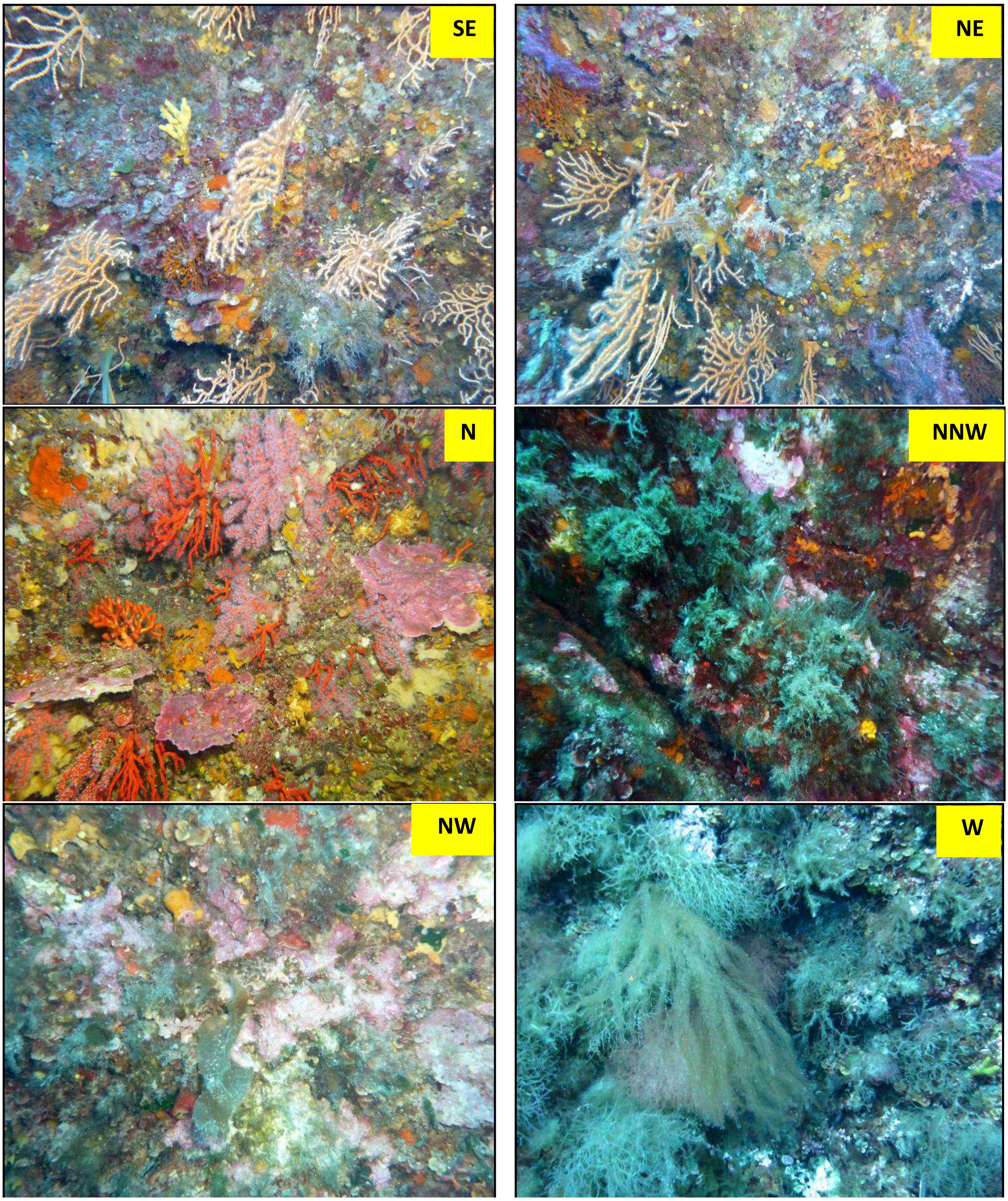


Fig. 1.5 Images of assemblages in the studied areas: SE: South-East, NE: north-East, N; North, NNW: North-North-West, NW: North-West, W: West.

Finally, to avoid any misleading investigation, an extensive work aimed at characterizing the different biogeographic areas of the coralligenous habitat at Mediterranean scale should be done, so that the use of specific indicators and reference conditions should be addressed depending on the biogeographic area to be monitored.

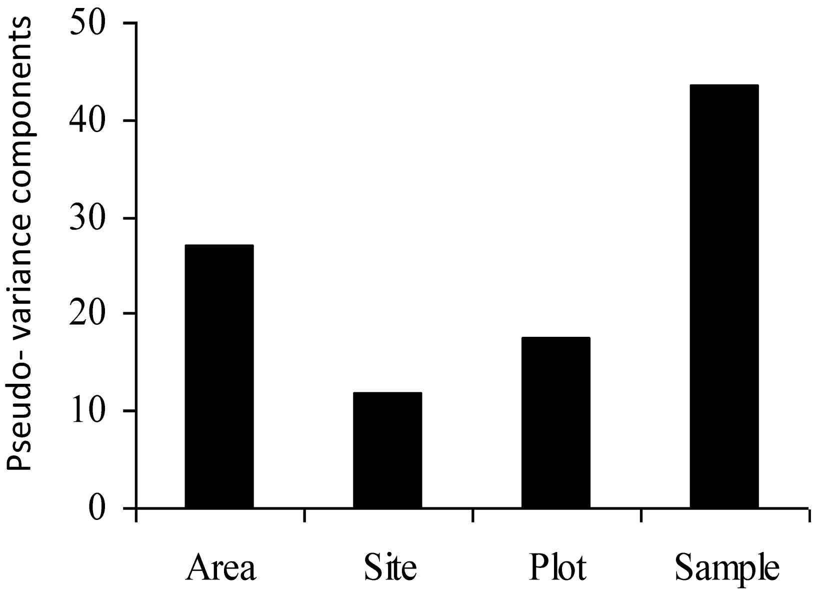


Fig. 1.6 Pseudo variance components at the spatial scales investigated.

CHAPTER 2

Vertical variation of coralligenous cliff assemblages in marine biogeographic areas

2.1 Abstract

Estimating spatial patterns of variability in coastal marine priority habitats may allow to plan monitoring programs and impact evaluation studies and to optimize sampling designs in environmental investigations. In this study the spatial variability of the vertical distribution (18 m, 23 m, 28 m, 33 m, and 38 m of depth) of coralligenous cliff assemblages was estimated in three marine biogeographic areas of the Mediterranean Sea: the Sardinia Sea, the Tyrrhenian Sea and the Bonifacio Strait. Sampling sites were selected in the West, North, and East coast of Sardinia, all in pristine conditions (far from any anthropogenic sources of influence and in highly oligothrophic water). Important variations among areas in the vertical zonation of the coralligenous cliffs have emerged, especially at the shallower depths, and the dominant taxa have been highlighted. Despite these unconsistencies, a common increase in the number of taxa/groups per sample was found with depth. Thermal environment and hydrodynamics have been discussed as the most likely important drivers of such variability. Overall, these data support the hypothesis that coralligenous cliff assemblages unaffected by local anthropogenic disturbance may be relevantly different in structure and indicate that the lack of gorgonians and bryozoans (commonly used as ecological indicators) is not necessarily a sign of local human impact, as it may be the result of biogeographic patterns.

2.2 Introduction

Estimating spatial patterns of variability in coastal marine assemblages and drivers of these patterns is a main ecological goal, crucial to discriminate between natural changes and human-induced effects (Hewitt et al., 2001; Benedetti-Cecchi, 2001; Fraschetti et al., 2005). Thus, the knowledge of these patterns may allow to plan monitoring programs and impact evaluation studies and to optimize sampling designs in environmental investigations (Irving and Connel, 2002; Benedetti-Cecchi et al., 2003; Diez et al., 2003). This issue is particularly important for priority habitats, whose status has to be assessed within international legislations (EU, 2008). The distribution of marine organisms may be regulated by gradients of physical factors, such as light, water movement, temperature, sedimentation and nutrient availability (Pérès and Picard, 1964). Depth regulates the importance of these physical factors and it may be considered the main cause of variation in marine life (Garrabou et al., 2002; Konar et al., 2009; Terlizzi et al., 2010). Therefore, important vertical variations in terms of community structure and species richness have been described in all main subtidal habitats, such as temperate rocky bottoms (Vadas and Steneck, 1988), seagrass meadows (Nesti et al., 2016) and coral reefs (Edmunds and Leichter, 2016), highlighting that vertical zonation may often represent the main driver of species distribution (Chappuis et al., 2014).

Coralligenous reefs are deep subtidal systems of the Mediterranean Sea, characterized by calcareous structures edified by encrusting Rhodophyta (thalli of *Lithophyllum*, *Lithothamnion*, *Mesophyllum*, *Neogoniolithon* and *Spongite*, Ballesteros, 2006) a secondary substrate that facilitates the settlement of several algae and sessile invertebrates and that increases the biodiversity of the coastal system (Cocito, 2004; Ballesteros, 2006;). Coralligenous reefs, due to their extent, species diversity, productivity and role played in the carbonate cycle, are recognized as one of the most important habitats of the Mediterranean Sea (Laborel, 1987; Martin et al., 2014; UNEP, 2017). Coralligenous assemblages can develop both on rocky and soft bottom in relatively homogeneous conditions of temperature, currents, salinity and under reduced irradiance (Garrabou and Ballesteros, 2000). Two main coralligenous reefs may be distinguished: cliffs are vertical or near-vertical walls from a steep littoral rock face mostly developing between 20 and 50 m of depth (Piazzi et al., 2019b), while banks are isolated outcrops surrounded by sand or biogenic sediments found down to about 150 m of depth (Ballesteros, 2006).

Most of the human pressures affecting coastal areas, such as pollution, fishing, anchoring, sedimentation, biological invasions, and thermal anomalies, may impact coralligenous reefs (Bavestrello et al., 1997; Piazzi et al., 2012) leading to severe shifts in the structure of assemblages and erosion of biodiversity (Balata et al., 2007; Piazzi et al., 2019a; Gatti et al., 2015b). Coralligenous reefs are therefore considered as habitats of interest under the Habitat Directive, being part of the habitat type 1170 “reefs”, and they are included among the “special habitat types” under the Marine Strategy Framework Directive (MSFD, EC, 2008). The MSFD requests the EU members to maintain or improve the ecological quality of the main marine coastal habitats, and the development of monitoring programs represents a fundamental step to achieve these objectives (Gatti et al., 2012; Cecchi et al., 2014; Deter et al., 2012a; Piazzi et al., 2017; Sartoretto et al., 2019). In this context, knowledge of spatial variability of coralligenous assemblages may be useful to define the ecological status of reefs and to evaluate human-caused changes (Gatti et al., 2015a; Piazzi et al., 2018, 2019a).

Spatial variability of coralligenous cliff assemblages has been investigated in relation to specific components (Piazzi et al., 2004; Casoli et al., 2019) and at different scales (Virgilio et al., 2006; Ponti et al., 2011; Casas-Guell et al., 2015, 2016; Piazzi et al., 2016, 2021b). However, coralligenous assemblages are still less well-known compared to shallower temperate rocky assemblages and spatial variability of the vertical distribution of cliff assemblages remains to be adequately estimated. Previous investigations highlighted that species distribution differed across depths (Deter et al 2012b) and that such variability was also dependent on the scale (Ferdeghini et al., 2000; Balata et al., 2006) and/or the community descriptor (alpha or beta taxonomic, functional or phylogenetic diversity, Doxa et al., 2016). Moreover, other studies have highlighted that depth-related patterns may change in relation to different levels of human pressure (Piazzi and Balata, 2011). Thus, many aspects concerning the relation between vertical and horizontal spatial patterns of coralligenous structure need to be assessed.

This study aims at assessing natural spatial patterns of coralligenous cliff assemblages in relation to depth. At this aim coralligenous cliffs of the Sardinia Sea and the Tyrrhenian Sea biogeographic regions, with the addition of the Bonifacio Strait (part of the Liguro-Provencal region, Manca et al., 2004), were considered. The following hypotheses were tested: 1) the structure of the coralligenous assemblage changes along a depth gradient in terms of the main taxa/morphological groups composition and richness, and 2) the vertical variation of the coralligenous assemblages differed depending on the Sardinia biogeographic regions and sites within each region, independently of the geographic distance.

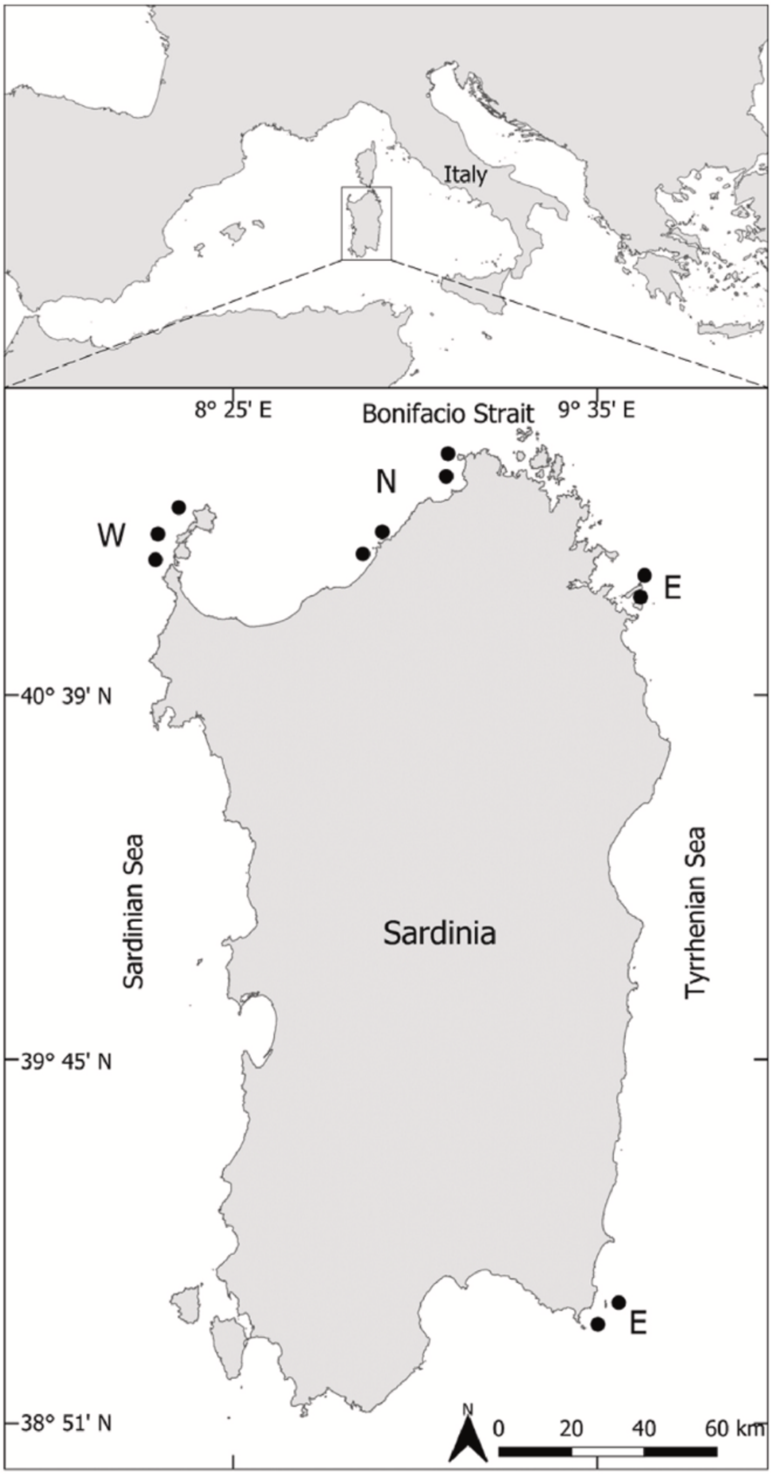


Fig. 2.1 Map of the study site (black dots) in each Sardinia coastal area (N=North, W=West and E=East).

2.3 Material and methods

The study was conducted along Sardinia coasts (Mediterranean Sea, Italy). The West (W), North (N) and East (E) Sardinia areas were considered, corresponding to the Sardinia Sea, the Bonifacio Strait and the Tyrrhenian Sea, respectively (Fig. 2.1). Although these three areas are quite close to each other, they belong to different biogeographic regions (Manca et al., 2004; Bianchi, 2007; Coll et al., 2010). They are also distinguished by important variations in sea temperature conditions during the warm season, when thermocline occurs (Table S2.1, Ceccherelli et al., 2020). In fact, the western and northern coasts directly receive Atlantic waters through the Western Mediterranean Surface Current, while the eastern coast is affected by the Algerian Current (Pinardi et al., 2013). In correspondence of the north-western Sardinia corner, the Atlantic flow segregates in two branches affecting the northern and the western coast of the Island, respectively. The western coast is also influenced by upwelling currents causing a decrease in sea surface temperature (Olita et al., 2013). Overall, these features support different subtidal communities (Piazzi et al., 2021a). Several sites (10 km apart) were selected within each area: three in the W and four in both the N and E area. The selected sites are located either in marine protected areas (Asinara Island, Capo Testa-Punta Falcone, Tavolara Punta Coda Cavallo and Capo Carbonara) or in pristine areas (Costa Paradiso, Piazzi et al., 2017) (Fig. 2.1). All sites were selected far from any anthropogenic source of influence (urbanization, industries, aquaculture, harbors, mining and dredging, Piazzi et al., 2017, 2021a) and in highly oligothrophic conditions (Barisiello et al., 2002; Regione Autonoma della Sardegna, 2016), so that coralligenous assemblages in pristine conditions could be examined.

In each site, ten photographs of 0.2 m^2 areas were collected using a camera with a frame on vertical rocky bottom at five depths: 18 m, 23 m, 28 m, 33 m, and 38 m. Organisms easily identified in photographic samples were considered as taxa, while those displaying similar morphological features were assembled into morphological groups (Table S2.2, Piazzi et al., 2019b, 2021b). The percentage cover of the main taxa/morphological groups was evaluated through the ImageJ software by means of the "patches" mosaic method (Cecchi et al., 2014): each taxon or group is outlined and the area obtained is filled with a specific color; the software then calculates the surface of each patch allowing to obtain the total cover of each taxon/group in each image.

Spatial differences in the structure of assemblages (percent cover of taxa/groups) were analysed by a permutational analysis of variance (Primer6 + PERMANOVA, Anderson, 2001) based on Bray-Curtis resemblance matrix of fourth root transformed percent cover data to also detect the contribution of the least abundant taxa/groups to dissimilarities. A 3-way model was used with Area (W, N, and E) and Depth (18 vs 23 vs 28 vs 33 vs 38) as fixed and crossed factors, and Site (three or four levels) as random factor nested in the Area. The pairwise test was used to discriminate between levels of significant factors. Taxa/morphological groups were also pooled in major categories (Table S2.1) and a SIMPER test was run in order to discriminate the main categories contributing to dissimilarities among areas and depths which were shown by an MDS ordination. The number of taxa/groups per sample was analysed by PERMANOVA based on Euclidean distance using the same model of the multivariate analysis.

2.4 Results

A total of 35 taxa/morphological groups were identified, 15 macroalgae and 20 sessile invertebrates (7 Bryozoans, 5 Anthozoans, 4 Porifera, 2 Polychaeta, 1 Ascidian and 1 Hydrozoan) (Table S2.2).

The structure of the coralligenous cliff assemblages was deeply influenced by the combination of the specific depth and area condition (significant interaction AxD, Table 2.1), although important variation was also found at the scale of site. The pairwise test has indicated significant differences among the three areas at all depths (Table 2.1), but some common vertical patterns were also identified. In fact, at all the areas a homogeneous structure was found from 28 m to 38 m of depth, while larger differences were found among shallower assemblages, though differently depending on the area: specifically, in the N area, the 18 m assemblage differed from the 23 m, while in the E and W area a significant discontinuity was found between 23 and 28 m of depth (Table 2.1).

Although a clear vertical zonation was highlighted in each area (Fig. 2.2), important differences were found in the dominant taxa (Fig. 2.3 and Table 2.2). The largest variation among taxa zonation regards the secondary calcareous substrate constituted by encrusting Rhodophyta, which was always well developed below 30 m of depth, although in the N area it was present in the whole vertical profile starting from 18 m. Furthermore, the shallower assemblages were dominated by *Parazoanthus axinellae* (Schmidt, 1862) in the E area, by Udoteaceae in the N area and by erect algae in the W area (Fig. 2.3 and Table 2.2). The deeper assemblages were mostly characterized by gorgonians (both *Paramuricea clavata* (Risso, 1826) and *Eunicella cavolini* (Koch, 1887)) and erect bryozoans (mostly *Smittina cervicornis* (Pallas, 1776)) in the E area, by encrusting calcareous Rhodophyta and *Corallium rubrum* (Linnaeus, 1758) in the N area, and by erect algae in the W area (Fig. 2.3 and Table 2.2). *Peyssonnelia* spp. was widespread, but particularly abundant in the shallower assemblages of the N area. Sponges were abundant everywhere and no clear patterns were detected.

The number of taxa/groups per sample significantly increased with depth (Table 2.3), starting from about 10 at 18 m up to about 15 at 38 m of depth (Fig. 2.4). This pattern was significantly affected by the site, but no differences were detected among areas (Table 2.3).

Table 2.1 PERMANOVA results on the composition and abundance of taxa/groups of coralligenous assemblages. E=eastern area, N=northern area, W=western area; numbers (18, 23, 28, 33, and 38) refer to depths. Significant effects are in bold.

Source	*df*	*MS*	*Pseudo-F*	*P(perm)*
Area = A	2	89706	8.84	**0.0001**
Depth = D	4	17800	4.60	**0.0001**
Site(A) = S(A)	8	10147	23.94	**0.0001**
AxD	8	8880	2.29	**0.0004**
DxS(A)	32	3863	9.11	**0.0001**
Residual	494	423		
Pairwise test (AxD)	18:	E≠N≠W	E: 18=23≠28=33=38	
	23:	E≠N≠W	N: 18≠23=28=33=38	
	28:	E≠N≠W	W: 18=23≠28=33=38	
	33:	E≠N≠W		
	38:	E≠N≠W		

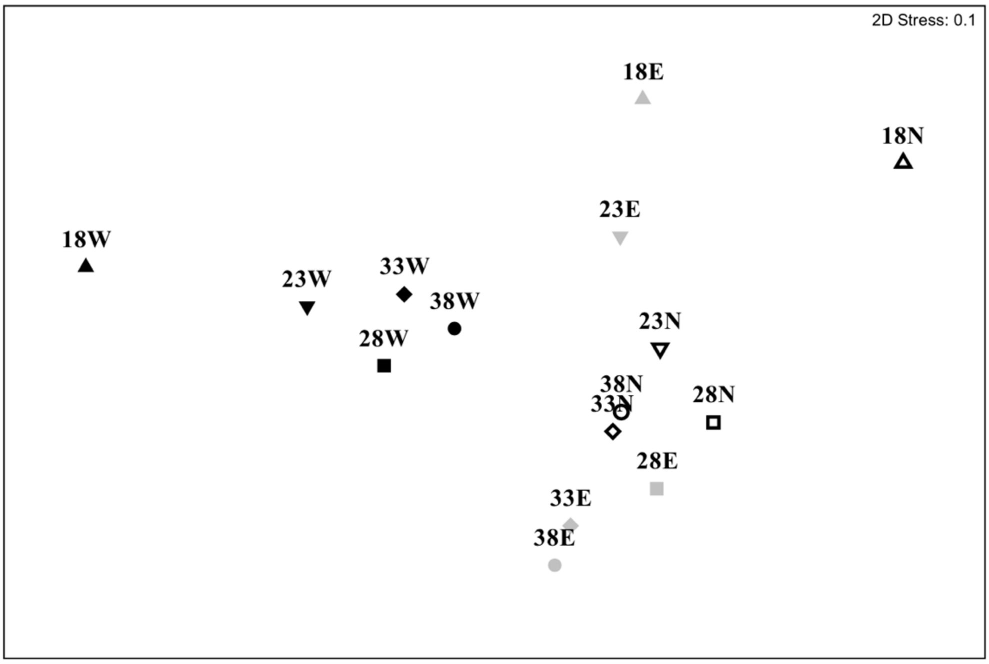


Fig. 2.2 MDS ordination on the structure of the coralligenous assemblages: E = eastern area, N = northern area, W = western area. Numbers (18, 23, 28, 33, and 38) refer to depth.

2.5 Discussion

Results highlighted the vertical zonation of the coralligenous cliff assemblage in Sardinia, showing relevant variations among the W, N and E coastal areas. The occurrence of a depth gradient in coralligenous assemblages has been already described in many studies (Ferdeghini et al., 1999; Balata et al., 2006; Piazzi and Balata, 2011; Doxa et al., 2016), but to what extent this pattern was consistent among biogeographic areas was never investigated. A typical vertical zonation of coralligenous cliffs, with gorgonians dominating the assemblages in the deep and zoantharians in the shallow areas was observed only in the E area, similarly to Cocito et al. (2002) for the North Tyrrhenian Sea. In the N area, the deep assemblage was characterized by *Corallium rubrum*, completely absent in the other studied sites: *C. rubrum* is widely distributed in western Mediterranean Sea (Casas-Guell et al., 2016), but mechanisms related to spatial patterns of distribution are not completely known (Giannini et al., 2003) as factors, including harvesting and mortality event, may contribute to the local abundance (Garrabou et al., 2001; Montero-Serra et al., 2015). The bryozoans were well represented in each area confirming their important role in structuring coralligenous cliffs (Casoli et al., 2020), but different vertical patterns occurred among areas. The variability in the vertical distribution of bryozoans has been already described (Ferdeghini et al., 1999; Balata et al., 2006), but further investigations are needed to detect the mechanisms involved. A high abundance of Udoteaceae in shallow coralligenous assemblages would be considered a common pattern (Ballesteros, 1991; Balata et al., 2006; Piazzi and Balata, 2011), but this was observed only in the N area and partially in the E area. On the contrary, the W area was characterized by a dominance of erect Ochrophyta, highlighting a very peculiar pattern for coralligenous cliffs. In fact, although deep stands of Fucales have been described (Ballesteros et al., 1998, 2009), they are considered locally distributed and related to specific environmental conditions, such as the presence of unidirectional currents (Ballesteros et al., 2009).

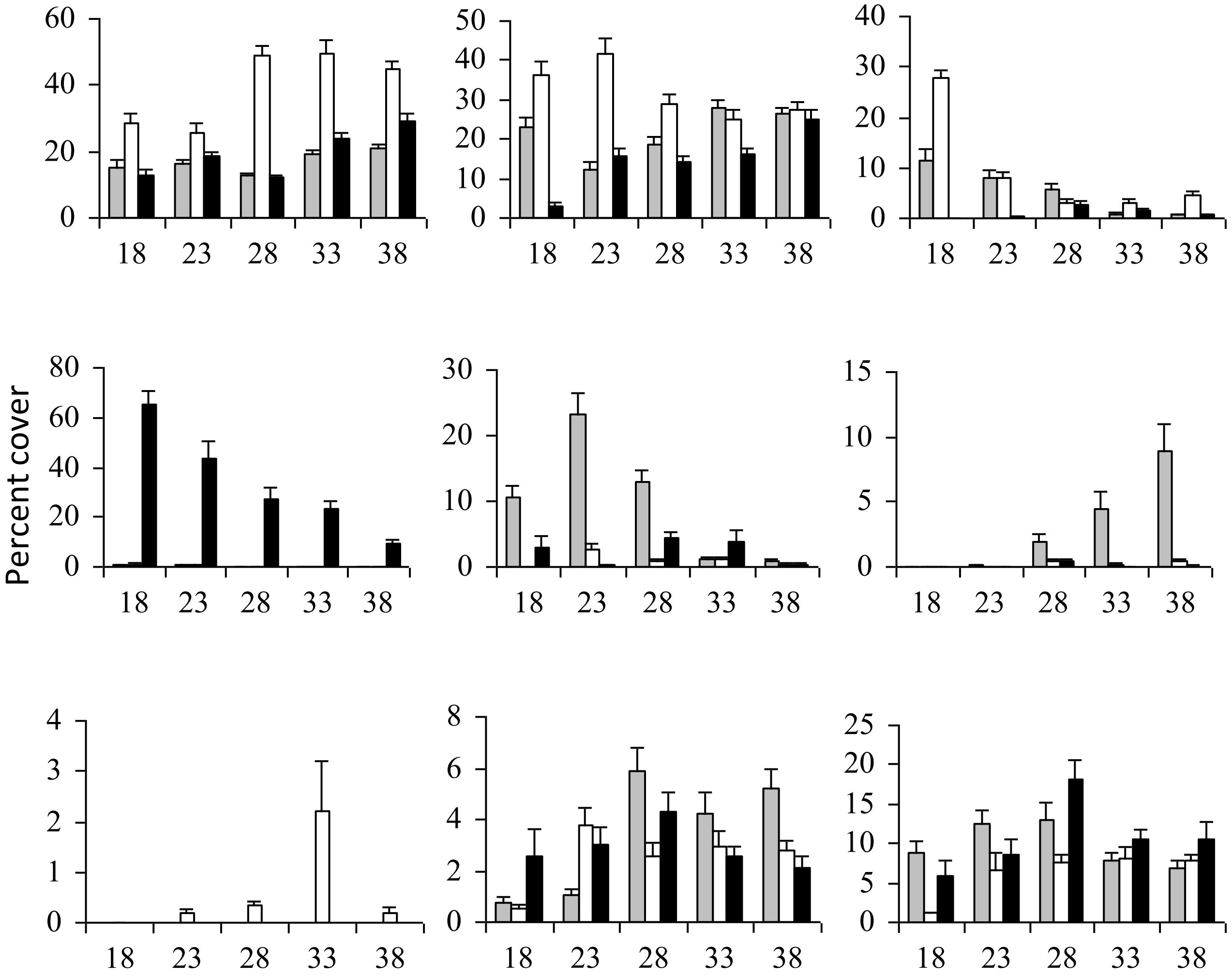


Fig. 2.3 Mean (+SE) abundance of the main taxa /groups across depths in each area. Grey = eastern area, white = northern area, black = western area.

The number of taxa/morphological groups per sample was consistently dependent on depth, with an increase of diversity from the shallow to the deep coralligenous. Different patterns were found for the French coast where taxonomic and functional diversity was unaffected and decreased with depth, respectively, despite the bathymetric range (0-70m) was not the same of the present study (Doxa et al., 2016). On the contrary, similar patterns to those observed in the present study have been already described for macroalgae (Piazzi and Ceccherelli, 2020), and attributed to the increase of habitat heterogeneity in deep subtidal, likely due to the development of calcareous structures.

In fact, calcareous structures may create microhabitats which allow the concurrent presence of many organisms with different requirements (Cocito, 2004). Moreover, the homogenous conditions characterizing deeper habitats may allow the spread of sensitive organisms that may be limited in shallower systems (Teixido et al., 2001) enhancing the diversity of the assemblages.

One of the most interesting finding of this study was the vertical variation of calcareous biocostructions, as in the N sites massive calcareous structures characterized all the depths while in E and W areas they were only present below 30 m of depth. The growth of calcareous thalli of encrusting Rhodophyta is considered mostly related to light (Martin et al., 2013), but this factor alone cannot explain the large differences observed among areas, where the water column is particularly clear for the high oligotrophy and low sedimentation rates. Thus, the observed patterns might be related to other factors, such as inter-specific features of coralline algae (Garrabou and Ballesteros, 2000), which would deserve further studies, as already partially highlighted by recent investigations (Pezzolesi et al., 2019).

By comparing assemblages of the same depth, results have corroborated the differences among Sardinia coastal areas already highlighted for deeper coralligenous assemblages (Piazzi et al., 2021a). The segregation of different biogeographic regions around Sardinia may be mostly related to local temperature and hydrodynamic conditions (Ceccherelli et al., 2020; Piazzi et al., 2021a): these two factors may act both selecting different organisms and modifying vertical patterns of distribution (Novosel et al., 200; Pagès-Escolà et al., 2018). Temperature is a fundamental factor for most stenoecius coralligenous organisms living in the bathymetric belt affected by thermocline (Lombardi et al., 2006; Crisci et al., 2011; Gomez-Gras et al., 2019), as it deeply influences the assemblages vulnerable to heating events (Cerrano et al., 2000; Coma et al., 2006; Garrabou et al., 2009; Verdura et al., 2019). During summer, the presence and persistence of the thermocline depth changes depending on the area (Table S3.1, Ceccherelli et al., 2020). On the W area, summer upwellings can also hamper water stratification (Olita et al., 2013) and this process likely affects the diversity and productivity of the macroalgae component of the assemblage. This would partially explain the highest abundance of the erect algae in the W, compared to the N and E areas. However, whether the thermal environment represents a physical and/or a physiological barrier will remain unknown.

This study consolidates the establishment of the Sardinia Sea and Tyrrhenian Sea biogeographic regions by contributing to characterize the subtidal vertical patterns of the coralligenous cliffs. At present, thirteen marine biogeographic sectors have been recognized in the Mediterranean Sea on the basis of the physical features of the water and specific assemblages and species composition (Bianchi, 2007; Coll et al., 2010). However, the spatial patterns of the taxa/groups considered in this study suggest that in the Bonifacio Strait the patterns of distribution of subtidal assemblage differ from the Sardinia and the Tyrrhenian Sea. The vertical variation of the coralligenous assemblage harbours a wealth of peculiarities, such as the distribution of the encrusting coralline algae and, in the shallow, abundance of Udoteaceae and Peyssonelliaceae. Geographic straits (*i.e.* Gibraltar and Messina, in the Mediterranean Sea) are often recognized as marine biogeographic regions (Bianchi 2007) that, although small in extension, offer interesting features for the species distribution and for the structure of trophic groups. This also opens the scenario that differences in the Bonifacio Strait would also be found in species distribution through the depth gradient and we highlight the importance that further investigations will consider analysing specimens at the lowest taxonomic resolution possible.

Table 2.2 Results of the SIMPER test showing the importance of taxa/morphological groups to patterns of multivariate analysis. SE = shallow eastern area (18-23m), DE = deep eastern area (28-38 m), SN = shallow northern area (18 m), DN = Deep northern area (23-38 m) SW = shallow western area (18-23 m), DW = deep western area (28-38 m).

Taxa/morph. groups	Av.Abund	Av.Abund	Contrib%
	SE	**DE**	
Peyssonnelia spp.	17.58	24.17	20.85
Parazoanthus axinellae	16.96	5.01	19.53
Encrusting Corallinales	15.84	17.64	12.11
Udoteaceae	9.66	2.36	12.07
Encrusting sponges	10.62	8.9	12.06
Gorgonians	0.05	5.1	6.24
Bryozoans	0.92	5.11	5.30
	SN	**DN**	
Udoteaceae	27.69	4.7	27.31
Encrusting Corallinales	23.85	44.07	27.27
Encrusting sponges	1.05	6.55	7.12
	SW	**DW**	
Erect algae	54.41	21.28	41.72
Peyssonnelia spp.	9.37	18.46	16.32
Encrusting Corallinales	15.82	22.03	13.03
Encrusting sponges	6.22	12.32	12.3
Parazoanthus axinellae	1.58	2.91	4.21
	SE	**SN**	
Encrusting Corallinales	15.84	23.85	22.1
Peyssonnelia spp.	17.58	28.98	21.49
Udoteaceae	9.66	27.69	21.19
Parazoanthus axinellae	16.96	0	16.53
Encrusting sponges	10.62	1.05	9.66
	SE	**SW**	
Erect algae	1.25	54.41	41.46
Parazoanthus axinellae	16.96	1.58	13.28
Peyssonnelia spp.	17.58	9.37	12.59
Encrusting sponges	10.62	6.22	8.72
Udoteaceae	9.66	0.24	7.42
	SN	**SW**	
Erect algae	1.23	54.41	37.29
Udoteaceae	27.69	0.24	19.34
Peyssonnelia spp.	28.98	9.37	16.89
Encrusting Corallinales	35.64	15.82	15.56
Encrusting sponges	1.05	6.22	4.48
	DE	**DN**	
Encrusting Corallinales	17.64	44.07	33.53
Peyssonnelia spp.	24.17	28.93	21.83
Udoteaceae	2.36	4.7	6.36
Parazoanthus axinellae	5.01	1.26	6.16
Gorgonians	5.1	0.26	6.08
Bryozoans	5.11	3.00	4.89

	DE	**DW**	
Erect algae	0.94	21.28	23.22
Peyssonnelia spp.	24.17	18.46	18.98
Encrusting Corallinales	17.64	22.03	14.11
Encrusting sponges	8.9	12.32	12.67
Parazoanthus axinellae	5.01	2.91	7.08
Gorgonians	5.1	0.18	5.94
Bryozoans	5.11	3.04	4.72
	DN	**DW**	
Encrusting Corallinales	44.07	22.03	27.67
Peyssonnelia spp.	28.93	18.46	20.59
Erect algae	1.64	21.28	19.97
Encrusting sponges	6.55	12.32	11.15
Udoteaceae	4.7	1.65	4.75

Although the sites investigated are not influenced by local human activities, it is not known to what extent the trajectories of climate change (such as global warming and marine heat waves) have been influencing the assemblages investigated and whether this influence has had similar pressure on the different areas, as if upwelling areas could be less affected. In fact, for the E area some quantitative information about gorgonian mortalities concomitant to summer heating events have been collected (Ponti et al., 2014, 2021c), but whether such mortalities have happened in the other coastal areas of Sardinia (W and N) is unknown. Therefore, because every single heating event may select coralligenous thermo-tolerant species (Verdura et al., 2019), it is important to consider the structure of the coralligenous assemblages investigated pristine to local anthropogenic impacts, but not necessarily to climate change, issues that we believe should be distinguished. However, the present study has estimated the variation in the vertical profile of pristine coralligenous assemblages across biogeographical regions highlighting that at the same depth the assemblages can be dominated either by animals, such gorgonians and bryozoans, or macroalgae, such as encrusting or erect Rhodophyta and Udoteaceae (Piazzi et al., 2021a; Montefalcone et al., 2017). Therefore, the presence of an elevate layer (gorgonians and bryozoans) is not the only indicator of high ecological conditions, as pristine areas may host assemblages lacking in erect organisms (Piazzi et al., 2019b).

These patterns should be absolutely considered in monitoring programs and in impact evaluation studies: in fact, although the status of gorgonians or bryozoans is commonly used as ecological indicators (Deter et al., 2012a; Gatti et al., 2015a; Piazzi et al., 2019a), their absence may not be the consequences of their loss and thus it does not mandatorily indicate the occurrence of environmental alterations, suggesting that a larger number of sensitive taxa should be used.

Table 2.3 PERMANOVA results on the number of taxa/groups per sample. Numbers (18, 23, 28, 33, and 38) refer to depths. Significant effects are in bold.

Source	*df*	*MS*	*Pseudo-F*	*P(perm)*
Area = A	2	3.36	0.016	0.9875
Depth = D	4	352.48	15.13	**0.0001**
Site(A) = S(A)	8	205.17	47.03	**0.0001**
AxD	8	21.43	0.92	0.5099
DxS(A)	32	23.29	5.33	**0.0001**
Residual	494	4.36		
Pairwise test (D)	18≠23≠28=33=38			

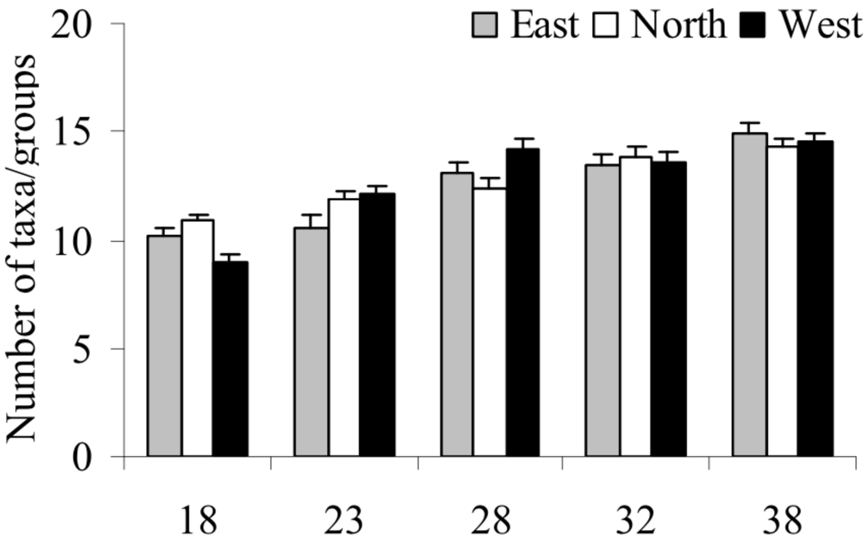


Fig. 2.4 Mean (+SE) number of taxa/groups per samples across depths and areas.

CHAPTER 3

The constraint of ignoring the subtidal water climatology in evaluating the changes of coralligenous reef due to heating events

3.1 Abstract

Predicting community-level responses to seawater warming is a pressing goal of global change ecologists. How far such predictions can be derived from a fine gradient of thermal environments needs to be explored, even if ignoring water climatology does not allow estimating subtidal marine heat waves. In this study insights about the influence of the thermal environment on the coralligenous community structure were gained by considering sites (Sardinia, Italy) at different temperature conditions. Heating events were measured (by loggers at 18m, 23m, 28m, 33m and 38m deep) and proxies for their duration (the maximum duration of events warmer than the 90th percentile temperature), intensity (the median temperature) and variability (the number of daily ΔT larger than the mean daily ΔT, and the number of heating events larger in ΔT than the 90th percentile ΔT) were selected by GAM models. Reliable predictions of decrease in coralligenous richness of taxa/morphological groups, with relevant increment in turfs and encrusting coralline algae abundance at the expenses of bryozoans were made. Associations to the different types of heating descriptor have highlighted the aspect (intensity, duration, or variability) of the heating events and the threshold for each of them responsible for the trajectories of change.

3.2 Introduction

Predicting community-level responses to sea water warming is a pressing goal of global change ecologists. A large amount of studies have reported that this pressure is exerting an overwhelming impact on marine ecosystems worldwide (Walter 2010; Poloczanska et al. 2013; Hoegh-Guldberg and Poloczanska 2017; Bruno et al. 2018), revealing that the majority of the changes are occurring rapidly with an increased risk of sudden nonlinear transformations (Hoegh-Guldberg and Bruno 2010). Understanding the response to warming of marine communities is of critical importance because of their complexity, as often they comprise highly divergent taxa (from microbes to metazoans), different phyla, trophic levels and functional groups (Smale et al., 2017; Gauzens et al., 2020), and because warming may affect differently the processes leading to unpredictable shifts in the structure and function of the ecosystem.

The speed of climate change has become a more important driver of change in biodiversity this century, leading to an accelerating rate of species loss (Sahney and Benton 2008; Urban 2012; Wiens 2016; Pinsky et al., 2019). Indeed, the thermal stress to which marine communities are subjected may not be able to keep up in terms of adaptation with important consequences on biodiversity and the economy associated. Warming, through both gradual increases in temperature and short-term extreme events, influences processes across all biological scales and can lead to step-wise shifts in ecosystem structure and functioning (Smale and Wernberg 2013; Wernberg et al., 2013; Hobday et al., 2016). Concurrent with long-term persistent warming, discrete prolonged periods of anomalously warm seawater (*i.e.* marine heat waves MHWs, periods of at least five consecutive days of water temperatures exceeding the 90th percentile according to the local climatology (Hobday et al., 2016) have increased significantly in frequency and duration since the early twentieth century (Oliver et al., 2018), with the projection to further increase for the anthropogenic climate change (Oliver et al., 2019). Several regions on the Globe seem particularly vulnerable to MHWs intensification due to the coexistence of high levels of biodiversity, a prevalence of species found at their warm range edges or concurrent non-climatic human impacts (Smale et al., 2019): in these areas MHWs have deleterious impacts across a range of biological processes and taxa, including critical foundation species such as corals (Eakin et al., 2010; Bruno and Valdivia 2016), seagrasses (Marbà and Duarte 2010; Thomson et al., 2015; Hyndes et al., 2019) and kelps (Babcock et al., 2019; Rogers-Bennett and Catton 2019).

In the Mediterranean Sea, the coralligenous reef is one of the most important benthic ecosystems, whose conservation is a major challenge for the management of coastal marine systems

(E.C., MSFD 2008). Coralligenous reefs are hot-spots of biodiversity (Martin et al., 2015) being produced by carbonate deposition of encrusting coralline algae (*Lithophyllum*, *Lithothammnium*, and *Mesophyllum*) and by several invertebrates, mostly Cnidaria, Polychaeta, Porifera and Bryozoa Ballesteros et al., 2006; Kružić 2014). Coralligenous reefs are habitats of European Community interest (E.C., Council Directive 92/43/EEC Habitat Directive) due to the ecological services they provide for fisheries and their important role in the balance of CO_2 (E.C.,MSFD 2008; Ballesteros et al., 2006; Martin and Gattuso 2009; Boudouresque et al., 2016) and to their vulnerability to anthropogenic local stressors, such re-suspension of nearby sediments, eutrophication due to wastewater discharge or aquaculture, direct habitat destruction through fishing, anchoring, and coastal construction activities (including submarine cables) (Coma et al., 2004; Ballesteros et al., 2006; Piazzi et al., 2016). At a wider scale, climate change is also known to affect the coralligenous reef by increasing the incidence of warming events with direct and indirect consequences on several species (Cerrano et al., 2000; Garrabou et al., 2009; Gatti et al., 2015). In particular, mortalities of gorgonians have been recorded in recent decades (Cerrano et al., 2000; Coma et al., 2006; Huete-Stauffer et al., 2011) and have been linked to different water heating events, during water stratification seasons (Martin et al., 2001; Garrabou et al., 2009; Crisci et al., 2011; Huete-Stauffer et al., 2011). Overall, thermal tolerance has been highlighted mainly for gorgonians, bryozoans and sponges species, and lethal and sublethal responses (*e.g.* necrosis or decreased polyps activity) to the exceeding of heating thresholds or to manipulated duration of heating events have been identified (Torrents et al., 2008; Pagès-Escolà et al. 2018; Gómez-Gras et al. 2019). Overall, the survival horizon of specific taxa as well as of the whole coralligenous reef is considered strongly dependent on heat waves occurrence (Galli et al., 2017).

In general, the assessment of vulnerability of marine habitats to warming has been mainly based on changes in satellite-derived sea-surface temperature (SST) and recently on detection of MHWs, identified as SST anomalies and categorized for intensity, duration and frequency based on the local climatology (Smale and Wernberg 2013; Hobday et al., 2018; Pansch et al., 2018; Roberts et al., 2019). Satellite-derived SST is undoubtedly a useful tool for subtidal habitats and its usefulness as proxy for very shallow water temperature is allowed; however, depending on the ecological questions to ask, benthic ecologists are encouraged to use loggers to rely on accurate and precise temperature estimates, as deep water temperature can be scarcely predicted from SST (Smale and Wernberg 2013;). The use of loggers poses a great limit on the testable hypotheses in marine ecology, as if on the one hand we can deal with reliable measurements, on the other hand we cannot know the water climatology at the desired depth. As a matter of fact, most of the investigations testing the effect of warming on subtidal species have manipulated the temperature in mesocosms either testing a wide range of tolerable condition (Bruno et al., 2015; Silbiger et al., 2019) or reproducing field conditions measured from loggers (Linares et al., 2013), but ignoring the climatology at the depth of interest and thus the temperature anomalies. This scenario prevents the possibility of detecting and categorizing the real subtidal MHWs for any subtidal locality.

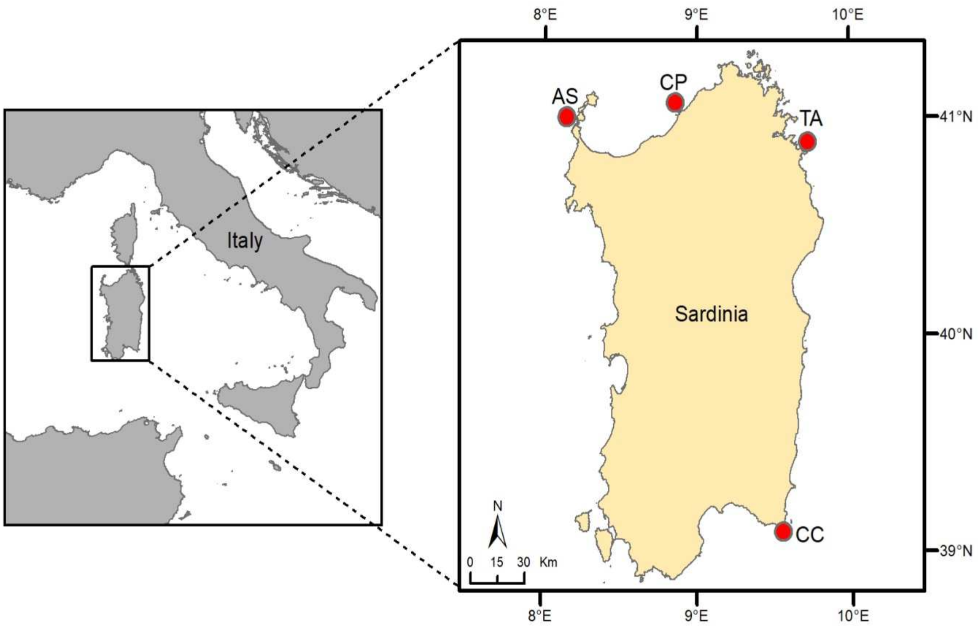


Fig. 3.1 The study sites (AS, CP, TA and CC) in Sardinia (western Mediterranean): AS 'Isola dell'Asinara MPA', CP 'Costa Paradiso', TA 'Tavolara Punta Coda Cavallo MPA' and CC 'Capo Carbonara MPA'.

The present study was carried out from May to October 2019 in four sites of Sardinia Island (Western Mediterranean, Fig. 3.1): Isola dell’Asinara Marine Protected Area (AS), Costa Paradiso (CP), Tavolara Punta Coda Cavallo Marine Protected Area (TA) and Capo Carbonara Marine Protected Area (CC). All the sites are far from any anthropogenic source of influence (*i.e.* urbanization, industries, aquaculture, harbors, mining and dredging) and are characterized by high level of oligotrophy. All of them support high diverse coralligenous reefs, which are coveted destinations of scuba tourists (Piazzi et al 2017). Recent investigations have provided evidence that the assemblage structure (taxa composition and relative abundance) of these coralligenous reefs is strongly dependent on the combination of site and depth (Ceccherelli et al., 2019), which might correspond to the specific thermal environment (Fig. 3.2). In the present work, temperature conditions (during water stratification May-October 2019) associated with site×depth context were measured by loggers so to identify several descriptors of the duration, intensity and variability of heating events and to test their influence on the coralligenous community structure. The aim was twofold: the first was to evaluate if such heating descriptors can be useful predictors of the coralligenous reef community structure, while the second was to identify the structure and the taxa of the community associated to the current heating events, so to provide tools to draw the trajectories of change of this community due to future warming scenarios. The results may contribute to identifying heating descriptors relevant to any kind of subtidal habitat vulnerability, for which MHWs metrics cannot be applied for the lack of climatological multi-year data.

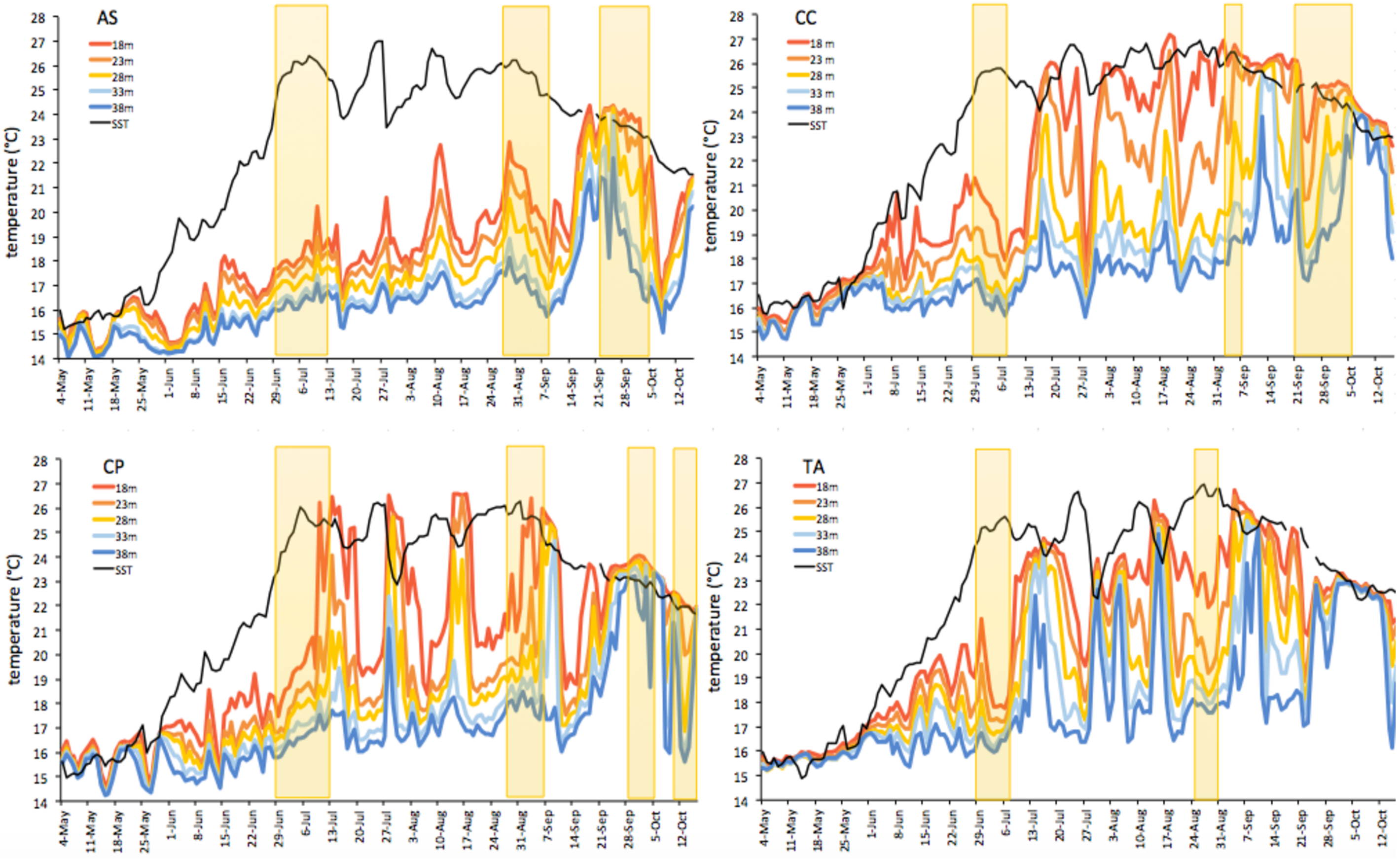


Fig. 3.2 Daily temperature from May 4 to October 16 2019 at the four sites (AS, CP, TV, and CC), at each depth (from loggers, at 18m, 23m, 28m, 33m and 38m). In black SST (from satellites). Yellow squared areas indicate MHWs (categorized in Table S3.2).

3.3 Materials and methods

3. 3. 1 Thermal environment

The thermal environment was estimated by deploying in situ high-resolution (hourly records) temperature loggers (HOBO Pendant Temp/Light MX2202) at five depths (18m, 23m, 28m, 33m and 38m) on the coralligenous reef of each site. The hobos were anchored by scuba divers to the substratum using steel nails where the coralligenous layer was sufficiently thick, otherwise a two-component epoxy underwater filler. The data logger recorded from the 4th of May until the 16th of October 2019, for a total of 166 days. The data obtained gave information on the variability in water stratification in the four study sites. Furthermore, thirty-years satellite-derived SST data were obtained (AVHRR, http://apdrc.soest.hawaii.edu) and used to detect the 2019 MHWs at each site and to explore the correlative pattern with subtidal water temperature.

3. 3. 2. Biota data collection

Samplings of the coralligenous community structure were done in May 2019 on vertical rocky walls using a non-destructive photographic method (underwater camera Lumix TZ30 with lighting achieved using two electronic strobes fitted with diffusers). At each site, two areas (about 100m distant) were selected and at each depth (18m, 23m, 28m, 33m, 38m) ten photographic samples of 0.2 m^2 of vertical surface were taken (Piazzi et al 2019). Organisms easily detectable from the photograph samples were identified to the lowest possible taxonomic level, while those not easily recognized were identified according to morphological groups (Piazzi et al., 2017). In order to run reliable models, the cover of several unconspicuous taxa/groups was pooled in six categories (encrusting coralline algae, red algae, green algae, turf algae, sponges and bryozoans), based on the sample size and affinities (Table 3.1). Red and green algae categories were mainly composed of Peyssonneliaceae and Udoteaceae, respectively, while turfs were algae smaller than 1 cm.

The percent cover of each taxon/morphological group was estimated in each picture by ImageJ software (https://imagej.nih.gov/ij/). Richness of taxa/morphological groups and evenness index were calculated from the data acquired.

3. 3. 3 Temperature descriptors

A total of 26 temperature descriptors for all sitexdepth conditions were considered to estimating the duration of heating events, their intensity and temperature variability (Table 3.2). Overall, arbitrary thresholds were set choosing 1) temperature intensity for estimating S23-S27 (the number of days of daily temperature) and D23-D27 (the maximum heating duration) over 23°C-27°C, respectively, 2) 4°C as shift intensity for NHS and 3) two days of time for shifts in LTH. However, to estimate differences among sitexdepth conditions in terms of temperature anomalies, the daily temperature data were also explored to identify the number of days of maximum duration of a heating event (D90 and D95), the number of days of high temperature (S90 and S95) and the number of heating events (F90 and F95) respect to the 90th and 95th percentile, calculated on the temperature data collected during 2019. The temperature variability was measured by other several descriptors: NHS, the number of times that heating shifts occurred in two days in a row were larger than 4° C; LTH, the largest heating event (ΔT, in °C) occurred in two days in a row; NDD, the number of daily shifts larger than the daily mean shift; LDH the largest daily heating (in °C, Table 3.2).

3. 3. 4 Data analysis

Data exploration was carried out following (Zuur et al., 2009). Outliers were inspected with Cleveland dot-plots and normality with histograms and Q-Q plots. Collinearity between continuous explanatory variables was inspected with pair-plots, and variance inflation factors (VIFs) were calculated. All covariates were highly correlated with the exception of MED, D90, F90, NDD, and LTH (VIFs < 2); thus, only these covariates were considered in the analyses. Conditional scatterplots were used to investigate the potential relationship between the explanatory variables: i) continuous variables: MED, D90, F90, NDD, and LTH; ii) Site (categorical with four levels: AS, CC, TA, CP; iii) Depth (categorical with five levels: A=18m, B=23m, C=28m, D=33m, E=38m) and the interactions between covariates and factors with the coralligenous response variables.

Since data exploration indicated non-linear relationships between each response variable and the explanatory variables, generalized additive models (GAMs) were run to correlate separately the different response variables with the explanatory variables, allowing detection of the eventual effects of Site and Depth on the continuous variables. GAMs are nonparametric extensions of linear regression models that allow the evaluation of highly non-linear relationships between explanatory and response variables thanks to the use of smooth functions (Hastie et al., 1990). To avoid over-dispersion, a negative binomial distribution was applied to all the response variables, with the exception of S (Poisson distribution) and evenness (gaussian distribution). The choice of the best fitting explanatory variables used in the final model was undertaken using AIC (Akaike information criterion), following a forward selection approach (Zuur et al., 2009). Model validations were run calculating and plotting the Pearson residuals against (i) the fitted values, (ii) each explanatory variable in the model, (iii) each explanatory variable not in the model (Zuur et al., 2009) (supplementary material 3.2).

3.4 Results

3. 4. 1. Thermal regimes at the sites and heating descriptors

Important differences in the thermal regimes among sites depending on the depth were evidenced by graphical inspection (Fig. 3.2). AS was the site with the least differences in temperature among depths and the coolest maximum temperature at the shallower depth (24.36°C at 18m), while CP was the site with the largest variations in temperature (at the least down to 28m). CC was the site with the largest differences in temperature among depths and TA was the site where water stratification was complete, as at the end of the summer temperature was homogeneous from the surface down 38m deep (Fig. 3.2 and Supplementary 1).

Table 3.1 Presence (+) or absence (-) of coralligenous taxa/morphological groups at all the sites (AS, CP, TA and CC) and depth (18, 23, 28, 33 and 38m). Taxa categories (Cat.) of GAM models are indicated by the letters B=bryozoans, C=encrusting coralline algae, G=green algae, S=sponges, R= red algae and T=turf algae.

Taxa/morphological groups	**Cat.**	**AS**					**CP**					**TA**					**CC**				
		18	23	28	33	38	18	23	28	33	38	18	23	28	33	38	18	23	28	33	38
Articulated Coralline Algae	C	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	-	-	+	+
Asparagopsis sp.	R	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caulerpa cylindracea	G	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Codium spp.	G	+	+	-	+	-	+	+	+	-	-	-	-	-	+	-	-	-	+	+	+
Dictyotales		+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	-
Encrusting Coralline Algae	C	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Encrusting Ochrophyta		+	+	+	+	+	-	-	-	+	+	-	-	+	-	+	-	+	+	-	-
Erect flattened Rhodophyta	R	-	+	+	+	+	-	-	-	-	-	-	-	-	+	+	-	+	-	-	+
Erect terete Ochrophyta		+	+	+	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
Erect terete Rhodophyta	R	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-	+	+	+
Flabellia petiolata	G	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+
Fucales		+	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halimeda tuna	G	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	-	-
Palmophyllum crassum	G	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Peyssonnelia sp.	R	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pseudoclorodesmis furcellata/Bryopsis sp	G	-	+	-	+	+	+	+	+	-	+	-	+	-	-	+	-	-	-	+	-
Turf algae	T	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Valonia sp.	G	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Aedonella calveti	B	-	-	+	+	+	-	-	-	+	+	-	+	+	+	+	-	+	+	+	+
Encrusting bryozoans	B	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Myriapora truncata	B	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	-	-	-	+	+
Pentapora fascialis	B	+	+	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	+	+	+
Ramified bryozoans	B	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Reteporella grimaldii	B	-	-	+	-	+	+	+	+	+	+	-	-	+	+	+	-	-	+	+	+
Smittina cervicornis	B	+	+	+	+	+	-	-	+	+	+	-	+	+	+	+	-	-	+	+	+
Hydrozoans		-	+	+	+	+	-	-	-	-	+	+	+	+	+	+	-	-	+	+	+
Alcyonum coralloides		-	-	+	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	+
Corallium rubrum		-	-	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
Eunicella cavolini		-	-	+	+	+	-	-	+	+	+	-	+	+	+	+	-	-	+	+	+
Paramuricea clavata		-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	+	+
Parazoanthus axinellae		+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+
Azooxantellate individual scleractinians		+	+	+	+	+	-	+	+	+	-	+	-	+	+	+	-	-	+	+	+
Zooxantellate scleractinians		+	+	+	+	+	-	+	+	+	-	+	-	+	+	+	-	-	+	+	+
Large serpulids		-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Salmacina-Filograna complex		-	+	-	-	-	-	+	-	+	+	+	+	+	+	+	-	+	+	+	+
Arborescens/massive sponges	S	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	-	-	+	+	+
Bushy sponges	S	+	+	+	+		-	+	+	+	+	+	+	+	-	+	-	-	-	+	+
Encrusting sponges	S	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Perforating sponges	S	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-	-	+	-	+
Prostrate sponges	S	-	-	-	+	-	+	+	+	+	+	+	+	-	+	-	-	+	+	+	+
Erect ascidians		-	+	+	+	+	-	+	-	+	+	+	+	+	+	+	+	+	+	-	+
Encrusting ascidians		-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-

Table 3.2 List of all temperature descriptors tested as explanatory variables for the duration of heating events, temperature intensity and variability. In bold are the descriptors selected by the models.

Descriptor type	TAG	Temperature descriptors
Duration	**D90**	**Max duration (days) > 90th percentile**
Duration	D95	Max duration (days) > 95th percentile
Duration	D27	Max duration (days) of heat event >27° C
Duration	D26	Max duration (days) of heat event >26° C
Duration	D25	Max duration (days) of heat event >25° C
Duration	D24	Max duration (days) of heat event >24° C
Duration	D23	Max duration (days) of heat event >23° C
Intensity	MAXT	Max T
Intensity	AT	Average T
Intensity	MINT	Min T
Intensity	**MED**	**Median T**
Intensity	S95	Sum of days >95th percentile
Intensity	S90	Sum of days >90th percentile
Intensity	S27	Sum of days >27° C
Intensity	S26	Sum of days >26° C
Intensity	S25	Sum of days >25° C
Intensity	S24	Sum of days >24° C
Intensity	S23	Sum of days >23° C
Variability	**F90**	**# of heating events >90th percentile**
Variability	F95	# of heating events >95th percentile
Variability	F24	# of heating events >24° C
Variability	**NDD**	**# daily ΔT > mean daily ΔT**
Variability	NHS	# of heating shifts (> 4° ΔT) in two days
Variability	SD	Standard deviation
Variability	LDH	Largest daily heating (ΔT, in °C)
Variability	LTH	Largest heating (ΔT, in °C) in two days

A more accurate description of such relevant heterogeneity in thermal regimes among depths and sites was entrusted to the four heating descriptors (D90, MED, NDD and F90, the explanatory variables) selected by the models (from a set of 26, Table 3.1). Therefore, aspects of the heating events were quantified by each descriptor: 1) duration by D90, the maximum duration (in days) of events warmer than the 90th percentile temperature; 2) heat intensity by MED, the median temperature and 3) temperature variability by NDD, the number of daily ΔT larger than the mean daily ΔT, and by F90 the number of heating events larger in ΔT than the 90th percentile ΔT (Table 3.1 and Fig. 3.3). Consequently, AS is clearly ranked the coldest, while CC and TA are the hottest sites (with CP in between), for the consistency of MED patterns among depths. However, in terms of duration of heating events AS is the one with the longest D90 consistently across depths, while at CC D90 is quite variable and increases with depth; at TA and CP large variations among depths were estimated, and not following a depth gradient. Moreover, NDD and F90 have measured different aspects of temperature variability: AS had the highest NDD and the lowest F90, TA had increasing F90 with depth, but homogeneous and low NDD, and CC had a clear pattern only for F90 which decreased with depth.

Furthermore, based on the SST climatology of the four sites, May-October 2019 SST data (Fig. 3.2) were used to detect and characterize the MHWs during the study (Hobday et al., 2016; Hobday et al., 2018): three MHWs were found in AS and CC, four in CP and two in TA. MHWs differed in intensity and duration: some strong waves have occurred at all the sites, but they were not directly traceable in the subtidal temperature (Table 3.1 and Fig. S3.2, supplementary 2).

3. 4. 2. Coralligenous structure-heating descriptors models

A total of 42 taxa/morphological groups composing the coralligenous reef community were identified at several taxonomic levels (18 macroalgae, 7 anthozoans, 7 bryozoans, 5 sponges, 2 polychaete, 2 tunicates and 1 hydrozoan, Table 3.2) and used to calculate the community richness and evenness. The models have highlighted the significant influence of the site on the community (in terms of taxa richness and evenness) and on all the categories of taxa considered, while depth only affected a few of the response variables: encrusting coralline algae, red algae, turf algae, sponges and bryozoans (Table 3.3 and supplementary material Fig. S3.3). However, the most interesting result was about the influence of the selected explanatory variables (D90, MED, F90 and NDD), alone or in interaction with site and depth on the coralligenous community structure (richness and evenness) and every single conspicuous category (supplementary material 3.2). Surprisingly, all the coralligenous response variables were influenced by some of the heating descriptors (Table 3.3). In fact, both intensity and variability of heating events influenced the number of taxa of the community, as richness was negatively influenced by the MED larger than 18.5°C, while it had a non-linear response to NDD (Figs. 3.4, 3.5 and Table 3.3). Conversely, the community evenness was only affected by MED intensity depending on the site, except for TA (Table 3.3 and Fig. 3.4).

Particularly, the duration of heating events (D90) has influenced all the categories of taxa (except for the green algae), though interactively with depth or site (Fig. 3.6). D90 had a positive influence on the abundance of turf algae at all depths (with 10 being the most common threshold) and encrusting coralline algae only at 18m, while deeper the influence had an opposite direction, with the same threshold (10). Furthermore, the site also changed the type of D90 influence on some categories (red algae were negatively influenced at CC and CP, but positively at AS, while sponges were positively influenced at both AS and CP and bryozoans negatively at TA), although exceeding 10 D90 always seemed to make a difference.

The 18.5°C MED intensity of heating events seemed to be an important threshold as encrusting coralline algae and bryozoans received a positive and negatively effect, respectively, for temperature larger than 18.5°C. Furthermore, the type of effect on the green algae depended on the site but 18.5°C remained the threshold (Table 3.3 and Fig. 3.4).

Moreover, variability in heating events did have an influence on some categories: turf and red algae were negatively affected by NDD larger than 28 and F90 larger than 4.5, while the same descriptors had a positive influence on bryozoans and sponges again for NND larger than 28 and F90 larger than 4.5 (Fig. 3.5 and Table 3.3).

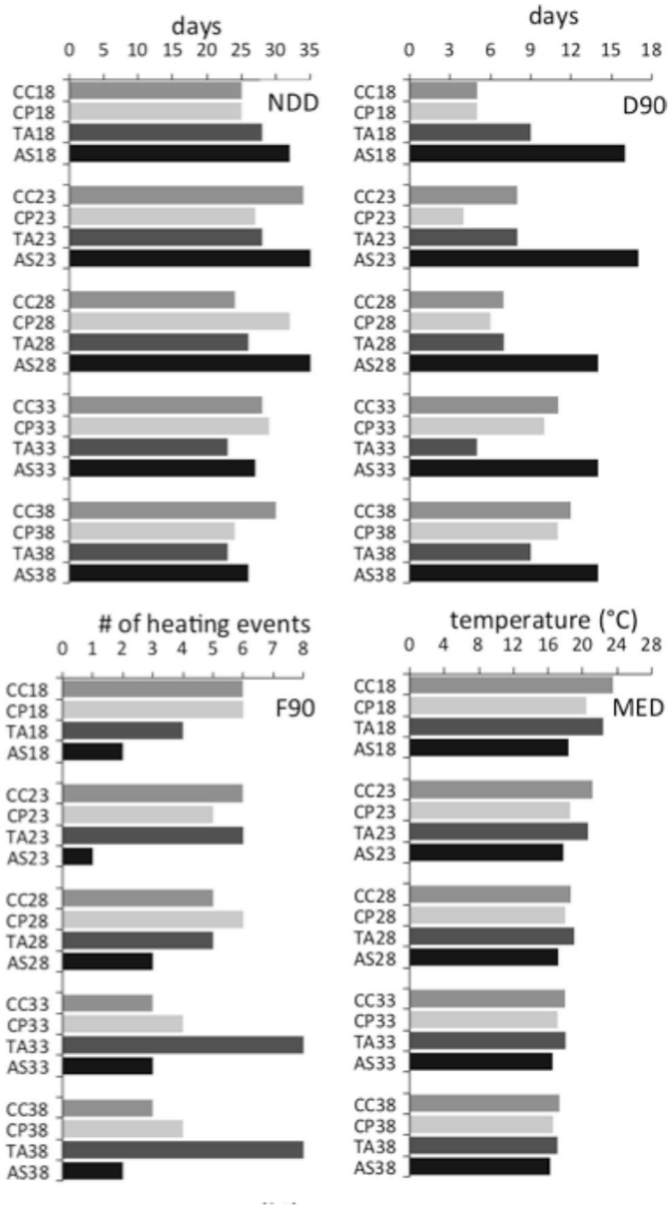


Fig. 3.3. Variability of the explanatory variables considered (D90, MED, NDD and F90) at each site (AS, CP, TV, and CC) and depth (18m, 23m, 28m, 33m and 38m).

3.5 Discussion

In a temperate location like Sardinia, the dynamics of subtidal temperature changes relevantly among sites and depths during the water stratification period. The whole study refers to the heating events that have occurred in the water column independently of the surface MHWs, whose lag of influence in time and space on the deep water temperature has likely been driven by several hydrodynamic mechanisms (Holbrook et al., 2019): at each study site, satellite-derived SST was correlated with logger measures down to 38m deep (Table S3.2 supplementary material), but this did not allow accurate predictions on the thermal subtidal environment (Smit et al., 2013; Brewin et al., 2018). Therefore, having detected the MHWs during the study period was useful to characterize the surface conditions, although their direct effects on the deeper thermal environment still remain to be deeply explored.

The objective limitation of not having long time-series of subtidal temperature data has forced to find proxies of heating events, resembling the MHWs metrics (Coma et al., 2009; Verdura et al., 2019). All the heating descriptors here selected, D90, MED, NDD and F90, influenced several coralligenous response variables either of the community or the main categories, so that they all might be considered useful predictors for climate change investigations on the coralligenous reef. The possibility of exploiting the use of such descriptors of heating events for other subtidal efforts should be investigated, in addition to MHWs metrics for the surface (Hobday et al., 2016; Hobday et al., 2018). Currently, the response of other subtidal community/species to the thermal environment is being examined based on satellite-derived SST, if the systems investigated are very shallow (Kendrick et al., 2019). Alternatively, studies for deeper systems have relied on *in situ* loggers measures where, for very specific locations, temperature data have started to be collected long before the study was really designed and where researchers could formulate the hypotheses only *a posteriori* (Coma et al., 2009; Kim et al., 2009; Verdura et al., 2019; Kendrick et al., 2019; Johnson et al., 2011; Saha et al., 2020). However, estimating subtidal temperature anomalies based on the subtidal climatology by long-time series of field temperature data has to be supported, although it will concern a limited number of localities: the recent promotion of research projects or temperature monitoring programs (*i.e.* TMED for the Mediterranean, http://t-mednet) that have extensively implemented logger data acquisition will be fundamental to gain information in wide areas and will enable detecting the role of sea water warming on relevant ecological patterns (*i.e.* mass mortalities) by correlative analyses (Garrabou et al., 2019).

Overall, the arbitrary choices made to define the D90, MED, NDD and F90 descriptors were striking, as far as there have been many significant associations with the coralligenous response variables selected. Among the whole portfolio of the coralligenous taxa/morphological groups initially considered (before pooling data) in the analyses, none could be considered due to the negligible sample size for most of them and results could be obtained only from models run on conspicuous groups of taxa (obtained by data pooling).

This represents a relevant bias of the methodology, especially for this habitat since the coralligenous community is importantly structured by a multitude of taxa with a natural very low area of occupancy (Hartley and Kunin 2003) and this approach does not allow deriving any prediction for uncospicuous taxa. This aspect involves even the cnidarian species, iconic taxa to the habitat, that have been repeatedly affected in the Mediterranean by relevant mortality events during summer-autumn heat waves (*i.e.* in 1985, 1999, 2003 and 2008) (Cerrano et al., 2000; Garrabou et al., 2009; Galli et al., 2017; Ponti et al., 2014) and whose disappearance may cause shifts in the community composition, favoring filamentous algae (Ponti et al., 2014). Change in the structure of coralligenous reefs with loss of species (lower richness and diversity) is a wide described phenomenon (Verdura et al., 2019). Although for the study sites there is lack of historical complete quantitative data, information about gorgonians mortalities gained for TA site (Cerrano et al., 2000; Garrabou et al., 2009; Huete-

Stauffer 2011) and CC [FP, personal observation], induce inferring that even the structure of the communities currently under focus is the product of pressing climate alteration.

Table 3.3 Summary of the significant GAMs results showing only the significant explanatory selected variables: site, depth and the temperature descriptors for the heating duration, temperature intensity and variability. N=400. Dev= the deviance explained by the models. “X”= interaction.

Response variable			**Heating duration**	**Heating Intensity**	**Heating variability**		**Dev.**
Community							
Richness	Site		D90	MED	NDD		58.20%
Evenness	Site			MEDXSite			25.50%
Category							
Green algae	Site			MEDXSite			65.40%
Bryozoans	Site	Depth	D90XSite	MEDXDepth	NDD		38.70%
Turf algae	Site	Depth	D90XDepth		NDD		34.80%
Red algae	Site	Depth	D90XSite			F90	29.70%
Sponges	Site	Depth	D90XSite			F90	29.00%
Encr Coralline algae	Site	Depth	D90XDepth	MED			26.70%

Nevertheless, the approach used in this study can only lead formulating predictions on large categories of taxa. In general, the expectation about the coralligenous community change to heating events, based on the overall vulnerability to warming treatments (Coma et al., 2006; Coma et al., 2009; Gatti et al., 2015; Gómez-Gras et al., 2019), concerns the reduction of sea fan and encrusting sponge species abundance and the consequent increase of algae such as turfs or fast growing weeds (Verdura et al., 2019). In this study, although with the limit of the taxonomic resolution, some unequivocal predictions of the effects of heating events on the coralligenous community could be made, as there was a consistence response across sites and depths of associations (descriptor-coralligenous): these include the high predictive power of the median temperature for the taxa richness, for the encrusting coralline algae and bryozoans. Based on these, increases in temperature intensity would drive to a lower number of taxa and, among the categories composing the community, to an increase and decrease of encrusting coralline algae and bryozoans, respectively.

This prediction is in accordance with the recent investigations on the whole community (Verdura et al., 2019) and on bryozoans (Lombardi et al., 2006), although for these latter temperature tolerance seems species-dependent Pagès-Escolà et al., 2018) and varies among areas (Novosel et al., 2004). Conversely, experimental evidence on the response of encrusting coralline algae to heat is badly needed (Rindi et al., 2019). Moreover, in the projection of longer lasting heating events, turf algae will increase the spread, as they were positively associated to D90, evidencing that the duration longer than 10 days is likely the key aspect of heating events responsible for the increase in turfs on the coralligenous reefs (Verdura et al., 2019).

Measures of heating variability, NDD and F90, have provided some further important insights, as they were good predictors for the decrease in turf (NDD over 28 daily temperature shifts larger than the mean daily shift) and red algae (F90 over 4.5 heating events larger than the 90th percentile), and increase in sponges (F90 larger than 4.5) and bryozoans (NDD larger than 28). This result may be seen in apparent contrast with expectations, but the most likely interpretation is that large values of these two descriptors correspond to breaks to the trajectories of change driven by increases in intensity and duration of heating events, stressing the need of not neglecting heat variability in studies of community responses to sea water warming. At this regards it seems important to highlight that NDD and F90 do not estimate the frequency of heating events, an aspect of heating events that was not taken into consideration in this study.

Certainly, important thresholds for whatever type of effect (negative or positive) on the coralligenous community were found for all the temperature descriptors: 18.5°C for the median temperature, 28 for NDD, 4.5 for F90 and 10 for D90. Although related to the specific study period that does not include the cold months, all these thresholds together provide evidence for formulating predictions on the coralligenous reef community on the basis of the heating events. In fact, independently of their absolute values, they seem edges highly consistent across the response variables of the community investigated, suggesting that specific temperature intensity, variability and duration of heating events affect the coralligenous community, both as a whole and its conspicuous taxa.

Overall, discriminating the effect and quantifying the specific magnitude of influence of the heating events, whether the duration, intensity or variability represents one of the main results of the approach used. The other output regards the context-dependence of several predictions, either on the community or the categories of taxa, as the type of associations (negative or positive) changed among sites or depths. However, the categories of taxa are composed of numbered species whose contribution in abundance changes depending on the sitexdepth context and, because vulnerability to the heating may be species specific (Pagès-Escolà et al., 2018; Gómez-Gras et al., 2019) and often depends on local adaptation (Crisci et al., 2017), the interpretation of unconsistent patterns could only be very oddly and speculative, until the relevancy of each single species is assessed.

The present study uses the approach of relating different coralligenous communities to their thermal environment in order to contribute drawing the trajectories of change of the coralligenous community due to future warming scenarios.

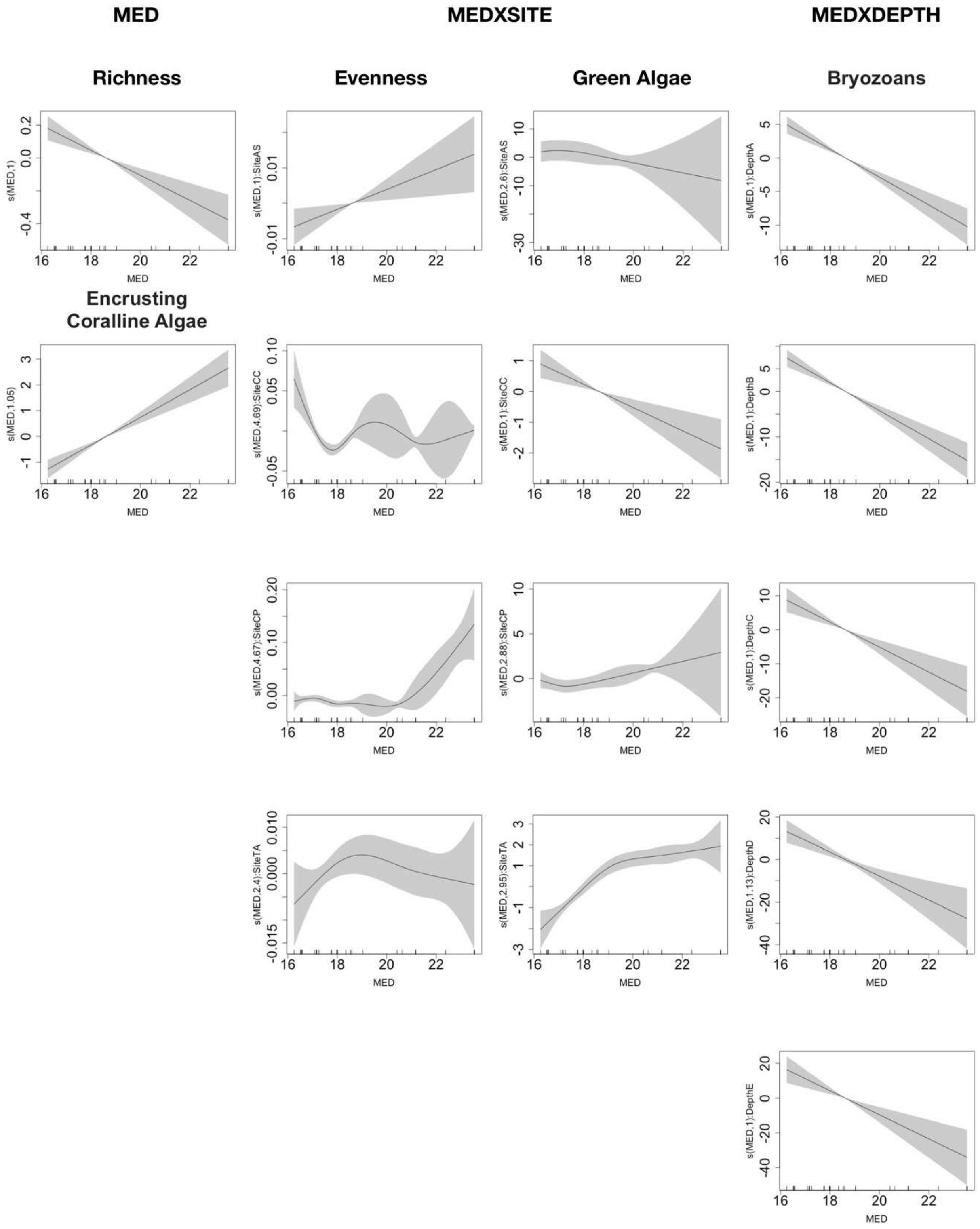


Fig. 3.4 Summary of GAM results showing only the significant explanatory variables of the models: MED both, as a main factor and MED x SITE (AS, CP, TV, and CC), and x DEPTH (18m=A, 23m=B, 28m=C, 33m=D and 38m=E). The y-axis represents the additive predictor by GAM, which is a smoothed function for MED and for the interaction. The solid line is the smoother and the dotted lines are 95% point-wise confidence bands.

The innovative approach consists in providing some descriptors of heating events and the thresholds to which for this community would change. The same approach could be similarly applied to investigate the responses of any other subtidal community/species to climate change. The need of disentangling the effects due to the intensity, duration and variability of the heating events is stressed, as well as the importance of gaining spatially and temporally wide databases, both of the thermal environment and the biota. We hope the present contribution my also assist the implementing of persistent monitoring nets of subtidal habitats.

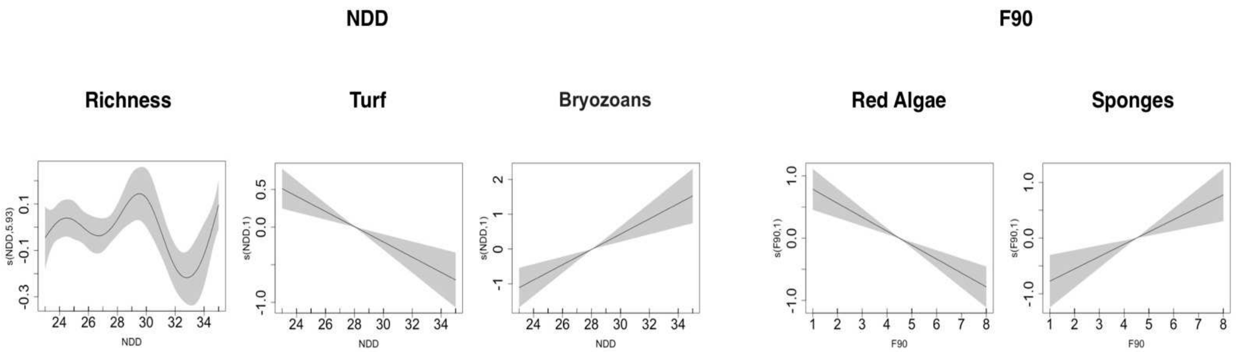


Fig. 3.5 Summary of GAM results showing only the significant explanatory variables of the models: NDD and F90. The y-axis represents the additive predictor by GAM, which is a smoothed function for NDD and for the interaction. The solid line is the smoother and the dotted lines are 95% point-wise confidence bands.

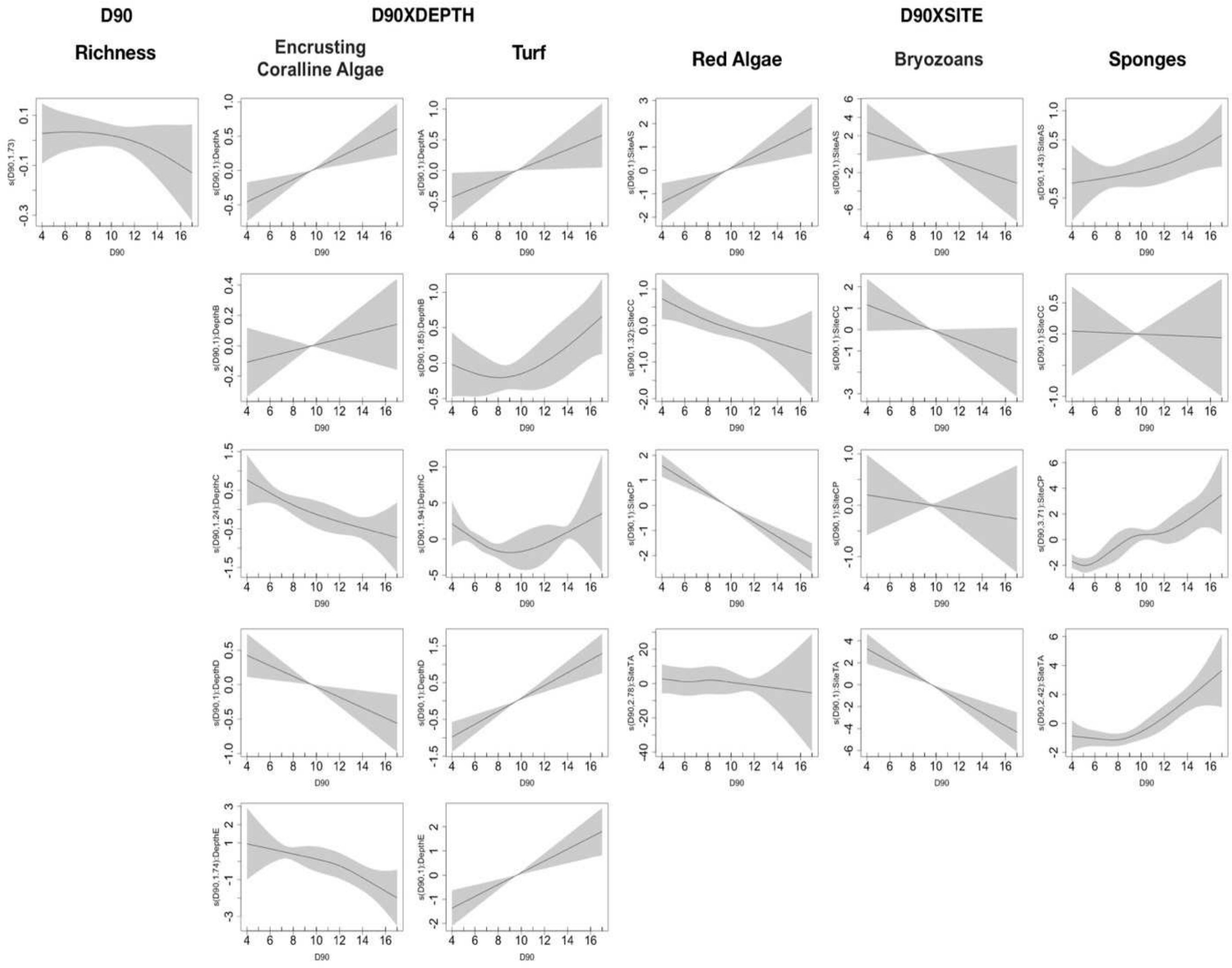


Fig. 3.6 Summary of GAM results showing only the significant explanatory variables of the models: D90 both as main factor and D90 x DEPTH (18m=A, 23m=B, 28m=C, 33m=D and 38m=E), and x SITE (AS, CP, TV, and CC). The y-axis represents the additive predictor by GAM, which is a smoothed function for D90 and for the interaction. The solid line is the smoother and the dotted lines are 95% point-wise confidence bands.

CHAPTER 4

The Mediterranean bioconstructor *Lithophyllum stictiforme* showed adaptability to future warming

4.1 Abstract

Understanding how coralline algae may acclimatize to ocean warming is important to understand their survival over the coming century. Taking advantage of natural differences in temperature conditions between coastal areas in Sardinia (Italy) and between depths, the responses to warming of the crustose coralline alga *Lithophyllum stictiforme*, a key bioconstructor of coralligenous reefs in the Mediterranean, were evaluated in the field by two innovative transplant experiments where translocated specimens were used as controls. Results of the first experiment (algae cross transplanted between a cold and a warm site at two depths, 23 and 34 m) showed that the marginal growth of the alga was not affected by transplants, although natural differences existed between sites and depths, while the growth in thickness in algae transferred from the cold site to the warm one was higher at 34 m of depth. Furthermore, the number of conceptacles was significantly different depending on the site per treatment combination. Results of the second experiment (algae transplanted from 34 m to 15 m of depth under different light irradiance manipulations) evidenced a positive effect of high temperature on marginal growth and on the number of conceptacles, even with an increase of +4°C compared to the control conditions, and a negative effect of high light irradiance. These results suggest an overall good adaptability of *L. stictiforme* at warmer conditions, which encourages considering the use of this bioconstructor transplants in future restoration actions of coralligenous habitats.

4.2 Introduction

Climate variability is expected to increase as anthropogenic global warming continues, and climate models predict that temperature peaks will become more extreme, more frequent and more prolonged in time in many regions (Oliver et al., 2018; Smale et al., 2019; IPCC, 2021). Temperature affects organisms in several ways from the individual level (ecophysiology) to the population and species levels (changes in geographic distribution) (Poloczanska et al., 2013; Bruno et al., 2015; Scheffers et al., 2016; Gauzens et al., 2020). Ocean warming (OW) is altering important physical and structural features of many ecosystems (Hoegh-Guldberg and Poloczanska, 2017; Bruno et al., 2018; Smale et al., 2019) and is perceived as a major threat to key foundation species such as corals (Carpenter et al., 2008; Hughes et al., 2018; Kubicek et al., 2019), kelps (Assis et al., 2016; Wernberg et al., 2016), seagrasses (Marbà and Duarte, 2010; Thomson et al., 2015), and coralline algae (Ragazzola et al., 2012; Ordoñez et al., 2014; McCoy and Kamenos, 2015; Kim et al., 2020). The climate impacts are expressed at various levels of biological organization and often are due to changes in local or regional environmental conditions affecting biological processes such as reproduction and survival (Ådhal et al., 2006). Species may respond differently to climate change because of a variety of factors, such as evolutionary history, species interactions, physiology, genetic architecture, behavior, and habitat-mediated environmental effects on individuals (Etterson and Shaw, 2001; McCoy and Ragazzola, 2014; Louthan and Morris, 2021). Local habitat conditions can mediate the effects of climate, so populations living in different habitats may exhibit different responses to global changes (Crozier et al., 2008).

Coralline algae (CA) are calcareous red algae, belonging to the orders Corallinales, Corallinapetrales, Hapalidiales and Sporolithales, widespread in the photic zone of rocky shores in both hemispheres (Steneck, 1986; Rindi et al., 2019; Schubert et al., 2020). Their morphological habits include encrusting forms (crustose coralline algae, CCA), free-living thalli (rhodolith-maerl) and geniculate articulated thalli; species with these morphologies occur both in intertidal and subtidal habitats and some act as important ecosystem engineers (Steneck, 1986; Nelson, 2009; Fragkopoulou et al., 2021). Some CCA, in particular, are important habitat builders, as their calcified thalli create and stabilize reefs and greatly increase benthic diversity by providing hard substrate for other organisms to settle on (Foster, 2001; Teichert, 2014). Bioconstructor CA are slow-growing and long-lived organisms and occur from the intertidal zone down to 270 m in the tropics, occurring commonly at all latitudes on modern carbonate shelves worldwide (Bosence, 1983; Littler and Littler 1984; Nelson, 2009; Teichert et al., 2012; Foster et al., 2013). Many CA species are experiencing a loss of vitality (Blanfuné et al., 2018) and are considered highly vulnerable to long-term climate change (Cornwall et al., 2019; Rindi et al., 2019). Mineralogical changes have also been evidenced, as the Mg content in CA varies as a function of the sea water temperature (Halfar et al., 2008; Kamenos et al., 2008; Hetzinger et al., 2009; Ragazzola et al., 2020) which is believed to exert primary control by determining incorporation of Mg into the CA cell walls (Kamenos et al., 2008; Caragnano et al., 2014; Diaz-Pulido et al., 2014; Ragazzola et al., 2020).

CCA have occurred in the Mediterranean Sea for ∼140 My and are well-represented in the subsequent fossil record (Chatalov et al., 2015). Among the living taxa, species of the genus *Lithophyllum* (Corallinales) are key bioconstructors, greatly contributing to the formation of coralligenous concretions (Garrabou and Ballesteros, 2000; Ballesteros, 2006). Coralligenous reefs are the most important deep subtidal habitat in the Mediterranean and provide important ecosystem services, acting as hot spots of marine biodiversity (Ådhal et al., 2006; Ballesteros, 2006; Piazzi and Ceccherelli, 2020), carbon sinks (Martin et al., 2014), and providing habitat for economically valuable species (Canals and Ballesteros, 1997; Ballesteros, 2006; Rindi et al., 2019). In coralligenous reefs, CCA constitute a secondary substrate which hosts highly diverse assemblages (Ballesteros, 2006). Spatial analyses of assemblages associated to CCA have evidenced biogeographical patterns (Piazzi et al., 2021), supporting the hypothesis that temperature is a key driver affecting the horizontal and vertical distribution of these communities (Ceccherelli et al., 2020; Pinna et al., 2021). On the contrary, little is known about the influence of temperature on CCA presence and distribution in the

Mediterranean Sea, although several diseases referable to thermal effects have been reported (Hereu and Kersting, 2016) and a time-integrated thermogeographic model has been proposed by Adey and Steneck (2001) to demonstrate conditions under which CCA assemblages evolve biogeographic patterns in their distribution and abundance.

At present, only laboratory studies about vulnerability of CCA at increased greenhouse gas conditions have been conducted (Anthony et al., 2008; Martin and Gattuso, 2009; Rodríguez-Prieto, 2016; Vásquez-Elizondo and Enríquez, 2016; Martin and Hall-Spencer, 2017; Kim et al., 2020). Experiments performed on *Lithophyllum* species have investigated how warming affects growth, respiration, photosynthesis, calcification, and mineralogical responses (Martin and Gattuso, 2009; Martin et al., 2013a; Martin et al., 2013b; Nash et al., 2016; Rodríguez-Prieto, 2016). Thus, despite some knowledge on survival, growth rates and geochemistry of *Lithophyllum*, it is not yet clear how environmental changes translate into the distribution of Mediterranean populations. The need for further insights is also driven by the results of recent molecular studies (De Jode et al., 2019; Pezzolesi et al., 2019). *Lithophyllum stictiforme* (Areschoug) Hauck and *Lithophyllum cabiochiae* (Boudouresque & Verlaque) Athanasiadis, the two main species of the genus in coralligenous concretions, were recently shown to represent a striking case of cryptic diversity: although in the past most authors separated these species, recent treatments (Cormaci et al., 2017; Pezzolesi et al., 2019; Guiry and Guiry, 2022) consider *L. cabiochiae* and *L. stictiforme* conspecific. Both Pezzolesi et al. (2019) and De Jode et al. (2019) concluded that these entities belong to a complex of cryptic species, several of which have a geographic distribution seemingly restricted to a particular area or site (Rindi et al., 2019). Therefore, the need of a better knowledge of the biology of the *Lithophyllum stictiforme* complex in relation to future scenarios is therefore more important and urgent than ever. Indeed, a better understanding of CCA responses to warming is critical to predict how CCA-based communities may change in response to global environmental changes.

Nowadays, there is a growing need of field experiments which may serve as useful bridge between laboratory results and natural environmental processes (Chave, 2013). Taking advantage of natural differences in temperature conditions between coastal areas in Sardinia (Italy, Western Mediterranean, Pansini et al., 2021) and along depth gradients (Ceccherelli et al., 2020), we performed crossed transplants of *L. stictiforme* to examine the temperature effects in terms of mortality, growth, and reproductive structures for the first time in the field. Two experiments were conducted: in the first (between sites experiment, BSE), to evaluate the adaptability of the alga to a different thermal regime, we transplanted algae from a cold site to a warmer one considering two depths; in the second (between depths experiment, BDE), transplants were done within the same site from a deeper to a shallower depth under different light irradiance manipulations to evaluate the influence of the thermocline, which could be increasingly deeper and persistent due to global climate change effects (Cerrano et al., 2000; Collins et al., 2010). The main goal was to understand if *L. stictiforme* is adaptable to changes in thermal conditions and to distinguish the effects of light irradiance from temperature conditions on the algal performance. This species was chosen because it is the most common CCA in the coralligenous concretions considered and occurs throughout in the Mediterranean. The results provide pivotal information collected in the field on the biology of the alga, allowing us to forecast whether future changes in temperature will affect its performance and to propose hypotheses about performances at the population level for the future. Finally, these data may also contribute to draw up future guidelines for a restoration of the coralligenous habitat by transplantation of this foundation species.

4.3 Materials and methods

The two manipulative experiments, BSE and BDE, were both conducted in Sardinia. The BSE was carried out from November 2020 to October 2021 on coralligenous reefs of two sites, Costa Paradiso (CP, 41°04'N, 08°57'E) and Capo Carbonara Marine Protected Area (CC, 39°05'N, 09°31’E, Fig. 4.1), belonging to two different biogeographic regions (Coll et al., 2010; Piazzi et al., 2021). The BDE was done from June to November 2021 on the coralligenous reefs at the CP site. Both sites are far from any anthropogenic sources of disturbance and are characterized by a high oligotrophy (Barisiello et al., 2002; Regione Autonoma della Sardegna 2016). However, large differences in sea water temperature were evidenced between the sites in the Sea Surface Temperature (SST) climatology and water stratification during the hot season in terms of duration, temperature intensity and variability (Ceccherelli et al., 2020). Probably due also to such differences, the coralligenous assemblages of the two sites have different geomorphological structures (Piazzi et al., 2021): in particular, CP is characterized by massive bioconstructions from 15 m of depth, while in CC the same type of constructions is found only deeper than 30 m (Pinna et al., 2021).

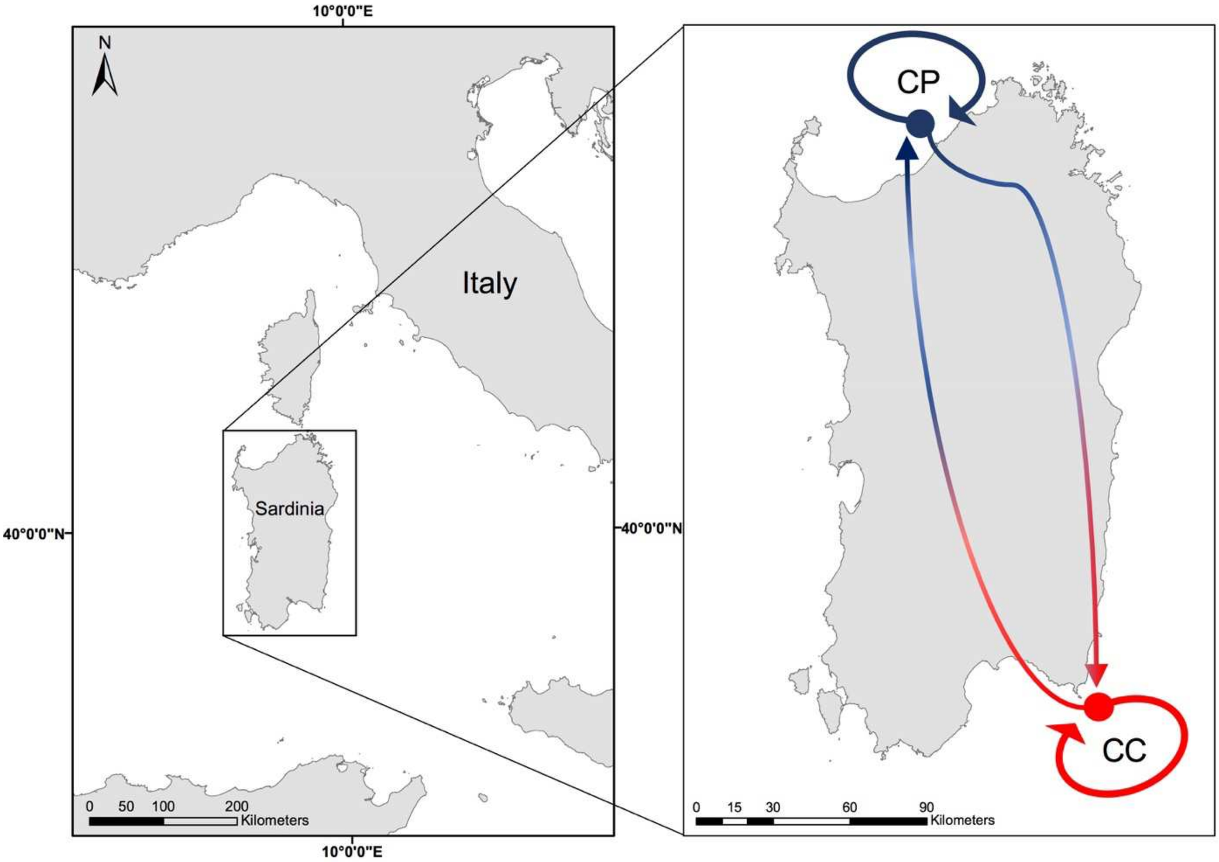


Fig. 4.1 Map of the study sites: Costa Paradiso (CP) in blue = cold site and Capo Carbonara (CC) in red = warm site. Arrows indicate the translocated and transplanted treatments in the BSE.

4. 3. 1. Morphology and identification of the material used for the experiments

Due to the complex taxonomic nature of the *L. stictiforme* complex, great care was taken to ensure that all specimens used in the experiments belonged to the same species. The specimens used in this study were identified as *L. stictiforme* based on the circumscription of this species provided by Pezzolesi et al. (2019). They consisted of lobed lamellae, often superimposed, up to 1.5 mm thick, with a smooth to undulate surface, violet to dark pink in colour (Fig. 4.2). Using DNA sequence data, Pezzolesi et al. (2019) showed that specimens exhibiting this habit represent the genuine *L. stictiforme* and demonstrated that this species is widespread in the central Mediterranean. For this study it was not possible to sequence all specimens used in the experiments; however, DNA sequence data (partial *rbc*L sequences) were obtained for a few representative specimens from CP, confirming the assignment to *L. stictiforme* (Caragnano and Rindi, unpublished data). It is likely that the specific identity of the specimens reported as *L. cabiochiae* by Martin and Gattuso (2009) and Martin et al. (2013a; 2013b) and Rodríguez-Prieto (2016) corresponds to that of the specimens that we used in this study.

Fig. 4.2 Specimen of the algae *L. stictiforme* in its natural enviromental at Costa Paradiso at 34 meters of depth.

4. 3. 2. Sampling design and experiment set up

In the BSE a cross-transplant experiment of *L. stictiforme* was performed between CP and CC maintaining the origin depth (*i.e.* 23 and 34 m). Based on temperature variations measured by Ceccherelli et al. (2020), CC has considerably warmer water than CP, and the rationale of the BSE relies on the fact that, at the same depth, the algae of the two sites can experience different temperatures for several months, at least from May to November (Ceccherelli et al., 2020). At each combination of site and depth, eight *L. stictiforme* thalli were fixed on the substratum: four transplanted from the other site (same depth) and four translocated (same site and same depth, *sensu* Chapman, 1986). The experimental design consisted of three factors (Fig. 4.3): 1) Site, with two levels (cold=CP and warm=CC); 2) Depth, with two levels (23 and 34 m); 3) Treatment, with two levels (transplanted and translocated).

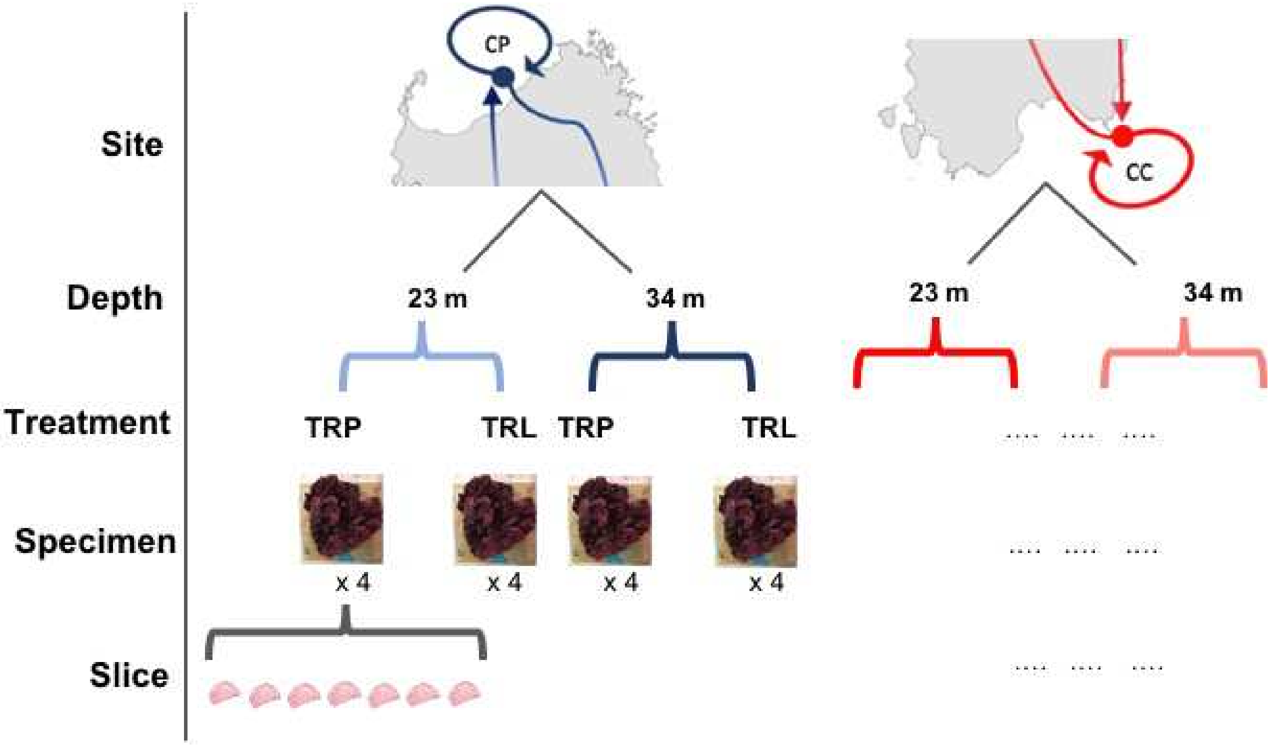


Fig. 4.3 Sampling design of the BSE. Site: CP=cold site, CC=warm site; Depth: 23 and 34 m; Treatment: TRP=transplant, TRL=translocation.

In the BDE, to evaluate the influence of warm water on 34 m depth algae simulating the effects of the near future deeper thermocline, and to disentangle the effects of irradiance from those of the temperature, four treatments were used by transplanting or translocating *L. stictiforme* (4 replicated treatments) between two depths at CP site: 1) *L. stictiforme* was transplanted from 34 m to 15 m depth and placed in a natural cavity within the bioconstruction (L TRP=transplanted at low irradiance), so that the algae could experience the 34 m light irradiance but water temperature above the thermocline; 2) *L. stictiforme* was translocated at the same depth of origin (34 m, L TRL=translocated at low irradiance); 3) *L. stictiforme* was transplanted from 34 m to 15 m on a exposed substratum (H TRP=transplanted at high irradiance); 4) *L. stictiforme* was translocated at the same depth of origin (15 m, H TRL=translocated at high irradiance). The L TRP and L TRL treatments simulate the temperature and irradiance conditions that occur at 34 m of depth in the future and current scenario, respectively; the comparison between L TRP and H TRP algae allows disentangling the effect of temperature from light irradiance, while the comparison between the H TRL and H TRP treatments allow to assess the adaptability of algae from different depths to high temperature and high irradiance conditions.

For the setup of both experiments, healthy *L. stictiforme* (about 8 cm in diameter) with no signs of damage or bleaching were carefully collected (detaching their basal parts using hammer and chisel) by SCUBA diving (Fig. 4.4a) and transported in insulated aquaria to the laboratory within one hour, where they were cleaned from epiphytes and rinsed with new seawater. Afterwards, they were placed in aquaria with oxygenators, kept at the temperature of their origin environment and stained using Alizarine-Red stain (Sigma-Aldrich, Steinheim, Germany) 0.25 $g \cdot l^{-1}$ for 24 h (Blake and Maggs, 2003; Rivera et al., 2004). The stained *L. stictiforme* thalli were transported to the receiving sites and glued with a two-component epoxy underwater filler (Sub Coat Veneziani) on granite tiles which were attached on horizontal substrates in the field (Fig. 4.4a). Both CP and CC host extensive populations of healthy *L. stictiforme* occupying a relatively wide bathymetric range and the collection of the specimens used for the experiments did not compromise the vitality of the populations.

For both experiments, two data loggers (HOBO Pendant Temp/Light MX2202, Onset Computer Corporation, USA) per treatment were fixed to record water temperature and light irradiance (only for the BDE) during the whole experimental time. The loggers were checked and cleaned from epiphytes every two months. At the end of the experimental period, each thallus was recollected from the field and transported to the laboratory, where mortality was evaluated by visually inspecting the color of the thallus surface._Thalli were considered dead when a total bleaching of the surface occurred, since the colour change does not indicate thallus deterioration, as the concentration of phycobilin can vary in relation to the exposure. Then algae were rinsed with fresh water, air dried and individually embedded into epoxy resin mold (Kit EpoFix Struers; Fig. 4.4b).

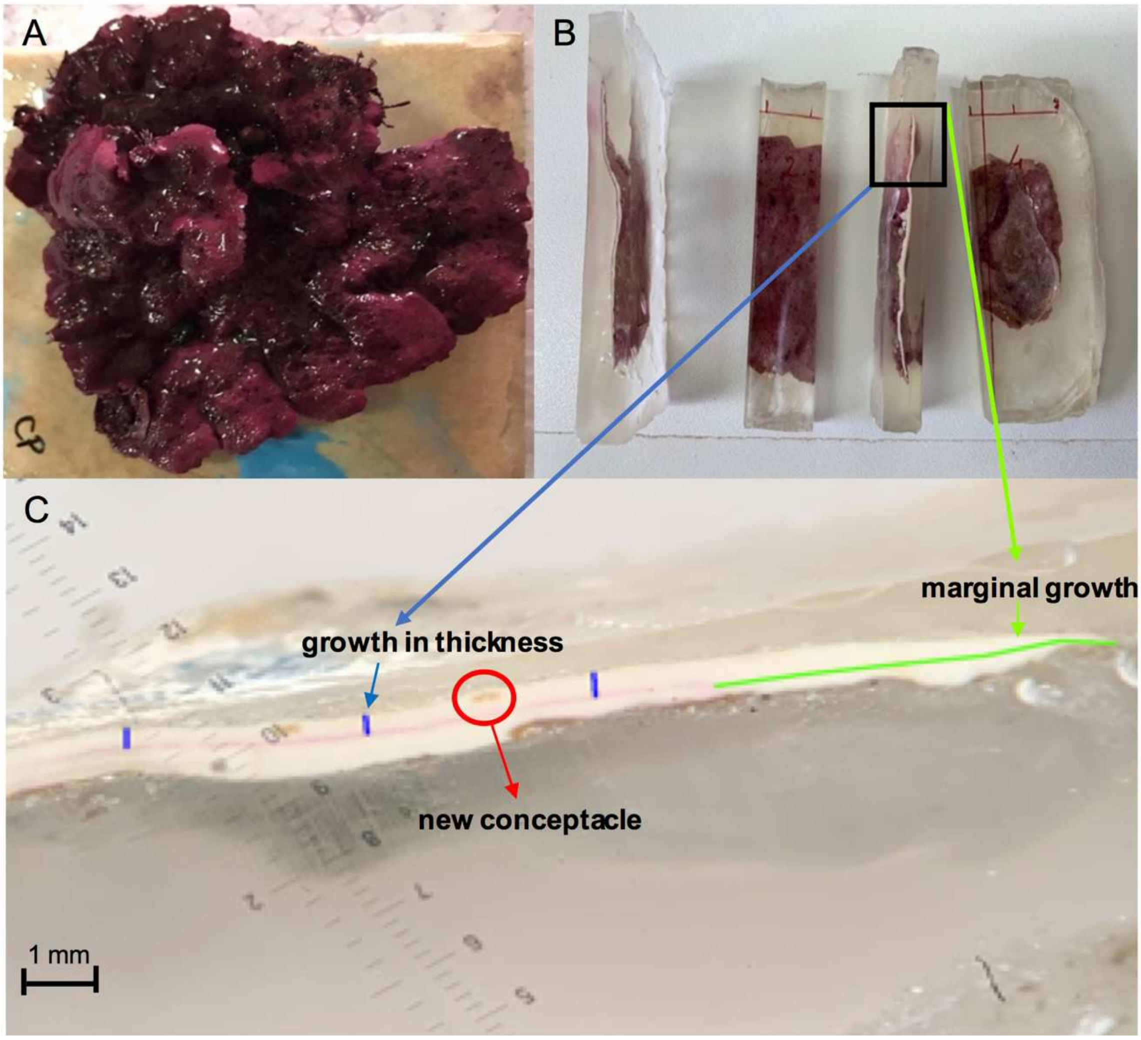


Fig. 4.4 *Lithophyllum stictiforme*: A) thallus on tile; B) embedded into epoxy resin mold; C) thallus slice under the binocular (in green = marginal growth, in blue = growth in thickness).

4. 3. 3. Data collection

From each thallus seven slices (about 1 cm wide) were obtained using a circular rock saw, and each slice was polished using a machine with abrasive papers of different grain size (*i.e.* from 30 to 15 μm) on the longitudinal axes and photographed under the binocular. Then thallus marginal growth and growth in thickness were estimated on the images through ImageJ software (https://imageJ.nih.gov, Fig. 4.4c) by measuring the thallus new portions from the Alizarine stain. A total of five measurements at equal distances (approximately 3 mm) were taken along the cross-section of each slice and averaged to obtain the growth in thickness measurements. Furthermore, in the portion of the alga grown during the experiment, the abundance of conceptacles was checked, and the number of conceptacles was calculated for each section. For both experiments, each slice image was considered a replicate (Fig. 4.4b).

4. 3. 4. Data analysis

In order to assess thermal differences between sites (CC and CP), two approaches were used: i) the daily temperature recorded by loggers was analyzed by a three-way permutational analysis of variance (Primer 7 + PERMANOVA, Anderson, 2001) based on Euclidean distance using an orthogonal design where site (two levels), depth (two levels) and season (four levels) were fixed factors (n = 28); ii) SST data were used to describe marine heat waves (MHWs) in both sites according with Hobday et al. (2016, 2018), using heatwaveR packages in R (Schlegel and Smit, 2018).

Growth data of *L. stictiforme* of the BSE were analysed by two three-way analyses of variance (ANOVAs) where site (CC and CP), depth (23 and 34 m), and treatment (TRL and TRP) were fixed orthogonal factors. Twenty-eight measurements (n=28, pooling data from specimens under the same conditions) were used for each combination of factors. Since, for ‘number of conceptacles’, ANOVA assumptions were not verified, a PERMANOVA based on Euclidean distance with the same design was performed.

In BDE, the effects of treatments on the marginal growth were assessed by one-way ANOVA where treatment (L TRL, L TRP, H TRP, and H TRL) was a fixed factor with fifty-six replicates (n= 56, pooling data obtained from both slice sides of specimens at the same conditions). Due to the absence of new reproductive structures in H TRL and H TRP thalli, the ANOVA on the number of conceptacles was run with only two levels (L TRL and L TRP). Since, for growth in thickness, ANOVA assumptions were not verified, a PERMANOVA based on Euclidean distance with the same design on marginal growth, was performed.

In both experiments, Barlett's test was used to check for homogeneity of variances. For *a posteriori* comparisons of the means, Tukey's test was run after ANOVAs (Underwood, 1997) and Pair-Wise comparison after PERMANOVAs (Anderson, 2001).

4.4 Results

4. 4. 1 Between Site Experiment

Temperature data collected from loggers estimated the temperature differences between CP and CC at the two depths during the study period (Fig. 4.5). Differences between sites in terms of annual average temperature were overall larger at 23 m depth (1.30°C) than at 34 m (0.68°C, Table 4.1). Significant differences in temperature were found between sites, depths, and seasons highlighting that CC site was significantly warmer than CP for most of the study period (Table 4.2 and Fig. 4.5).

Table 4.1 BSE: season and year (1 November 2020 – 31 October 2021) average water temperature of sea surface temperature (SST from satellites) and *in situ* at 23 and 34 m of depth (from loggers) at Costa Paradiso=CP and Capo Carbonara=CC.

	Winter	Spring	Summer	Autumn	year
SST CP	14.56	15.26	24.06	22.24	18.91
SST CC	15.42	16.03	25.22	23.65	19.93
CP 23	14.49	15.06	19.82	20.93	17.46
CP 34	14.52	14.85	17.06	19.16	16.34
CC 23	15.23	15.31	21.09	22.50	17.91
CC 34	15.14	15.34	19.44	18.26	17.22

In addition, during the study period eight MHWs occurred at each of the sites, but not simultaneously: at CP two MHWs during the cooler period (Nov 2020-Apr 2021) and six during the warmer (May-Oct 2021), while in CC four MHWs in each of the periods. Overall, the highest MHW intensity category was recorded at CC during October 2021 (Fig. S4.1).

Table 4.2 Results of PERMANOVA testing difference in temperature between Site (CP and CC); Depth (23 and 34) and Season (Winter, Spring, Summer, and Autumn) and Pair wise tests on the interactions Dept x Site and Site x Season.

Source of variation	***df***	***MS***	***Pseudo-F***	***P(perm)***
Site = si	1	254.9	68.0	0.001
Depth = de	1	480.7	128.2	0.001
Season = se	3	2365.7	631.1	0.001
sixde	1	13.5	3.6	0.067
sixse	3	163.5	43.6	0.001
dexse	3	101.4	27.1	0.001
sixdexse	3	12.8	3.4	**0.018**
Residual	1236	3.7		

Results of Pair wise test

Dept x Season			Site x Season		
23 m	winter	CP < CC	CP	winter	23 = 34
	spring	CP = CC		spring	23 = 34
	summer	CP < CC		summer	23 > 34
	autumn	CP = CC		autumn	23 > 34
34 m	winter	CP = CC	CC	winter	23 > 34
	spring	CP = CC		spring	23 = 34
	summer	CP < CC		summer	23 > 34
	autumn	CP < CC		autumn	23 > 34

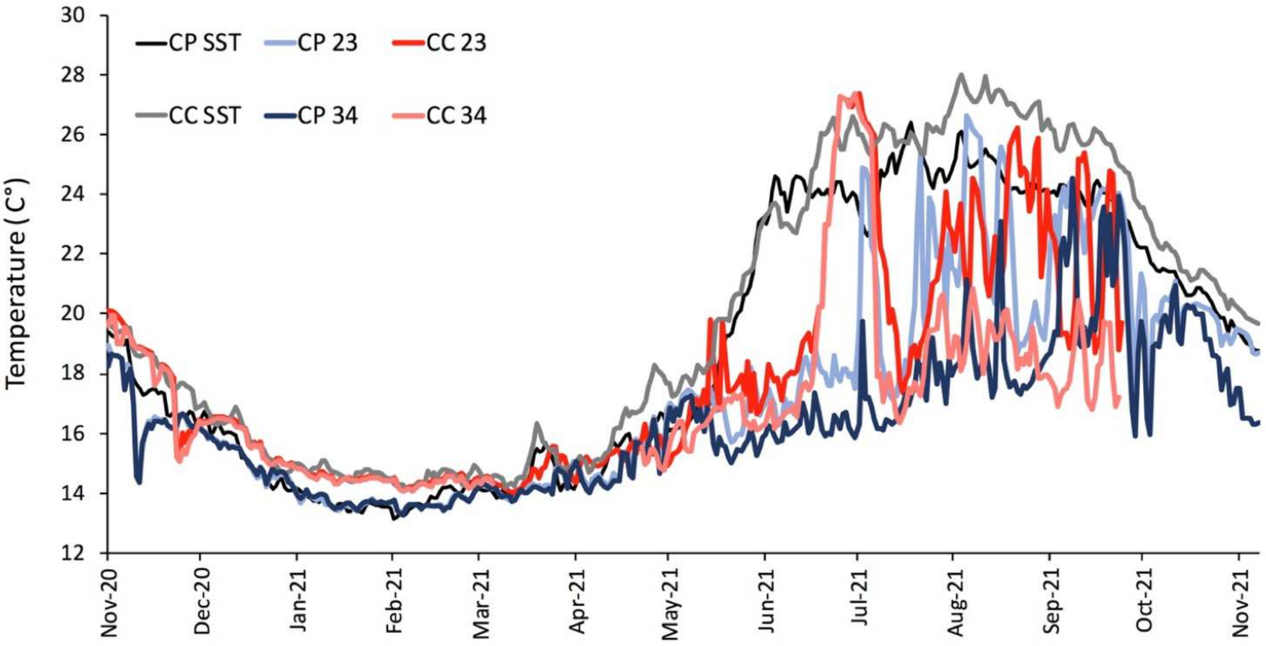


Fig. 4.5 BSE: Daily temperature from November 2020 to October 2021 at the two sites (CP and CC), each depth (23 and 34 m from loggers). In black and grey SST (for CP and CC, respectively) from satellites.

All algae were found healthy at the end of the study and no mortality was recorded. The marginal growth was significantly different depending on the site per depth and site per treatment combination (Table 4.3): *L. stictiforme* at 23 m of depth exhibited a higher marginal growth at CP site than at CC, while no difference between sites was evidenced at the 34 m of depth. Furthermore, at CP a higher marginal growth was observed at 23 m than at 34 m deep, but at CC no difference between depths was found (Fig. 4.5a).

However, the most important result consisted in the comparison between transplanted and translocated thalli: at both sites the algae transplanted had a marginal growth similar to the translocated, even though differences were found between sites for the translocated algae (higher marginal growth at CP). Moreover, no difference between transplanted algae was detected between sites (Fig. 4.5a).

Table 4.3 BSE: results of ANOVA testing the effect of Site (CP vs CC), Depth (23 vs 34 m) and Treatment (transplant=TRP vs translocated=TRL) on *L. stictiforme* thallus marginal growth and Tukey test on the interaction Site x Depth and Site x Treatment.

Source of variation	*Df*	*MS*	*F-value*	*P- value*
Site = S	1	3.568	14.565	0.0002
Depth = D	1	0.698	2.851	0.0928
Treatment = T	1	0.088	0.360	0.5490
S x D	1	1.891	7.718	**0.0060**
S x T	1	1.150	4.695	**0.0313**
D x T	1	0.446	1.822	0.1784
S x D x T	1	0.235	0.958	0.3288
Residual	216	0.245		

Tukey test of the interaction Site x Depth

(i) Site	(ii) Depth
CP: 23 > 34	34: CP = CC
CC: 23 = 34	23: CP > CC

(i) Site	(ii) Treatment
CP: TRL = TRP	TRL: CP > CC
CC: TRL = TRP	TRP: CP = CC

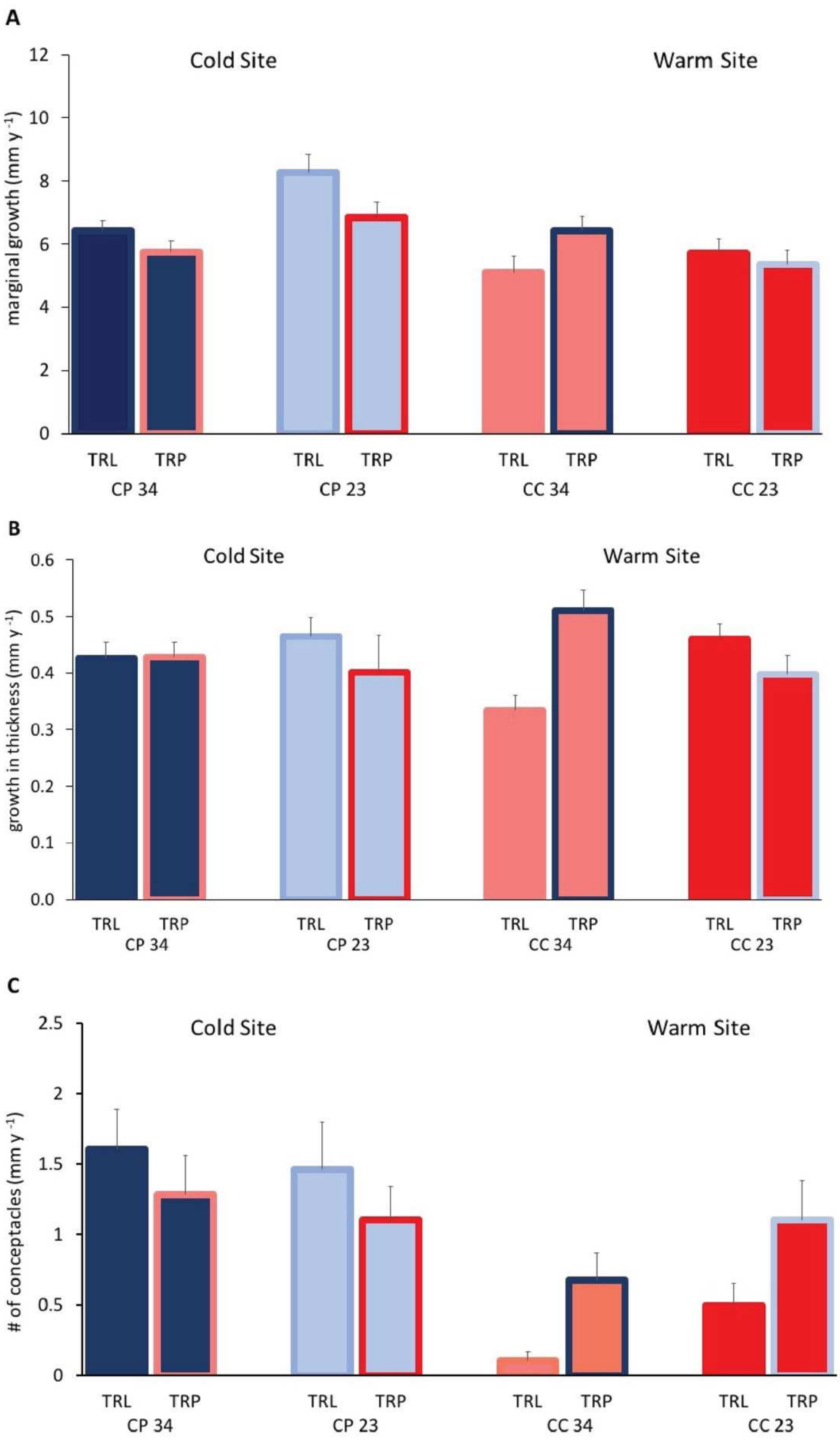


Fig. 4.5 BSE: Average (+SE) *L. stictiforme* A) marginal growth, B) growth in thickness and C) number of new conceptacles at the two sites (CP and CC), two depths (23 and 34 m), and between treatments (TRL = translocated and TRP = transplanted).

Growth in thickness of *L. stictiforme* was influenced by the interaction of all conditions (site, depth, and treatment, Table 4.4). In particular, at CP there was no difference between treatments at 34 m of depth, while at 23 m algae translocated exhibited a thicker growth than algae coming from the warm site (Fig. 4.5b). At 34 m of depth at CC, algae transplanted from CP had a higher growth than the translocated, but at the shallower level (23 m) there was no difference between treatments. Again, the result that should be highlighted is the differences in growth in thickness found at the CC site: transplanted specimens and translocated specimens at 23 m of depth had a similar growth, whereas at 34 m the transplanted algae exhibited a higher growth than the local algae. Overall, at 23 m of depth there was no difference between sites, whereas at 34 m the algae that grew the most were those of CP, either translocated or transplanted to the warmer site (Fig. 4.5b).

The number of conceptacles was significantly different depending on site per treatment combination (Table 4.5). Specifically, algae originating from CP seemed to have naturally more new conceptacles than thalli originating from CC, while no difference between transplants was observed. However, in the comparison between treatments, no difference was detected between the thalli originating from CP and those transplanted from CC to CP (Table 5 and Fig. 4.5c), while at CC the thalli transplanted from CP showed a higher number of conceptacles than the thalli originating from CC.

Table 4.4 BSE: results of ANOVA testing the effect of Site (CP vs CC), Depth (23 vs 34 m) and Treatment (transplant=TRP vs translocated=TRL) on *L. stictiforme* thallus growth in thickness and Tukey's test on the interaction Site x Depth x Treatment.

Source of variation	***Df***	***MS***	***F- value***	***P- value***
Site = S	1	0.00365	0.313	0.5761
Depth = D	1	0.00150	0.129	0.7200
Treatment = T	1	0.00295	0.254	0.6148
S x D	1	0.00111	0.096	0.7576
S x T	1	0.08275	7.116	0.0082
D x T	1	0.24039	20.670	0.0000
S x D x T	1	0.06699	5.760	**0.0172**
Residual	216	0.01163		

Tukey Test of the interaction Site x Depth x Treatment

(i) Site x Depth
CP34: TRL = TRP
CC34: TRL < TRP
CP23: TRL > TRP
CC23: TRL = TRP

(ii) Site x Treatment
CP TRL: 23 = 34
CC TRL: 23 > 34
CP TRP: 23 = 34
CC TRP: 23 < 34

(iii) Depth x Treatment
23TRL: CP = CC
23TRP: CP = CC
34TRL: CP > CC
34TRP: CP < CC

Table 4.5 BSE: results of PERMANOVA testing the effect of Site (CP vs CC), Depth (23 vs 33 m) and Treatment (transplant=TRP vs translocated=TRL) on *L. stictiforme* number of conceptacles and Pair-Wise comparison test on the interaction Site x Treatment.

Source	***Df***	***Mean Sq***	***Pseudo-F***	***P(perm)***
Site	1	33.02	20.94	0.0001
Depth	1	0.87	0.55	0.4563
Treatment	1	0.87	0.55	0.4555
SxD	1	4.57	2.90	0.0923
SxT	1	12.07	7.66	**0.0055**
DxT	1	-3.91E-15	1.50E-14	1.0000
SxDxT	1	0.02	0.011	0.9151
Residuals	216	1.58		

Pair-Wise test

Site x Treatment
CP TRL > CC TRL
CP TRP = CC TRP
CP TRL = CP TRP
CC TRP > CC TRL

4. 4. 2 Between Depths Experiment

The temperature experienced by *L. stictiforme* at 15 m (L TRP, H TRP and H TRL) was warmer than at 34 m (L TRL) in terms of both maximum and average temperature, the difference being 2.08 °C and 4.23 °C, respectively (Fig. 4.6a). Light irradiance between the L TRL and L TRP was similar, indicating that the natural cavity used for the experiment was adequate to reproduce the 34 m irradiance (the highest intensities recorded were 36.67 and 36.36 µmol m^{-2} s^{-1}, for the two treatments, respectively), while irradiance levels at the exposed 15 m treatments (H TRL and H TRP) were much higher (highest intensity 160.49 µmol m^{-2} s^{-1}, Fig. 6b).

All algae appeared healthy for the whole study period of the BDE. A higher marginal growth was found in L TRP compared to the L TRL *L. stictiforme* (Table 4.6 and Fig. 4.7a). Furthermore, the lowest growth was found in the high irradiance treatments (H TRP and H TRL), regardless of the origin of the algae (Fig. 4.7a). The higher irradiance clearly inhibited the growth in thickness, but no difference between L TRP and L TRL algae was found (Table 4.6 and Fig. 4.7b). Algae produced conceptacles only where irradiance condition was low, although transplanted algae had a higher number than the translocated (L TRP and L TRL, one way ANOVA, $F_{1,112}$=48.4, P= 0.029, Fig.4.7c).

Table 4.6 BDE: results of ANOVA testing the effect of treatment (L TRL, L TRP, H TRP, and H TRL) at CP on *L. stictiforme* marginal growth and PERMANOVA on *L. stictiforme* growth in thickness.

	Marginal growth ANOVA				**Growth in thickness PERMANOVA**		
Source of variation	***Df***	***MS***	***F-value***	***P-value***	***MS***	***Pseudo-F***	***P(perm)***
Treatment	3	116.29	46.29	**<2e-16**	0.687	64.17	**0.0001**
Residuals	224	2.51			0.011		

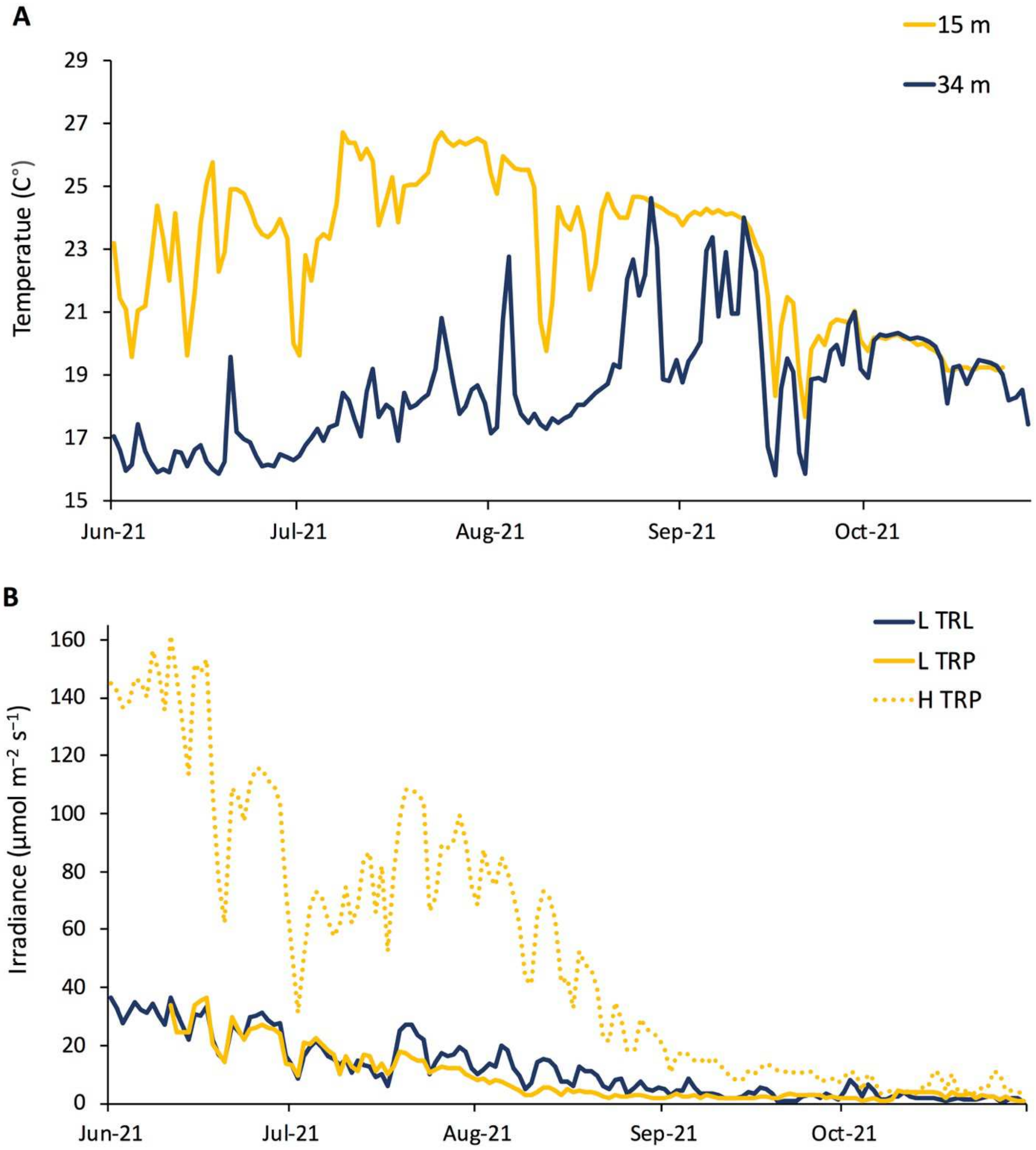


Fig. 4.6 BDE: Daily A) seawater temperature and B) irradiance from June to November 2021: conditions at 34 m of depth L TRL in blue, at 15 m L TRP in solid yellow and H TRL and H TRP in dotted yellow.

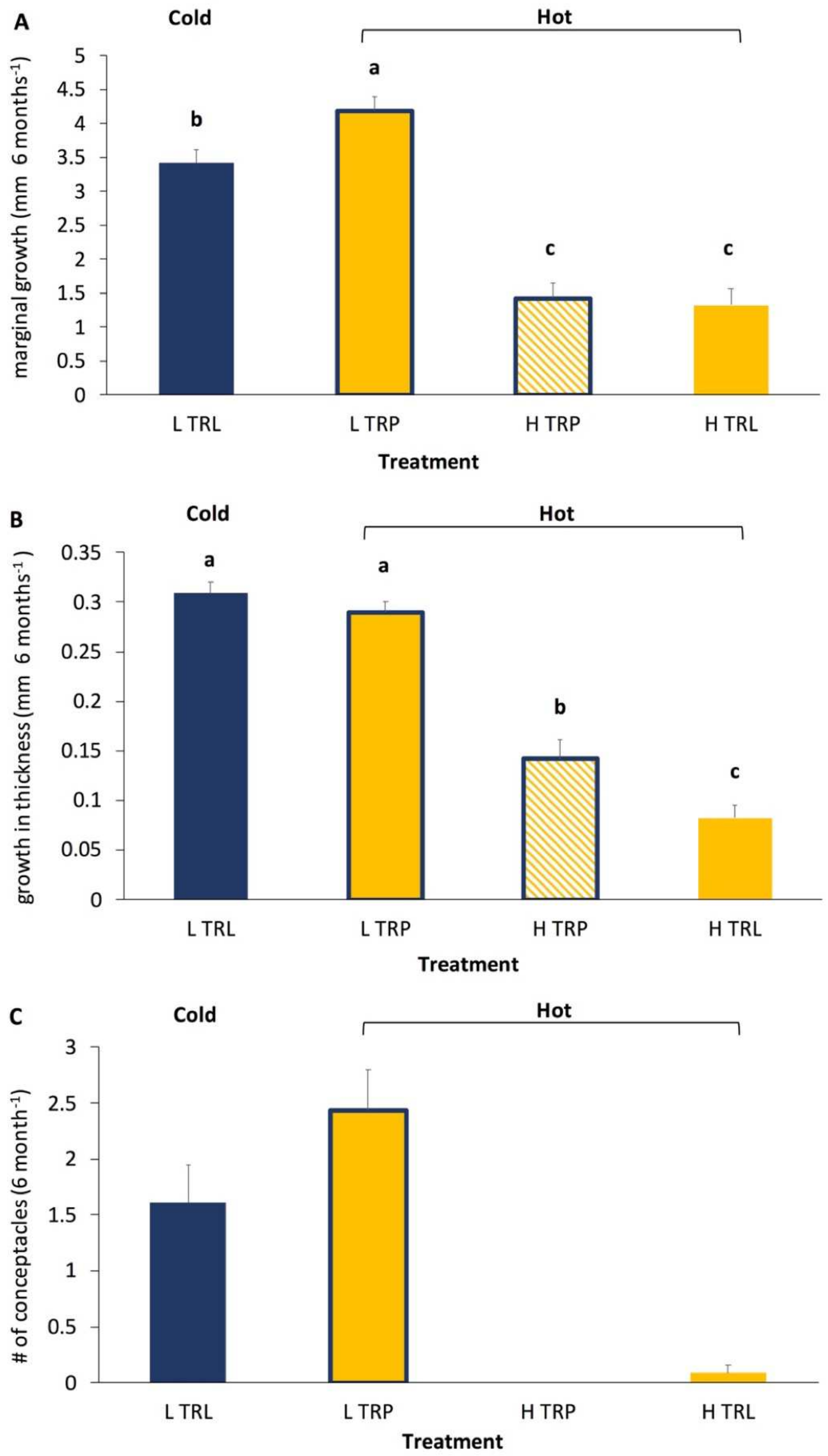


Fig. 4.7 BDE: Average (+SE) *L. stictiforme* A) marginal growth, B) growth in thickness, and C) number of conceptacles at the four treatments (L TRL =translocated at low irradiance, L TRP= transplanted at low irradiance, H TRP =transplanted at high irradiance and H TRL=translocated at high irradiance). Blue refers to cold and yellow to warm conditions. Letters indicate significant results of Tukey's test and pair-wise comparisons.

4.5 Discussion

This study provides in situ data on the performance of an important bioconstructor of Mediterranean coralligenous reefs by examining the responses of the red crustose alga *L. stictiforme* to different temperature and light conditions. First, it was shown that *L. stictiforme* mainly exhibits marginal growth rather than increase in thickness, confirming that this species invests in lateral expansion of thalli, although some natural differences both in growth and in conceptacles production between sites were evidenced in the BSE. Both thallus growth and number of conceptacles of *L. stictiforme* had a better performance at the cold site (CP); in terms of differences between depths no variation was found at CP, while at the warmer CC a higher thickening was recorded at 23 m of depth. Overall, the growth values found in the present study for *L. stictiforme* exceed those reported in the literature for specimens of CCA probably referable to the same species (Garrabou and Ballesteros, 2000; Basso and Rodondi, 2007).

The treatments provided several interesting insights. In the BSE the marginal growth of the CP algae at the warm CC site was comparable to that of the controls (the CC translocated algae), as well as the growth in thickness at 23 m depth. Conversely, a higher increase in thickness was observed in the deeper CP algae (34 m) compared to the controls. Therefore, temperature experienced at the warm site not only was tolerated, but the performance indicates a good adaptability of the CP specimens to the warmer environment. The fact that a higher thickness of CP algae seemed promoted by the warmer conditions only at the deeper CC areas opens several scenarios. First, the possibility that at the CC site the high light irradiance at 23 m could depress the growth promoted by the warm temperature, while algae at 34 m of depth could benefit from a darker environment: in fact, evidence gained by a laboratory experiment on this species supported the interacting effect of temperature and irradiance, providing information about the importance of levels for each of the two factors to make accurate predictions on their effects (Rodríguez-Prieto, 2016). However, comparing the conditions that the algae experienced in the field during the BSE with those set in the laboratory experiments can be misleading, because the real natural variability cannot be reproduced in aquaria and because the specimens used in Rodríguez-Prieto's study were collected in Catalonia (eastern Spain). Although probably belonging to the same species, they may be adapted to different local conditions compared to the CP specimens. On the other hand, differences between TRP and TRL at the two depths in CC could be attributed to different adaptations of the CP algae (23 m vs 34 m) and therefore to different performance thresholds. In order to interpret whether the different performance (growth in thickness) of the CP algae in the BSE depended on temperature and irradiance conditions, the data collected should be integrated by testing the two factors on the algal performance across gradients likely using chambers (*e.g.* Anton et al., 2020): much of the experimental evidence gained in laboratory on *L. stictiforme* (or *L. cabiochae*) is not based on gradients, but only on increases of 3°C over the ambient temperature (Martin and Gattuso, 2009; Diaz-Pulido et al., 2012; Martin et al., 2013a; Martin et al., 2013b; Nash et al., 2016), because they tested hypotheses derived from modelling predictions for the end of the century (IPCC, 2019).

However, in this regard, results obtained from the BDE have provided solid evidence that the 15 m temperature during summer and autumn (warm) had positive effects on the 34 m algae only in low irradiance conditions (L TRP compared to L TRL). The comparison between H TRP e and L TRP allowed disentangling the interaction between temperature and irradiance, as the 15 m irradiance had a negative effect on the *L. stictiforme* performance, regardless of the origin (15 or 34 m) of the algae. In particular, the most affected trait was the formation of reproductive structures since no new conceptacles were detected at the end of experiment. Accordingly, Rodriguez Prieto (2016), highlighted that irradiance was the most limiting factor when compared with temperature. Furthermore, it is noteworthy that no trade-off has been found on the growth and formation of conceptacles. A possible explanation is that all the considered response variables depend on the same calcification dynamics and L TRP conditions were too harsh for *L. stictiforme* tolerance thresholds. By fact, such insights support the hypothesis that future deepening of the thermocline (Hoegh-Guldberg and Bruno, 2010) would promote the marginal growth of the algae and the conceptacle formation, even though growth in thickness will not be affected. This fact would agree with the theory that marginal growth and growth in thickness are the result of a trade-off in CCA (Dethier and Steneck, 2001), probably as a result of energetic constraints and biotic interactions effects that incur different maintenance costs (McCoy and Ragazzola, 2014). Our results also provide evidence that *L. stictiforme* may be more resistant to the effects of OW than widely believed. This expectation is also supported by the fact that conceptacles of *L. stictiforme* developed in warmer conditions, even if at the moment it is unknown whether their abundance may not necessarily reflect neither their reproductive strategy (spores or gametes) nor their effectiveness. Nevertheless, as thick CCA such as *L. stictiforme* are foundation species, their adaptability could also favor the establishment of other species of the coralligenous reefs due to an increase in substrate availability.

Interestingly, comparing the performance of algae across the two experiments for the deepest bathymetry in the CP site (the marginal growth was 6.31 mm ± 0.8 in 12 months, *i.e.* 0.53 mm per month^{-1} in the BSE, and 3.42 ± 0.19 in 6 months, *i.e.* 0.57 mm month^{-1} in the BDE), no seasonal growth pattern is suggested. This result would not be in accordance with Martin et al. (2013a), who obtained a higher growth rate in the hot seasonal period (in L TRL in the BDE). Therefore, further information is needed to estimate the seasonal performance of this species, even because some contrasting evidence was provided by the BSE and BDE for the growth in thickness (0.42 mm and 0.31 mm on average in the 12 months and in the hot 6 months, respectively), supporting the theory that the performance of *L. stictiforme* depends on complex mechanisms.

The healthy status and survival of the manipulated specimens in the BSE and BDE are overall quite unexpected and encouraging in the warming scenario: studies focusing on temperate (Martin and Gattuso, 2009) and tropical CCA (Anthony et al., 2008; Diaz-Pulido et al., 2012) highlighted that 3°C over the ambient temperature have a negative effect, especially for the tropical ones, as they live close to their thermal limit (Pörtner, 2010), while in the present study all algae were found alive and healthy, including those that were exposed for 6 months to 4°C above the control condition (BDE). This wide tolerance of temperature variation, especially to the combination + 4°C plus MHWs is particularly noteworthy for a deep subtidal species, especially for specimens distributed under the thermocline depth (such as the 34 m *L. stictiforme*), as it would rather be expected for macroalgae living in much more variable conditions, such as in intertidal habitats (Pakker et al., 1995). Overall, although evidence will need to be corroborated with other field experiments, the adaptability of *L. stictiforme* here highlighted between sites and depths is encouraging even in relation to the possible use of transplants of this bioconstructor for future restoration actions.

CONCLUDINGS REMARKS

There is a growing body of evidence that anthropogenic global change impacts a range of ecological systems and is a major source of disruption to global marine biodiversity (Poloczanska et al., 2016; Hughes et al., 2018; Smale et al., 2019). Many effects of climate change on the functioning of marine ecosystems are directly or indirectly due to changes in the physiology and structure of foundation species, especially in coastal marine habitats (Harley et al., 2006).

In the Mediterranean Sea, many important benthic marine habitats such as coralligenous reefs, are profoundly transformed mainly by continuous warming (Marbà et al., 2015). Thus, the knowledge of their structure and biodiversity, together with the assessment of their response to an increase in warming, are crucial for ecologists and managers to maintain their functioning, enabling their conservation (Kleypas et al., 2001; Hughes et al., 2003; Martin et al., 2014).

My doctoral dissertation has contributed to improving the knowledge of spatial variability of coralligenous reefs under climate current conditions and of how this variability could change in a global warming scenario in Sardinia, through assessment of patterns ranging from local to biogeographic scale and at different depths, and through the evaluation of the performance of the main biocostructor of this habitat, *Lithophyllum stictiforme,* to warming.

The general hypothesis that the structure of coralligenous assemblages changes spatially across different biogeographic areas was met. In particular, it was found that differences in the dominant taxa and that the number of morphological groups increased significantly with depth (chapter 2). These differences were also linked to the thermal variations of the different study areas, since the biogeographical patterns are related to thermal environment (chapter 1 and 2). Particularly, differences in the structure of the coralligenous community were found strongly dependent on the combination of site and depth, in correspondence to specific temperature averages and variability (chapter 3). I have also related the differences in coralligenous spatial patterns to the thermal environment. In fact, richness in taxa was negatively influenced by median temperature (corroborating findings of chapter 2) and providing evidence that an increase in temperature intensity is associated to an increase and decrease of CCA and bryozoans, respectively. In addition, the results found in Chapter 3 suggest that the thermal anomalies, identified by D90 temperature descriptor, will lead to decline in percentage coverage of key taxa/morphological groups especially upon exceeding certain temperature thresholds. Under these circumstances, opportunistic and turf species could potentially increase their coverage to spaces that used to be occupied by species vulnerable to heat. Thus, the coralligenous community would be not only totally different (taxonomically and functionally) from the original one, but also many feedbacks maintaining ecosystem stability could be replaced and return to the initial status would be very difficult.

The results of Chapter 3 were also in agreement with the observed performance of one of the main CCA of the coralligenous reef (chapter 4), as *L. stictifome* showed a good adaptability to warming, even at temperature on average 4°C higher than control conditions for a whole season. Furthermore, these findings have substantially contributed to filling the existing knowledge gap on several basic aspects of the biology and ecology of Mediterranean coralline algae, with the aim of predicting the responses of these algae to future warming.

To date, we know that the effects of global warming on the coralligenous habitat have negative effects in terms of a decrease in biodiversity and a decrease in functional traits that provide this habitat with important ecosystem functions (Cerrano et al., 2000; Garrabou et al., 2019; Verdura et al., 2019; Gomez-Grass et al., 2021); therefore, the decline of some coralligenous key species could lead to imbalances in ecosystem functioning. Furthermore, the differences in the structure of coralligenous assemblages found between areas and depths reflect an excellent ecological status of the coralligenous cliffs (Piazzi et al., 2022), underlines that responses of coralligenous assemblages to global warming can have different context-dependence trajectories of change, highlighting the importance to improve monitoring programs and generate more accurate indicators for each type of coralligenous assemblage. Finally, these findings are of fundamental importance as they allow us to hypothesize that the current coralligenous configurations may be the result of the thermal history of the different biogeographical areas.

In conclusion, although these results suggest that temperature plays a crucial role in the spatial distribution of coralligenous assemblages and the adaptability of its main bioconstructor, other biotic and abiotic factors may interplay with temperature effects. For example, an increase in temperature could affect intraspecific and interspecific interactions and thus species distribution patterns, community structure, ecosystem processes, and properties (Kordas et al., 2011; Nelson et al., 2013; Bruno et al., 2015). Further studies will be needed to corroborate these results, implementing information about the species' vulnerability to warming, as coralligenous assemblages are particularly complex and adaptations can be species-specific and location dependent. Furthermore, the need of disentangling the effects due to the intensity, duration, and variability of heating events is stressed, as well as the importance of gaining spatially and temporally wide databases, both of the thermal environment and the biota. In this context, it is necessary to continue the monitoring effort to trace the changes in the benthic marine communities, paying particular attention to spatial differences that do not necessarily return univocal information on the status of the habitats.

REFERENCES

Ådal, E., Lundberg, P. and Jonzèn, N. 2006. From climate change to population change: the need to consider annual life cycles. Global Change Biology 12, 1627-1633.

Adey, W. H. and Steneck, R. S. 2001. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. Journal of Phycology 37, 677-698.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Australian Ecology. 26, 32-46.

Anderson, M. J. and Robinson, J. 2003. Generalized discriminant analysis based on distances. Australian and New Zealand Journal of Statistics 45, 301-318.

Anderson, M. J., Ellingsen, K. E. and McArdle, B. H. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9, 683-693.

Andrades, R., Machado, F. S., Reis-Filho, J. A., Macieira, R. M. and Giarrizzo, T. 2018. Intertidal biogeographic subprovinces: local and regional factors shaping fish assemblages. Frontiers in Marine Science 5, 412.

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S. and Hoegh-Guldberg, O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. Proceeding of the Natural Academy of Science 105(45), 17442–17446.

Anton, A., Randle, J. L., Garcia, F. C., Rossbach, S., Ellis, J. I., Weinzierl, M. and Duarte, C. M. 2020. Differential thermal tolerance between algae and corals may trigger the proliferation of algae in coral reefs. Global Change Biology 26(8), 4316–4327.

Assis, J., Lucas, A. V., Bárbara, I. and Serrão, E. Á. 2016. Future climate change is predicted to shift long-term persistence zones in the cold-temperate kelp *Laminaria hyperborea*. Marine Environmental Research 113, 174–182.

Babcock, R. C., Bustamante, R. H., Fulton, E. A., Fulton, D. J., Haywood, M. D. E., Hobday, A. J., Kenyon, R., Matear, R. J., Plagányi, E. E., Richardson, A. J. and Vanderklift, M. A. 2019. Severe continental-scale impacts of climate change are happening now: extreme climate events impact marine habitat forming communities along 45% of Australia's coast. Frontiers in Marine Science 6, 411.

Balata, D., Piazzi, L., Cecchi, E. and Cinelli, F. 2005. Variability of Mediterranean coralligenous assemblages subject to local variation in sediment deposition. Marine Environmental Research 60, 403-421.

Balata, D., Acunto, S. and Cinelli, F. 2006. Spatio-temporal variability and vertical distribution of a low rocky subtidal assemblage in the north-west Mediterranean. Estuarine Coastal and Shelf Science 67, 553-561.

Balata, D., Piazzi, L. and Benedetti-Cecchi, L. 2007. Sediment disturbance and loss of beta diversity on subtidal rocky reefs. Ecology 88, 2455-2461.

Ballesteros, E. 1991. Seasonality of growth and production of a deep-water population of *Halimeda tuna* (Chlorophyceae, Caulerpales) in the North-western Mediterranean. Botanica Marina 34, 291-302.

Ballesteros, E., Sala, E., Garrabou, J. and Zabala, M. 1998. Community structure and frond size distribution of a deep water stand of *Cystoseira spinosa* (Phaeophyta) in the northwestern mediterranean. European Journal of Phycology 33, 121-128.

Ballesteros, E. 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanography and Marine Biology 44, 123-195.

Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E. and Sala, E. 2009. Deep-water stands of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: Insights into assemblage structure and population dynamics. Estuarine Coastal and Shelf Science 82, 477–484.

Barisiello, O., Bernabei, S., Bucci, M., Casazza, G., Cavalieri, S., Comperini, W., De Vincenzi, S., Fabiani, C., Franceschini, S., Giovanardi, F., Mancini, L., Manzini, E., Marzani, A., Mazzoni, M., Melley, A., Ress, M., Siligardi, M., Silvestri, C., Spaggiari, R. and Volpi, E. 2002. Qualità delle acque marino costiere. Annuario dei dati ambientali. Agenzia Nazionale per la Protezione dell'Ambiente, pp 256-274.

Basso, D. and Rodondi G. 2007. Valutazione del tasso di crescita in coltura delle alghe clacaree *Lithophyllum stictaeformae* e *Mesophyllum lichenoides*: primi risultati. Biologia Marina Mediterranea 14(3), 172–173.

Bavestrello, G., Bertone, S., Cattaneo-Vietti, R., Cerrano, C., Gaino, E. and Zanzi, D. 1994. Mass mortality of *Paramuricea clavata* (Anthozoa, Cnidaria) on Portofino Promontory cliffs, Ligurian Sea, Mediterranean Sea. Marine Life 4, 15–19.

Bavestrello, G., Cerrano, C., Zanzi, D. and Cattaneo-Vietti, R. 1997. Damage by fishing activities to the gorgonian coral *Paramuricea clavata* in the Ligurian Sea. Aquatic Conservation: Marine Freshwater Ecosystem 7, 253-262.

Benedetti-Cecchi, L., Bulleri, F. and Cinelli, F. 2000. The interplay of physical and biological factors in the north-west Mediterranean. Oecologia 123, 406-417.

Benedetti-Cecchi, L., Maggi, E., Bertocci, I., Vaselli, S., Micheli, F., Osio, G.C. and Cinelli, F. 2003. Variation in rocky shore assemblages in the northwestern Mediterranean: Contrasts between islands and the mainland. Journal of Experimental Marine Biology and Ecology 293, 193-215.

Bensoussan, N., Romano, J. C., Harmelin, J. G. and Garrabou, J. 2010. High resolution characterization of northwest Mediterranean coastal waters thermal regimes: to better understand responses of benthic communities to climate change. Estuarine Coastal and Shelf Science 87, 431–441.

Betti, F., Bavestrello, G., Bo, M., Ravanetti, G., Enrichetti, F., Coppari, M., Cappanera, V, Venturini, S. and Cattaneo-Vietti, R. 2020. Evidences of fishing impact on the coastal gorgonian forests inside the Portofino MPA (NW Mediterranean Sea). Ocean and Coastal Management 187, 105105.

Bianchi, C. N. 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580, 7-21.

Blake, C. and Maggs, C. A. 2003. Comparative growth rates and internal banding periodicity of maerl species (Corallinales, Rhodophyta) from northern Europe. Phycologia 42(6), 606–612.

Blanchette, C.A., Miner, C.M., Raimondi, P.T., Lohse, D., Heady, K.E.K. and Broitman, B.R. 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. Journal of Biogeography 35, 1593-1607.

Blanfuné, A., François Boudouresque, C., Thibaut, T. and Verlaque, M. 2018. The sea level rise and the collapse of a Mediterranean ecosystem, the *Lithophyllum byssoides* algal rim. The Mediterranean Region under Climate Change 285–289.

Boudouresque, C. F., Blanfunè, A., Harmelin-Vivien, M., Personnic, S., Ruitton, S., Thibaut and T., Verlaque, M. 2016. Where seaweed forests meet animal forests: the examples of macroalgae in coral reefs and the Mediterranean coralligenous ecosystem marine animal forests in Marine Animal Forests (Springer) 1-28.

Bosence, D. W. J. 1983. Coralline algal reef frameworks. Journal of the Geological Society 140 (3) 365–376.

Breeman, A. M. 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. Helgolander Meeresunters 42, 199-241.

Brewin, R. J. W., Smale, D.A., Moore, P. J., Dall'Olmo, G., Miller, P. I., Taylor, B. H., Smyth, T. J., Fishwick, J. R. and Yang, M. 2018. Evaluating operational AVHRR sea surface temperature data at the coastline using benthic temperature loggers. Remote Sensing 10, 925.

Bruno, J. F. and Carr, L. A., O'Connor, M. I. 2015. Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96, 3126–3140.

Bruno, J. F. and Valdivia, A. 2016. Coral reef degradation is not correlated with local human population density. Scientific Reports 6, 29778.

Bruno, J. F., Bates, A. E., Cacciapaglia, C., Pike, E. P., Amstrup, S. C., Van Hooidonk, R., Henson, S. A. and Aronson, R. B. 2018. Climate change threatens the world's marine protected areas. Nature Climate Change 8(6), 499–503.

Bustamante, R. H, Branch, G. M. and Eekhout, S. 1997. The influences of physical factors on the distribution and zonation patterns of South African rocky-shore communities, South African Journal of Marine Science 18, 119-136.

Canals, M. and Ballesteros, E. 1997. Production of carbonate particles by phytobenthic communities on the Mallorca-Menorca shelf, northwestern Mediterranean Sea. Deep-Sea Research Part II: Topical Studies in Oceanography 44(3–4), 611–629.

Caragnano, A., Basso, D., Jacob, D. E., Storz, D., Rodondi, G., Benzoni, F. and Dutrieux, E. 2014. The coralline red alga *Lithophyllum kotschyanum f.* affine as proxy of climate variability in the Yemen coast, Gulf of Aden (NW Indian Ocean). Geochimica et Cosmochimica Acta 124-1,17.

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J. C., DeVantier, L., Edgar, G. J., Edwards, A. J., Fenner, D., Guzmán, H. M., Hoeksema, B. W., Hodgson, G., Johan, O., Licuanan, W. Y., Livingstone, S. R., Lovell, E.R., Moore, J. A., Obura, D. O., Ochavillo, D., Polidoro, B. A., Precht, W. F., Quibilan, M. C., Reboton, C., Richards, Z. T., Rogers, A. D., Sanciangco, J., Sheppard, A., Sheppard, C,, Smith, J., Stuart, S., Turak, E., Veron, J. E., Wallace, C., Weil, E. and Wood, E. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321(5888), 560–563.

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R. and Largier, J. L. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications 13, S90-S107.

Casas-Güell, E., Teixidó, N., Garrabou, J. and Cebrian, E. 2015. Structure and biodiversity of coralligenous assemblages over broad spatial and temporal scales. Marine Biology 162, 901-912.

Casas-Guëll, E., Cebrian, E., Garrabou, J., Ledoux, J. B., Linares, C. and Teixidó, N. 2016. Structure and biodiversity of coralligenous assemblages dominated by the precious red coral *Corallium rubrum* over broad spatial scales. Scientific Reports 6.

Casoli, E., Nicoletti, L., Mastrantonio, G., Jona-Lasinio, G., Belluscio, A. and Ardizzone, G. D. 2017. Scuba diving damage on coralligenous builders: Bryozoan species as an indicator of stress. Ecological Indicator 74, 441-450.

Casoli, E., Piazzi, L., Nicoletti, L., Jona-Lasinio, G., Cecchi, E., Mancini, G., Belluscio, A. and Ardizzone, G. 2020. Ecology, distribution and demography of erect bryozoans in Mediterranean coralligenous reefs. Estuarine Coastal and Shelf Science 235, 106573.

Cau, A., Follesa, M. C., Moccia, D., Alvito, A., Bo, M. Angiolillo, M., Canese, S., Paliaga, E. M., Orrù, P. E., Sacco, E. and Cannas, R. 2015. Deepwater corals biodiversity along roche du large ecosystems with different habitat complexity along the south Sardinia continental margin (CW Mediterranean Sea). Marine Biology 162, 1865-1878.

Ceccherelli G., Pinna, F., Cinti, M. C., Pansini A., Roselli, C. and Piazzi L. 2019. Vertical gradient and spatial variability of Coralligenous reefs in Sardinia: the interactive effect of depth and location. S.It.E. (Italian Society of Ecology) conference (Ferrara, Italy 10-12 September 2019) https://www.ecologia.it/wp-content/uploads/2019/09/AbstractBook-SItE-Ferrara-2019.pdf, 124.

Ceccherelli, G., Pinna, F., Pansini, A., Piazzi, L. and La Manna, G. 2020. The constraint of ignoring the subtidal water climatology in evaluating the changes of coralligenous reefs due to heating events. Scientific Reports 10, 17332.

Cecchi, E., Gennaro, P., Piazzi, L., Ricevuto, E. and Serena, F. 2014. Development of a new biotic index for ecological status assessment of Italian coastal waters based on coralligenous macroalgal assemblages. European Journal of Phycology 49, 298-312.

Cerrano, C., Bavestrello, G., Bianchi, C. N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P., Sara, G., Schiaparelli, S., Siccardi, A. and Sponga, F. 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean). Ecology Letters 3(4), 284–293.

Chapman, M. G. 1986. Assessment of some controls in experimental transplants of intertidal gastropods. Journal of Experimental Marine Biology and Ecology 103(1–3), 181–201.

Chappuis, E., Terradas, M., Cefalì, M. E., Mariani, S. and Ballesteros, E. 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. Estuarine Coastal and Shelf Science 147, 113-122.

Chatalov, A., Bonev, N. and Ivanova, D. 2015. Depositional characteristics and constraints on the mid-Valanginian demise of a carbonate platform in the intra-Tethyan domain, Circum-Rhodope Belt, northern Greece. Cretaceous Research 55, 84–115.

Chave J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology Letters 16, 4–16.

Cinar, M. E., Féral, J. P., Arvanitidis, C., Davis, R., Sini, M., Doğan, A., Gerovasileiou, V., Evcen, A., Chenuil, A., Dağli, E., Aysel, V., Issaris, Y., Bakir, K., Nalmpantı, M., Sartoretto, S., Salomidi, M., Sapouna, A., Açik, S., Dimitriadis, C., Koutsoubas, D., Katağan, T., Öztürk, B., Koçak, F., Erdogan-Dereli, D., Önen, S., Özgen, O., Türkçü, N., Kirkim, F. and Önen, M. 2020. Coralligenous assemblages along their geographical distribution: Testing of concepts and implications for management. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 1578-1594.

Cocito, S., Sgorbini, S. and Bianchi, C. N. 1997. Zonation of a suspension-feeder assemblage on a temperate rocky shoal: the influence of water current and bottom topography. In: Hawkins, L. E., Hutchinson, S. (eds.), The response of marine organisms to their environments, University of Southampton, UK. pp. 183-192.

Cocito, S., Bedulli, D. and Sgorbini, S. S. 2002. Distribution patterns of the sublittoral epibenthic assemblages on a rocky shoal in the Ligurian Sea (NW Meditteranean). Scientia Marina 66, 175-181.

Cocito, S. 2004. Bioconstruction and biodiversity: their mutual influence. Scientia Marina 68, 137-144.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F. B. R., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B. S., Gasol, J. M., Gertwage, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M. S., Koukouras, A., Lampadariou, N., Laxamana, E., de la Cuadra, C. M. L. F., Lotze, H. K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J. I., Vicente, C. S., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R. and Voultsiadou, E. 2010. The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. PLoS One 5, 0011842.

Collins, M., An, S. Il, Cai, W., Ganachaud, A., Guilyardi, E., Jin, F. F., Jochum, M., Lengaigne, M., Power, S., Timmermann, A., Vecchi, G. and Wittenberg, A. 2010. The impact of global warming on the tropical Pacific Ocean and El Nĩno. Nature Geoscience 3(6), 391–397.

Coma, R., Pola, E., Ribes, M. and Zabala, M. 2004. Long-term assessment of temperate octocoral mortality patterns, protected vs. unprotected areas. Ecological Application 14, 1466–1478.

Coma, R., Linares, C., Ribes, M., Diaz, D., Garrabou, J. and Ballesteros, E. 2006. Consequences of a mass mortality in populations of *Eunicella singularis* (Cnidaria: Octocorallia) in Menorca (NW Mediterranean). Marine Ecology Progress Series 327, 51-60.

Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J. and Pascual, J. 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. Proceeding of the National Academy of Sciences of the United States of America 106, 6176 – 6181.

Cormaci, M., Furnari, G., and Alongi, G. 2017. Flora marina bentonica del Mediterraneo: Rhodophyta (*Rhodymeniophycidae* escluse). *Bullettin of the Gioenia Accademy of Natural Science of Catania*. *50*(380), 1–391.

Cornwall, C. E., Diaz-Pulido, G. and Comeau, S. 2019. Impacts of ocean warming on coralline algae: Knowledge gaps and key recommendations for future research. Frontiers in Marine Science 6(186), 1–10.

Costello, M. J., Tsai, P., Wong, P. S. Cheung, A. K. L., Basher, Z. and Chaudhary, C. 2017. Marine biogeographic realms and species endemicity. Natural Communities 8, 1057.

Crisci, C., Bensoussan, N., Romano, J. C. and Garrabou, J. 2011. Temperature anomalies and mortality events in marine communities: Insights on factors behind differential mortality impacts in the NW Mediterranean. PLoS One 6, e23814.

Crisci, C., Ledoux, J. B., Mokhtar- Jamaï, K., Bally, M., Bensoussan, N., Aurelle, D., Cebrian, E., Coma, R., Féral, J. P., La Rivière, m., Linares, C., López-Sendino, P., Marschal, C., Ribes, M., Teixidó, N., Zuberer F. and Garrabou J. 2017. Regional and local environmental conditions do not shape the response to warming of a marine habitat-forming species. Scientific Reports 7, 5069.

Crozier, L. G., W. Zabel, R. and Hamlet, A. F. 2008. Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. Global Change Biology 14, 236–249.

De Frenne, P., Graae, B. J., Rodríguez-Sanchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D.A. and Verheyen, K. 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. Journal of Ecology 101, 784-95.

De Jode, A., David, R., Haguenauer, A., Cahill, A. E., Erga, Z., Guillemain, D., Sartoretto, S., Rocher, C., Selva, M., Le Gall, L., Féral, J. P. and Chenuil, A. 2019. From seascape ecology to population genomics and back. Spatial and ecological differentiation among cryptic species of the red algae *Lithophyllum stictiforme/L. cabiochae*, main bioconstructors of coralligenous habitats. Molecular Phylogenetics and Evolutions 137, 104–113.

Deter, J., Descamp, P., Ballesta, L., Boissery, P. and Holon, F. 2012a. A preliminary study toward an index based on coralligenous assemblages for the ecological status assessment of Mediterranean French coastal waters. Ecological Indicators 20, 345-352.

Deter, J., Descamp, P., Boissery, P., Ballesta, L. and Holon, F. 2012b. A rapid photographic method detects depth gradient in coralligenous assemblages. Journal of Experimental Marine Biology and Ecology 418–419, 75-82.

Dethier, M. N. and Steneck, R. S. 2001. Growth and persistence of diverse intertidal crusts: Survival of the slow in a fast-paced world. Marine Ecology Progress Series 223, 89–100.

Diaz-Pulido, G., Anthony, K. R. N., Kline, D. I., Dove, S. and Hoegh-Guldberg, O. 2012. Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. Journal of Phycology 48(1), 32–39.

Diaz-Pulido, G., Nash, M. C., Anthony, K. R. N., Bender, D., Opdyke, B. N., Reyes-Nivia, C. and Troitzsch, U. 2014. Greenhouse conditions induce mineralogical changes and dolomite accumulation in coralline algae on tropical reefs. Nature Communications 5.

Díez, I., Santolaria, A. and Gorostiaga, J. M. 2003. The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). Estuarine Coastal and Shelf Science 56, 1041-1054.

Doxa, A., Holon, F., Deter, J., Villéger, S., Boissery, P. and Mouquet, N. 2016. Mapping biodiversity in three-dimensions challenges marine conservation strategies: The example of coralligenous assemblages in North-Western Mediterranean Sea. Ecological Indicators 61, 1042-1054.

E.C., Council Directive 92/43/EEC (Habitat Directive) of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official Journal of European Communities 22/7/1992, L206, 7 (1992).

E.C., MSFD 2008/56/EC of the European Parliament and of the Council, 17 June 2008, establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of European Communities 25/6/2008, L164/19, 22 (2008).

Eakin, C. M. et al. Morgan, J. A., Heron, S. F., Smith, T. B., Liu, G., Alvarez-Filip, L., Baca, B., Bartels, E., Bastidas, C., Bouchon, C., Brandt, M., Bruckner, A.W., Bunkley-Williams, L., Cameron, A., Causey, B. D., Chiappone, M., Christensen, T. R. L., Crabbe, M. J. C., Day, O., De la Guardia, E., Díaz-Pulido, G., DiResta, D., Gil-Agudelo, D. L., Gilliam, D. S., Ginsburg, N. R., Gore, S., Guzmán, H. M., Hendee, J. C., Hernández-Delgado, E. A., Husain, E., Jeffrey, C. F. G., Jones, R. J., Jordán-Dahlgren, E., Kaufman, L. S., Kline, D. I., Kramer, P. A., Lang, J. C., Lirman, D., Mallela, J., Manfrino, C., Maréchal, J. P., Marks, K., Mihaly, M., Miller, W. J., Mueller, E. M., Muller, E. M., Orozco Toro, C. A., Oxenford, H. A., Ponce-Taylor, D., Quinn, N., Ritchie, K. B., Rodríguez, S., Ramírez, A. R., Romano, S., Samhouri, J. F., Sánchez, J. A., Schmahl, G. P., Shank, B. V., Skirving, W. L., Steiner, S. C. C., Villamizar, E., Walsh, S. M., Walter, C., Weil, E., Williams, E. H., Roberson, K. W. and Yusri Yusuf, Y. 2010. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PLoS One 5, e13969.

Edmunds, P. J. and Leichter, J. J. 2016. Spatial scale-dependent vertical zonation of coral reef community structure in French Polynesia. Ecosphere 7, 1-14.

Etterson, J. R. and Shaw, R. G. 2001. Constraint to adaptive evolution in response to global warming. Science 294(5540), 151–154.

Ferdeghini, F., Acunto, S., Cocito, S. and Cinelli, F. 2000. Variability at different spatial scales of a coralligenous assemblage at Giannutri Island (Tuscan Archipelago, northwest Mediterranean). Hydrobiologia 440, 27-36.

Ferrigno, F., Appolloni, L., Russo, G. F. and Sandulli, R. 2018. Impact of fishing activities on different coralligenous assemblages of Gulf of Naples (Italy). Journal of Marine Biological Association of the United Kingdom 98, 41-50.

Foster, M. S. 2001. Rhodoliths: Between rocks and soft places. Journal of Phycology 37(5), 659–667.

Foster, M., Amado Filho, G. M., Kamenos, N. A., Riosmena-Rodríguez, R. and Steller D. L. 2013. Smithsonian Contributions to the Marine Sciences, no. 39 Chapter: Rhodoliths and Rhodolith Beds. Smithsoninan Institution.

Fragkopoulou, E., Serrão, E. A., Horta, P. A., Koerich, G. and Assis, J. 2021. Bottom Trawling Threatens Future Climate Refugia of Rhodoliths Globally. Frontiers in Marine Science 7, 1–11.

Fraschetti, S., Terlizzi, A. and Benedetti-Cecchi, L. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Marine Ecology Progress Series 296, 13-29.

Galli, G., Solidoro, C. and Lovato, T. 2017. Marine heat waves hazard 3D maps and the risk for low motility organisms in a warming Mediterranean Sea. Frontiers in Marine Science 4, 136.

Garrabou, J. and Ballesteros, E. 2000. Growth of *Mesophyllum alternans* and *Lithophyllum frondosum* (Corallinales, Rhodophyta) in the northwestern Mediterranean. European Journal of Phycology 35,1-10.

Garrabou, J., Ballesteros, E. and Zabala, M. 2002. Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. Estuarine Coastal and Shelf Science 55, 493-508.

Garrabou, J., Perez, T., Sartoretto, S. and Harmelin, J. G. 2001. Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). Marine Ecology Progress Series 217, 263-272.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M. C., Kersting, D. K., Ledoux, J. B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J.C., Serrano, E., Teixido, N., Torrents, O., Zabala, M., Zuberer, F. and Cerrano, C. 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. Global Change Biology 15, 1090-1103.

Garrabou, J., Gómez-Gras, D., Ledoux, J.-B., Linares, C., Bensoussan, N., López-Sendino, P., Bazairi, H., Espinosa, F., Ramdani, M., Grimes, S., Benabdi, M., Souissi, J. B., Soufi, E., Khamassi, F., Ghanem, R., Ocaña, O., Ramos-Esplà, A., Izquierdo, A., Anton, I., Rubio-Portillo, E., Barbera, C., Cebrian, E., Marbà, N., Hendriks, I. E., Duarte, C. M., Deudero, S., Díaz, D., Vázquez-Luis, M., Alvarez, E., Hereu, B., Kersting, D. K., Gori, A., Viladrich, N., Sartoretto, S., Pairaud, I., Ruitton, S., Pergent, G., Pergent-Martini, C., Rouanet, E., Teixidó, N., Gattuso, J. P., Fraschetti, S., Rivetti, I., Azzurro, E., Cerrano, C., Ponti, M., Turicchia, E., Bavestrello, G., Cattaneo-Vietti, R., Bo, M., Bertolino, M., Montefalcone, M., Chimienti, G., Grech, D., Rilov, G., Tuney Kizilkaya, I., Kizilkaya, Z., Eda Topçu, N., Gerovasileiou, V., Sini, M., Bakran-Petricioli, T., Kipson, S. and Harmelin, J. G. 2019. Collaborative Database to Track Mass Mortality Events in the Mediterranean Sea. Frontiers in Marine Science 6, 707.

Gatti, G., Bianchi, C. N., Morri, C., Montefalcone, M. and Sartoretto, S. 2015. Coralligenous reefs state along anthropized coasts: application and validation of the COARSE index, based on a rapid visual assessment (RVA) approach. Ecological Indicators 52, 567-576.

Gatti, G., Montefalcone, M., Rovere, A., Parravicini, V., Morri, C., Albertelli, G. and Nike Bianchi, C. 2012. Seafloor integrity down the harbor waterfront: The coralligenous shoals off Vado Ligure (NW Mediterranean). Adance in Oceanography and Limnology 3, 51-67.

Gatti, G., Bianchi, C. N., Parravicini, V., Rovere, A., Peirano, A., Montefalcone, M., Massa, F. and Morri, C. 2015b. Ecological change, sliding baselines and the importance of historical data: Lessons from combing observational and quantitative data on a temperate reef over 70 years. PLoS One 10, e0118581.

Gauzens, B., Rall, B. C., Mendonça, V., Vinagre, C. and Brose, U. 2020. Biodiversity of intertidal food webs in response to warming across latitudes. Nature Climate Change. 10, 264–269.

Giaccone, G. and Geraci, R. M., 1989. Biogeografia delle alghe del Mediterráneo. Anales Jardín Botánico de Madrid, 46, 27-34.

Giannini, F., Gili, J. M. and Santangelo, G. 2003. Relationships between the spatial distribution of red coral *Corallium rubrum* and coexisting suspension feeders at Medes Islands Marine Protected Area (Spain). Italian Journal of Zoology 70, 233-239.

Golikov, A. N., Dolgolenko, M. A., Maximovich, N. V. and Scarlato, O. A. 1990. Theoretical approaches to marine biogeography. Marine Ecology Progress Series 63, 289-301.

Gómez-Gras, D., Linares, C., de Caralt, S., Cebrian, E., Frleta-Valić, M., Montero-Serra, I., Pagès-Escolà, M., López-Sendino, P. and Garrabou, J. 2019. Response diversity in Mediterranean coralligenous assemblages facing climate change: Insights from a multispecific thermotolerance experiment. Ecology and Evolution 9, 4168-4180.

Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J. S., Brambilla, V., Ledoux, J.-B., López-Sendino, P., Bensoussan, N. and Garrabou, J. 2021. Climate change transforms the functional identity of Mediterranean coralligenous assemblages. Ecology Letters 24, 1038-1051.

Guiry, M. D. and Guiry, G. M. 2022. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org; searched on 2 April 2022.

Halfar, J., Steneck, R. S., Joachimski, M., Kronz, A., and Wanamaker, A. D. 2008. Coralline red algae as high-resolution climate recorders. Geology *36*(6), 463–466.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L., and Williams, S. L. 2006. The impacts of climate change in coastal marine systems. Ecololgy Letters 9, 228–241.

Hartley, S. and Kunin, W. E. 2003. Scale Dependency of rarity, extinction risk, and conservation priority. Conservetion Biology 17, 1559–1570.

Hastie, T. and Tibshirani, R. Generalized additive models. (Taylor and Francis Ltd,1990).

Hereu, B. and Kersting, D. K. 2016. Diseases of coralline algae in the Mediterranean Sea. Coral Reefs 35, 713.

Hetzinger, S., Halfar, J., Kronz, A., Steneck, R. S., Adey, W., Lebednik, P. A. and Schöne, B. R. 2009. High-resolution Mg/Ca ratios in a coralline red alga as a proxy for Bering Sea temperature variations from 1902 to 1967. Palaios 24(6), 406–412.

Hewitt, J. E., Thrush, S. E. and Cummings, V. J. 2001. Assessing environmental impacts: Effects of spatial and temporal variability at likely impact scales. Ecological Applications 11, 1502-1516.

Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C., Benthuysen, J. A., Burrows, M. T., Donat, M., feng, M., Jessica A. Benthuysen, Michael T. Burrows, Markus G. Donat, Feng, M., Neil J. Holbrook, N. J., Moore, P. J., Scannel, H. A., Sen Gupta, A. and Wernberg, T. 2016. A hierarchical approach to defining marine heatwaves. Progress in Oceanography 141, 227-238.

Hobday, A. J., Oliver, E. C. J., Sen Gupta, A., Benthuysen, J. A., Burrows, M. T., Donat, M. G., Holbrook, N. J., Moore, P. J., Thomsen, M. S., Wernberg, T. and Smale, D. A. 2018. Categorizing and naming marine heatwaves. Oceanography 31(2), 162–173.

Hoegh-Guldberg, O. and Bruno, J. F. 2010. The impact of climate change on the world's marine ecosystems. Science 328(5985), 1523–1528.

Hoegh-Guldberg, O. and Poloczanska, E. S. 2017. Editorial: The effect of climate change across ocean regions. Frontiers in Marine Science 4, 361.

Holbrook, N. J., Scannell, H. A., Sen Gupta, A., Benthuysen, J. A., Feng, M., Oliver, E. C. J., Alexander, L. V., Burrows, M. T., Donat, M. G., Hobday, A. J., Moore, P.J., Perkins-Kirkpatrick, S. E., Smale, D. A., Straub, S. C. and Wernberg, T. 2019. A global assessment of marine heatwaves and their drivers. Nature Communications 10, 2624.

Huete-Stauffer, C., Vielmini, I., Palma, M., Navone, Panzalis, A. P., Vezzulli, L., Misic, C. and Cerrano C. 2011. *Paramuricea clavata* (Anthozoa, Octocorallia) loss in the Marine Protected Area of Tavolara (Sardinia, Italy) due to a mass mortality event. Marine Ecology 32, 107–116.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B., Kleypas, J., Lough, J. M. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301,929-933

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Liu, G., McWilliam, M. J., Pears, R. J., Pratchett, M. S., Skirving, W. J., Stella, J. S. and Torda, G. 2018. Global warming transforms coral reef assemblages. Nature 556(7702), 492–496.

Hyndes, G. A. et al. Heck, K. L., Jr., Vergés, A., Harvey, E. S., Kendrick, G. A., Lavery, P. S., McMahon, K., Orth, R. J., Pearce, A., Vanderklift, M., Wernberg, T., Whiting, S. and Wilson, S. 2016. Accelerating tropicalization and the transformation of temperate seagrass meadows. Bioscience 66, 938–945.

IPCC 2019. Special Report on the Ocean and Cryosphere in a Changing Climate. Pörtner, H. O., Roberts, D. C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E. K., Mintenbeck, K., Alegría, A., Okem, A., Petzold, J. Rama B. and Wever, M. N (eds). in press.

IPCC 2021. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press. In Press.

Irving, A. D. and Connell, S. D., 2002. Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: Algal versus invertebrate dominated assemblages. Marine Ecology Progress Series 245, 83-91.

Johnson, C. R., Banks, S. B., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., Frusher, S. D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K. L., Holbrook, N. J., Hosie, G. W., Last, P. R., Ling, S. D., Melbourne-Thomas, J., Miller, K., Pecl, G. T., Richardson, A., Ken R. Ridgway, Rintoul, S. R., Ritz, D. A., D., Ross, J., Sanderson, J. C., Shepherd, S. A., Slotwinski, A., Swadling, K. M. and Taw, N. 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experiments Marine Biology and Ecology 400, 17–32.

Kamenos, N. A., Cusack, M. and Moore, P. G. 2008. Coralline algae are global palaeothermometers with bi-weekly resolution. Geochimica and Cosmochimica Acta 72(3), 771–779.

Kendrick, G. A., Nowicki, R. J., Olsen, Y. S., Strydom, S., Fraser, M. W., Sinclair, E. A., John Statton, J., Hovey, R. K., Thomson, J. A., Burkholder, D. A., McMahon, K. M., Kilminster, K., Hetzel, Y., Fourqurean, J. W., Heithaus, M. R. and Orth R. J. 2019. A systematic review of how multiple stressors from an extreme event drove ecosystem-wide loss of resilience in an iconic seagrass community. Frontiers in Marine Science 6, 455.

Kim, J. B., Park, J. I., Jung, C. S., Lee, P. Y. and Lee, K. S. 2009. Distributional range extension of the seagrass *Halophila nipponica* into coastal waters off the Korean peninsula. Aquatic Botany 90, 269–272.

Kim, J. H., Kim, N., Moon, H., Lee, S., Jeong, S. Y., Diaz-Pulido, G., Edwards, M. S., Kang, J. H., Kang, E. J., Oh, H. J., Hwang, J. D. and Kim, I. N. 2020. Global warming offsets the ecophysiological stress of ocean acidification on temperate crustose coralline algae. Marine Pollution Bullettin 157, 111324.

Konar, B., Iken, K. and Edwards, M. 2009. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. Marine Ecology 30, 63-73.

Kordas R. L., Harley, C. D. G., O'Connor, M. I. 2011. Journal of Experimental Marine Biology and Ecology 400, 218–226

Kružić, P. 2014. Bioconstructions in the Mediterranean: present and future in The Mediterranean sea: its history and present challenges (ed. Goffredo, S. and Dubinsky, Z) 435-447.

Kubicek, A., Breckling, B., Hoegh-Guldberg, O. and Reuter, H. 2019. Climate change drives trait-shifts in coral reef communities. Scientific Reports 9(1), 1–10.

Laborel, J. 1987. Marine biogenic constructions in the Mediterranean. A review. Travaux Scientifique du Parc National Port-Cros. 13, 97-127.

Linares, C., Coma, R., Garrabou, J., Diaz, D. and Zabala, M. 2008. Size distribution, density and disturbance in two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis.* Journal of Applied Ecology 45, 688-699.

Linares, C., Cebrian, E., Kipson, S. and Garrabou, J. 2013. Does thermal history influence the tolerance of temperate gorgonians to future warming? Marine Environmental Research 89, 45–52.

Littler, M. M. and Littler, D. S. 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. Journal of Experimental Marine Biology and Ecology 74, 13-34.

Lombardi, C., Cocito, S., Occhipinti-Ambrogi, A. and Hiscock, K. 2006. The influence of seawater temperature on zooid size and growth rate in *Pentapora fascialis* (Bryozoa: *Cheilostomata*). Marine Biology 149, 1103-1109.

Lourie, S. and Vincent A. C. J. 2004. Using biogeography to help set priorities in marine conservation. Conservation Biology 18, 1004-1020.

Louthan, A. M. and Morris, W. 2021. Climate change impacts on population growth across a species' range differ due to nonlinear responses of populations to climate and variation in rates of climate change. PLoS ONE 16, 1–20.

Manca, B., Burca, M., Giorgetti, A., Coatanoan, C., Garcia, M. J. and Iona, A. 2004. Physical and biochemical averaged vertical profiles in the Mediterranean regions: An important tool to trace the climatology of water masses and to validate incoming data from operational oceanography. Journal of Marine System 48, 83-116.

Marbà, N. and Duarte, C. M. 2010. Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. Global Change Biology 16(8), 2366–2375.

Marbà, N., Jordà, G., Agustí, S., Girard, C. and Duarte, C. M. 2015. Footprints of climate change on Mediterranean Sea biota. Frontiers in Marine Science 2:56.

Martin, C. S., Giannoulaki, M., De Leo, F., Scardi, M., Salomidi, M., Knittweis, L., Pace, M. L., Garofalo, G., Gristina, M., Ballesteros, E., Bavestrello, G., Belluscio, A., Cebrian, E., Gerakaris, V., Pergent, G., Pergent-Martini, C., Schembri, P. J., Terribile, K., Rizzo, L., Souissi, J. Ben, Bonacorsi, M., Guarnieri, G., Krzelj, M., Macic, V., Punzo, E., Valavanis, V. and Fraschetti, S. 2014. Coralligenous and maërl habitats: Predictive modelling to identify their spatial distributions across the Mediterranean Sea. Scientific Reports 4, 6646.

Martin, S. and Gattuso, J. P. 2009. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. Global Change Biology 15, 2089–2100.

Martin, S. and Hall-Spencer, J. M. 2017. Effects of ocean warming and acidification on rhodolith/maërl beds. In Coastal Research Library (Vol. 15).

Martin, S., Charnoz, A. and Gattuso, J. P. 2013. Photosynthesis, respiration and calcification in the Mediterranean crustose coralline alga *Lithophyllum cabiochae* (Corallinales, Rhodophyta). European Jounrnal of Phycology 48, 163-172.

Martin, S., Cohu, S., Vignot, C., Zimmerman, G. and Gattuso, J. P. 2013b. One-year experiment on the physiological response of the Mediterranean crustose coralline alga, *Lithophyllum cabiochae*, to elevated pCO2 and temperature. Ecology and Evolution 3(3), 676–693.

Martin, Y., Bonnefont, J. L. and Chancerelle, L. 2001. Gorgonians mass mortality during the 1999 late summer in French Mediterranean coastal waters: the bacterial hypothesis. Water Research 36, 779–782.

McCoy, S. J. and Ragazzola, F. 2014. Skeletal trade-offs in coralline algae in response to ocean acidification. Nature Climate Change 4(8), 719–723.

McCoy, S. J. and Kamenos, N. A. 2015. Coralline algae (Rhodophyta) in a changing world: Integrating ecological, physiological, and geochemical responses to global change. Journal of Phycology 51(1), 6–24.

Montefalcone, M., Morri, C., Bianchi, C.N., Bavestrello, G. and Piazzi, L. 2017. The two facets of species sensitivity: Stress and disturbance on coralligenous assemblages in space and time. Marine Pollution Bullettin 117, 229-238.

Montero-Serra, I., Linares, C., García, M., Pancaldi, F., Frleta-Valić, M., Ledoux, J. B., Zuberer, F., Merad, D., Drap, P. and Garrabou, J. 2015. Harvesting effects, recovery mechanisms, and management strategies for a long-lived and structural precious coral. PLoS One 10, 1-14.

Nash, M. C., Martin, S. and Gattuso, J. P. 2016. Mineralogical response of the Mediterranean crustose coralline alga *Lithophyllum cabiochae* to near-future ocean acidification and warming. Biogeosciences 13(21), 5937–5945.

Nelson, E. J., Kareiva, P., Ruckelshaus, M., Arkema, K., Geller, G., Girvetz, E., Goodrich, D., Matzek, V., Pinsky, M., Reid, W., Saunders, M., Semmens, D. and Tallis, H. 2013. Climate change's impact on key ecosystem services and the human well-being they support in the US. Frontiers in Ecology and the Environment 11: 483-893

Nelson, W. A. 2009. Calcified macroalgae critical to coastal ecosystems and vulnerable to change: A review. Marine Freshwater Research 60(8), 787–801.

Nesti, U., Piazzi, L. and Balata, D. 2009. Variability in the structure of epiphytic assemblages of the Mediterranean seagrass *Posidonia oceanica* in relation to depth. Marine Ecology 30, 276-287.

Novosel, M., Požar-Domac, A. and Pasarić, M. 2004. Diversity and distribution of the Bryozoa along underwater cliffs in the Adriatic Sea with special reference to thermal regime. Marine Ecology 25, 155-170.

Olita, A., Ribotti, A., Fazioli, L., Perilli, A. and Sorgente, R. 2013. Surface circulation and upwelling in the Sardinia Sea: A numerical study. Continental Shelf Research 71, 95-108.

Oliver, E. C. J., Burrows, M. T., Donat, M. G., Sen Gupta, A., Alexander, L. V., Perkins-Kirkpatrick, S. E., Benthuysen, J. A., Hobday, A. J., Neil J. Holbrook, N. J., Moore, P. J., Thomsen, M. S., Wernberg, T. and Smale, D. A. 2019 Projected Marine Heatwaves in the 21st Century and the Potential for Ecological Impact. Frontiers in Marine Science 6, 1–12.

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C. and Wernberg, T. 2018. Longer and more frequent marine heatwaves over the past century. Nature Communications 9(1), 1–12.

Ordoñez, A., Doropoulos, C. and Diaz-Pulido, G. 2014. Effects of ocean acidification on population dynamics and community structure of crustose coralline algae. The Biological Bullettin 226(3), 255–268.

Pagès-Escolà, M., Hereu, B., Garrabou, J., Montero-Serra, I., Gori, A., Gómez-Gras, D., Figuerola, B. and Linares, C. 2018. Divergent responses to warming of two common co-occurring Mediterranean bryozoans. Scientific Reports 8, 17455.

Pakker, H., Breeman, A. M., Prud'homme van Reine, W. F. and van den Hock, C. 1995. A Comparative Study of Temperature Responses of Caribbean Seaweeds from Different Biogeographic Groups. Journal of Phycology 31(4), 499–507.

Pansch, C., Scotti, M, Barboza, F. R, Al-Janabi, B., Brakel, J., Briski, E., Bucholz, B., Franz, M., Ito, M., Paiva, F., Saha, M., Sawall, Y., Weinberger, F. and Wahl M. 2018. Heat waves and their significance for a temperate benthic community: a near-natural experimental approach. Global Change Biology 24, 4357–4367.

Pansini, A., La Manna, G., Pinna, F., Stipcich, P. and Ceccherelli, G. 2021. Trait gradients inform predictions of seagrass meadows changes to future warming. Scientific Reports 11(1), 1–12.

Pezzolesi, L., Peña, V., Le Gall, L., Gabrielson, P. W., Kaleb, S., Hughey, J. R., Rodondi, G., Hernandez-Kantun, J. J., Falace, A., Basso, D., Cerrano, C. and Rindi, F. 2019. Mediterranean *Lithophyllum stictiforme* (Corallinales, Rhodophyta) is a genetically diverse species complex: implications for species circumscription, biogeography and conservation of coralligenous habitats. Journal of Phycology 55, 473-492.

Piazzi, L. and Balata, D. 2011. Coralligenous habitat: patterns of vertical distribution of macroalgal assemblages. Scientia Marina 75, 399-406.

Piazzi, L. and Ceccherelli, G. 2020. Alpha and beta diversity in Mediterranean macroalgal assemblages: relevancy and type of effect of anthropogenic stressors vs natural variability. Marine Biology 167.

Piazzi, L., Gennaro, P. and Balata, D. 2011. Effects of nutrient enrichment on macroalgal coralligenous assemblages. Marine Pollution Bulletin 62, 1830-1835.

Piazzi, L., Gennaro, P. and Balata, D. 2012. Threats to macroalgal coralligenous assemblages in the Mediterranean Sea. Marine Pollution Bullettin 64, 2623-2629.

Piazzi, L., Balata, D., Pertusati, M. and Cinelli, F. 2004. Spatial and temporal variability of Mediterranean macroalgal coralligenous assemblages in relation to habitat and substratum inclination. Botanica Marina 47, 105–115.

Piazzi, L., La Manna, G., Cecchi, E., Serena, F. and Ceccherelli, G. 2016. Protection changes the relevancy of scales of variability in coralligenous assemblages. Estuarine Coastal and Shelf Science 175, 62–69.

Piazzi, L., Cecchi, E., Cinti, M. F., Stipcich, P. and Ceccherelli, G. 2019a. Impact assessment of fish cages on coralligenous reefs through the use of the STAR sampling procedure. Mediterranean Marine Science 20, 627-635.

Piazzi, L., Atzori, F., Cadoni, N., Cinti, M. F., Frau, F. and Ceccherelli, G. 2018. Benthic mucilage blooms threaten coralligenous reefs. Marine Environmental Research 140, 145-151.

Piazzi, L., Gennaro, P., Cecchi, E., Serena, F., Nike Bianchi C., Morri C. and Montefalcone, M. 2017. Integration of ESCA index through the use of sessile invertebrates. Scientia Marina 81, 283–290.

Piazzi, L., Gennaro, P., Montefalcone, M., Bianchi, C. N., Cecchi, E., Morri, C. and Serena, F. 2019b. STAR: an integrated and standardized procedure to evaluate the ecological status of coralligenous reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 29, 189-201.

Piazzi, L., Bianchi, C. N., Cecchi, E., Gatti, G., Guala, I., Morri, C., Sartoretto, S., Serena, F. and Montefalcone, M. 2017a. 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. Aquatic Conservations in Marine Freshwater Ecosystems 27, 1091-1100.

Piazzi L., Cinti M. F., Guala I., Grech D., La Manna G., Pansini A., Pinna F., Stipcich P. and Ceccherelli G. 2021a. Variations in coralligenous assemblages from local to biogeographic spatial scale. Marine Environmental Research 169, 105375.

Piazzi, L., Gennaro, P., Cecchi, E., Bianchi, C. N., Cinti, F., Gatti, G., Guala, I., Morri, C., Sartoretto, S., Serena, F. and Montefalcone, M. 2021. Ecological Status of Coralligenous Assemblages: ten years of application of the ESCA index from local to wide scale validation. Ecological Indicators 121, 107077.

Piazzi, L., Bonaviri, C., Castelli, A., Ceccherelli, G., Costa, G., Curini-Galletti, M., Langeneck, J., Manconi, R., Montefalcone, M., Pipitone, C., Rosso, A. and Pinna, S. 2018. Biodiversity in canopy-forming algae: structure and spatial variability of the Mediterranean Cystoseira assemblages. Estuarine Coastal and Shelf Sciences 207, 132-141.

Piazzi, L., Ferrigno, F., Guala, I., Cinti, M. F., Conforti, A., De Falco, G., De Luca, M., Grech, D., La Manna, G., Pascucci, V., Pansini, P., Pinna, F., Pireddu, L., Puccini, A., Russo, G. F., Sandulli, R., Santonastaso, A., Simeone, S., Stelletti, M., Stipcich, P., Ceccherelli, G. 2022. Inconsistency in community structure and ecological quality between platform and cliff coralligenous assemblages. Ecological Indicators 136,108657

Pinardi, N., Zavatarelli, M., Adani, M., Coppini, G., Fratianni, C., Oddo, P., Simoncelli, S., Tonani, M., Lyubartsev, V., Dobricic, S. and Bonaduce, A. 2015. Mediterranean Sea large-scale low-frequency ocean variability and water mass formation rates from 1987 to 2007: A retrospective analysis. Progress in Oceanography 132, 318-332.

Pinna, F., Piazzi, L., Cinti, M. F., Pansini, A., Stipcich, P. and Ceccherelli, G. 2021. Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. Estuarine Coastal and Shelf Science 261, 107554.

Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. and Sunday, J. M. 2019. Vulnerability to warming of marine versus terrestrial ectotherms. Nature 569, 108–111.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V, O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A. and Richardson, A. J. 2013. Global imprint of climate change on marine life. Nature Climate Change 3(10), 919–925.

Poloczanska E. S., Burrows M. T., Brown C. J., García Molinos J, Halpern B. S., Hoegh-Guldberg O., Kappel C. V., Moore P. J., Richardson A. J., Schoeman D. S. and Sydeman W. J. 2016. Responses of Marine Organisms to Climate Change across Oceans. Frontiers in Marine Science 3:62

Ponti, M., Turicchia, E., Ferro, F., Cerrano, C. and Abbiati, M. 2018. The understorey of gorgonian forests in mesophotic temperate reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 28, 1153-1166.

Ponti, M., Perlini, R. A., Ventra, V., Grech, D., Abbiati, M. and Cerrano, C. 2014. Ecological shifts in Mediterranean coralligenous assemblages related to gorgonian forest loss. PLoS One 9.

Pörtner, H.-O. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. Journal of Experimental Biology 213 (6), 881–893.

Ragazzola, F., Caragnano, A., Basso, D., Schmidt D. N. and Fietzke, J. 2020. Establishing temperate crustose early Holocene coralline algae as archives for paleoenvironmental reconstrunctions of the shallow water habitats of the Mediterranean Sea. Palaeontology 63, 155–170.

Ragazzola, F., Foster, L. C., Form, A., Anderson, P. S. L., Hansteen, T. H. and Fietzke, J. 2012. Ocean acidification weakens the structural integrity of coralline algae. Global Change Biology 18(9), 2804–2812.

RCoreTeam. R: A Language and Environment for Statistical Computing. (R Foundation for Statistical Computing, 2018).

Regione Autonoma della Sardegna, 2016. Riesame e aggiornamento del piano di gestione del distretto idrografico della Sardegna. Monitoraggio e classificazione delle acque marino-costiere. Monitoraggio e classificazione delle acque superficiali, pp. 121-148.

Rindi, F., Braga, J. C., Martin, S., Peña, V., Le Gall, L., Caragnano and A., Aguirre, J. 2019. Coralline algae in a changing Mediterranean Sea: how can we predict their future, if we do not know their present? Frontiers in Marine Science 6, 723.

Rivera, M. G., Riosmena-Rodrìfguez, R. and Foster, M. S. 2004. Age and growth of *Lithothamnion muelleri* (Corallinales, Rhodophyta) in the southwestern Gulf of California, Mexico. Ciencias Marinas 30.

Roberts, S. D., Van Ruth, P. D., Wilkinson, C., Bastianello, S. S. and Bansemer, M. S. 2019. Marine heatwave, harmful algae blooms and an extensive fish kill event during 2013 in South Australia. Frontiers in Marine Science 6, 610.

Rodríguez-Prieto, C. 2016. Light and temperature requirements for survival, growth and reproduction of the crustose coralline *Lithophyllum stictaeforme* from the Mediterranean Sea. Botanica Marina 59(2–3), 95–104.

Rogers-Bennett, L. and Catton, C. A. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific Reports 9, 15050.

Saha, M., Barboza F. R., Somerfield P. J., Al-Janabi B., Beck M., Brakel J., Ito M., Pansch C., Nascimento-Schulze J. C., Jakobsson Thor S., Weinberger F. and Sawall Y. 2020. Response of foundation macrophytes to near-natural simulated marine heatwaves. Global Change Biology 26, 417–430.

Sahney, S. and Benton, M. J. 2008. Recovery from the most profound mass extinction of all time. Proceeding of the Royal Society B Biological Science 275, 759–765.

Sales, M., Ballesteros, E., Anderson, M. J., Ivesa, I. and Cardona, E. 2012. Biogeographical patterns of algal communities in the Mediterranean Sea: *Cystoseira crinita*-dominated assemblages as a case study. Journal of Biogeography 39, 140-152.

Salomidi, M., Katsanevakis, S., Borja, A., Braeckman, U., Damalas, D., Galparsoro, I., Mifsud, R., Mirto, S., Pascual, M., Pipitone, C., Rabaut, M., Todorova, V., Vassilopoulou, V. and Vega Fernandez, T. 2012. Assessment of goods and services, vulnerability, and conservation status of European seabed biotopes: a stepping stone towards ecosystem-based marine spatial management. Mediterranean Marine Science 13, 49–88.

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. and Gatti, G. 2017. An integrated method to evaluate and monitor the conservation state of coralligenous habitats: The INDEX-COR approach. Marine Pollution Bullettin 120, 222-231.

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D. and Watson, J. E. M. 2016. The broad footprint of climate change from genes to biomes to people. Science 354(6313).

Schlegel, W. R. and Smit, J. A. 2018. heatwaveR: A central algorithm for the detection of heatwaves and cold-spells. Journal of Open Source Software 3(27), 821.

Schubert, N., Schoenrock, K. M., Aguirre, J., Kamenos, N. A., Silva, J., Horta, P. A. and Hofmann, L. C. 2020. Editorial: Coralline Algae: Globally Distributed Ecosystem Engineers. Frontiers in Marine Science 7, 7–9.

Shears, N. T., Smith, F., Babcock, R. C., Duffy, C. A. J. and Villouta, E. 2008. Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal marine environment. Conservation Biology 22, 467-481.

Silbiger, N. J., Goodbody-Gringley, G., Bruno, J. F. and Putnam, H. M. 2019.Comparative thermal performance of the reef-building coral *Orbicella franksi* at its latitudinal range limits. Marine Biology 166, 126.

Smale, D. A. and Wernberg, T. 2009. Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. Marine Ecology Progress Series 387, 27–37.

Smale, D. A. and Wernberg, T. 2013. Extreme climatic event drives range contraction of a habitat-forming species. Proceeding of the Royal Society B: Biological Science 280, 20122829.

Smale, D. A., Taylor, J. D., Coombs, S. H., Moore, G. and Cunliffe, M. 2017. Community responses to seawater warming are conserved across diverse biological groupings and taxonomic resolutions. Proceedings of the Royal Society B: Biological Sciences 284, 20170534.

Smale, D. A., Wernberg, T., Oliver, E. C. J. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N.

J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L. and Moore, P. J. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nature Climate Change 9(4), 306–312.

Smit, A. J., Roberts, M., Anderson, R. J., Dufois, F., Dudley, S. F.J., Bornman. T. G., Olbers, J. and Bolton J. J. 2013. A coastal seawater temperature dataset for biogeographical studies: large biases between in situ and remotely-sensed data sets around the coast of South Africa. PLoS One 8, e81944.

Steinbauer, M. J., Schweiger, A. H. and Irl, S. D. H. 2016. Biogeography, patterns. In: Encyclopedia of Evolutionary Biology. Kliman, R.M. (ed.), Oxford Academic Press, UK, pp. 221-230.

Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. Annual Review of Ecology Evolution and Systematics Vol. 17, 18, 273–303.

Teichert, S., Woelkerling, W. J., Rüggeberg, A., Wisshak, M., Piepenburg, D., Meyerhöfer, M., Form, A. and Freiwald, A. 2012. Rhodolith beds (Corallinales, Rhodophyta) and their physical and biological environment at 80◦31′ N in Nordkappbukta (Nordaustlandet, Svalbard Archipelago, Norway), Phycologia 51, 371–390.

Teichert, S. 2014. Hollow rhodoliths increase Svalbard’s shelf biodiversity. Scientific Reports 4, 1–5.

Teixido, N., Garrabou, J. and Harmelin, J. G. 2011. Low dynamics, high longevity and persistence of sessile structural species dwelling on Mediterranean coralligenous outcrops. PLoS One 6, e23744.

Terlizzi, A., Anderson M. J., Fraschetti, S. and Benedetti-Cecchi, L. 2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. Marine Ecology Progress Series 332, 25-39.

Thierry de Ville d’Avray, L., Ami, D., Chenuil, A., David, R. and Feral, J. P. 2019. Application of the ecosystem service concept at a small-scale: the cases of coralligenous habitats in the North-western Mediterranean Sea. Marine Pollution Bulletin 138, 160-170.

Thomson, J. A., Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Fraser, M. W., Statton, J. and Kendrick, G. A. 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Global Change Biology 21(4), 1463–1474.

Toonen, R. J., Bowen, B. W., Iacchei, M. and Briggs, J. C. 2016. Biogeography, Marine. In: Kliman, R. M. (ed.), Encyclopedia of Evolutionary Biology. Kliman, R.M. (ed.), Oxford Academic Press, UK, pp. 166-178.

Torrents, O., Tambutté, E., Caminiti, N. and Garrabou, J. 2008. Upper thermal thresholds of shallow vs. deep populations of the precious Mediterranean red coral *Corallium rubrum* (L.): assessing the potential effects of warming in the NW Mediterranean. Journal of Experiments in Marine Biology and Ecology 357, 7–19.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. In Cambridge University Press, Cambridge.

UNEP, 2017. Action plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea. UNEP/MAP Athens, GR.

Urban, M. C. 2012. Accelereting extinction risk from climate change. Science 348, 571-573.

Vadas, R. L. and Steneck, R. S. 1988. Zonation of deep water benthic algae in the Gulf of Maine. Journal of Phycology 24, 338-346.

Vásquez-Elizondo, R. M. and Enríquez, S. 2016. Coralline algal physiology is more adversely affected by elevated temperature than reduced pH. Scientific Reports 6, 1–14.

Verdura, J., Linares, C., Ballesteros, E., Coma, R., Uriz, M. J., Bensoussan, N. and Cebrian, E. 2019. Biodiversity loss in a Mediterranean ecosystem due to an extreme warming event unveils the role of an engineering gorgonian species. Scientific Reports 9, 5911.

Virgilio, M., Airoldi, L. and Abbiati, M. 2006. Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. Coral Reefs 25, 265-272.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transaction of the Royal Society B: Biological Science 365, 2019–2024.

Wernberg, T., Smale, Dan A. Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., Bennett, S. and Rousseaux, C. S. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change 3, 78–82.

Wernberg, T., Bennett, S., Babcock, R. C., Bettignies, T. De, Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. a, Radford, B., Santana-garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A. and Tuya, F. 2016 Climate-driven regime shift of a temperate marine ecosystem. Science 353(6295), 169–172.

Wiens, J. J. 2016. Climate-related local extinctions are already widespread among plant and animal species. PLoS Biology 14, e2001104.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. (Springer, 2009).

Appendix A: Supporting Information Chapter 1

Tab. S1.1 List of taxa/morphological groups. The mean percent cover in each area is given for each area.

TAXA	SE	NE	N	NNW	NW	W
Macroalgae						
Pseudochlorodesmis furcellata (Zanardini) Børgesen	0.10	0.03	0.00	0.02	0.13	0.07
Dyctiotales	5.07	0.53	0.04	2.90	4.37	4.44
Encrusting Corallinales	25.92	38.32	58.08	21.66	40.02	12.54
Articulated Corallinales	0.29	0.00	0.04	0.27	0.06	0.00
Peyssonnelia spp.	56.12	22.95	20.29	15.29	32.23	29.15
Valonia spp.	0.01	0.03	0.03	0.05	0.04	0.02
Codium spp.	0.15	0.01	0.06	0.00	0.26	0.02
Flabellia petiolata (Turra) Nizamuddin	0.54	3.06	1.70	0.93	4.43	1.79
Erect terete Ochrophyta	0.01	0.02	0.02	27.03	2.87	17.03
Encrusting Ochrophyta	0.03	0.11	0.08	0.10	0.82	0.54
Palmophyllum crassum (Naccari) Rabenhorst	0.17	0.81	1.21	0.88	1.89	0.74
Erect terete Rhodophyta	0.62	0.10	0.03	1.37	1.95	7.60
Erect flattened Rhodophyta	0.02	2.97	0.09	0.51	0.80	1.24
Halimeda tuna (J.Ellis & Solander) J.V.Lamouroux	0.11	5.75	0.80	0.06	0.32	0.46
Fucales	0.00	0.00	0.00	0.58	0.00	0.40
Phyllariopsis brevipes (C.Agardh) E.C.Henry & G.R.Sout	0.00	0.00	0.00	0.00	0.22	0.23
Sessile invertebrates						
Hydrozoans	0.36	0.85	0.10	0.02	0.00	0.00
Encrusting sponges	5.45	6.06	6.88	14.16	4.88	9.18
Encrusting briozoans	1.16	1.14	1.11	1.19	0.11	0.05
Sponges prostrate	0.14	0.37	0.34	0.77	0.59	0.27
Large serpulids	0.37	0.11	0.05	0.02	0.01	0.00
Parazoanthus axinellae (Schmidt, 1852)	0.14	0.94	0.64	1.47	0.41	2.36
Azooxantellate individual scleractinians	0.43	0.34	0.45	0.04	0.21	0.11
Small ramified bryozoans	0.89	1.17	0.35	0.23	0.05	0.04
Arborescens/massive sponges	0.12	0.17	0.34	0.40	0.10	0.09
Salmacina-Filograna complex	0.21	0.08	0.02	0.00	0.00	0.00
Myriapora truncata (Pallas, 1766)	0.02	0.09	0.36	0.19	1.60	0.11
Erect ascidians	0.01	0.39	0.33	0.05	0.08	0.02
Corallium rubrum (Linnaeus, 1758)	0.00	0.00	2.34	0.00	0.00	0.10
Paramuricea clavata (Risso, 1826)	1.05	0.99	0.00	0.00	0.00	0.00
Pentapora fascialis (Pallas, 1766)	0.32	0.45	0.06	0.00	0.05	0.03
Eunicella cavolini (Koch, 1887)	4.72	1.41	0.33	0.02	0.06	0.00
Reteporella grimaldii (Jullien, 1903)	0.23	0.12	0.17	0.00	0.02	0.18
Smittina cervicornis (Pallas, 1766)	0.37	0.22	0.25	0.06	0.01	0.00

Appendix B: Supporting Information Chapter 2

Table S2.1 Mean temperature at each area (East, North and West) and depth (18, 23, 28, 33 and 38 m) during the warm period (May-October 2019) calculated from Ceccherelli et al., 2020.

	18m	**23m**	**28m**	**33m**	**38m**
East	21.56	20.54	19.32	18.61	17.82
North	20.49	19.16	18.48	17.67	17.06
West	18.65	18.12	17.44	16.66	16.33

Table S2.2 List of the taxa/morphological groups identified

Taxa/morphological groups	**West**					**North**				**East**				
	18	**23**	**28**	**33**	**38**	**18**	**23**	**28**	**33**	**18**	**23**	**28**	**33**	**38**
Macroalgae														
Encrusting Coralline Algae	10.89	15.54	9.78	21.98	26.75	23.85	21.17	43.85	46.08	12.70	12.93	8.64	11.10	
Encrusting non calcareous algae														
Palmophyllum crassum	0	0.48	1.24	1.17	0.88	0.12	1.38	1.15	0.71	0.65	0.55	0.83	1.28	
Encrusting Ochrophyta	0.17	0.06	0.01	0.02	0.25	0	0	0.03	0.16	0	0.02	0.03	0	
Peyssonnelia spp.	3.10	15.61	13.97	15.97	24.87	36.35	41.84	28.94	24.99	22.87	12.29	18.43	27.82	
Turf algae	5.37	7.61	14.41	12.95	15.57	3.35	8.58	5.56	4.80	21.74	23.16	25.87	29.65	
Siphonous with vesicle-like thallus														
Codium spp.	0.41	0.42	0	0	0	0.24	0.02	0.09	0.13	0	0	0.6	0.04	0.03
Valonia sp.	0	0.07	0.03	0.06	0.08	0.47	0.06	0.03	0.03	0.03	0.02	0.03	0.01	0.3
Erect algae														
Articulated Coralline Algae	0.87	1.17	0.21	0.40	0.36	0.84	0.27	0.15	0.09	0.07	0.03	0.12	0.02	0.09
Erect terete Rhodophyta	22.04	8.58	0.54	2.22	1.74	0.27	0.25	0.03	0.06	0.60	0.59	0.01	0.07	
Erect flattened Rhodophyta	0	0	0.08	0.20	0.98	0	0	0	0	0	0	0	0.2	14.39
Dictyotales	1.62	1.17	0.83	3.48	2.96	0	0.1	0	0.1	4.65	0.65	0.14	0.44	0.14
Fucales	26.43	21.92	2.89	1.24	0.12	0	0	0	0	0	0	0	0	0.03
Erect terete Ochrophyta	14.11	10.66	22.99	19.47	6.29	0	0.05	0	0.03	0	0	0.01	0.02	0
Udoteaceae														
Halimeda tuna	0	0.02	0.02	0.07	0.11	24.71	4.05	0.62	0.67	7.61	5.34	2.96	0.03	0.04
Flabellia petiolata	0.06	0.39	2.75	1.41	0.55	2.98	3.83	2.48	2.54	3.83	2.53	2.72	0.78	0.57
Sessile invertebrates														
Sponges														
Encrusting sponges	4.78	7.66	16.97	9.85	10.17	1.05	5.98	5.95	7.48	8.86	12.39	12.84	7.60	
Prostrate sponges	0	0	0.33	0.29	0.26	0	0.56	1.47	0.21	0.01	0.03	0.01	0.02	
Arborescens/massive sponges	0.88	0.32	0.06	0.01	0.31	0.04	0.04	0.05	0.39	0	0.06	0.14	0.08	
Bushy sponges	0.14	0.59	0.86	0.36	0.09	0.01	0.05	0.01	0.04	0	0.03	0.02	0.1	
Hydrozoans	0	0.07	0.02	0.02	0.04	0.01	0	0.14	0.03	0.08	0.03	0.40	1.78	0.59
Parazoanthus axinellae	2.92	0.23	4.36	3.93	0.34	0	2.73	0.87	1.08	10.67	23.26	12.87	1.18	
Azooxantellate individual scleractinians	0	0.03	0.07	0.01	0.09	0	0.03	0.03	0.96	0	0	0.36	0.19	
Corallium rubrum	0	0	0	0	0	0	0.18	0.33	2.20	0	0	0	0	
Gorgonians														
Eunicella cavolini	0	0	0.47	0.01	0.05	0	0.03	0.43	0.19	0	0.10	1.96	3.26	
Paramuricea clavata	0	0	0	0	0	0	0	0	0	0	0	0.03	1.20	
Polychaetes														
Large serpulids	0	0.01	0.04	0.02	0.04	0.04	0.02	0	0.06	0.05	0.11	0.16	0.15	
Salmacina-Filograna complex	0	0.07	0	0	0	0	0.10	0	0.04	0.27	0.12	0.47	0.21	
Bryozoans														
Encrusting bryozoans	1.68	2.19	3.27	2.19	1.33	0.32	1.45	1.26	1.63	0.42	0.68	2.75	1.71	
Thin ramified bryozoans	0	0.39	0.50	0.21	0.46	0.08	0.15	0.33	0.47	0.35	0.35	2.41	1.71	
Aedonella calveti	0	0	0.03	0.07	0.01	0	0.01	0	0.21	0	0.01	0.13	0.16	0.41
Myriapora truncata	0.76	0.15	0.22	0.15	0.27	0.13	1.76	0.41	0.45	0	0.3	0.07	0.06	0.13
Pentapora fascialis	0.10	0.24	0.30	0.01	0	0	0.04	0.09	0.02	0	0	0.1	0.32	0.78
Reteporella grimaldii	0	0	0	0	0.01	0	0.10	0.13	0.23	0	0	0.05	0.24	0.19
Smittina cervicornis	0	0	0.01	0.02	0.09	0	0.24	0.33	0.15	0	0.01	0.48	0.21	0.21
Erect ascidians	0	0.05	0.05	0.05	0.01	0.04	0.09	0.07	0.14	1.81	1.21	0.34	0.58	0.30

Appendix C: Supporting Information Chapter 3

Table S3.1 List of all MHWs detected from the 4th of May to the 16th of October 2019 at the sites (AS, TA, CC and CP). For each of them the duration and the intensity category (moderate, strong, severe or extreme) was calculated based on Hobday et al 2018. The letters a, b, c and d refer to the MHW of each site, counting from May through October in sequence. Category I and II refer to the MHW intensity. *P* is the percentage of time spent in each of the MHW categories over the duration of the event.

site	MHW	category	peak date	Duration (days)	Max Intensity (°C)	*P* moderate	*P* strong	*P* severe	*P* extreme
CC	a	II	06-Jul	11	0.96	91	9		
	b	I	05-Sept	5	0.50	100			
	c	II	26-Sept	12	1.03	92	8		
TA	a	II	06-Jul	12	1.51	83	17		
	b	I	27-Aug	6	0.88	100			
CP	a	II	05-Jul	13	1.78	85	15		
	b	II	31-Aug	10	0.81	90	10		
	c	I	28-Sept	8	0.45	100			
	d	I	13-Oct	5	0.38	100			
AS	a	II	08-Jul	14	1.92	86	14		
	b	II	31-Aug	14	0.89	93	7		
	c	I	25-Sept	11	0.66	100			

Table S3.2 Temperature (°C) of the 90th percentile used to calculate D90 for each site x depth combination.

Depth	Site			
	CC	TA	CP	AS
18m	26.14	24.97	25.40	22.90
23m	25.30	24.23	23.66	22.29
28m	23.43	23.39	23.22	20.90
33m	22.34	22.37	22.03	18.89
38m	20.38	22.38	19.97	18.16

Table S3.3 Correlations (all $p<0.05$) between SST (by satellite) and deep temperature (by loggers) in N=166 days.

	Site			
	CC	**TA**	**CP**	**AS**
Depth				
18m	r =0.83	r =0.84	r =0.71	r =0.65
23m	r =0.73	r =0.72	r =0.57	r =0.61
28m	r =0.56	r =0.61	r =0.51	r =0.58
33m	r =0.48	r =0.52	r =0.43	r =0.57
38m	r =0.42	r =0.40	r =0.40	r =0.58

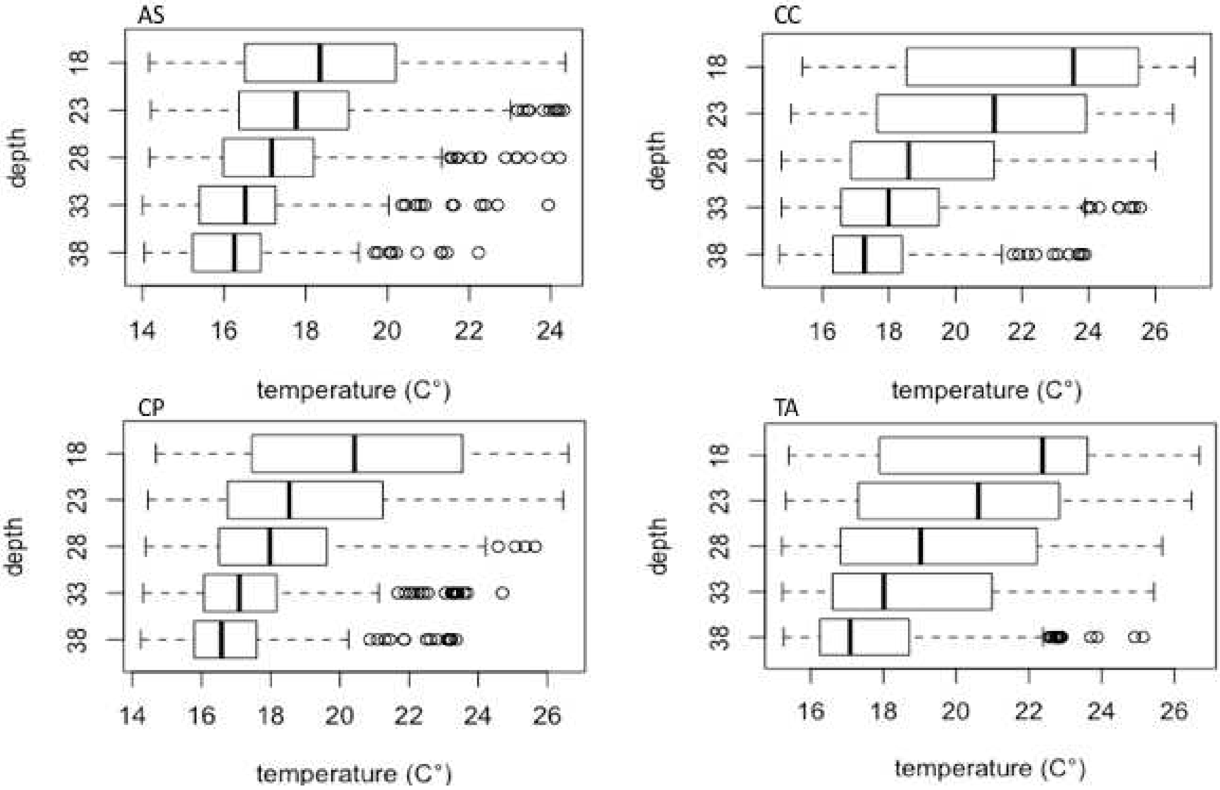


Figure S3. Variability of the temperature (°C) as function of the site (AS, CP, TV, and CC) and depth (18m, 23m, 28m, 33m and 38m).

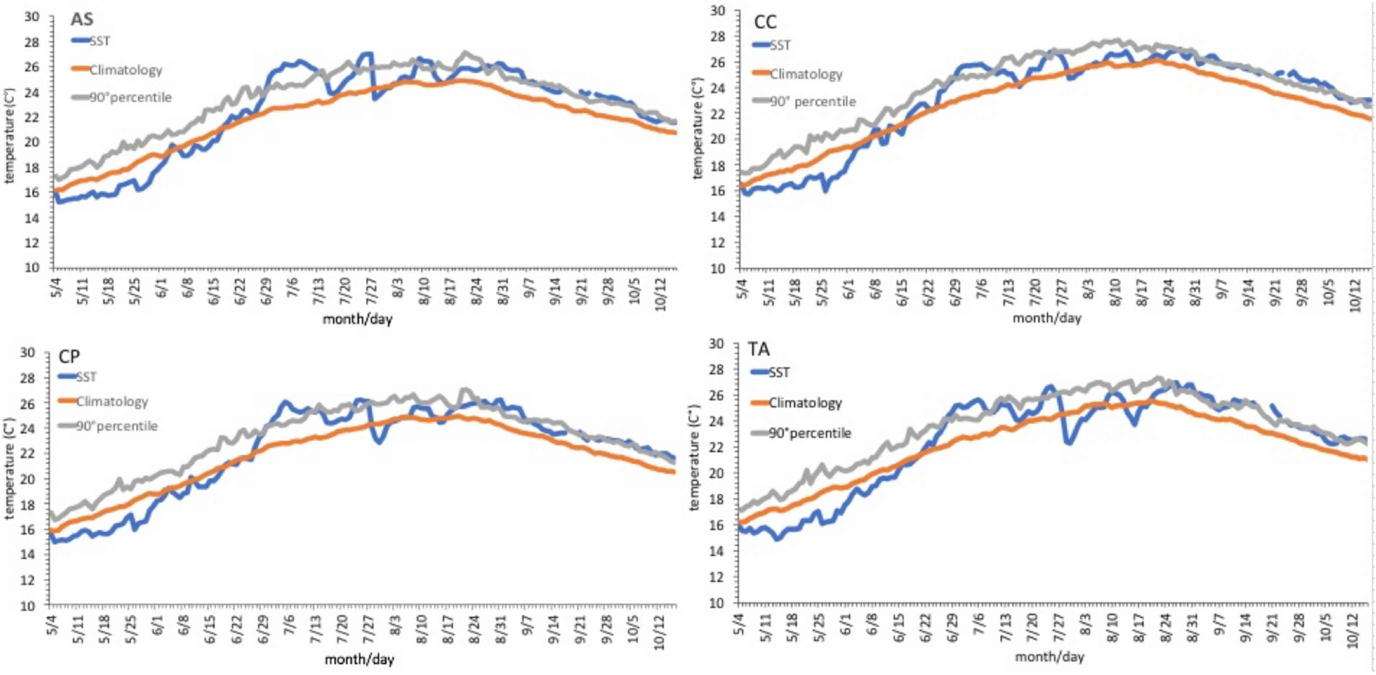
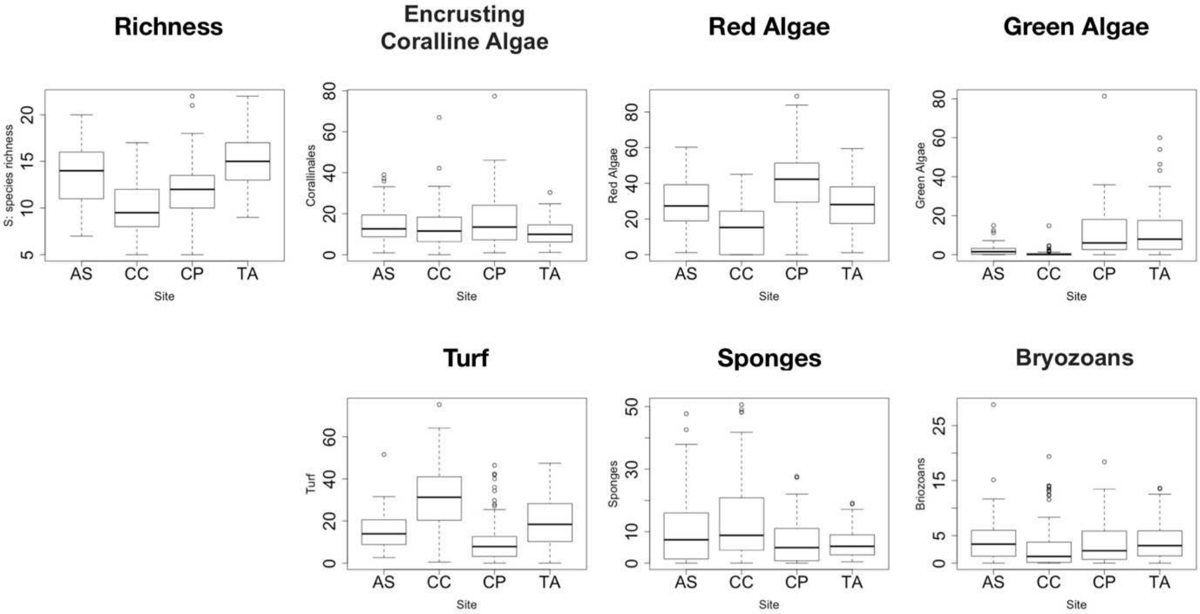


Figure S3.2 Daily temperature from May 4 to October 16 2019 at the four sites (AS, CP, TV, and CC): in blue SST (from satellites) of 2019, in orange the SST climatology and in grey the SST 90th percentile.

SITE



DEPTH

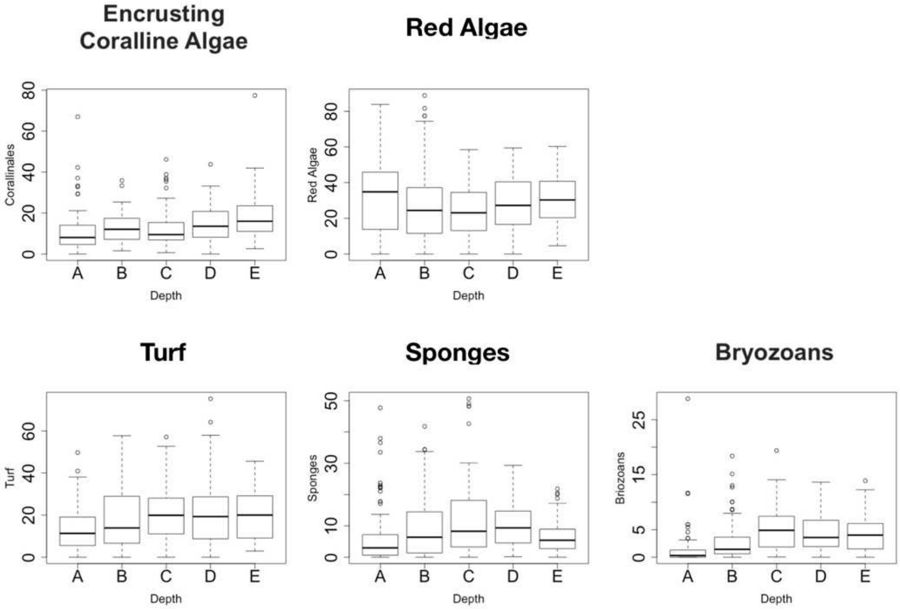


Figure S3.3 Variability of the response variables as function of the site (AS, CP, TV, and CC) and depth (18m, 23m, 28m, 33m and 38m).

MODEL RESULTS

Table S4. Statistical details for smooth and parametric terms of the final GAM models for richness.

S3.3 Statistical details for smooth and parametric terms of the final GAM models for richness.

Richness				
Smooth term	**df**	**Chi-square**	**P-value**	
s(MED)	1	24.047	**< 0.0001**	
s(D90)	2.092	1.982	0.424132	
s(NDD)	6.964	29.505	**0.000125**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
Intercept	2.57852	0.07595	33.95	**< 0.0001**
factor(Site)CC	-0.25896	0.10168	-2.547	**0.0109**
factor(Site)CP	-0.1813	0.10558	-1.717	0.086
factor(Site)TA	0.15334	0.10875	1.41	0.1586
Deviance explained: 58.2% n= 400				

Table S3.4 Statistical details for smooth and parametric terms of the final GAM models for Evenness

Evenness				
Smooth term	**df**	**F**	**P-value**	
s(MED):SiteAS	1.000	5.474	**0.0198**	
s(MED):SiteCC	3.953	6.469	**< 0.0001**	
s(MED):SiteCP	3.587	2.983	**0.02**	
s(MED):SiteTA	2.480	1.603	0.2329	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
Intercept	0.966973	0.002715	356.113	**< 0.0001**
factor(Site)CC	-0.007981	0.009253	-0.863	0.389
factor(Site)CP	-0.016361	0.012728	-1.285	0.199
factor(Site)TA	-0.002207	0.003145	-0.702	0.483
Deviance explained: 25.6% n= 400				

Table S3.5 Statistical details for smooth and parametric terms of the final GAM models for Coralline algae.

Corallinales				
Smooth term	**df**	**Chi-square**	**P-value**	
s(MED)	1.103	59.434	**< 0.0001**	
s(D90):DepthA	1.001	10.291	**0.00134**	
s(D90):DepthB	1.001	0.897	0.34372	
s(D90):DepthC	1.420	10.715	**0.00155**	
s(D90):DepthD	1.001	7.354	**0.00669**	
s(D90):DepthE	2.038	18.928	**0.00011**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	2.035	0.152	13.386	**< 0.0001**
factor(Site)CC	-1.534	0.237	-6.482	**< 0.0001**
factor(Site)CP	-0.596	0.194	-3.071	**0.00214**
factor(Site)TA	-1.854	0.256	-7.251	**< 0.0001**
factor(Depth)B	1.020	0.144	7.080	**< 0.0001**
factor(Depth)C	1.509	0.228	6.615	**< 0.0001**
factor(Depth)D	2.295	0.287	8.008	**< 0.0001**
factor(Depth)E	3.044	0.484	6.296	**< 0.0001**
Deviance explained: 26.7% n= 400				

Table S3.6 Statistical details for smooth and parametric terms of the final GAM models for Green Algae

Green Algae				
Smooth term	**df**	**Chi-square**	**P-value**	
s(MED):SiteAS	3.12	19.21	**0.00031**	
s(MED):SiteCC	1.002	15.05	**0.000105**	
s(MED):SiteCP	3.349	59.79	**< 0.0001**	
s(MED):SiteTA	3.409	122.31	**< 0.0001**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	-1.1834	1.7975	-0.658	0.5103
factor(Site)CC	0.7531	1.8041	0.417	0.6764
factor(Site)CP	3.6104	1.8296	1.973	**0.0485**
factor(Site)TA	2.6524	1.8018	1.472	0.141
Deviance explained: 65.4% n= 400				

Table S3.7 Statistical details for smooth and parametric terms of the final GAM models for Red Algae

Red Algae				
Smooth term	**df**	**Chi-square**	**P-value**	
s(D90):SiteAS	1.000	11.383	**0.000735**	
s(D90):SiteCC	1.561	8.597	0.044318	
s(D90):SiteCP	1.000	50.974	**< 0.0001**	
s(D90):SiteTA	2.953	3.430	0.387428	
s(F90)	1.004	22.655	**< 0.0001**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	1.2867	0.4534	2.838	**0.004541**
factor(Site)CC	0.9738	0.3941	2.471	**0.013467**
factor(Site)CP	1.606	0.3753	4.279	**< 0.0001**
factor(Site)TA	0.5404	4.0025	0.135	0.892605
factor(Depth)B	-0.4482	0.1287	-3.483	**0.000497**
factor(Depth)C	0.2158	0.1331	1.621	0.104991
factor(Depth)D	0.5951	0.1699	3.502	**0.000462**
factor(Depth)E	0.7615	0.1689	4.509	**< 0.0001**
Deviance explained: 29.7% n=400				

Table S3.8 Statistical details for smooth and parametric terms of the final GAM models for Turfs.

Turf				
Smooth term	**df**	**Chi-square**	**P-value**	
s(D90):DepthA	1.000	4.805	**0.028398**	
s(D90):DepthB	1.978	8.569	**0.022097**	
s(D90):DepthC	1.996	21.318	**< 0.0001**	
s(D90):DepthD	1.000	23.336	**< 0.0001**	
s(D90):DepthE	1.000	13.709	**0.000214**	
s(NDD)	1.003	14.852	**0.000118**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	1.8303	0.1578	11.600	**< 0.0001**
factor(Site)CC	1.4303	0.2108	6.787	**< 0.0001**
factor(Site)CP	0.1005	0.2087	0.482	0.6302
factor(Site)TA	0.9886	0.2186	4.523	**< 0.0001**
factor(Depth)B	0.6208	0.1505	4.126	**< 0.0001**
factor(Depth)C	0.9312	0.4452	2.092	**0.0365**
factor(Depth)D	0.2488	0.1178	2.112	**0.0347**
factor(Depth)E	0.1530	0.2041	-0.750	0.4534
Deviance explained: 34.8% n= 400				

Table S3.9 Statistical details for smooth and parametric terms of the final GAM models for Bryozoans.

Briozoans				
Smooth term	**df**	**Chi-square**	**P-value**	
s(MED):DepthA	1.000	56.866	**< 0.0001**	
s(MED):DepthB	1.000	60.112	**< 0.0001**	
s(MED):DepthC	1.000	23.901	**< 0.0001**	
s(MED):DepthD	1.251	16.251	**< 0.0001**	
s(MED):DepthE	1.000	18.387	**< 0.0001**	
s(D90):SiteAS	1.000	2.299	0.1294	
s(D90):SiteCC	1.000	3.58	0.0585	
s(D90):SiteCP	1.001	0.265	0.6068	
s(D90):SiteTA	1.000	23.063	**< 0.0001**	
s(NDD)	1.000	15.205	**< 0.0001**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	2.666	1.7341	1.537	0.1242
factor(Site)CC	5.431	2.251	2.412	**0.0158**
factor(Site)CP	1.060	1.5716	0.674	0.5000
factor(Site)TA	5.156	2.1002	2.455	**0.0141**
factor(Depth)B	-2.205	0.4794	-4.599	**< 0.0001**
factor(Depth)C	-5.856	0.989	-5.921	**< 0.0001**
factor(Depth)D	-10.856	2.0505	-5.294	**< 0.0001**
factor(Depth)E	-15.816	3.3712	-4.691	**< 0.0001**
Deviance explained: 38.7% n= 400				

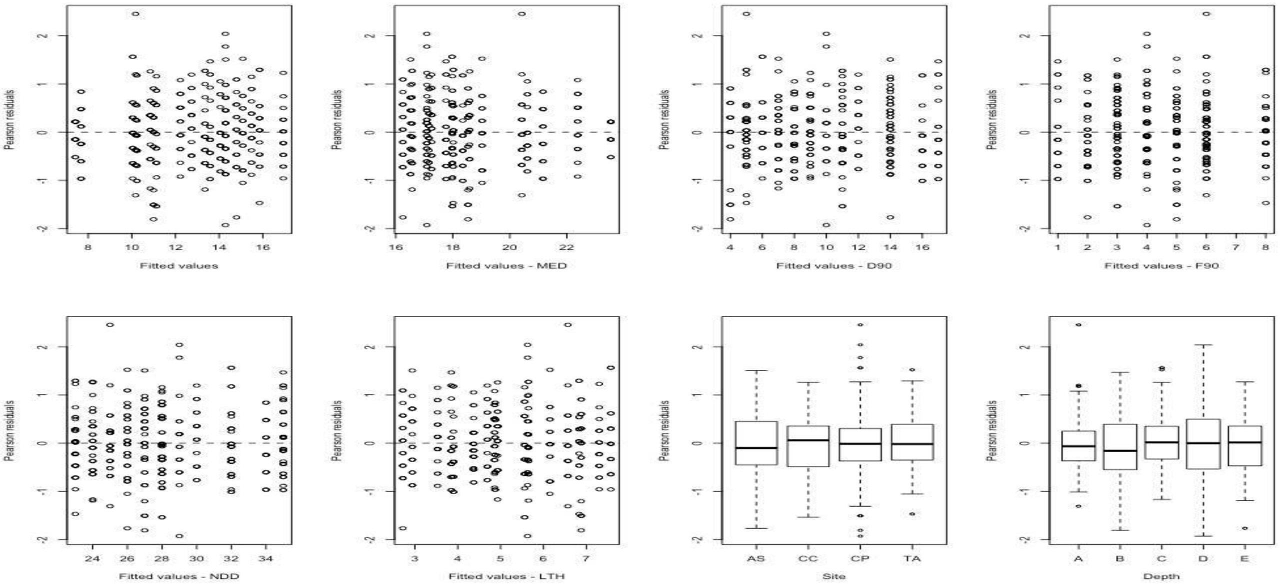
Table S3.10 Statistical details for smooth and parametric terms of the final GAM models for Sponges.

Sponges				
Smooth term	**df**	**Chi-square**	**P-value**	
s(D90):SiteAS	1.001	4.726	**0.0293**	
s(D90):SiteCC	1.003	0.028	0.8675	
s(D90):SiteCP	3.598	53.557	**< 0.0001**	
s(D90):SiteTA	1.001	0.032	0.8582	
s(F90)	1.001	15.565	**< 0.0001**	
Parametric terms	**Estim.**	**Std. Er.**	**Z-value**	**P-value**
(Intercept)	1.51219	0.58409	2.589	**0.00963**
factor(Site)CC	0.74953	0.51028	1.469	0.14187
factor(Site)CP	-0.01079	1.29332	-0.008	0.99334
factor(Site)TA	-0.37037	0.58555	-0.633	0.52706
factor(Depth)B	0.27842	0.17709	1.572	0.11591
factor(Depth)C	0.72273	0.184	3.928	**< 0.0001**
factor(Depth)D	0.16529	0.25432	0.65	0.51575
factor(Depth)E	-0.17573	0.24119	-0.729	0.46625
Deviance explained: 29% n= 400				

MODEL SELECTION AND VALIDATION

Richness model selection. "x" = interaction; "s" = smoother. Distribution: Poisson. In bold the model selected. The model order follows an increasing AIC.

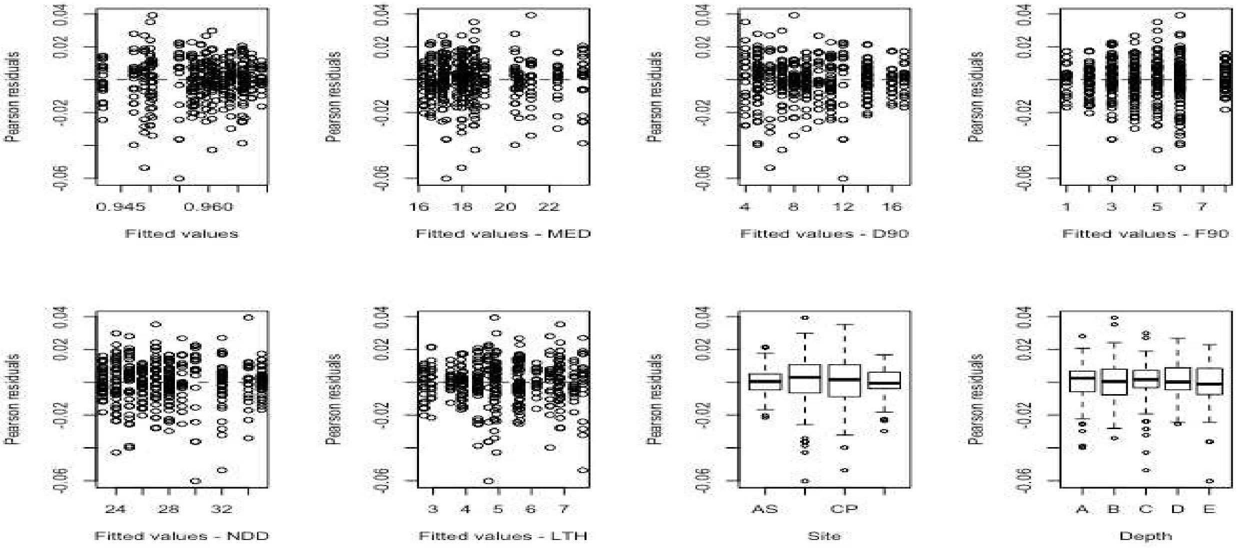
Model	Df	AIC	ΔAIC	Dev
R ~ factor(Site) + s(MED) + s(D90) + s(NDD)	**12.67**	**1929.71**	**0.00**	**58.2**
R ~ factor(Site) + s(MED) + s(NDD)	10.79	1930.24	0.54	57.2
R ~ factor(Site) + s(MED)+ s(NDD) + s(F90)	12.40	1930.51	0.81	57.9
R ~ factor(Site) + s(MED) + s(D90) + s(F90) + s(NDD)	13.56	1931.21	1.50	58.3
R ~ factor(Site) + s(D90) + s(NDD)	15.41	1934.05	4.34	58.5
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	16.20	1935.40	5.70	58.6
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDDxDepth)	17.27	1936.36	6.66	58.9
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90xSite) + s(F90) + s(NDD)	17.16	1936.38	6.68	58.8
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	16.82	1936.54	6.83	58.6
R ~ s(MED) + s(D90) + s(NDD)	16.78	1936.56	6.85	58.6
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90) + s(NDD)	17.90	1937.68	7.97	58.8
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90xDepth) + s(NDD)	17.94	1937.69	7.98	58.9
R ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90) + s(NDD)	18.22	1937.69	7.99	59.0
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	16.25	1937.90	8.20	58.0
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90xSite) + s(NDD)	18.33	1938.19	8.48	58.9
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDDxSite)	18.29	1938.19	8.48	58.9
R ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90) + s(NDD)	18.37	1938.30	8.59	58.9
R ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	18.44	1938.95	9.24	58.8
R ~ factor(Site) + factor(Depth) + s(MED)	15.67	1939.06	9.35	46.3
R ~ factor(Site) + s(MED) + s(D90)	18.79	1939.30	9.60	58.9
R ~ factor(Site) + factor(Depth)	8.00	1954.05	24.34	49.9
R ~ factor(Site)	4.00	2035.50	105.80	27.7



Richness model validation

Evenness model selection. “x” = interaction; “s” = smoother. Distribution: Gaussian. In bold the model selected. The model order follows an increasing AIC.

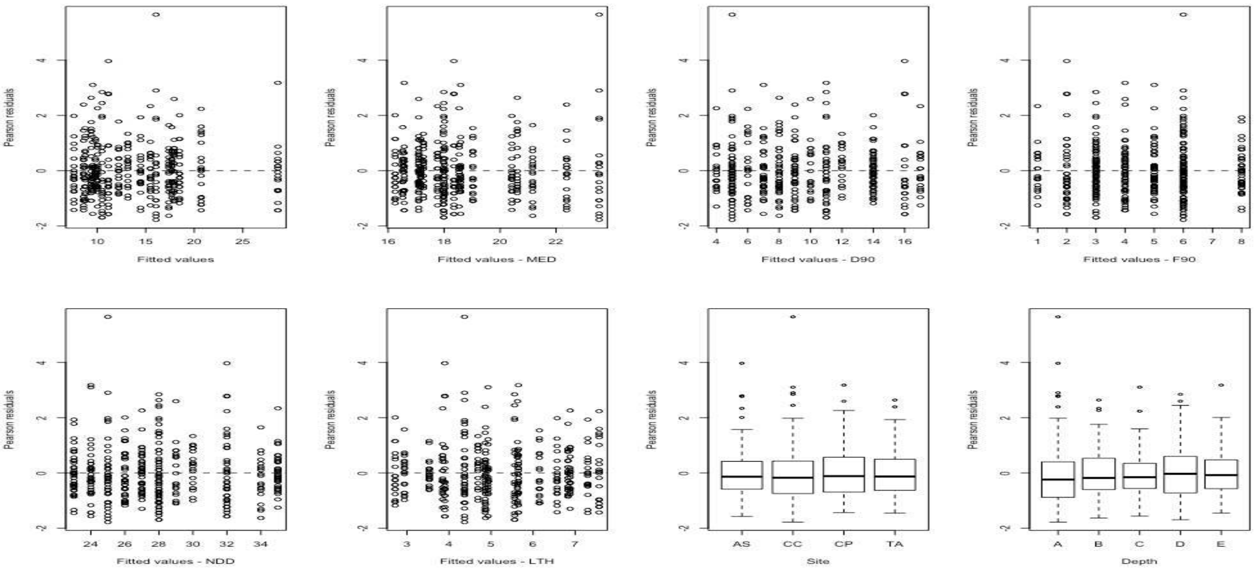
Model	Df	AIC	ΔAIC	Dev
evenness ~ factor(Site) + s(MED, by = Site)	**17.81**	**-2316.95**	**0**	**25.6**
evenness ~ factor(Site) + s(MED, by = Site) + s(LTH)	15.02	-2316.38	1	25.4
evenness ~ factor(Site) + s(MED, by = Site) + s(F90) + s(LTH)	15.98	-2314.82	2.23	25.50
evenness ~ factor(Site) + s(MED, by = Site) + s(F90) + s(LTH, by= Site)	16.85	-2314.15	2.90	25.70
evenness ~ factor(Site) + s(MED) + s(F90) + s(LTH)	16.24	-2314.13	2.92	25.30
evenness ~ factor(Site) + s(MED, by = Depth) + s(F90) + s(LTH)	17.58	-2314.11	2.94	26.00
evenness ~ factor(Site) + s(MED, by = Site) + s(F90) + s(LTH, by= Depth)	17.97	-2313.81	3.24	26.10
evenness ~ factor(Site) + s(MED, by = Site) + s(F90)	17.29	-2313.76	3.29	25.80
evenness ~ factor(Site) + s(MED, by = Site) + s(F90, by=Site) + s(LTH)	17.57	-2313.20	3.85	26.00
evenness ~ factor(Site) + s(MED, by = Site) + s(F90, by=Depth) + s(LTH)	17.85	-2312.53	4.52	25.80
evenness ~ factor(Site) + s(MED) + s(F90) + s(D90) + s(NDD) + s(LTH)	17.53	-2312.10	4.95	25.60
evenness ~ factor(Site) + s(MED) + s(F90) + s(NDD) + s(LTH)	17.77	-2311.59	5.46	25.50
evenness ~ factor(Site) + s(MED) + s(F90) + s(D90)	17.74	-2311.23	5.82	25.50
evenness ~ factor(Site) + s(MED, by = Depth)	18.83	-2310.93	6.12	25.80
evenness ~ factor(Site) + s(MED) + s(F90) + s(D90) + s(NDD)	18.79	-2310.76	6.29	25.80
evenness ~ factor(Site) + s(MED) + s(F90)	19.65	-2310.17	6.88	26.00
evenness ~ factor(Site) + s(MED) + s(LTH)	17.30	-2307.07	9.98	24.60
evenness ~ factor(Site) + s(MED)	11.78	-2290.26	26.79	19.10
evenness ~ factor(Site) + s(MED) + s(F90)	13.24	-2289.52	27.53	19.60
evenness ~ factor(Site)	5.00	-2272.15	44.91	12.40
evenness ~ factor(Site) + factor(Depth)	9.00	-2268.54	48.51	13.40



Evenness model validation

Corallinales model selection. “x” = interaction; “s” = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC.

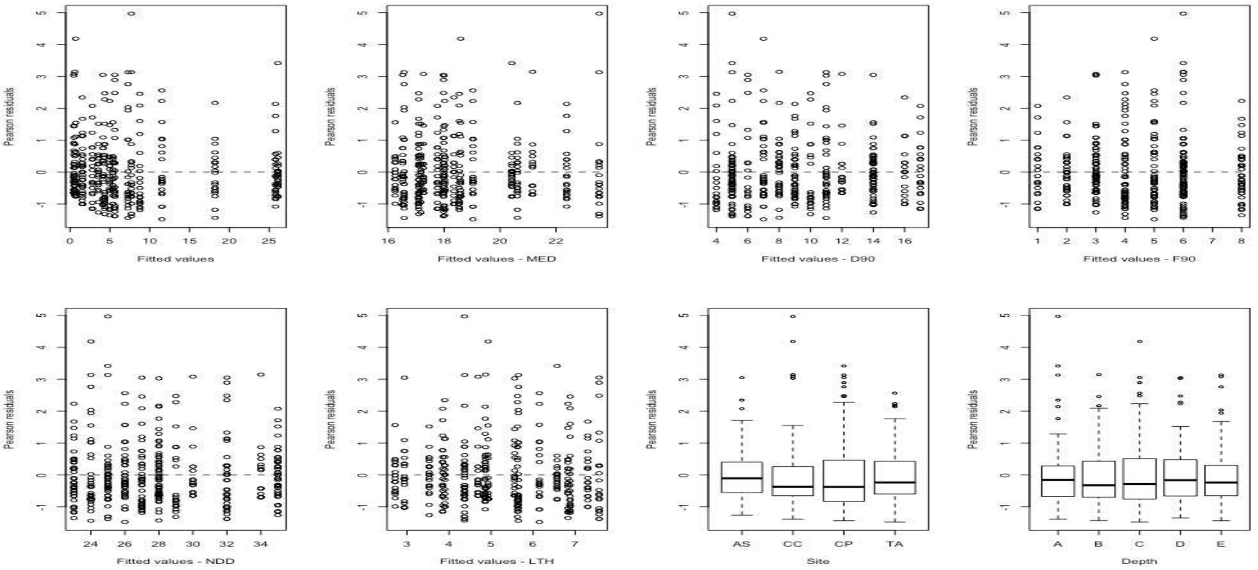
Model	AIC	ΔAIC	df	Dev
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth)	**2700.23**	**0.00**	**16.56**	**26.7**
CorallinalesTot ~ factor(Site) + factor(Depth)+ s(MED) + s(D90xDepth) + s(NDD)	2700.59	0.35	18.40	27.2
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xDepth) + s(F90) + s(NDD)	2701.83	1.59	19.23	27.3
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED + s(D90) + s(F90) + s(NDD)	2702.03	1.79	19.13	27.2
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	2702.60	2.37	19.41	27.2
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90) + s(NDD)	2702.71	2.47	19.42	27.2
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90xSite) + s(NDD)	2702.98	2.74	20.00	27.4
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90) + s(NDDxSite)	2703.39	3.16	20.01	27.3
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90) + s(NDD)	2703.49	3.26	19.76	27.2
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	2704.17	3.94	19.00	26.8
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED:Depth) + s(D90) + s(F90) + s(NDD)	2704.24	4.01	20.45	27.3
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90) + s(NDDxDepth)	2704.60	4.36	21.00	27.5
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90xDepth) + s(NDD)	2704.60	4.36	21.00	27.5
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	2704.81	4.58	18.75	26.6
CorallinalesTot ~ factor(Site) + factor(Depth) + s(MED)	2715.26	15.03	17.07	24.2
CorallinalesTot ~ factor(Site) + factor(Depth)	2759.57	59.34	9.00	12.4
CorallinalesTot ~ factor(Site)	2782.05	81.82	5.00	5.91



Corallinales model validation

Green algae model selection. "x" = interaction; "s" = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC.

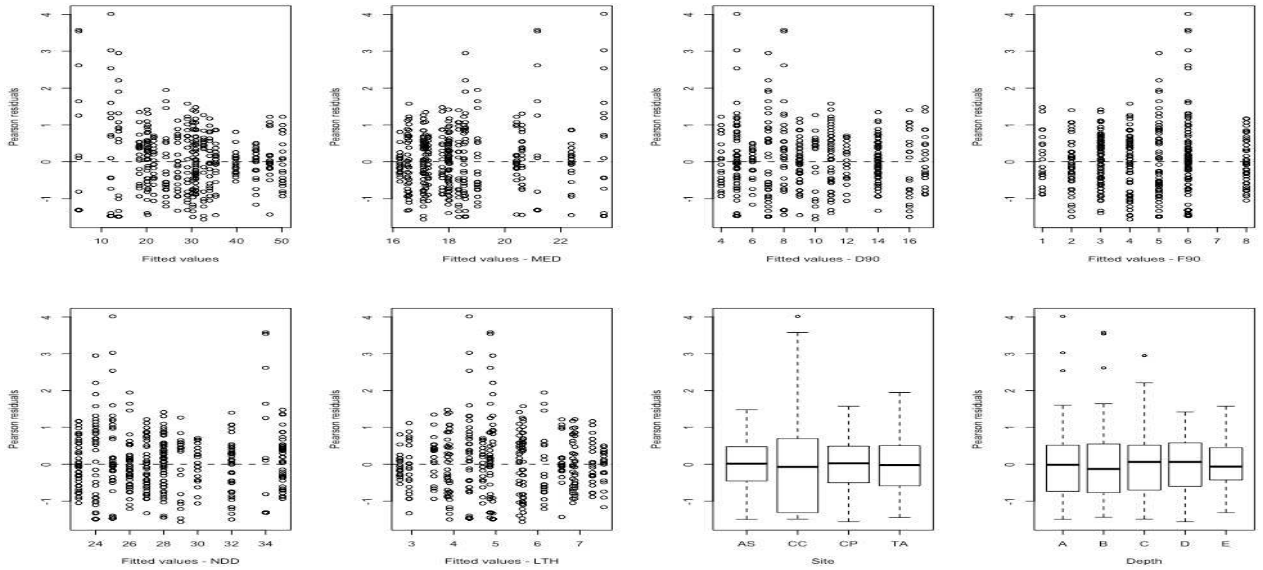
Model	Df	AIC	ΔAIC	Dev
GreenAlgae ~ factor(Site) + s(MEDxSite)	15.88	1834.27	0.00	65.4
GreenAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite)	17.08	1834.33	0.06	65.6
GreenAlgae ~factor(Site) + factor(Depth) + s(MEDxSite) + s(LTH)	18.13	1835.08	0.81	65.8
GreenAlgae ~factor(Site) + factor(Depth) + s(MEDxSite) + s(NDD)	17.70	1835.72	1.46	65.6
GreenAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(F90)	17.95	1835.90	1.63	65.6
GreenAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90)	18.05	1836.08	1.81	65.6
GreenAlgae ~ factor(Depth) + s(MEDxSite)	18.55	1837.12	2.86	65.6
GreenAlgae ~ factor(Site) + factor(Depth) + s(MEDxDepth)	19.89	1837.81	3.54	65.8
GreenAlgae ~ factor(Site) + factor(Depth) + s(MED)	17.96	1838.39	4.13	65.4
GreenAlgae ~ s(MEDxSite)	19.13	1838.70	4.43	65.6
GreenAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	20.93	1839.93	5.66	65.8
GreenAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	20.14	1840.07	5.80	65.6
GreenAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	20.59	1840.29	6.02	65.7
GreenAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	20.01	1842.58	8.32	65.4
GreenAlgae ~ factor(Site) + factor(Depth)	9.00	1978.12	143.85	47.5
GreenAlgae ~ factor(Site)	5.00	2864.46	1030.20	25.0



Green Algae model validation

Red algae model selection. "x" = interaction; "s" = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC

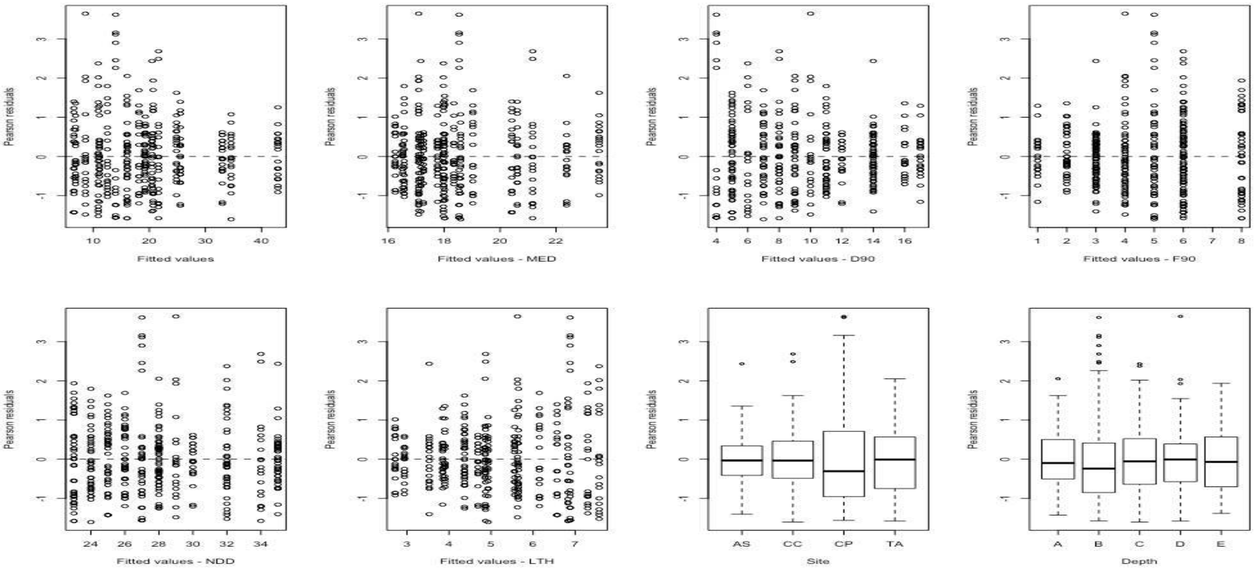
Model	Df	AIC	ΔAIC	Dev
RedAlgae ~ factor(Site)+ factor(Depth) + s(D90xSite) + s(F90)	**16.52**	**3315.72**	**0.00**	**29.7**
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90)	18.00	3316.81	1.09	30.0
RedAlgae ~ factor(Site) + s(MEDxSite) + s(D90xSite) + s(F90)	18.28	3318.03	2.31	29.9
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite)+ s(F90)	18.48	3318.14	2.42	30.0
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90) + s(NDD)	19.00	3318.15	2.43	30.1
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90) + s(NDD)	19.25	3318.96	3.24	30.1
RedAlgae ~ factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90)	18.88	3319.11	3.39	29.9
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90) + s(NDD)	19.51	3319.33	3.61	30.1
RedAlgae ~ factor(Site)+ factor(Depth) + s(D90xSite)	16.78	3319.66	3.94	29.2
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite)	18.82	3319.93	4.21	29.8
RedAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	18.92	3320.13	4.41	29.8
RedAlgae ~ factor(Site) + factor(Depth) + s(MED)	17.25	3321.01	5.29	29.2
RedAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	18.49	3321.24	5.52	29.5
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(NDD)	19.85	3321.36	5.64	29.9
RedAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	19.67	3321.52	5.80	29.8
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xDepth) + s(F90) + s(NDD)	21.00	3321.79	6.07	30.1
RedAlgae ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	18.66	3322.52	6.80	29.4
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90xSite) + s(NDD)	22.00	3323.75	8.03	30.1
RedAlgae ~ factor(Site) + factor(Depth) +s(MEDxSite) + s(D90xSite) + s(F90xDepth) + s(NDD)	22.00	3323.75	8.03	30.1
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90) + s(NDDx Site)	22.00	3323.75	8.03	30.1
RedAlgae ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90xSite) + s(F90) + s(NDDxDepth)	22.00	3323.75	8.03	30.1
RedAlgae ~ factor(Site)+ factor(Depth) + s(F90)	14.91	3338.47	22.75	25.8
RedAlgae ~ factor(Site) + factor(Depth)	9.00	3370.89	55.17	18.5
RedAlgae ~ factor(Site)	5.00	3374.38	58.67	16.5



Red Algae model validation

Turf model selection. "x" = interaction; "s" = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC.

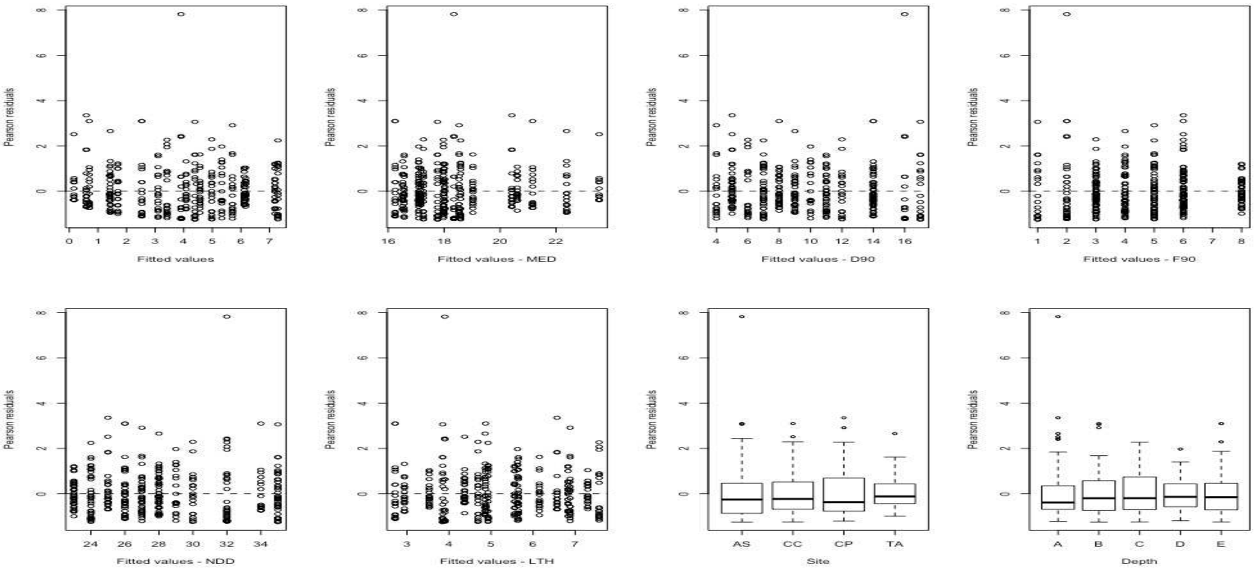
Model	Df	AIC	ΔAIC	Dev
Turf ~ factor(Site) + factor(Depth)+ s(D90xDepth) + s(NDD)	**16.98**	**2976.65**	**0.00**	**34.8**
Turf ~ factor(Site) + factor(Depth)+ s(D90xDepth) + s(F90) + s(NDD)	17.24	2976.75	0.10	34.8
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90) + s(NDD)	18.24	2978.17	1.53	34.9
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	19.08	2979.86	3.21	34.9
Turf ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90) + s(NDD)	19.57	2980.68	4.03	34.9
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	19.04	2980.74	4.09	34.8
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xSite) + s(F90) + s(NDD)	19.69	2981.32	4.67	34.9
Turf ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90) + s(NDD)	20.19	2981.54	4.89	35.0
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90xDepth) + s(NDD)	21.00	2982.29	5.64	35.1
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90) + s(NDDxDepth)	21.00	2982.29	5.64	35.1
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90) + s(NDDxSite)	20.97	2982.40	5.75	35.1
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90xDepth) + s(F90xSite) + s(NDD)	20.92	2982.41	5.76	35.1
Turf ~ factor(Site) + factor(Depth)+ s(F90) + s(NDD)	16.44	2982.53	5.78	33.7
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(NDD)	17.83	2984.15	7.50	33.9
Turf ~ factor(Site) + factor(Depth) + s(D90) + s(NDD)	16.46	2984.44	7.80	33.5
Turf ~ factor(Site) + factor(Depth)+ s(NDD)	15.12	2985.97	9.32	32.8
Turf ~ factor(Site) + factor(Depth)+ s(D90xDepth) + s(F90)	17.58	2986.79	10.15	33.4
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	17.61	2987.38	10.73	33.4
Turf ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	17.53	2987.58	10.93	33.3
Turf ~ factor(Site) + factor(Depth)+ s(D90xDepth)	15.81	2990.84	14.20	32.3
Turf ~ factor(Site) + factor(Depth) + s(MED)	12.10	3003.23	26.58	29.2
Turf ~ factor(Site) + factor(Depth)	9.00	3008.36	31.71	27.3
Turf~ factor(Site)	5.00	3029.06	52.42	22.5



Turf model validation

Briozoans model selection. "x" = interaction; "s" = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC.

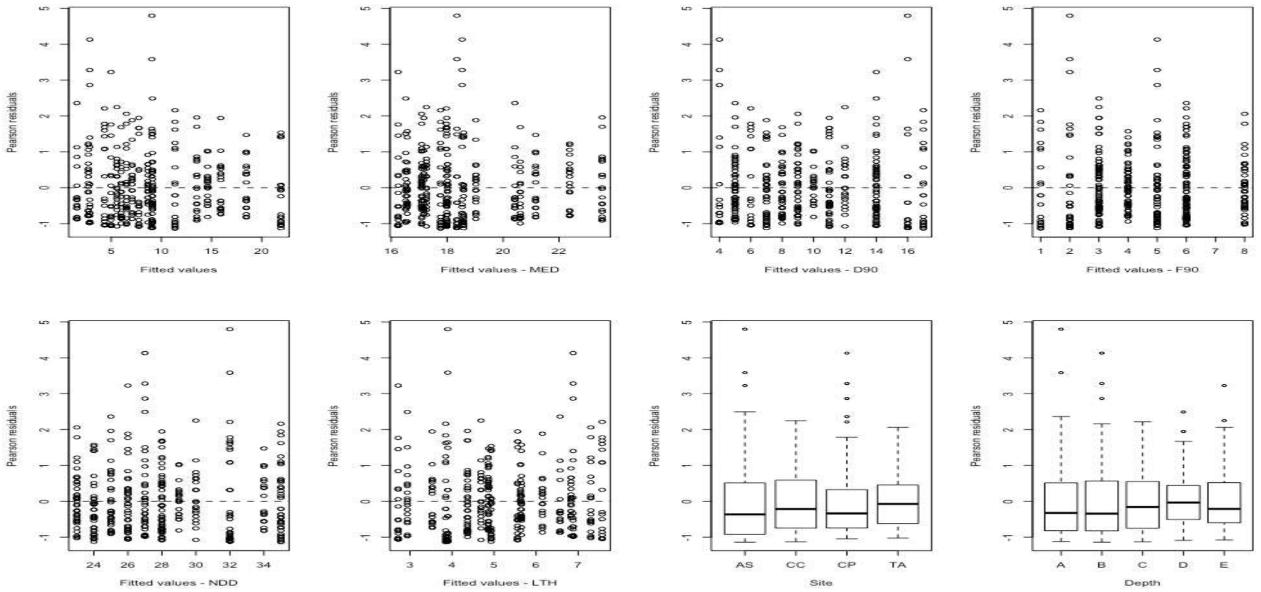
Model	Df	AIC	ΔAIC	Dev
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(NDD)	**19.25**	**1768.82**	**0.00**	**38.7**
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90) + s(NDD)	20.09	1770.47	1.65	38.7
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90) + s(NDD)	20.39	1770.98	2.15	38.7
Briozoans ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	19.58	1771.03	2.21	38.5
Briozoans ~ factor(Site) + factor(Depth) + s(MEDx Depth) + s(D90xSite)	20.59	1771.34	2.52	38.7
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xDepth) + s(F90) + s(NDD)	21.00	1771.43	2.61	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(D90xSite) + s(NDD)	20.86	1771.69	2.87	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(NDD)	20.41	1771.88	3.06	38.6
Briozoans ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(LTH)	18.50	1772.06	3.24	38.0
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90) + s(NDD)	20.82	1772.15	3.33	38.7
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90xSite) + s(NDD)	22.00	1773.41	4.58	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90xDepth) + s(NDD)	22.00	1773.41	4.58	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90) + s(NDDxSite)	22.00	1773.41	4.58	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90) + s(NDDxDepth)	22.00	1773.41	4.58	38.8
Briozoans ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	16.23	1781.64	12.82	36.0
Briozoans ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	15.59	1786.20	17.37	35.1
Briozoans~ factor(Site) + factor(Depth) + s(MED)	14.11	1789.52	20.70	34.2
Briozoans ~ factor(Site) + factor(Depth)	9.00	1891.12	122.30	15.5
Briozoans ~ factor(Site)	5.00	1956.10	187.28	1.31



Briozoans model validation

Sponges model selection. “x” = interaction; “s” = smoother. Distribution: Negative binomial. In bold the model selected. The model order follows an increasing AIC.

Model	Df	AIC	ΔAIC	Dev
SpongesTot ~ factor(Site) + factor(Depth) + s(D90xSite) + s(F90)	**16.60**	**2482.03**	**0.00**	**29.0**
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90)	20.00	2482.59	0.56	29.9
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(F90)	19.93	2482.84	0.81	29.9
SpongesTot ~ factor(Site) + s(D90xSite) + s(F90)	16.80	2482.87	0.84	28.9
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90) + s(F90)	20.06	2482.94	0.91	29.9
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite)	19.74	2482.97	0.94	29.8
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xDepth) + s(F90)	20.01	2483.08	1.05	29.9
SpongesTot ~ factor(Depth) + s(D90xSite) + s(F90)	16.65	2483.71	1.68	28.7
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90)	18.47	2484.17	2.14	29.2
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD) + s(LTH)	20.42	2484.92	2.89	29.7
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(NDD)	19.89	2485.11	3.08	29.5
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxSite) + s(D90) + s(F90)	18.59	2485.16	3.13	29.1
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(F90) + s(NDD)	20.37	2485.19	3.16	29.6
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90)	20.39	2485.68	3.65	29.6
SpongesTot ~ factor(Site) + factor(Depth) + s(D90xSite)	17.75	2485.72	3.69	28.7
SpongesTot ~ factor(Site) + factor(Depth) + s(MED) + s(D90) + s(LTH)	20.13	2486.07	4.04	29.4
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90xSite)	22.00	2486.21	4.18	30.0
SpongesTot ~ factor(Site) + factor(Depth) + s(MEDxDepth) + s(D90xSite) + s(F90xDepth)	22.00	2486.21	4.18	30.0
SpongesTot ~ factor(Site) + factor(Depth) + s(MED)	17.35	2509.25	27.22	24.7
SpongesTot ~ factor(Site) + factor(Depth) + s(F90)	14.97	2511.20	29.18	23.6
SpongesTot ~ factor(Site) + factor(Depth)	9.00	2563.24	81.21	12.1
SpongesTot ~ factor(Site)	5.00	2578.78	96.75	7.52



Sponges tot model validation

Appendix D: Supporting Information Chapter 4

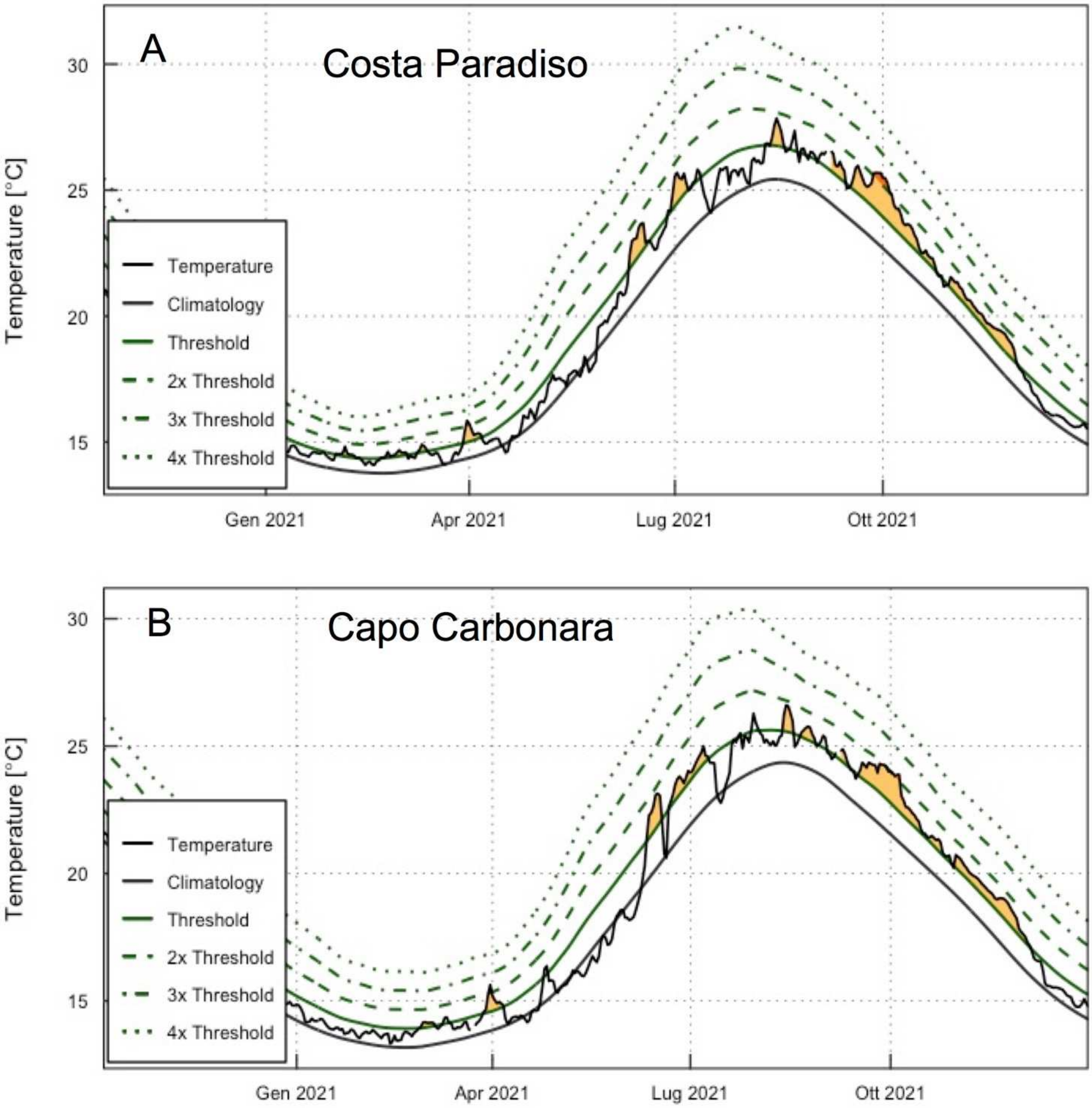


Fig S4.1 MHWs (yellow and orange areas) occurred during the study period at CC (A) and CP (B) SST. Note that the y axes have different scales.

Appendix E: Activities during the PhD

Seminars and Conferences

1. Trasformazioni urbane, processi di desertificazione e cambiamento climatico. Prof. V. Pascucci, Prof. G. Ceccherelli. 22/01/2019. University of Sassari. 4 hours.
2. Cerimonia di conferimento delle pergamene di Dottore di ricerca e Inaugurazione dell'anno accademico della Scuola di Dottorato di Ricerca. Prof. Massimo Carpinelli, Prof. Antonello Cannas, Prof. Massimo Onofri, Prof. Giovanni Sotgiu. 07/02/2019. University of Sassari. 3 hours
3. Il Public Engagement e il ruolo dell'Università nella società. Prof. M. Carpinelli, Prof. P.A. Serra, Dott. G. Demuro, Dott.ssa A. del Bello, Prof. R. Furesi. 11/02/2019. University of Sassari. 6 hours.
4. Celebrazioni dei 500 anni dalla morte di Leonardo da Vinci | Leonardo innovatore, inventore e ingegnere. 03/05/2019. University of Sassari. 3 hours.
5. Seminar, Cambiamenti Climatici: Passato, presente e futuro. Prof V. Pascucci, Prof S. Andreucci, Prof.ssa L. Dallai, Dott. D. Sechi, Dott.ssa Giulia Cossu. 14/05/2019. University of Sassari. 4 hours.
6. Seminar, Remote Sensing: a major technological revolution for ecology. Dott. Marco Malavasi. 21/05/2019. University of Sassari. 2 hours
7. Conference, Impacts of Alien Species on Sardinian Ecosystem. 29/05/2019. University of Cagliari. 5 hours.
8. Seminar, Ocean warming is shifting community composition and functioning via species - and functional group - specific thermal tolerances. Prof. John F. Bruno. 01/09/2019. University of Sassari. 2 hours.
9. Seminar, Does location protection increase coral reef resilience to climate change? Prof. John F. Bruno. 02/09/2019. University of Sassari. 2 hours.
10. Seminar, *Uso sostenibile degli oceani: dal disturbo alle soluzioni.* Prof. Antonio Pusceddu. Società Italiana di Ecologia. 26/03/2021. University of Cagliari. 1 hour
11. Seminar, *Ecologia quantitativa: dai dati ai modelli.* Prof. Marino Gatto. Società Italiana di Ecologia. 23/04/2021. Politecnico di Milano. 1 hour
12. Seminar, GAUSS- *SEM-TEM taglio biologico.* Dott. Salvatore Marceddu. 21/05/2021. University of Sassari. 1 hour.

13. Seminar, GAUSS- *Microscopi SEM ad ultra alta risoluzione (UHR-Feg).* Dott. Giuliano Casati. 4/06/2021. University of Sassari. 1 hour
14. Seminar, GAUSS- *Microcopia SEM e TEM per le scienze dei materiali.* Prof. Sebastiano Garroni. 29/10/2021. University of Sassari. 1 hour.
15. Seminar, *Zeiss microscopia e interfaccia Zen.* Dott.ssa Silvia contessi. 16/09/2021. University of Sassari. 1 hour
16. Seminar, *Withstanding climate change: the resilience of marginal populations of coralline algae.* Prof.ssa Federica Ragazzola. 30/11/2021. University of Sassari. 2 hours.
17. Seminar, *Ecological restoration.* Prof.ssa *Simonetta Fraschetti.* Società Italiana di Ecologia. 17/12/2021. University of Napoli Federico II. 1 hour.
18. Seminar, *Cambiamenti climatici: la risposta della Natura e gli effetti sulla Società Umana.* Prof.ssa Annalisa Fano. Società Italiana di Ecologia. 17/12/2021. University of Ferrara. 1 hour.
19. Seminar, *Sulle tracce di Darwin a scoprire le iguane rosa delle Galapagos.* Prof. Gabriele Gentile. Società Italiana di Ecologia. 1/04/2022. UniRoma Torvergata. 1 hour.

Courses and Workshops

1. Workshop, Organizzazione e gestione della ricerca. Prof. Andrea Vargiu, Prof. M. Bresadola. 12/02/2019. University of Sassari. 6 hours.
2. Workshop, Competenze per il mondo del lavoro I. Dott. Tommaso Aiello. 25/02/2019, Incubatore Uniss at University of Sassari. 8 hours.
3. Workshop, Competenze per il mondo del lavoro II. Dott. Tommaso Aiello. 26/02/2019. Incubatore Uniss at University of Sassari. 8 hours.
4. Workshop, Tavolo Tecnico: tematica della gestione di *P. lividus* in Area Marina Protetta di Alghero. 25/03/2019. 4 hours.
5. Workshop, Tavolo Tecnico: tematica della conservazione di *P. nobilis*, Marine Protected Area Penisola del Sinis- Isola di Maldiventre, Carbras (OR). 26/03/2019. 4 hours.
6. Course, Multivariate Analysis in Ecology. Prof. Marti J. Anderson, Dr. Paul Somerfield. 09/09/2019 to 20/09/2019. University of Trieste. 56 hours.
7. Course, Scientific Writing. Dr. A. H. D. Francesconi. 21/01/2020 to 20/02/2020. University of Sassari. 16 hours.
8. Course, Multivariate Analysis. Prof. C. Dimauro. 23/01/2020. University of Sassari. 24 hours.
9. Course, Statistics. Prof. Nicolò Pier Paolo Macciotta. 11/02/2020. University of Sassari. 32 hours.
10. Course, R software and statistics. Dott.ssa Gabriella La Manna. 20/05/2021 to 25/05/2021. University of Sassari. 16 hours.
11. Geomatica e le possibili applicazioni in ambiente marino. Dott.ssa Erica Nocerino. 19/11/2021. University of Sassari. 4 hours.

Publications related to the Phd thesis

1. CHAPTER 1: Luigi Piazzi, Maria Francesca Cinti, Ivan Guala, Daniele Grech, Gabriella La Manna, Arianna Pansini, **Federico Pinna**, Patrizia Stipcich, Giulia Ceccherelli. 2021. Variations in coralligenous assemblages from local to biogeographic spatial scale. Marine Environmental Research 169, 105375 https://doi.org/10.1016/j.marenvres.2021.105375
2. CHAPTER 2: **Federico Pinna**, Luigi Piazzi, Maria Francesca Cinti, Arianna Pansini, Patrizia Stipcich, Giulia Ceccherelli. 2021. Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. Estuarine, Coastal and Shelf Science 261,107554 https://doi.org/10.1016/j.ecss.2021.107554
3. CHAPTER 3: Giulia Ceccherelli, **Federico Pinna**, Arianna Pansini, Luigi Piazzi, Gabriella La Manna. 2020. The constraint of ignoring the subtidal water climatology in evaluating the changes of coralligenous reefs due to heating events. Scientific Reports 10:17332 | https://doi.org/10.1038/s41598-020-74249-9
4. CHAPTER 4: **Federico Pinna** et al. 2022. The Mediterranean bioconstructor *Lithophyllum stictiforme* showed adaptability to future warming. Submitted to Frontier in Marine Science

Publications not related to the Phd thesis

Moreover, during the completion of this PhD, I have participated in the following additional scientific publications:

1. Giulia Ceccherelli, Piero Addis, Fabrizio Atzori, Nicoletta Cadoni, MarcoCasu, Stefania Coppa, Mario De Luca, Giuseppe Andrea de Lucia, Simone Farina, Nicola Fois, Francesca Frau, Vittorio Gazale, Daniele Grech, Ivan Guala, Mariano Mariani, Massimo SG Marras, Augusto Navone, Arianna Pansini, Pieraugusto Panzalis, **Federico Pinna**, Alberto Ruiu, Fabio Scarpa and Luigi Piazzi. 2022. Sea urchin harvest inside marine protected areas: an opportunity to investigate the effects of exploitation where trophic upgrading is achieved. PeerJ 10:e12971

2. Patrizia Stipcich, Lazaro Marin-Guirao, Arianna Pansini, **Federico Pinna**, Gabriele Procaccini, Antonio Pusceddu, Santina Soru, Giulia Ceccherelli 2022. Effects of current and future summer marine heat waves on Posidonia oceanica: plant origin matters? Frontiers in Climate 4:844831

3. Luigi Piazzi, Federica Ferrigno, Ivan Guala, Maria Francesca Cinti, Alessandro Conforti, Giovanni De Falco, Mario De Luca, Daniele Grech, Gabriella La Manna, Vincenzo Pascucci, Arianna Pansini, **Federico Pinna**, Laura Pireddu, Alessandra Puccini, Giovanni Fulvio Russo, Roberto Sandulli, Antonio Santonastasio, Simone Simeone, Myriam Stelletti, Patrizia Stipcich, Giulia Ceccherelli 2021. Inconsistency in community structure and ecological quality between platform and cliff coralligenous assemblages. Ecological Indicator 136(3):108657

4. Arianna Pansini, Gabriella La Manna, **Federico Pinna**, Patrizia Stipcich, Giulia Ceccherelli. 2021. Trait gradients inform predictions of seagrass meadows change to future warming. Scientific Reports 11:18107 | https://doi.org/10.1038/s41598-021-97611-x

5. Luigi Piazzi, Fabrizio Atzori, Nicoletta Cadoni, Maria Francesca Cinti, Francesca Frau, Arianna Pansini, **Federico Pinna**, Patrizia Stipcich, Giulia Ceccherelli. 2021. Animal Forest Mortality: Following the Consequences of a Gorgonian Coral Loss on a Mediterranean Coralligenous Assemblage. Diversity 13, 133. https://doi.org/10.3390/d13030133

Abstract and presentations during the PhD

1. **Pinna F**., Caragnano A., Piazzi L, Ragazzola F., Stipcich P., Rindi F., Ceccherelli G. 2022. The Mediterranean bioconstructor *Lithophyllum stictiforme* showed adaptability to future warming. Incontro Dottorandi in Ecologia e Scienze dei Sistemi Acquatici, Cagliari, 25-27 Maggio 2022. Comunicazione.

2. **Pinna F**., Caragnano A., Piazzi L., Cinti MF., Pansini A., Stipcich P., Ceccherelli G., Rindi F. 2021 - Coralligenous reef assemblages biodiversity: identification of crustose coralline algal species in different Sardinia biogeographic areas. Incontro Dottorandi in Ecologia e Scienze dei Sistemi Acquatici, Stazione Zoologica Anton Dohrn, Napoli, 13 - 15 Aprile 2021. Presentazione poster.

3. **Pinna F**., Piazzi L., Cinti MF., Pansini A., Stipcich P., Ceccherelli G. 2021 – Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. Incontro Dottorandi in Ecologia e Scienze dei Sistemi Acquatici, Stazione Zoologica Anton Dohrn, Napoli, 13 - 15 Aprile 2021. Comunicazione.

4. **Pinna F**., Atzori F., N. Cadoni N., Cinti M.F., Frau F., Piazzi L., Pansini A., Ceccherelli G. 2020 - Is it possible to forecast effects of sea surface temperature anomalies on Coralligenous Assemblages? 51° Congresso S.I.B.M. Trieste 8-12 Giugno 2020, Comunicazione accettata.
5. **Pinna F**., Cinti M.C., Pansini A., Piazzi L., Roselli C., Ceccherelli G. 2019 - Vertical gradient and spatial variability of Coralligenous reef in Sardinia: the interactive effect of depth and location. XXIX Congresso SiTE 2019 (Ferrara 10-12 Settembre 2019), presentazione poster.

Abstract and presentations before the PhD

1. **F. Pinna**, G. Ceccherelli, J.F. Bruno 2018 – Temperature influence on herbivory rate of the green and the pencil sea urchin in the Galapagos Island. XXVIII Congresso SiTE 2018 (Cagliari 12-14 Settembre 2018), presentazione poster.