CONSERVATION STATUS AND TRAJECTORIES OF CHANGE IN MARINE COASTAL ECOSYSTEMS

PhD thesis

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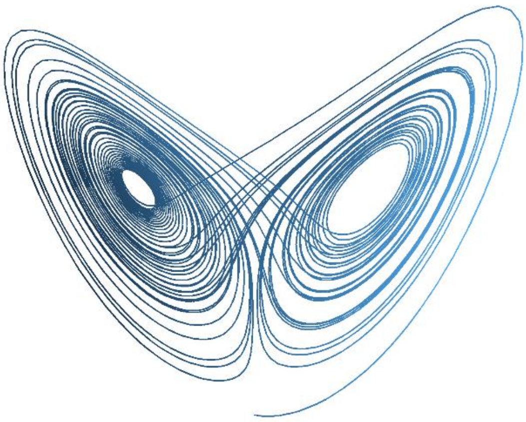
To me as a child,
Alla me da bambina,

"A butterfly flapping its wings in Brazil
can produce a tornado in Texas"

Edward N. Lorenz



"*Butterfly effect*"

Some complex dynamical systems

exhibit unpredictable behaviors

such that small variances in the initial conditions

could have profound and widely divergent effects

on the system's outcomes.

Because of the sensitivity of these systems,

outcomes are unpredictable.

(Chaos theory)

Abstract

Marine environments play a central role for the planet, yet an understanding of how climate change is affecting marine ecosystems has been poorly developed. There is now growing evidence that human activities are driving rapid changes from local to global scale. In last decades, the rates of change is accelerating and may exceed the potential tolerance of many organisms to adapt. Ecological systems and marine organisms have evolved under different regimes of stress and disturbances both of natural and anthropic origin and intrinsically connected. No ecosystem is unaffected and marine coastal habitats are particularly sensitive due to the convergence of multiple stressors.

The present work attempts to investigate how variable patterns of stress and disturbance influence the change in marine ecosystems, looking at two iconic coastal habitats: seagrass beds and coral reefs. Effects due to the anthropogenic pressure and a severe storm are here investigated as stress and disturbance respectively, on the endemic Mediterranean seagrass Posidonia oceanica*. Thermal anomalies causing repeated coral bleaching events are considered as disturbances on Maldivian coral reefs, while the reduced pH environment that is created at shallow hydrothermal vents of North Sulawesi (Indonesia) is seen as a stress simulating climate and human impact on benthic habitats. The study of change in coastal ecosystems has been carried out by means of several approaches including the comparison with long-time series, the use of indicators able to return a value of ecological status, retrospective analyses and modelling.*

The present work confirms the complexity of the interactions between stresses and disturbances, different in scale and intensity, operating on a same ecosystem.

The increase in seawater temperature starting from the 1980-90s can be identified as a common driver of change in both seagrass meadows and coral reefs ecosystems.

In P. oceanica *meadows of the Ligurian Sea, anthropic pressures remain the primary causes of impact, although, high intensity, pulse disturbances demonstrated that a single event is able to cause the same loss resulting from hundreds of years of chronic stress.*

Benthic habitats in close proximity to hydrothermal vents at tropical latitudes seem not negatively affected by the reduced pH as a chronic stress, while, in Maldivian coral reefs, the ability to cope with thermal disturbances seems to be dependent on coral genera.

Benthic ecosystems could develop a certain adjustment capacity to chronic stress to the detriment of an enhanced sensitivity towards disturbances but this is of concerns regarding the predicted increase of high intensity disturbances due to climate change.

Moreover, chronic stress and disturbances invariably co-occur, so it becomes difficult to assess which may be the proximate cause of ecosystem change.

Data on benthic communities suggest that marine habitats are experiencing phase-shifts toward alternative and unknown states. Consequently, future marine habitats will likely lose their original features acquiring a new different shape.

Continuing studies and long-term series of data will remain the most effective tool to validate these predictions and evaluate temporal patterns.

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General Introduction

Despite mounting evidence attest we are in the middle of a global change era, current conservation strategies and environmental policies seem unable to keep up with the modifications of the natural world (Pecl et al. 2017).

Temperature rise, pH reduction, and the drop in both the oxygen concentration and the food availability threaten oceans worldwide and their adaptive capacity to climate changes (Henson et al. 2017). Consequences of climate change can deeply affect marine habitats compromising their structure and functioning as well as causing the erosion of their ecological resilience (Wernberg et al. 2016). Marine ecosystems are changing at faster and faster rates under natural and human pressures and their trajectories are difficult to predict because of our limited understanding of the several processes involved (Somerfield 2018).

Physical disturbances and environmental stresses play central roles in determining the spatial and temporal dynamics of a variety of animal and plant communities (Pickett and White 1985, Osmond et al. 1986). The terms disturbance and stress have been used in various ecological contexts, often synonymously and ambiguously. A clear delimitation of their meaning has been hardly achieved and much depends on the intensity and duration of the external affectors involved (Montefalcone et al. 2017). According to Grime (1977) both are external agents: disturbances cause mortality or physical damage (subtraction of biomass), whereas stresses cause physiological alteration (reduction in productivity). Sensitivity to disturbance refers to the susceptibility of organisms to be physically injured or killed by exposure to specific external factors (e.g. mechanical impacts, climate anomalies). Sensitivity to stress refers to the organisms' capacity to tolerate and to cope with, and eventually adapt to, altered environmental quality (e.g. pollution, water turbidity) (Montefalcone et al. 2017).

Different stresses and disturbances altered survival and distribution of the marine biota, which aims to stay within its preferred environmental conditions. In recent decades, heat waves caused mass mortality events in sessile organisms and a consequent homogenization of the benthic community at a global scale (Cerrano et al. 2000; Cerrano and Bavestrello 2009; Lejeusne at al. 2010; Riegl et al. 2015; Morri et al. 2019). Some species were forced toward major depths, looking for their favourable thermal regime

(Graham et al. 2007; Dulvy et al. 2008; Smith et al. 2014, Assis et al. 2016; Morri et al. 2017) and new invaders ventured from tropical to temperate latitudes (Occhipinti-Ambrogi and Savini 2003; Montefalcone et al. 2010). The history of life on Earth is closely associated with environmental change on multiple spatial and temporal scales (Davis and Shaw 2001), but if on one hand changes have always been part of the natural evolution on the other hand, it is true that they occurred over a millennial time scale. The issue to deal with in the current age is the rate at which this change is happening. The Anthropocene has been recognised as a new geological era and it is widespread accepted that ecosystem dynamics are largely shaped by human actions (Uy and Shaw 2012). Until the '70s, oceans were overexploited for their resources, so when we felt the need to protect them it was already late. There is the exigence now to target the efforts in a way that allow the understanding of the magnitude and the direction of marine ecosystems shift, aiming to anticipate and adapt to changing conditions, as well as minimize negative consequences (Pecl et al. 2017).

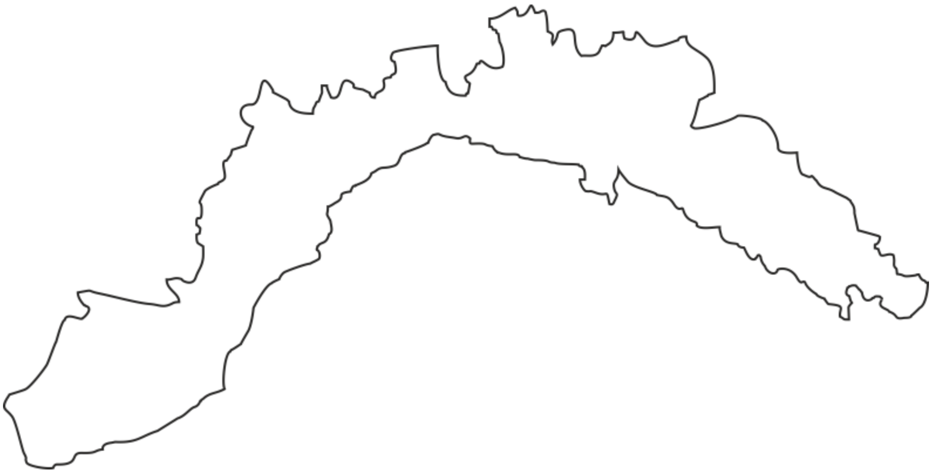
Health status assessment of marine ecosystems in an ever-changing world is challenging but it is a crucial step point to face the climate change.

The Ecological Status (ES) of a habitat can be evaluated differently according to the data availability. Usually, defining reference conditions is needed to measure a change (Borja et al. 2012). To this aim, the comparison with long-time series would be the best option even if historical data are rare and we often have to face with the diffused problem of the sliding baselines (Al-Abdulrazzak et al. 2012; Gatti et al. 2015b; Bianchi et al. 2019). An alternative way is to set some environmental targets for the habitat good status through the identification of indicators able to return a value of ES in terms of Ecological Quality Ratio (EQR) (Gobert et al. 2009).

Make predictions on ecosystems fate is likewise difficult, but there are some opportunities to figure out the incoming possible scenario. In this regard, studies on unique environments with peculiar abiotic characteristics and extreme environmental events, reproducing climate change effects, have proved to be useful to understand future impacts on marine habitats (Hall-Spencer et al. 2008; Teixido et al. 2013; Gera et al. 2014; Allen et al. 2017; Oprandi et al. 2019; Betti et al. 2020).

Healty marine ecosystems provide a number of services in terms of protein supply for the world's population and mitigation of climate change through the uptake and storage of atmospheric carbon dioxide. In particular, coastal ecosystems are “hot-spots” of environmental heterogeneity, biogeochemical transformations, and biological interactions, where dynamic exchanges of energy, mass, and nutrients occur between benthic and pelagic habitats (Griffiths et al. 2017). These transitional environments are among the world’s most productive ecosystems (Nixon, 1988; Berger et al., 1989; Costanza et al., 1995); they are characterized by a high biological diversity, however, by developing in the most densely populated areas, they experience multiple anthropogenic pressures at the same time. Additionally, the resulted impact due to human activities in coastal areas may grow further because of the combined effects of climate change and increasing anthropogenic pressure (Nepote et al. 2016).

The present work attempts to investigate how variable patterns of stress and disturbance influence the change in marine ecosystems, looking at two iconic coastal habitats: seagrass beds and coral reefs. The former specifically refers to *Posidonia oceanica* seagrass meadows in the Ligurian Sea (NW Mediterranean) and the latter to coral reefs in the Maldives archipelago (Indian Ocean) and Indonesia (North Sulawesi – Indo-Pacific Ocean). A focus on a Mediterranean rocky reef is here briefly presented in the context of “coral reefs”, with a case study on coralligenous assemblages of the Portofino Marine Protected Area (Eastern Ligurian Sea).



43°46'54.04"N 7°35'58.72"E
44° 7'54.70"N 9°38'36.06"E

PART ONE

POSIDONIA OCEANICA

The crucial role of seagrass ecosystems in coastal areas is largely recognised. The high level of productivity they support, guarantees the proper functioning of trophic cascade on which human population even depends for feeding. *Posidonia oceanica* L. Delile is the most important endemic seagrass of the Mediterranean Sea; its capacity to create a three-dimensional environment where an otherwise poor and less structured habitat would exist ensures an extensive array of biodiverse fauna (Unsworth et al. 2019). Among the benefits resulting from the presence of a stable and healthy *P.oceanica* meadow, refuge provision for the early life stages of valuable species and an effective protection from coastal erosion are included. Finally and yet importantly, the ability of seagrass meadows to store carbon within their "matte" represent a critical contribution in the mitigation of climate change (Duarte et al. 2013; Telesca et al. 2015; Carmen et al. 2019).

Thanks to all its qualities, *P. oceanica* is protected by several international directives and as a priority habitat (according to the Habitats Directive) it is worthy of conservation being included in management and monitoring plans. Moreover, its sensitivity to environmental changes makes it an optimal biological indicator largely used in the definition of water quality (Romero et al. 2007; Gobert et al. 2009; Montefalcone 2009; Lopez y Royo et al. 2010).

Despite increasing measures of protection adopted since the 1990s, seagrass meadows in the Mediterranean Sea experienced an overall decline attested by a general regression and a loss of their original extent (Boudouresque et al. 2009; Marbà et al. 2014; Pergent et al. 2014). The Ligurian Sea is among the northerner and colder sectors of the Mediterranean Sea and among the most anthropized areas as well, because of both industrial and touristic development (Burgos et al. 2017; Bianchi et al. 2019).

The study of change in *P. oceanica* ecosystem due to multiple anthropogenic pressures, invasive species and extreme weather event in the Ligurian Sea represents the core of the work here presented. The conservation status of *P. oceanica* meadows and their change over time have been evaluated through different methods: the use of indicators able to provide the measuring of the ES (Chapter 1), and the comparison between present and historical data (Chapter 2).

A retrospective technique has been applied to reconstruct trends in the sponge fauna associated to *P. oceanica* meadows up to hundreds of years in order to identify, through fluctuations in spicules abbundances, any natural or anthropic impact that possibly acted on the benthic habitat (Chapters 3).

Lastly, due to an unexpected and severe storm occurred on autumn 2018, it has been possible to investigate the effects of such extreme event on some *P. oceanica* meadows by comparing their status before and after the natural disturbance (Chapter 4).

Chapter 1 Ecological Status

1.1

Comparison of descriptors at different levels of ecological complexity to define the health status of *Posidonia oceanica* meadows in the Ligurian Sea (NW Mediterranean)

Additional resources:
In prep. manuscript. Extracted content:
A. Oprandi, C. N. Bianchi, O. Karayali, C. Morri, I. Rigo, M. Montefalcone. *Biologia Marina Mediterranea (2019) in press.*

Abstract

Posidonia oceanica (L.) Delile is an ideal biological indicator to define environmental quality. Due to the high urbanization of the coast, the *P. oceanica* meadows of Liguria are in decline. We assess the health status of 13 *P. oceanica* meadows using ecological descriptors at different complexity levels (i.e. species, population, community, and seascape); the consistence among indicators and indices has been evaluated, as well. In each meadow, cover data, type and depth of the meadow limits, shoots density and *P. oceanica* samples were collected. Field data and laboratory analyses on leaves, rhizomes and epiphytes allowed calculating 11 between indicators and indices, including the integrated index PREI (Posidonia Rapid Easy Index), the sole adopted by the national environmental agencies. Results provided inconsistent responses among descriptors, suggesting poor or bad ecological status at species and population levels, but high status at seascape level. The integrated index PREI, which includes different levels of complexity that gave contrasting answers when used singularly, mostly indicated good status. Our results suggest that the adoption of a more complete set of descriptors to accurately define the health status of *P. oceanica* meadows is highly recommended.

Introduction

The extensive use of biotic indices able to return a summary of the environmental quality has been highly supported by recent European directives. The Water Framework Directive (WFD 2000/60/EC) recommended achieving a good environmental status (GES) of coastal waters introducing, for the first time, the definition of ecological quality by means of a classification that encompassed five quality classes of ecological status: high, good, moderate, poor and bad. Since then, several indices have been developed basing on different biological, hydromorphological and physico-chemical quality elements suggested in the Annex V of the WFD (Moreno et al., 2001; Ballesteros et al., 2007; Fernandez-Torquemada et al., 2008; Lopez y Royo et al., 2009; Occhipinti-Ambrogi et al., 2009). In the frame of the biological ones, marine angiosperms, especially the endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile, are recognized as an optimal biological indicator of ecological quality due to their wide distribution and sensitivity to anthropic disturbances (Pergent et al., 1995; Pergent-Martini and Pergent, 2000; Romero et al., 2007; Gobert et al., 2009; Montefalcone, 2009). The subsequent Marine Strategy Framework Directive (MSFD 2008/56/EC) came into force as the first legislative instrument related to the protection of marine biodiversity and required monitoring planes to pursue the biological diversity maintenance (descriptor 1), healthy and abundant food webs (descriptor 4) and the seafloor integrity (descriptor 6) of seabed habitats.

Posidonia oceanica is a key species considered the most important coastal habitat of the Mediterranean Sea (Buia et al., 2004). Its meadows are the main source of primary production in the coastal waters nourishing many food chains and relative hundreds of species that depend on them. Moreover, as a nursery area they support very high levels of biodiversity (Boudouresque et al., 2006).

The increasing anthropic pressure that characterized Mediterranean coastal areas since the past century led to a global regression of *P. oceanica* meadows in the whole basin. In the Liguria region, the loss of meadows in terms of extension was estimated as the 50% of the original ones (Burgos et al., 2017). Nevertheless, recent evidences about some ligurian meadows seemed to prove that in the last decades the regression has stopped or slowed down thanks to the conservation policies encouraged by EU directives and the Marine Protected Areas establishment (Bianchi et al., 2019).

The complexity of *P. oceanica* ecosystem allow to process information at individual or species level, where the leaf biometry gives advices about plant growth (Marbà et al., 2006); at population level, where structure and morphology of the meadow reflect hydrodynamic and environmental conditions (Montefalcone et al., 2008); at community level, characterized by the associated flora and fauna as leaves epiphytes, considered early warning indicators of environmental alterations (Ruiz and Romero, 2001; Giovannetti et al., 2010) and at seascape level, where meadows' discontinuity as well as the presence of alien species give a measure of the ongoing degradation processes (Montefalcone 2009).

Monitoring the good status of *P. oceanica* meadows results useful to obtain information about the global environmental quality and on the efficacy of local or regional policies for the management of coastal environment.

To date, well-defined approach to monitor *P. oceanica* meadows are still lacking even if several efforts have been done under EU wishes and researches of new tools are ongoing.

As regards seagrass meadows, a multitude of methodologies, indices and metrics are available so rather than create new indicators it should be desirable to focus on what are suitable or not for monitoring purposes. In this respect, the aim of this work was to compare a set of eleven indices and descriptors able to provide a measure of the ecosystem' ecological status according to the quality classes proposed by the WFD and commonly used in the monitoring of Mediterranean *P. oceanica* meadows. To this end, we used data coming from thirteen seagrass meadows distributed along the Ligurian coast, aiming to obtain a measure of the efficiency and consistency of indices and descriptors that act at different levels of ecological complexity (species, population, community and seascape).

Materials and methods

Study area

The study was carried out in Liguria (NW Mediterranean) on thirteen *P. oceanica* meadows distributed along the coast of the whole regional territory. The investigated sites in geographical order moving eastward were: Ventimiglia (A 43° 47.387'N; 7° 34.968'E), Ospedaletti (B 43° 47.907'N; 7° 42.441'E), Sanremo (C 43° 48.241'N; 7° 45.152'E), Diano Marina (D 43° 54.440'N; 8° 5.485'E), Noli (E 44° 12.233'N; 8° 25.185'E), Bergeggi (F 44° 13.998'N; 8° 26.427'E), Vado Ligure (G 44° 14.970'N; 8° 27.264'E), Camogli (H 44° 20.518'N; 9° 9.075'E), Pedale (I 44° 19.215'N; 9° 12.790'E), Pagana (J 44° 20.426'N; 9° 13.467'E), Manara (K 44° 15.234'N; 9° 24.490'E), Framura (L 44° 12.363'N; 9° 32.304'E) and Monterosso (M 44° 8.516'N; 9° 38.551'E) (Fig. 1). In each meadow, two underwater transects were performed to collect data, totalling 26 transects in the study area.

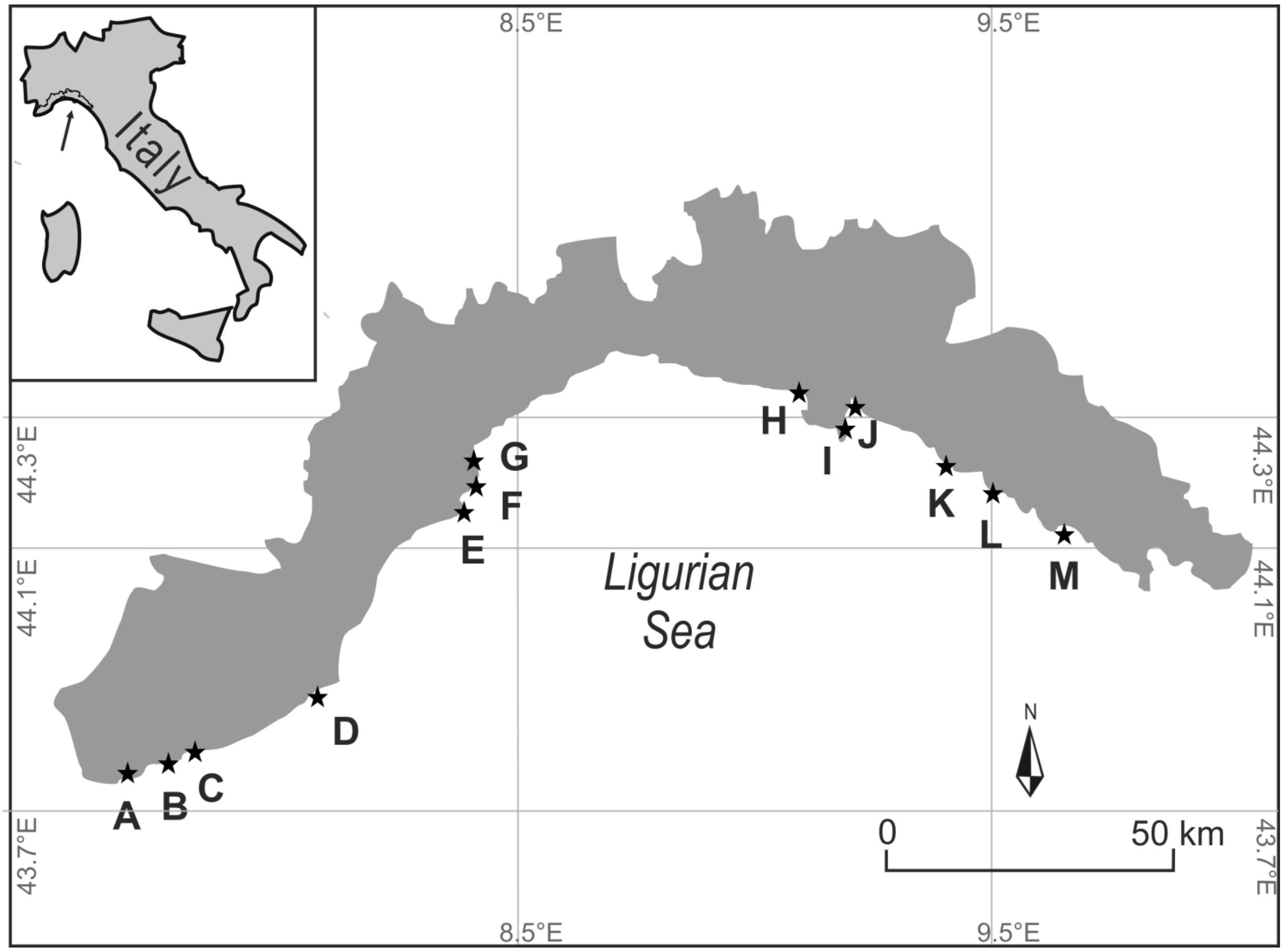


Fig. 1. Study area with location of the thirteen meadows investigated: Ventimiglia (A), Ospedaletti (B), Sanremo (C), Diano Marina (D), Noli (E), Bergeggi (F), Vado Ligure (G), Camogli (H), Pagana (I), Pedale (J), Manara (K), Framura (L), Monterosso (M).

Data collection

The field activity was carried out during the summer months of 2017 and 2018. In each meadow, the two transects were identified by a marked line that was lied down between the upper and the lower limit using an underwater compass to keep a perpendicular direction to the coast, according to known geographic coordinates from previous samplings. Two Scuba divers, trained to collect scientific data, detected each 10 m along the line, the type and depth of the seafloor substrate together with the percent cover of living *P. oceanica*, dead matte, sand, rock, and substituting species (e.g. *Cymodocea nodosa*, *Caulerpa cylindracea*, *Caulerpa taxifolia*). Due to its well-described relationship with water transparency the depth of the lower limit was also detected, while, type (Pergent et al., 1995) and cover of the lower limit were recorded as they may be indicative of the meadow health status. Additionally, at 15 m depth, that is supposed to be the mean depth to which *P. oceanica* reaches its maximum cover in each transect, 18 *P. oceanica* shoots were sampled for further laboratory analysis and shoots density (no. of shoot per m2) was estimated with in a sampling unit area of 0.016 m2 in nine replicates.

Field data elaboration and laboratory analysis

The total percent cover (Tx%) of each descriptors (e.g. living *P. oceanica*, dead matte, *C. Cylindracea*) along a transect, was calculated by the following formula:

$Tx\ \% = \sum(\% \bullet m) / TL$

Where % is the percent cover of the descriptor x detected between two consecutive points of distance m, and TL is the total length of the transect.

The Conservation Index (CI) (Moreno et al., 2001), the Substitution Index (SI) and the Phase Shift Index (PSI) (Montefalcone 2009) were calculated thanks to the percent cover data as informers of the meadows fragmentation and the presence of alien species, signs of degradation processes.

Laboratory analysis made on the 18 shoots collected in each transect allowed, through leaf biometry and lepidochronology, to estimate the average leaf surface per shoot ($cm^2 \bullet shoot^{-1}$), the average leaves number produced per year (no. leaves • y^{-1}) and the average rhizome elongation per year ($mm \bullet y^{-1}$) that are important parameters in the plant growth. Furthermore, leaf epiphytes were accurately scraped off from both the inner and the outer leaves layers to thus be dried and weighted. The resulted epiphyte biomass (mg_{dw} • cm^2) was adopted as indicator of the changing environment since it respond quickly to stresses compared to the plant itself (Giovannetti et al., 2010).

Thanks to both field and laboratory data we were able to calculate the Posidonia Rapid Easy Index (PREI) (Gobert et. al., 2009) that is the most used by the environmental agencies (ARPA) to predict the water quality at national level. PREI encompassing different metrics (leaf surface, shoot density, lower limit depth, lower limit type, epiphyte biomass and leaves biomass) produced a value on the Ecological Quality Ratio (0-1) scale.

Indices and descriptors at different level of ecological complexity

Totally, we used a set of eleven indices and descriptors grouped according to their affinity to the complexity level and summarized as follow.

At Individual level, we considered the leaf surface LS (cm^2 • $shoot^{-1}$), the leaves number per year LN and the rhizome elongation RE (mm • y^{-1}). At population level, we considered the shoot density SD (no. of shoot per m^2) the lower limit depth LLD (m) and the percent cover at the lower limit LLC (%). At community level, we considered the epiphyte biomass EB (mg_{dw} • cm^{-2}). At seascape level, we considered the CI, the SI and the PSI and at last, PREI, due to its formula, was considered as a multilevel descriptor combining more metrics.

Each index and descriptor was compared with its recent reference classification that meets requirements of the WFD (Montefalcone 2009; Gobert et al., 2009; UNEP/MAP- RAC/SPA 2011). Thus, for all indices and descriptors, the ecological status was classified in one of the five quality classes from “High” to “Bad”.

Since for the epiphyte biomass no reference classification was available, we provided an attempt to classification based on the frequency distribution of our data whose empirical scale is shown in table 1.

Tab. 1. Epiphyte biomass classification (mg_{dw} • cm^{-2})

High	Good	Moderate	Poor	Bad
< 0.1	≥ 0.1	≥ 0.2	≥ 0.3	≥ 0.6

Results

At individual level, leaf surface in the most of the meadows investigated was scarce, not exceeding 218 cm^2 • $shoot^{-1}$, Manara stood out positively (445 cm^2 • $shoot^{-1}$) while Diano Marina with 102 cm^2 • $shoot^{-1}$ showed the lowest value on record. Leaves number per year and rhizome elongation displayed mostly moderate values. Leaves number varied from 5.4 (Pedale) to 8.1 (Vado Ligure); rhizome elongation from 5.1 mm • y^{-1} (Monterosso) to 12.4 mm • y^{-1} (Vado Ligure).

At Population level, lower limit was always located at rather shallow depths. The minimum value was 12.6 m (Pagana), while only Sanremo, Framua and Camogli meadows exhibited relatively higher values (25 - 28 m).

Contrarily, percent cover of *P. oceanica* at the lower limit was high (>50%) in nearly all the study sites: low values were observed only in Diano Marina (30%) and Sanremo (5%).

Shoot density showed great variability: In Framura, Diano Marina and Sanremo meadows, it exceeded 500 shoot per m^2, while in Bergeggi and Vado Ligure its value was only 200-250 shoot per m^2.

At community level, epiphyte biomass displayed great variability as well: the greatest values were reported in Vado Ligure (e.g. 0.88 mg_{dw} cm^{-2}) and the lowest ones in Diano Marina (e.g. 0.06 mg_{dw} cm^{-2}).

At seascape level, SI and PSI were equal to zero in the most of the meadows; both indices reached the maximum value of 0.1 in Diano Marina. CI mostly showed values greater than 0.7 except for the meadows of Pedale, Bergeggi, Manara and Pagana (the latter had the lowest score of 0.54).

Lastly, PREI exhibited values greater than 0.55 in most cases, with peak values in Framura (0.78) and Manara (0.79) and a minimum value in Bergeggi (0.48).

Tab. 1. Classification of the status of the *Posidonia oceanica* meadows of Liguria according to indices at the level of species (LS=leaf surface; LN=number of leaves; RE=rhizomes elongation), population (LLD=lower limit depth; LLC=cover of P. oceanica at the lower limit; SD=shoot density), community (EB=epiphyte biomass), seascape (CI=Conservation Index; SI=Substitution Index; PSI=Phase Shift Index), and integrated (PREI=Posidonia Rapid Easy Index).1 and 2 are the two transects.

	VADO LIGURE		BERGEGGI		NOLI		DIANO MARINA		SANREMO		OSPEDALETTI		VENTIMIGLIA	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2
LS	G	G	B	B	P	P	B	B	P	B	P	P	P	P
LN	M	G	M	M	M	M	M	P	M	M	M	M	G	M
RE	H	G	M	G	G	M	M	G	M	G	M	G	G	M
LLD	B	B	B	B	B	B	B	B	P	M	B	B	B	B
LLC	H	H	H	H	H	H	H	H	P	H	H	H	H	H
SD	M	P	P	M	G	M	H	G	M	H	M	M	G	G
EB	B	B	G	H	M	G	H	H	H	H	P	P	H	G
CI	H	G	M	G	G	G	H	G	G	G	G	H	H	H
SI	H	H	H	H	H	H	H	G	H	H	H	H	H	H
PSI	H	H	G	H	H	H	H	G	H	H	H	H	H	H
PREI	G	G	M	M	G	G	G	G	G	G	G	G	G	G

	FRAMURA		MONTEROSSO		PEDALE		CAMOGLI		PAGANA		MANARA	
	1	2	1	2	1	2	1	2	1	2	1	2
LS	P	P	P	P	P	P	P	P	P	P	H	G
LN	M	M	M	M	B	M	M	P	P	P	M	M
RE	G	M	M	M	M	M	G	M	M	M	G	M
LLD	M	P	B	P	B	B	P	M	B	B	B	B
LLC	H	H	H	H	H	H	H	H	H	H	H	H
SD	M	H	G	M	G	M	G	M	G	M	M	G
EB	M	M	G	G	P	B	M	G	M	P	P	P
CI	G	H	H	G	M	G	G	G	M	M	M	G
SI	H	H	H	H	H	H	H	H	H	H	H	H
PSI	H	H	H	H	H	H	H	H	H	H	H	H
PREI	G	H	G	G	M	M	G	G	M	M	H	G

H	High
G	Good
M	Moderate
P	Poor
B	Bad

Conclusions

The multilevel approach proposed in this study highlighted a remarkable inconsistency among indices and descriptors usually adopted in the ecological status assessment of *P. oceanica* meadows.

The greatest variability was observed at individual and population level. This can be partially explained by seasonality, from which some of the considered descriptors are highly influenced, and by the reference classification (UNEP/MAP-RAC/SPA, 2011), which encompasses class ranges possibly not suitable fot the Liguria region that represents the northernmost border of the *P. oceanica* spatial distribution. For instance, lower limit depth in the Ligurian Sea rarely exceeds 30 m (Bianchi e Peirano, 1995) but according to the reference classification, this value is barely enough.

Seascape indices (CI, SI, PSI) and PREI are consistent, although PREI, including different complexity levels into a single index tends to homogenize the outcome.

Overall, indices seem more consistent in meadows less affected by human impact, while they provide conflicting responses in the case of meadows severely compromised by multiple anthropogenic pressures.

Meadows that exhibit a better health status are those further away from the main urban areas (i.e. Framura, Ventimiglia, Manara) and those included in the Marine Protected Areas (MPA) (i.e. Camogli, Monterosso), with the exception of Bergeggi, that although it is located into a MPA (Oprandi et al., 2014a,b) shows a bad conservation status, comparable to seagrass meadows heavily affected by human activities like that of Pagana (Lasagna et al. 2011).

The findings of this study, underline the utility of the multilevel approach: several descriptors applied at different complexity levels provide complementary information allow obtaining a more proper evaluation of *P. oceanica* ecological status.

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Chapter 2 Change over time

2.1

Seagrass meadows

Additional resources:

Extracted content:

C. N. Bianchi, A. Azzola, M. Bertolino, F. Betti, M. Bo, R. Cattaneo-Vietti, S. Cocito, M. Montefalcone, C. Morri, A. Oprandi, A. Peirano, G. Bavestrello. Consequences of the marine climate and ecosystem shift of the 1980-90s on the Ligurian Sea biodiversity (NW Mediterranean). *The European Zoological Journal (2019) 86(1), 458-487. https://doi.org/10.1080/24750263.2019.1687765.*

Seagrass meadows are important coastal ecosystems in tropical and temperate seas worldwide, providing essential ecosystem services (Cullen-Unsworth et al. 2014). The Mediterranean endemic species *Posidonia oceanica* represents a most valuable example of natural capital (Vassallo et al. 2013) and is protected by several international initiatives and national laws, which call for its management and monitoring for conservation (Montefalcone 2009). Despite its importance as foundation species, its meadows are experiencing a well-documented regression in the Mediterranean due to multiple anthropogenic pressures and invasive species, worsened by the effect of climate change (Chefaoui et al. 2018, and references therein). The first studies on *P. oceanica* meadows of Liguria date back to the beginning of the XX century (Issel 1918) but the first detailed maps of their distribution became available only in the mid 1990s (Bianchi & Peirano 1995), evidencing a generalized regressive condition of the meadows. Combining a morphodynamic model, which predicts the extent of *P. oceanica* meadows in absence of any human influence (Vacchi et al. 2014, 2017, and references therein), with the available historical data (Burgos- Juan et al. 2016; Burgos et al. 2017), it has been possible to estimate that more than 50% of the original surface of the meadows of Liguria has been lost under the influence of human impacts (Peirano & Bianchi 1997; Peirano et al. 2005; Montefalcone et al. 2006a, 2006b, 2007a, 2008a, 2008b, 2009, 2010a).

A similar trend has been observed in the French part of the Ligurian Sea (Holon et al. 2015). In the last decades, possibly thanks to the adoption of protection measures, regression apparently halted, with even some signs of recovery (Figure 10(a)), as observed also in other regions (Carmen et al. 2019). Regular monitoring activities on the *P. oceanica* meadow of Monterosso-al-Mare from 1991 to 2007 (Peirano et al. 2001, 2011) and occasional surveys between 1991 and 2017 showed a sudden and lasting increase of cover and shoot density, respectively, in coincidence with the sea water warming of the 1980- 90s (Figure 11). The relationship between sea water warming and *P. oceanica* growth, however, is controversial (Montefalcone et al. 2013; Pergent et al. 2014). Decline of *P. oceanica* in Liguria has often been coupled with its replacement by the more tolerant seagrass *Cymodocea nodosa* (Bianchi & Peirano 1995; Montefalcone et al. 2006a; Barsanti et al. 2007): such a replacement might be favoured by sea water warming (Ontoria et al. 2019), but showed an obvious positive relationship with the increased artificialization of the coastline (Figure 10(b)).

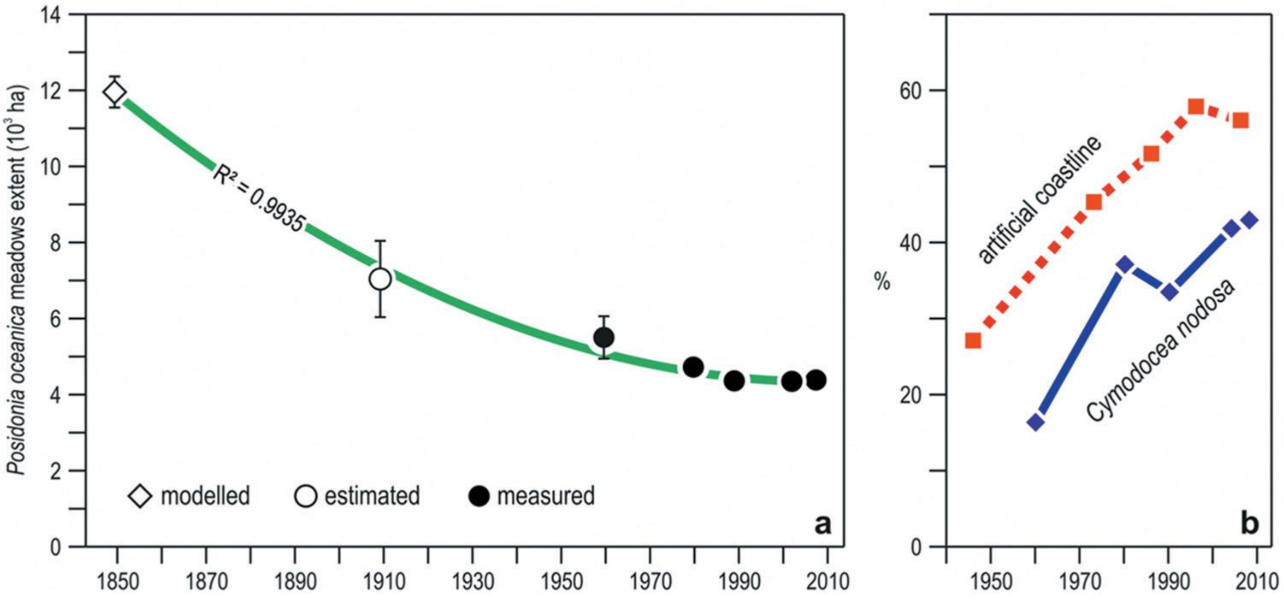

Figure 10. Changes in seagrass meadows of Liguria. (a) Time trend of *Posidonia oceanica* meadow extent since the mid of the XIX century, combining modelling, estimations, and quantitative cartographic measurements. The curve depicts the second degree polynomial fit of the data. (b) Time trend of the proportion of *Cymodocea nodosa* out of the total areal extent of seagrass meadows, and of the proportion of the linear extent of artificial structures on the coastline.

In recent years, *C. nodosa* was in turn partly replaced first by the native green alga *Caulerpa prolifera* and then by its two alien congeneric *C. taxifolia* and, especially, *C. cylindracea* (Montefalcone et al. 2007c, 2010b, 2015). The modifications underwent by the meadow of Prelo Cove in the last century represent a good example of such a series of substitutions. In the 1930s, the meadow of Prelo Cove had been severely impacted by the building of a jetty for pleasure craft (Lasagna et al. 2006a, 2006b, 2011). By the late 1950s, the areas of the cove's sea floor deprived of *P. oceanica* were colonized by *C. prolifera* (Tortonese 1962).

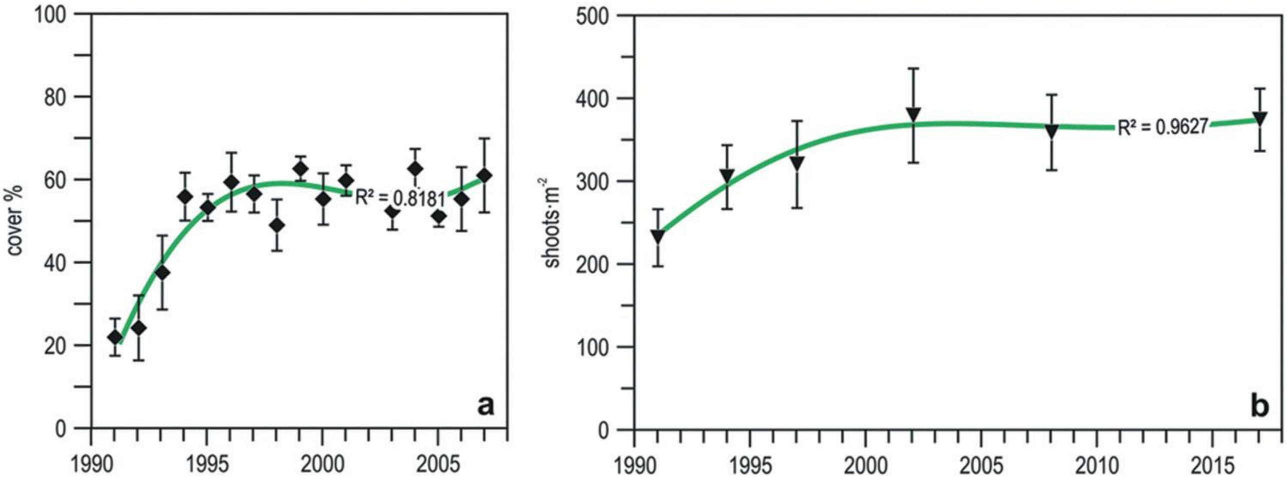

Figure 11. Trends in the Posidonia oceanica meadow at Monterosso. The curves depict the third degree polynomial fit of the data. (a) Yearly means (± se) of cover values, 1991–2006. (b) Discontinuous measures of mean shoot density (± se), 1991–2017. Data from Peirano et al. (2011) and Regione Liguria (http://www.cartografiarl.regione.liguria.it/SiraQualMare/script/PubRetePuntoParam.asp?_ga=2.97453724.2042002155.1518772812601063746.1517569932&fbclid=IwAR00qk1ShUaKXOxg0Hdi3lTtzAjMvUir-ryolOenpw9- v_yTP4wcl3wl2yk).

By 1979, *C. prolifera* disappeared to leave place to *C. nodosa*, which lasted there to at least 1986 (Morri et al. 1986). At this stage, the regressed meadow was therefore apparently following the secondary successional pattern envisaged by Molinier and Picard (1952), suggesting the possibly of recovery in the following years. By 1991, however, the pattern was reverted: *C. nodosa* was not found anymore, whilst *C. prolifera* was back again (Tunesi & Vacchi 1994). Being a thermophilic species, *C. prolifera* had been possibly favoured by the water warming of the 1980-90s, to remain abundant till at least 2004 (Montefalcone et al. 2006b). Notwithstanding persisting warm-water conditions, recent surveys in the 2010s did not find *C. prolifera* but *C. cylindracea* (Montefalcone et al. 2015), as predicted by the phase-shift model of Montefalcone et al. (2007c) and contrarily to both the successional and the warming hypotheses. The multidecal change observed in the Prelo meadow was mirrored in the modifications of the associated sponge fauna, as reconstructed through the analysis of the siliceous spicules trapped within the matte (Bertolino et al. 2012). The longest data series available on a Ligurian seagrass meadow, that of Bergeggi (Montefalcone et al. 2007b; Oprandi et al. 2014a, 2014b), illustrates well the present dualism of the health state of Ligurian *P. oceanica* meadows: on the one hand, the meadow has been recovering (in term of areal extent) since 2009 (Figure 12(a)); on the other hand, it has been suffering from substitution by *C. cylindracea*, which is deviating the recovery trajectory of the ecosystem towards a different basin of attraction (Figure 12(b)). Thus, information collected to date indicates hysteresis, rather than resilience (Montefalcone et al. 2011). Similarly, the resilience of seagrass ecosystems worldwide is becoming compromised by a range of local to global stressors (Unsworth et al. 2015).

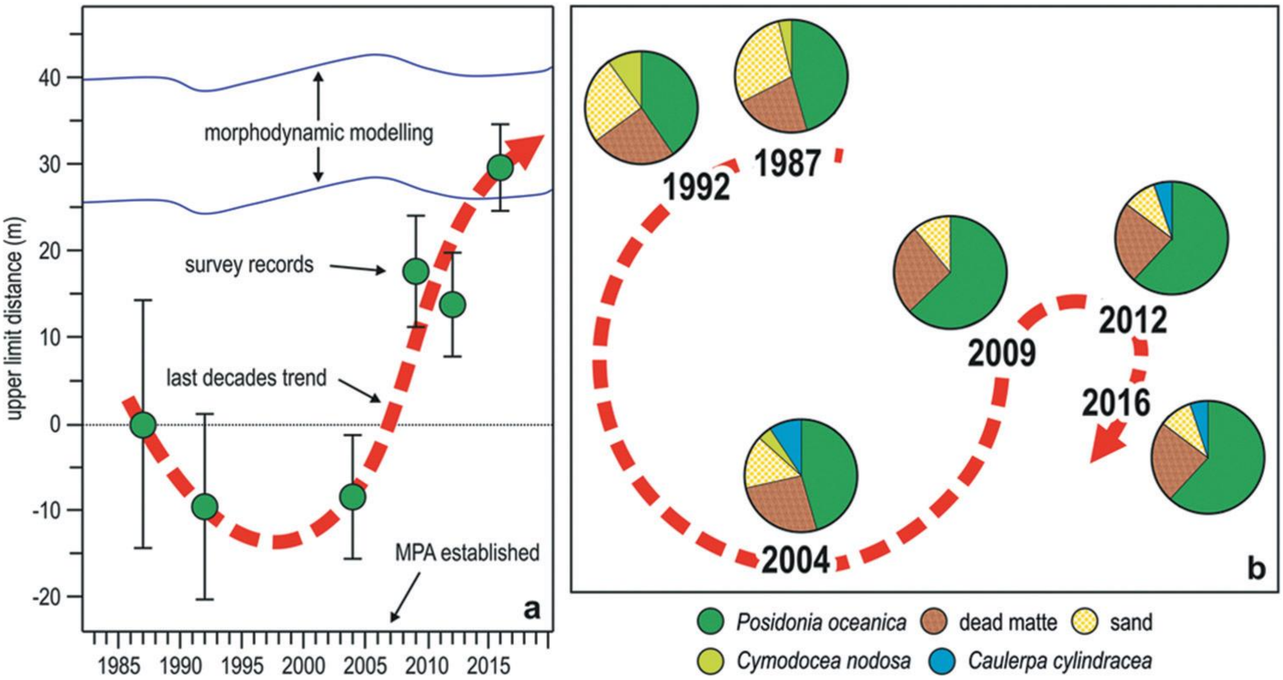

Figure 12. Changes in the *Posidonia oceanica* meadow of Bergeggi in 25 years. (a) Position of the meadow upper limit with respect to 1987. (b) Time trajectory of the meadow in the MDS ordination plane; pie diagrams illustrate the quantitative meadow composition. Redrawn and updated from Oprandi et al. (2014a, 2014b).

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2.2

What biotic indices tell us about ecosystem change: lessons from the seagrass *Posidonia oceanica*

Indices application on historical data

Additional resources:

I. Mancini, A. Oprandi, I. Rigo, M. Montefalcone, C. Morri, A. Peirano, P. Vassallo, C. Paoli, C. N. Bianchi. *Vie et Millieu.* Under review.

Abstract

Anthropogenic pressure on marine ecosystems is affecting water quality and seafloor integrity. Mediterranean seagrass meadows of endemic *Posidonia oceanica* (L.) Delile are considered a priority habitat under the European Directive 92/43/CEE, given their ecological and economic importance and being an environmental quality indicator. Availability of historical data on three *P. oceanica* meadows along the Ligurian coast (NW Mediterranean Sea) allowed assessing change in the meadow status over time. A number of indicators and ecological indices at different levels of ecological complexity, including the multimetric PREI (Posidonia Rapid Easy Index) adopted by the environmental agencies, were employed and compared.

This paper aims at a) defining the health status of the *P. oceanica* meadows and measuring their changes through time collating available historical information; b) evaluating the discriminating power of the different indices and assessing their consistency with each other.

The different indices adopted revealed little consistency thus suggesting that no single index can define the health status of *P. oceanica* meadows; as a consequence the use of an indices set is highly recommended to monitor meadow evolution over time.

Keywords: *Posidonia oceanica*; seagrass; Ligurian Sea; ecological indices; historical data.

Introduction

Biotic indices have long been used to assess the environmental quality of fresh water and terrestrial ecosystems (Cairns & Pratt 1993, Andreasen *et al.* 2001). The application of naturalistic information to elaborate biotic indices in support of marine management is still under development, while it is current practice on land (Bianchi *et al.* 2012). In the last decades, the use of indices to assess marine environmental status in Europe has become frequent, spurred by European directives. Indeed, EU rules (see Directive Proposal 1999/C 343/01, Official Journal of the European Communities 30/11/1999) emphasized the importance of biological indicators to establish the ecological quality of European seas and estuaries (Borja *et al.* 2000). The EU Water Framework Directive 2000/60/EC (WFD) underlined the need for biotic indices, which have been introduced in considerable number. More recently, the EU Marine Strategy Framework Directive 2008/56/EC (MSFD), introduced the concept of "seafloor integrity" to improve the assessment of ecological quality (Bianchi *et al.* 2012). Therefore, the use of seagrass as biological indicators has become a common practice to assess the environmental quality of coastal seas (Pergent *et al.* 1995, Short & Wyllie-Echeverria 1996, Hemminga & Duarte 2000).

Seagrass meadows are declining worldwide due to natural and human-induced events (Short & Wyllie-Echeverria 1996). The endemic Mediterranean seagrass *Posidonia oceanica* (L.) Delile is the most important and abundant seagrass and it is considered a priority habitat for both animals and plant communities, covering different substrata from the sea level down to 40 m depth (Boudouresque *et al.* 2006). There are many ecosystem services provided by *P. oceanica*: it represents an origin of food for many marine and shore organisms, but also plays fundamental roles such as nursery areas for fish and invertebrates and shoreline defence (Vassallo *et al.* 2013). Thus, *P. oceanica* is mentioned in the Habitat Directive 92/43/CEE and, since 1991, is included in the Red List of the International Union for Conservation of Nature (IUCN) as a threatened species of the Mediterranean Sea (www.iucnredlist.org).

A general regression of *P. oceanica* meadows has been recorded in the Ligurian Sea (Bianchi & Morri 2000). In fact, it has been estimated that in the past century the Ligurian

P. oceanica meadows lost 50% of their original extent (Peirano & Bianchi 1997, Peirano *et al.* 2005, Burgos *et al.* 2016). However, as a consequence of conservation policies enforced in the last decades, the regression of *P. oceanica* in the Ligurian Sea has possibly ceased or at least slowed down (Burgos *et al.* 2017, Bianchi *et al.* 2019).

This paper aims at a) defining the health status of three Ligurian *P. oceanica* meadows, using ecological indices and descriptors that work at different levels of complexity (i.e., individual, population, community, and seascape), and measuring their change through time collating all available historical information; b) evaluating the discriminating power of the different indices and assessing their consistency with each other.

Material and Methods

Study area

This study was carried out in Liguria, an administrative region in NW Italy, whose coast border the central and largest part of the Ligurian Sea. Three *Posidonia oceanica* meadows were analyzed, located in Monterosso (MM), Prelo (PR), and Bergeggi (BE) (Fig. 1), where historical data collected along underwater transects were available since the 1980s (Table I).

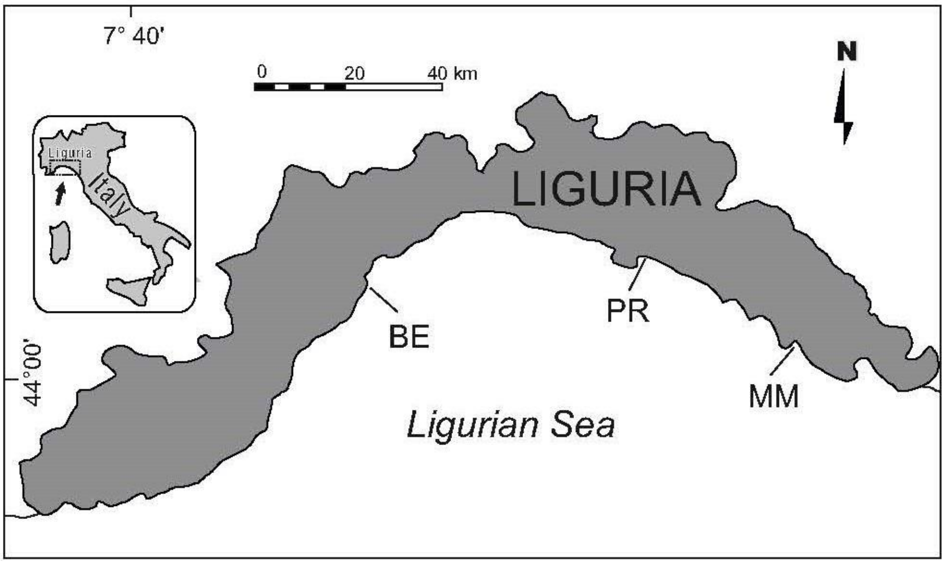


Fig. 1 Map of the study area and location of the three meadows investigated: Bergeggi (BE), Prelo (PR), and Monterosso (MM).

Field and laboratory activities

Historical data were compared with data collected more recently (2016 and 2017). All the historical and recent data considered in the analyses were collected during summer season, along underwater depth transects (Bianchi *et al.* 2004) located in the same area of previous studies (Table I). The sampling activity carried out along each transect consisted in a visual estimation, every 10 m along the marked line, of the percentage cover of the seafloor by living *P. oceanica*, dead matte, sand, rock, and possible substitutes (i.e., *Cymodocea nodosa*, *Caulerpa taxifolia*, *Caulerpa cylindracea*, and *Caulerpa prolifera*). The meadow shoot density was measured at 15 m depth, as recommended by ISPRA, the Italian higher institute for environmental protection and research (www.isprambiente.gov.it/files/icram/scheda-metodologia-posidonia-new.pdf). Altogether, 18 shoots were sampled for laboratory analyses through plant phenology and lepidochronology (Giraud 1977). Further analyses were also conducted on the associated epiphytic community: all the epiphytes were scratched from the leaves, then dried and weighed to assess their biomass.

Table I. Data sources for the three *Posidonia oceanica* meadows investigated.

Meadow	Year	References
Prelo	2002	Lasagna *et al.* 2006a,b
Prelo	2003	Lasagna *et al.* 2006a,b
Prelo	2004	Lasagna *et al.* 2006a,b
Prelo	2005	Lasagna *et al.* 2006a,b
Prelo	2006	Lasagna *et al.* 2011
Prelo	2013	Bianchi *et al.* 2019
Prelo	2017	Rigo *et al.* 2019
Bergeggi	1987	Vetere *et al.* 1989
Bergeggi	1992	Sandulli *et al.*1994
Bergeggi	2004	Montefalcone *et al.* 2007
Bergeggi	2009	Montefalcone *et al.* 2010
Bergeggi	2012	Oprandi *et al.* 2014
Bergeggi	2016	Bianchi *et al.* 2019
Monterosso	1991	Peirano *et al.* 1999
Monterosso	1992	Peirano *et al.* 1999
Monterosso	1994	Peirano *et al.* 2001
Monterosso	1996	Peirano *et al.* 2001
Monterosso	1997	Peirano *et al.* 2011
Monterosso	2002	Montefalcone *et al.* 2007
Monterosso	2008	Bianchi *et al.* 2019
Monterosso	2017	Bianchi *et al.* 2019

Ecological indices and descriptors assessment

Data obtained from field and laboratory activities were used to define the health status of the three *P. oceanica* meadows, through a set of descriptors and ecological indices working at different ecological complexity levels:

1. Leaf surface (cm2 shoot-1) at the individual level, to describe the physiological status of the plant (Leoni *et al.* 2007);
2. Shoot density (shoots m-2) and lower limit depth (m) at the population level, to understand dynamics in the meadow structure (Pergent *et al.* 1995);
3. Epiphyte biomass (mgDW cm-2) at the community level, which provides rapid information on changes in the water quality (Giovannetti *et al.* 2010);
4. Conservation Index (CI), Phase Shift Index (PSI), and Substitution Index (SI) at the seascape level, to evaluate changes over time of the meadow composition (Moreno *et al.* 2001, Montefalcone 2009);
5. Posidonia Rapid Easy Index (PREI, Gobert *et al.* 2009), which integrates different metrics (shoot density, leaf surface, epiphyte biomass, leaf biomass, and depth and type of the lower limit) and thus encompasses multiple ecological levels.

The above listed indices and descriptors were calculated also from historical data when information was available and complete. Results obtained for each index were then classified in five classes using the reference classifications of ecological quality status (Gobert *et al.* 2009, Montefalcone 2009, UNEP/MAP-RAC/SPA 2011): bad, poor, moderate, good, and high. Only for epiphyte biomass no classification is available.

Results

Meadows ecological quality and trend over time

At the individual level, analysis of the leaf surface (Fig. 3) showed a worsening in the ecological status in all the three meadows. The status of the *Posidonia oceanica* meadow at Prelo changed from good to poor in the last fifteen years. Also in Monterosso a decline in the meadow ecological status from good to moderate occurred from 1991 to 2017.

Regarding Bergeggi, data on leaf surface was available only for two periods: the meadow showed a moderate ecological status in 1992, a poor status in 2016.

At the population level (Fig. 4), all indices evidenced stability or even improvement, of the ecological status. Shoot density increased in Monterosso and Prelo meadows, and the ecological status passed from moderate to good in both meadows. Bergeggi maintained a moderate status, notwithstanding a reduction in shoot density values over time. With regard to the lower limit depth, the status remained poor over time in all the three meadows.

At the community level, epiphyte biomass showed a decrease of its values in all meadows, notwithstanding high temporal variability (Fig. 3).

At the seascape level, SI and PSI displayed highest temporal variability (Fig. 5). According to CI, Prelo meadow maintained a moderate ecological status, Monterosso showed a slight improvement passing from good to high status, whilst Bergeggi revealed a slight worsening of its status passing from good to moderate. SI evidenced a steady high ecological status in Prelo and Monterosso, but showed a high variability through time in Bergeggi, where it passed from high (1987), good (1992), and moderate (2004), to return again to a high ecological status in 2016.

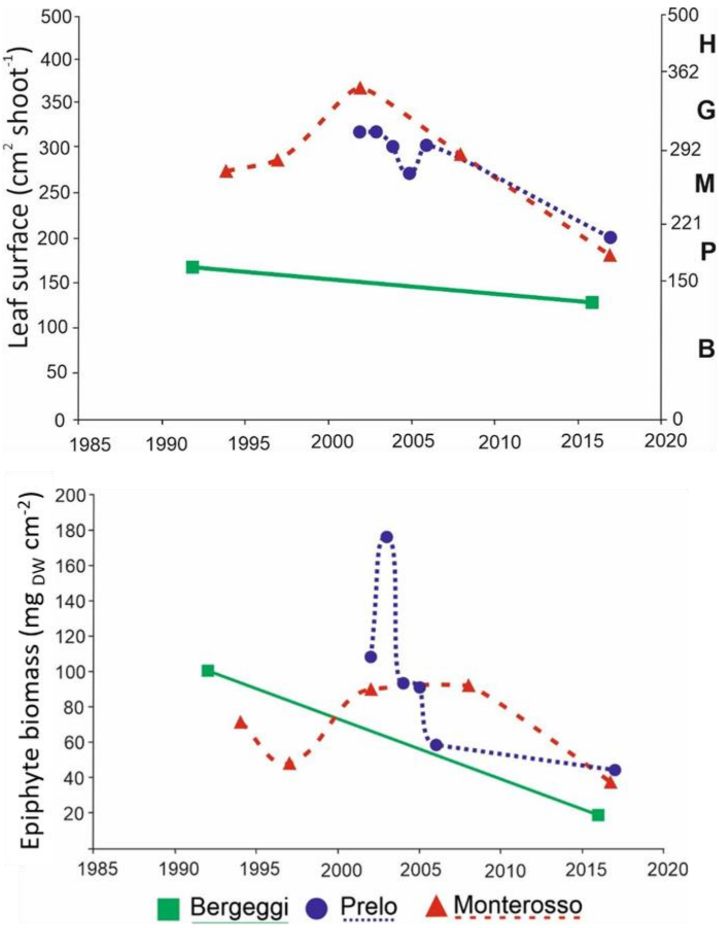


Fig.3.Trend over time of the indices at the individual (upper panel) and community (lower panel) level in the three meadows investigated. The y axis on the right side of the leaf surface graph reports reference values of the UNEP/MAP RAC/SPA (2011) classification: B = bad, P = poor, M = moderate, G = good, and H = high.

PSI showed different situations in the three meadows. A clear increase of its values was observed in Prelo, which changed from poor to high status. The status of the Bergeggi meadow dropped from high in 1987 to moderate in 2004 and 2017 according to PSI. The Monterosso meadow showed little variation in PSI values over time, always remaining in a bad status.

The multimetric PREI (Fig. 4) showed little or no important change in any of the three meadows. Monterosso ecological status was always classified as good, Bergeggi as moderate, whilst Prelo decreased from good to moderate with time.

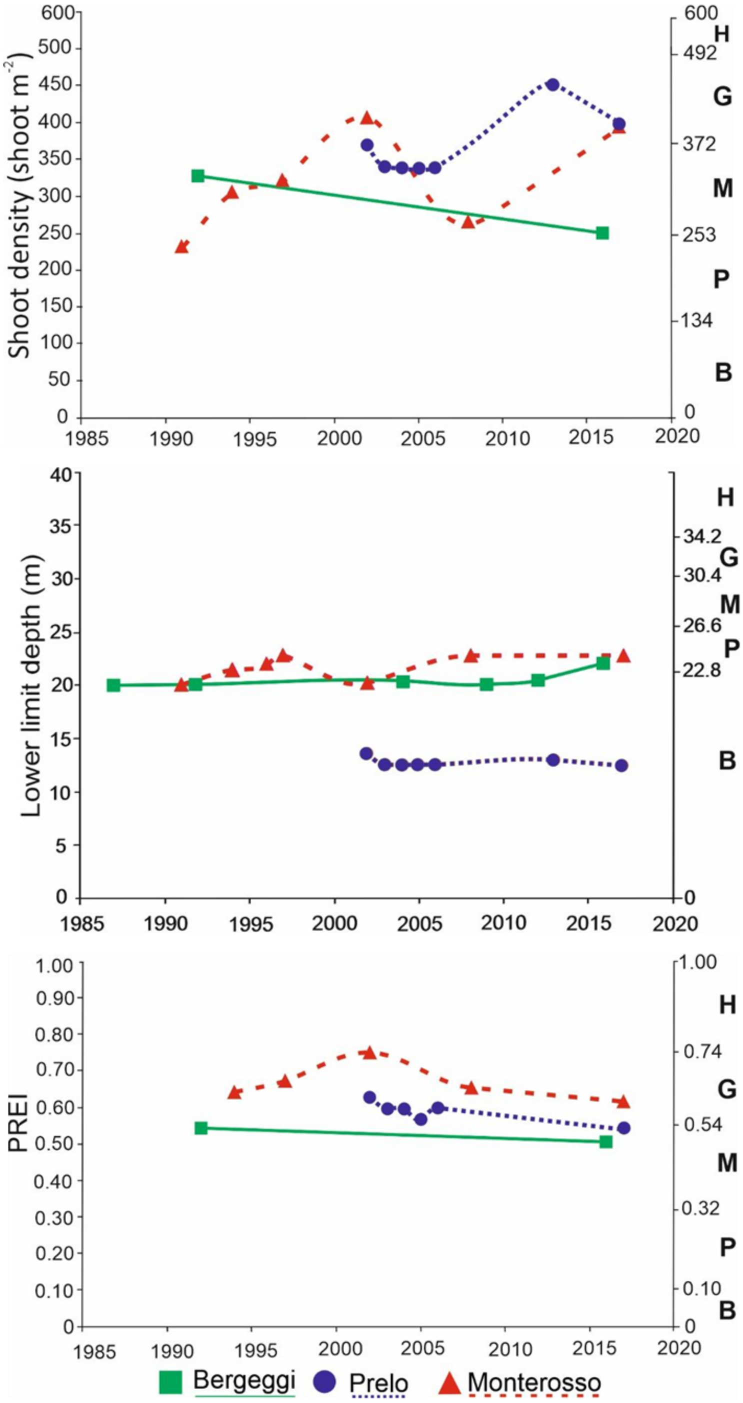


Fig 4. Trend over time of the indices at the population level (upper panel: shoot density; middle panel: lower limit depth) and of the multimetric index PREI (lower panel) in the three meadows investigated. The y axes on the right side of the shoot density and the lower limit depth graphs report reference values of the UNEP/MAP RAC/SPA (2011) classification, whilst that of PREI from Gobert *et al.* (2009) classification: B = bad, P = poor, M = moderate, G = good, and H = high.

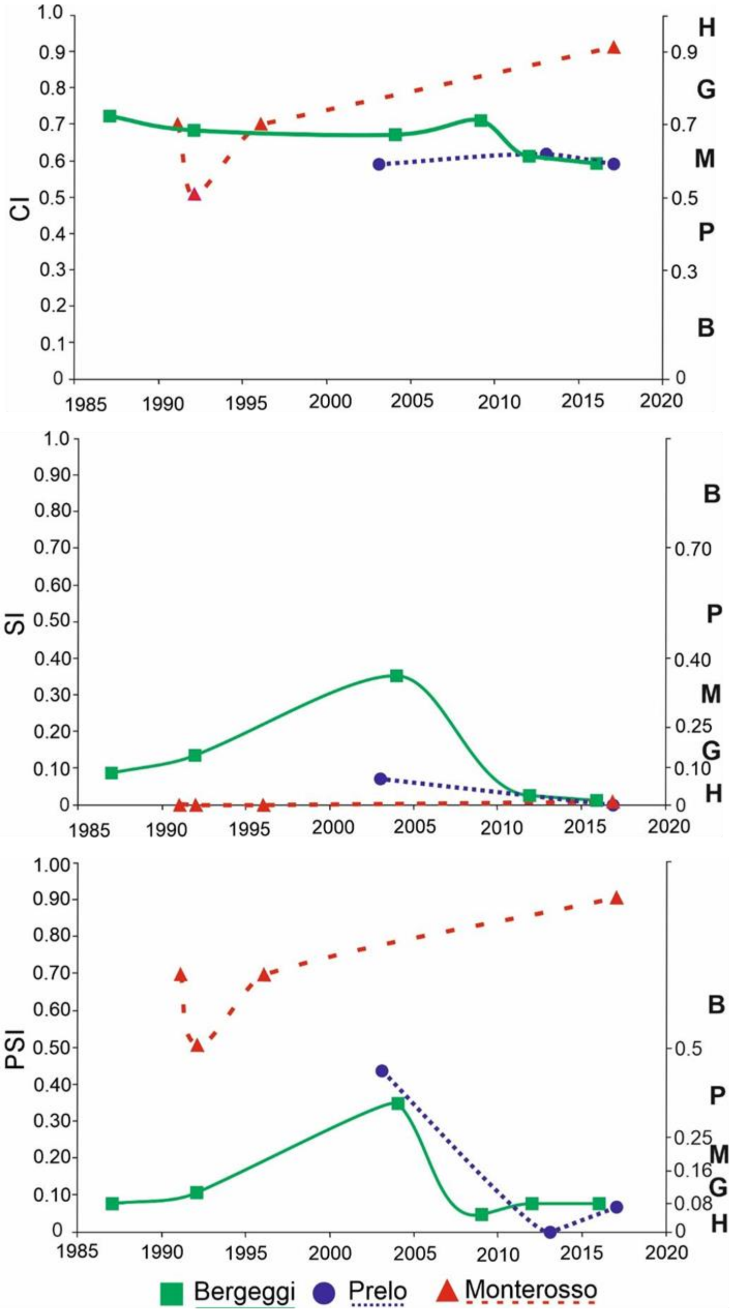
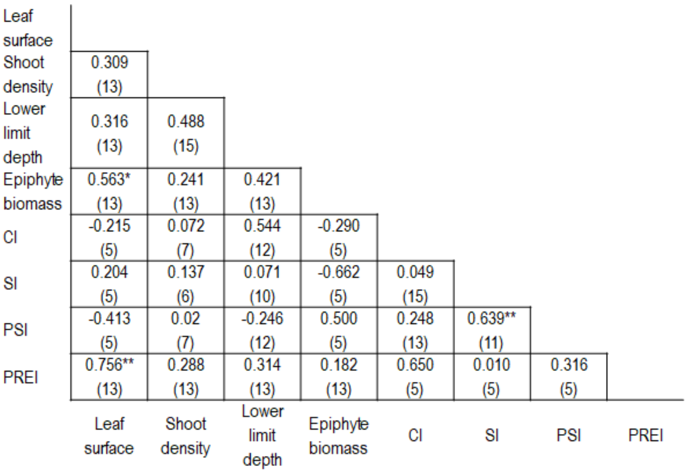


Figure 5. Trend over time of the indices at the seascape level (upper panel: CI; middle panel: SI; lower panel: PSI) in the three meadows investigated. The y axes on the right side of the CI, SI, and PSI report values of the classification by Montefalcone (2009): B = bad, P = poor, M = moderate, G = good, and H = high.

Consistency among indices

A significant correlation was found between PREI and leaf surface ($p < 0.01$, n = 13), between PSI and SI ($p < 0.05$, n = 11), and between leaf surface and epiphyte biomass ($p < 0.05$, n = 13) (Fig. 2).



	Leaf surface	Shoot density	Lower limit depth	Epiphyte biomass	CI	SI	PSI	PREI
Leaf surface								
Shoot density	0.309 (13)							
Lower limit depth	0.316 (13)	0.488 (15)						
Epiphyte biomass	0.563* (13)	0.241 (13)	0.421 (13)					
CI	-0.215 (5)	0.072 (7)	0.544 (12)	-0.290 (5)				
SI	0.204 (5)	0.137 (6)	0.071 (10)	-0.662 (5)	0.049 (15)			
PSI	-0.413 (5)	0.02 (7)	-0.246 (12)	0.500 (5)	0.248 (13)	0.639** (11)		
PREI	0.756** (13)	0.288 (13)	0.314 (13)	0.182 (13)	0.650 (5)	0.010 (5)	0.316 (5)	

Fig 2. Correlation matrix among the indices used in this study. * = p < 0.05; ** = p < 0.01. Numbers in parentheses are numbers of cases.

Discussion and Conclusions

Most of the indices adopted were consistent in displaying a worsening in the ecological status of the Bergeggi meadow, even though the sampling area is today located within the Marine Protected Area “Isola di Bergeggi”. Only SI showed a recovery trend from 2009, thanks to the reduction of the two substitutes *Caulerpa cylindracea* and *Cymodocea nodosa* (Montefalcone *et al.* 2007, Oprandi *et al.* 2014a,b). The Monterosso meadow showed different situations according to the index taken into account. All indices working at the individual and the community levels displayed a worsening trend in the last thirty years. The two indices at the population level, i.e. shoot density and lower limit depth, were discordant: the former showed a recovery, the latter a steady trend. All the indices working at the seascape level were consistent in showing an increase in the ecological quality of this meadow but SI, which always displayed low values due to the absence of substitutes. The Prelo meadow is affected by a high level of anthropogenic pressures (Lasagna *et al.* 2011). Only indices working at the individual and the community levels showed consistently a worsening in its ecological status during the last fifteen years. On the contrary, the two indices working at the population level and one at the seascape level (CI) showed a steady condition, whilst SI and PSI increased thanks to the reduction of substitutes.

Our results showed that it is not possible to define univocally a trend in the health status of the three *P. oceanica* meadows investigated. The consistency among all the indices was often low (Fig. 6), either considering the same sampling period or among different sampling periods, making even more difficult to identify clear trends over the last thirty years. Indices working at the individual level and the community level often displayed a similar behaviour. These indices can be viewed as early warning indicators (Giovannetti *et al*. 2010), responding quickly to disturbances and to environmental change, and thus being good indicators in short time-scales. Longer times are indeed necessary for descriptors and indices working at the population and the seascape level to show change in the meadow status. Shoot density and lower limit, despite referring to the same ecological level (i.e., population), did not show consistency, probably because the shoot density reacts faster than the lower limit.

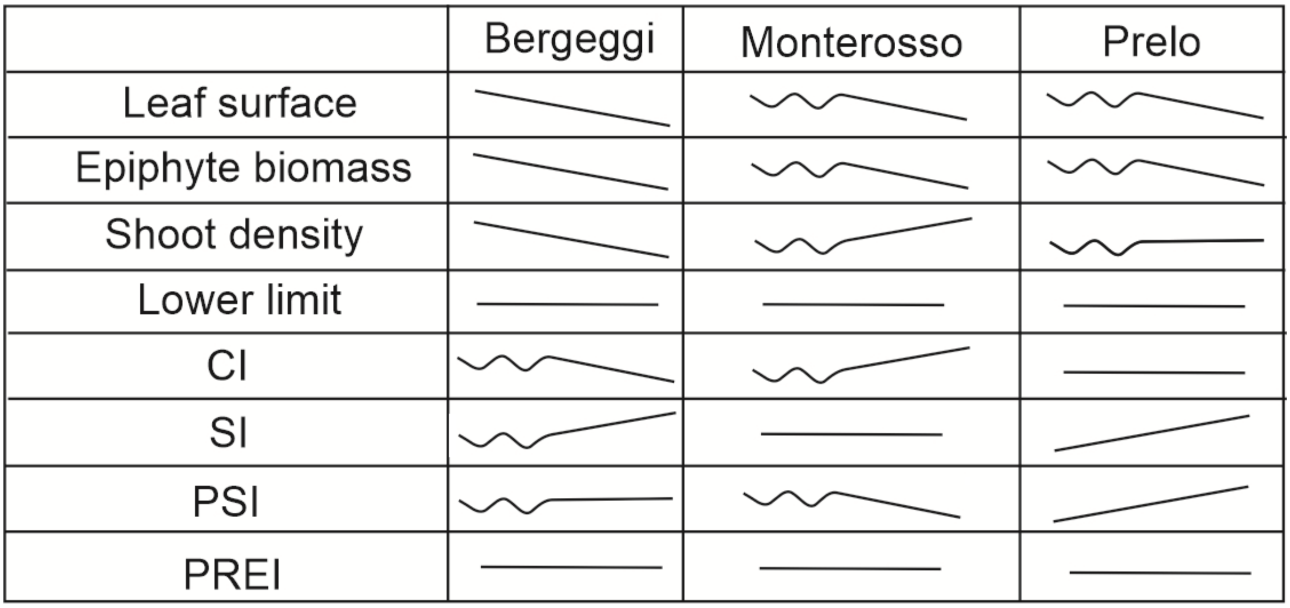


Fig. 6. Graphical representation of trend over time of each index applied in the three meadows investigated.

The Mediterranean classification used to define the meadow ecological status according to the lower limit depth (UNEP/MAP-RAC/SPA 2011) is possibly not suitable for the Ligurian Sea: along the Ligurian coast, *P. oceanica* meadows hardly exceed 30 m depth (Bianchi & Peirano 1995, Oprandi *et al.* 2019), thus resulting very often in a bad status. Local variability in this descriptor could be hidden if the classification at the Mediterranean spatial scale is used. This notwithstanding, the slight increase in the lower limit depth observed in Bergeggi and Monterosso may be a positive signal of meadows recovery.

Shoot density was often consistent with CI. Some authors recognised CI as an index working at population level (Romero *et al.* 2007a), being based on the evaluation of living *P. oceanica* cover along underwater depth transects. It may happen that when the meadow shoots density is high, divers record higher cover values by living plants. Concerning the other seascape indices, i.e. SI and PSI, they react to change only when substitutes are established and a shift in the *P. oceanica* meadow has occurred (Montefalcone 2009).

The multimetric PREI (Gobert *et al.* 2009) always showed a steady trend in all the three meadows, although the single metrics showed changes over time. This result can be due to different situations: i) all the composing metrics display the similar steady behaviour; ii) the metrics are discordant, so that a change in each single metric can be mutually counterbalanced by the other metrics in the PREI algorithm, and this is what happened in Monterosso and Prelo meadows; iii) when the majority of the metrics are concordant, as it happened in the Bergeggi meadow, a steady trend of PREI may result when the change is limited. It can thus be concluded that PREI averages and dampens the variability of the single metrics. Integrating a number of metrics into a synthetic index is very useful and effective for monitoring purposes, but it may homogenise the meadow condition. This result pointed out that PREI could not be appropriate, if used alone, to evidence punctual changes in the meadow health. PREI was also significantly correlated only with leaf surface, being the leaf surface one of the metrics used to build this index. Also PSI and SI were highly correlated, considering that PSI contains SI in its formula. Finally, correlation between leaf surface and epiphyte biomass is reasonable as the more the leaf grows the more the epiphytes have space to colonize.

In conclusion, it must be pointed out the importance of long time-series, which are usually very scarce, fragmentary and inhomogeneous, since historical data were collected under different kind of studies and sometimes also with different methodologies. Comparison of data trough time showed inconsistency among most indices, making it difficult to identify a consistent dynamic of Ligurian meadows over time. As a plethora of existing indices, adopting a single index is not recommended to assess the ecological status of *P. oceanica* meadows. All the indices investigated in this paper work at different ecological levels, thus providing different information. This is why many multimetric indices, such as the PosWare (Buia *et al.* 2005, Silvestre *et al*. 2006), the PoMi (Romero *et al.* 2007a,b), the Valencian CS (Fernandez Torquemada *et al*. 2008), the BiPO (Lopez y Royo *et al*. 2008), and PREI have been recently developed to address requirements of the EU directives. However, our study evidenced that using PREI alone would not have evidenced changes at both spatial and temporal scales. For this reason, flanking a multimetric index with other indices, such as for instance the seascape indices here adopted, should be recommended to collect complementary information and to better understand specific drivers of change in seagrass ecosystem.

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Chapter 3 Retrospective analysis

3.1

Using siliceous spicules in the *Posidonia oceanica* “matte” to discover past dynamics of the sponge community

Additional resources:

A. Oprandi, G. Costa, M. Pansini, G. Bavestrello, M. Bertolino. *Poster. 10th World Sponge Conference, NUI Galway, 25-30 June 2017.*

Introduction

The mineral skeleton of most of sponge species consist of siliceous spicules. After the sponge death, siliceous spicules persist for a long time in the sediments, partially withstanding dissolution and represent a valuable tool to assess the diversity of past sponge communities (Bertolino et al., 2012). The reduced re-suspension occurring within the *Posidonia oceanica* meadows makes these habitats a stable deposit for sponge spicules, where they are trapped inside the network of rhizomes progressively buried called “matte”, that is a sedimentary sequence interpretable on a temporal scale.

We investigated two *P. oceanica* meadows of the Eastern Ligurian Sea (North-West Italy) collecting samples of sediment at 0.5 m and 2 m depth along the matte profile. A quantitative study of the spicules detected in the matte layers was carried out, trying to identify the sponge genera. The aim of the study was to evaluate the differences in the past sponge assemblages possibly relating them with known local impacts.

Materials and Methods

The study area was located on the east side of Portofino Promontory in the Eastern Ligurian Sea. Both the meadows, that stretch for hundreds meters along the coast, in the Bay of Prelo and in Punta Pedale, present wide areas of thick living matte. By means of a vertical corer manually operated during sections of diving work, we collected six samples of sediment, three at each sampling depth (0,5 m and 2 m) along the matte profile. The core subsamples (weighing 0.05 g), in triplicate, were treated with nitric acid to eliminate the carbonate fraction then laid on microscope slides. Sponge spicule type and amount were evaluated by microscopical analyses, moreover, any marks of dissolution were reported.

Results

Significant differences in the number of entire spicules between the two investigated depths were found in both the meadows. The entire spicules collected at 0.5 m were 7756 ± 6457 per gram in Punta Pedale and 1446 ± 765 per gram in Prelo, whereas those from the 2 m depth were 2911 ± 1628 per gram in Punta Pedale and 163 ± 22 per gram in Prelo. The number of fragments resulted quite the same at the two different depths.

The percentage of spicules showing marks of dissolution never exceeded 15% of the total spicule number in all the studied samples.

Several sponge genera (*Chondrilla*, *Suberites*, *Cliona*, *Dercitus*, *Agelas* and *Crella)* were identified from the analyses of the spicules collected in the shallower layer (0.5 m). On the contrary, the only recognizable genus of demosponge found in the deeper layer was *Geodia,* identified on the base of its sterrasters. It is remarkable that *Geodia* is nowadays no more present in the *Posidonia* meadow area.

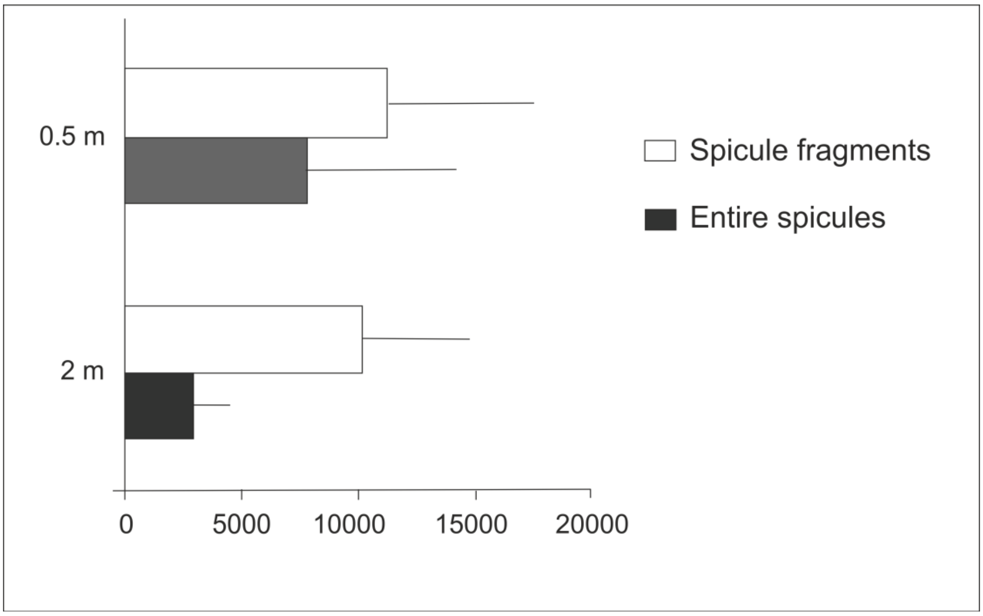

Fig.1 No. of spicule fragments and entire spicules at 0.5 mand 2 m depth in Punta Pedale

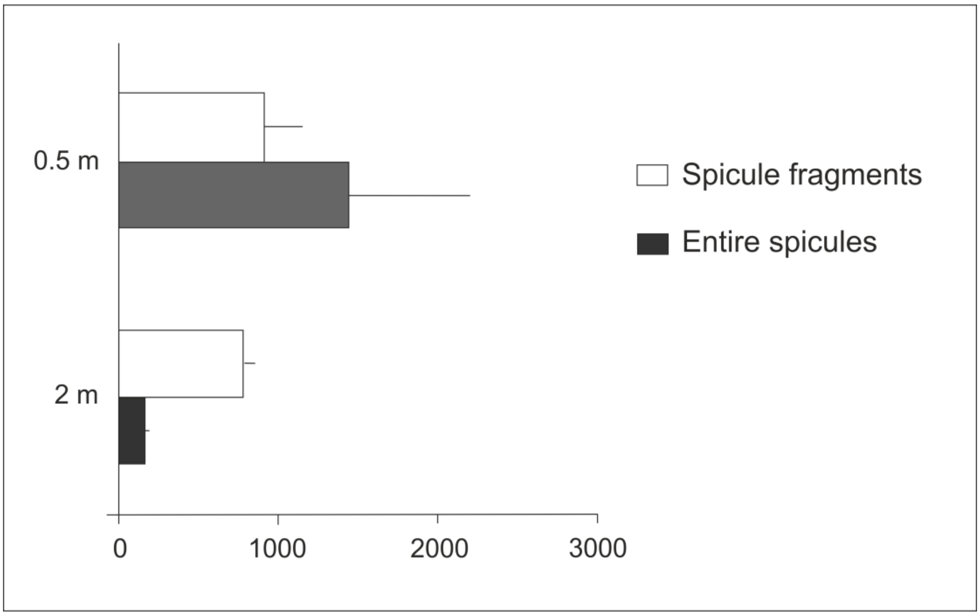

Fig.2 No. of spicule fragments and entire spicules at 0.5 mand 2 m depth in Prelo

Conclusions

The record of a layer of sediment rich in sponge spicules at a depth of 50-60 cm inside the mattes of *P. oceanica,* confirms previous data coming from the meadow of Prelo (Bertolino et al., 2012). The temporal variations of sponge abundance in the studied places, resulting from the spicule trend, is probably due to historical anthropogenic disturbances. In fact the low spicule content of the deep layer reflects the impact of the construction of the littoral road along the western board of the meadow occurred at the beginning of the twentieth century. The sponge rich layer could represent a period of recovering that was stopped by the rapid urban development that occurred in this part of the Ligurian Riviera in the sixties of 1900 with a deep impact on the littoral benthic assemblage of the area.

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3.2

Using biogenic silica to discover past dynamics of the sponge community associated to *Posidonia oceanica* meadows

Additional resources:

Alice Oprandi, Gabriele Costa, Maurizio Pansini, Giorgio Bavestrello and Marco Bertolino.
Poster. 50° Conference of the Italian Society in Marine Biology (S.I.B.M.). 10-14 Giugno 2019. Livorno, Italia.

Abstract

The skeleton of most of sponge species consist of siliceous spicules that, after the sponge death, persist for a long time in the sediment. The reduced suspension occurring within the meadows of the seagrass Posidonia oceanica, makes these habitats a stable deposit for sponge spicules, that are trapped inside the network of rhizomes progressively buried, named 'matte', a sedimentary sequence interpretable on a temporal scale. By means of a vertical corer we collected samples of sediment at 0.5, 1, 1.5 and 2 m depth along the matte profile in order to quantify the amount of biogenic silica used to assess past dynamics of the sponge community in four P. oceanica meadows of the Ligurian sea. The content in biogenic silica was determined by spectrophotometric analysis of the sediments. A general decreasing trend with depth was observed in the meadows of Prelo and Punta Pedale, while in the site of Punta Manara the major amount of silica was found deeper in the matte. The temporal variations of sponge abundance were probably due to historical anthropogenic disturbances. In the meadow of Bergeggi, silica' concentrations, significantly lower compare to all other sites, were likely caused from bottom currents in correspondence of the channel between Punta del Maiolo and the island of Bergeggi.

Introduzione

Lo scheletro della maggior parte delle specie di spugne è costituito da spicole silicee. Dopo la morte della spugna, le spicole silicee persistono nei sedimenti contrastando la dissoluzione, per questo motivo costituiscono un valido strumento per lo studio di dinamiche passate dei popolamenti di poriferi (Bertolino et al., 2012). La ridotta sospensione che si verifica all'interno delle praterie di *Posidonia oceanica*, rende questi habitat un deposito permanente di spicole, le quali rimanendo intrappolate nella fitta rete di rizomi progressivamente interrati che costituiscono la "matte", una sequenza sedimentaria coerente, restano accessibili per lungo tempo. È noto che le lunghe foglie di *P. oceanica* favoriscano la deposizione delle particelle in sospensione. La matte di *P. oceanica* presenta quindi una crescita verticale continua, interpretabile su scala temporale e controllata principalmente da fattori locali (Mateo et al. 1997). Nel presente lavoro è stato effettuato uno studio quantitativo della silice biogenica dovuta alla presenza di spicole lungo il profilo verticale della matte di *P. oceanica* a diverse profondità, 0.5, 1, 1.5 e 2 m, con l'obiettivo di determinare i cambiamenti nelle comunità di spugne associate a quattro praterie del mar Ligure ed interpretandoli su scala temporale, in relazione ad eventi di disturbo antropico e naturale.

Materiali e metodi

L'attività di campo ha previsto la raccolta di campioni di matte di *P. coeanica* in immersione subacquea per mezzo di un carotatore verticale azionato manualmente. Il sedimento è stato quindi prelevato (tre repliche) a 0,5, 1, 1,5 e 2 m di profondità nella matte di quattro praterie della riviera ligure: Punta Pedale, Prelo, Punta Manara e Bergeggi, per un totale di 48 carotaggi. In laboratorio, l'estrazione della silice biogenica dal sedimento è stata effettuata chimicamente seguendo la procedura di DeMaster (1981) e determinata tramite analisi spettrofotometrica dei campioni in duplice replica. Inoltre, soltanto sulla prateria di Punta Pedale, a causa dei lunghi tempi di analisi, è stato possibile contare e riconoscere le spicole presenti nei campioni raccolti a 0.5 e 2 m grazie all'analisi al microscopio ottico.

Risultati

I valori di silice biogenica riscontrati alle diverse profondità della matte di *P. oceanica* sono riportati in tabella (tab. 1). Tutte le praterie sono contraddistinte da un'elevata variabilità. A Bergeggi le concentrazioni di silice risultano più basse rispetto a tutti gli altri siti, raggiungendo un minimo assoluto alla profondità di 1.5 m con

4796 ± 1817 μM Si g^{-1}, nelle praterie di Punta Pedale e Prelo il valore massimo di silice, similmente, viene riscontrato alla profondità di 1.5 m con 35549 ± 9511 μM Si g^{-1} (Punta Pedale) e 22401 ± 7316 μM Si g^{-1} (Prelo) mentre a Punta Manara sembra essere lo strato più profondo (2 m) quello più ricco (42951 ± 8089 μM Si g^{-1}).

Tab. 1 – Biogenic silica concentration (μM Si g^{-1})

	BERGEGGI	PUNTA PEDALE	PRELO	PUNTA MANARA
0.5 m	8334 ± 3249	31323 ± 944	19898 ± 3991	31419 ± 4424
1 m	12646 ± 4078	22559 ± 5586	18064 ± 2242	27553 ± 2673
1.5 m	4796 ± 1817	35549 ± 9511	22401 ± 7316	36593 ± 2887
2 m	11145 ± 2312	21586 ± 2519	n.d.	42951 ± 8089

Dall'analisi al microscopio ottico sono emerse differenze nel numero di spicole intere tra le due profondità indagate nella prateria di Punta Pedale. Le spicole trovate alla profondità di 0.5 m erano 7756 ± 6457 spicole × g^{-1} di sedimento mentre a 2 m il numero di spicole risultava 2911 ± 1628 spicole x g^{-1}. Il numero di frammenti è risultato invece quasi lo stesso tra le due profondità. Diversi generi di spugna (*Chondrilla, Suberites, Cliona, Dercitus, Agelas e Crella*) sono stati identificati dai campioni raccolti a 0.5 m di profondità nella matte, mentre nello stato più profondo l'unico genere di demospongia che è stato possibile riconoscere era *Geodia*.

Conclusioni

Sebbene le concentrazioni di silice biogenica mostrino un andamento di difficile interpretazione a causa dell'elevata variabilità ambientale, si può ipotizzare che le differenze nell'abbondanza di spugne, relative a diversi periodi storici, nelle praterie di levante (Prelo, Punta Manara e Punta Pedale) siano principalmente dovute a disturbi di tipo antropico. A punta Pedale il minimo valore di silice riscontrato nello strato profondo e confermato anche dall'analisi al microscopio ottico potrebbe essere stato causato dall'impatto della costruzione della strada litoranea verificatosi all'inizio del XX secolo. Similmente, in tempi più recenti, lo sviluppo dei cantieri navali lungo il litorale di Riva Trigoso potrebbe aver causato una diminuzione nella popolazione di spugne della prateria di Punta Manara. La netta e generalizzata riduzione di spugne riscontrata a Bergeggi fa pensare che tale situazione sia legata a forzanti idrodinamiche di tipo locale, quale ad esempio la forte corrente di fondo che si genera in corrispondenza del canale tra Punta del Maiolo e l'isola di Bergeggi.

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Chapter 4 Extreme weather event

4.1

Effects of a severe storm on seagrass meadows

Additional resources:

A. Oprandi, L. Mucerino, F. De Leo, C. N. Bianchi, C. Morri, A. Azzola, F. Benelli, G. Besio, M. Ferrari, M. Montefalcone. *Science of the Total Environment. Under review.*

Abstract

Extreme environmental events can strongly affect coastal marine ecosystems but are typically unpredictable. Reliable data on benthic community conditions before such events are rarely available, making it difficult to measure their effects. At the end of October 2018, a severe storm hit the Ligurian coast (NW Mediterranean) producing million Euros damages to coastal infrastructures. Thanks to recent data collected just before the event on two *Posidonia oceanica* seagrass meadows hit by the storm, it has been possible to assess the impact of the event on one of the most valuable habitats of the Mediterranean Sea. By means of seagrass cover and depth data gathered along four depth transects positioned within the two meadows in areas differently exposed to the storm waves, and by using a model chain (WWWIII + SWAN + XBeach 1D) to evaluate the bed shear stress, we showed that meadows experienced erosion and deposition phenomena according to exposure. Meadows in good conditions suffered more damage as compared to those already suffering from previous local anthropogenic impacts. Besides the direct effect of waves in terms of plant uprooting, a major loss of *P. oceanica* was due to sediment burial in the deepest parts of the meadows. Overall, the loss of living *P. oceanica* cover amounted to about 50%. This result, if transformed into loss of natural capital, would equate 17,934,440 €•a^{-1}. Considering that previous research showed that the loss of the original surface of *P. oceanica* meadows in 150 years due to anthropogenic pressures was

similarly around 50%, the present study documented that an extreme environmental event can generate in a single day a loss of natural capital equal to that produced gradually by more than a century of human impact.

1. Inroduction

Despite short duration, episodic events can lead to dramatic changes in ecosystems if they are extreme in size and/or intensity (Turner et al., 1998). Due to their disruptive nature, extreme events are often judged negatively, and the increase in their frequency in recent decades, linked to climate change, raises concern for the future of local biological communities (Gillet et al., 2004; Gaertner et al., 2018). However, change is not always negative, as these events may represent driving forces in promoting diversity, evolution and renewal processes (Reed et al., 1988; Boero, 1996). In such a complex and variable scenario, it is central to understand the implications of these extreme events in the community dynamics.

The unpredictable nature of short-term episodic events leaves little scope for a proper evaluation of their effects. Ecosystems are known to respond to moderate and frequent disturbances with predictable trajectory of change (Glasby and Underwood, 1996; Scheffer et al., 2001), but reveal unexpected succession patterns when subjected to sudden disturbances differing for duration and intensity (Arens and West, 2008; Teixidó et al., 2013). Most available information focuses on terrestrial ecosystems, where extreme events such as forest fires, volcano eruptions, and floods have long been investigated (Turner et al., 1997a, b; Yin et al., 2009; del Moral and Magnússon, 2014).

In the marine realm, several studies exist that describe the effects of tropical hurricanes on coral reefs (Woodley et al., 1981; Harmelin–Vivien, 1994; Bythell et al., 2000; Gardner et al., 2005; Baird et al., 2018) but less is known on temperate marine ecosystems (Renaud et al., 1996). The Mediterranean Sea has been the theatre of severe storms since ancient times, but only recently these events have been recognized by meteorologist as Mediterranean hurricanes or ‘medicanes’ (Tous and Romero, 2013; Cavicchia et al., 2014; Gaertner et al., 2018).

Although the Mediterranean basin is considered among the regions with the highest cyclogenesis worldwide, especially during the boreal winter (Lionello et al., 2006), the effects of storms on marine habitats are rarely documented. The scanty available information concerns the impact of two big winter storms that struck the coasts of the north-western Mediterranean Sea in 1993 and 2008, respectively. Information on rocky reefs includes the near total mortality for the bryozoan *Pentapora fascialis* after the storm of 1993 (Cocito et al., 1998), and the change in species richness and benthic species cover after that of 2008 (Teixidó et al., 2013). Other evidences regarding the impact of the 2008 storm showed that it was able to move the organic carbon associated with fine particles from shallow to deep waters along with a large amount of sediment, with consequences on deep-sea habitats (Sanchez-Vidal et al., 2012). A study on the impact of the same storm on the meadows of the long-living seagrass *Posidonia oceanica* suggested that, due to the long return time of such exceptional events, those meadows might be able to recover in absence of other natural and anthropogenic stressors (Gera et al., 2014). As far as we know, no further information exists regarding the response of the endemic seagrass *P. oceanica* to extreme episodic events in the Mediterranean Sea.

P. oceanica represents a key species playing a major role in the coastal hydrodynamics: wave attenuation and sediment retention result in an effective protection of the shoreline from erosion (Vacchi et al., 2017, and references therein), and are among the major ecosystem services provided by *P. oceanica* meadows (Vassallo et al., 2013). Although meadows of *P. oceanica* develop in the most dynamic area of the seafloor, they are able to maintain beach stability by contrasting sediment transport; however, this balance comes to fail in the presence of episodic storm events that cause an increase in the nearshore energy (Vacchi et al., 2017). *P. oceanica* meadows experienced an alarming decline over the last decades because of its sensitivity to natural and anthropogenic pressures. A widespread regression of the meadows has been recorded throughout the Mediterranean Sea (Pergent et al., 2014; Montefalcone et al., 2019), and especially along the strongly urbanized coasts of Liguria region, in the northwestern basin (Burgos et al., 2017).

The delineation of seafloor habitats and associated hydrodynamic processes is fundamental for understanding how marine environments will respond to storms. In order to obtain spatially distributed and reliable measures, numerical models are emerging as an effective method to evaluate the storm-induced water levels and sediment transport on the nearshore. In particular, a fundamental parameter that can be efficiently modelled is the bed shear stress, which represents the bed resistance to the main flow (Barnes et al., 2009; Zhang et al., 2016). In coastal environments, bed shear stress is governed by wind and wave-driven currents, and waves (Kösters and Winter, 2014). Recently, hydrodynamic models have been applied to compute bed shear stresses that are capable of altering the distribution of sediments and benthic organisms (e.g., Hemer, 2006; Wölfl et al., 2014). Coastal hydrodynamic and morphodynamic models, such as XBeach, allow simulating a broad range of nearshore beach processes, including wave breaking, surf and swash zone processes and beach erosion (Roelvink et al., 2009). Models such as SWAN (Booij et al., 1999) and MIKE21SW allow computing sea waves parameters in shallow waters, taking into account the effects induced by the bathymetry and the orography of the investigated area. Models such as WavewatchIII (Komen et al., 1996; Tolman, 2009) allow reproducing the wave generation processes. Model chains obtained by coupling these models allow predicting inshore bed shear stress and sediment transport at local scale given offshore information about the meteorological conditions and wave height. Diaz et al. (2016) used model chain composed of WaveWatchIII, SWAN and XBeach to evaluate morphological processes induced by hurricanes impact in Varadero (Cuba). Wölfl et al. (2014) coupled ocean model FVCOM-SWAVE with SWAN to compute wave parameters to evaluate bed shear stress using Soulsby and Whitehouse (1997) formulation on subpolar bay to characterize marine habitats.

At the end of October 2018, a severe storm hit the Ligurian coast, between the coastal towns of Rapallo and Portofino (Bianchi and Peirano, 1995). This paper aims at evaluating the effects of the storm on the local *P. oceanica* meadows, by comparing field data collected immediately after the storm with previous information on seagrass cover and health status of the meadows, as well as the seabed profile. Using a model chain (WWWIII + SWAN + XBeach 1D) we provided bed shear stress estimates, which were related to seabed profile and changes observed in the meadows.

2. Material and methods

2.1. The storm

The storm of October 2018 was an extreme event recognized as one of the most destructive that hit the Ligurian coast in the last 50 years (Onorato, 2018). The coastal storm occurred in a context of general bad weather that was unusually long (5 days) and intense, involving the whole Italian territory.

On 29 October, the northward movement of a cyclone from the south of Mediterranean Sea reinforced the southeast wind of Sirocco. The wind intensity increased during the day, causing damages to the Rapallo harbour, where the waves torn down part of the breakwater dam. The storm peaked in the evening, with landfall between the Liguria and the French Riviera. Very low values of atmospheric pressure (980 hPa) were registered into the eye of cyclone, which moved gradually northward and caused an abrupt change in wind direction turning it into Libeccio (south-west). Under such conditions, the weather got even worse with torrential rains, wind gusts faster than 150 km•h^{-1} and storm waves, whose maximum height of 10.31 m has been measured from the buoy off Capo Mele (Savona), strongly affecting the coast and causing damages estimate of 180,000,000 € (Chamber of Commerce, Genoa).

2.2. Study area

The two *Posidonia oceanica* meadows investigated are located in the eastern coast of Liguria, an administrative region of NW Italy (Figure 1a, b), in the coves of San Michele di Pagana (Figure 1c) and Punta Pedale (Figure 1d). Along the coast, bordered to the north by the municipality of Rapallo and to the south by the eastern tip of the Portofino promontory, morphological and hydrodynamic forces influence the distribution of *P. oceanica* meadows developing in a shallow depth range. The vicinity of the Entella river mouth and the high degree of anthropogenic pressure cause sediment supply and water turbidity, fixing the lower limit of the meadows within 15 m depth (Coppo et al., 2020).

The cove of San Michele di Pagana (Figure 1c) hosts one of the most valuable meadows of the Ligurian Sea, which has been investigated since the 1960s (Bianchi and Peirano, 1995 and references therein). The meadow covers about 16 ha and is included in the marine SAC “Fondali Golfo di Rapallo” (IT1332673). On the west side of the cove, *P. oceanica* develops on a terrace of matte more than 1.5 m high; the natural barrier resulting from seafloor elevation protects the inner and shallow part of the meadow from waves, allowing plant leaves to reach the surface and forming the so-called ‘fringing reef’ (Pérès and Picard, 1964). Despite the high ecological value of this reef-like structure, this meadow has been subjected to anthropogenic impacts that compromised its health status (Montefalcone et al., 2006a; Lasagna et al., 2011).

Punta Pedale cove is part of the UE Special Area of Conservation (SAC) “Fondali Monte Portofino” (IT1332674) and is included in the zone C (partial reserve) of the national Marine Protected Area (MPA) of Portofino. The meadow stretches along the coast for 800 m with a total surface area of about 20 ha, and includes large mosaic areas of *P. oceanica* and dead matte (Figure 1d). Notwithstanding the establishment of the MPA, the ban of anchoring is not in force and the meadow is threatened by nautical tourism.

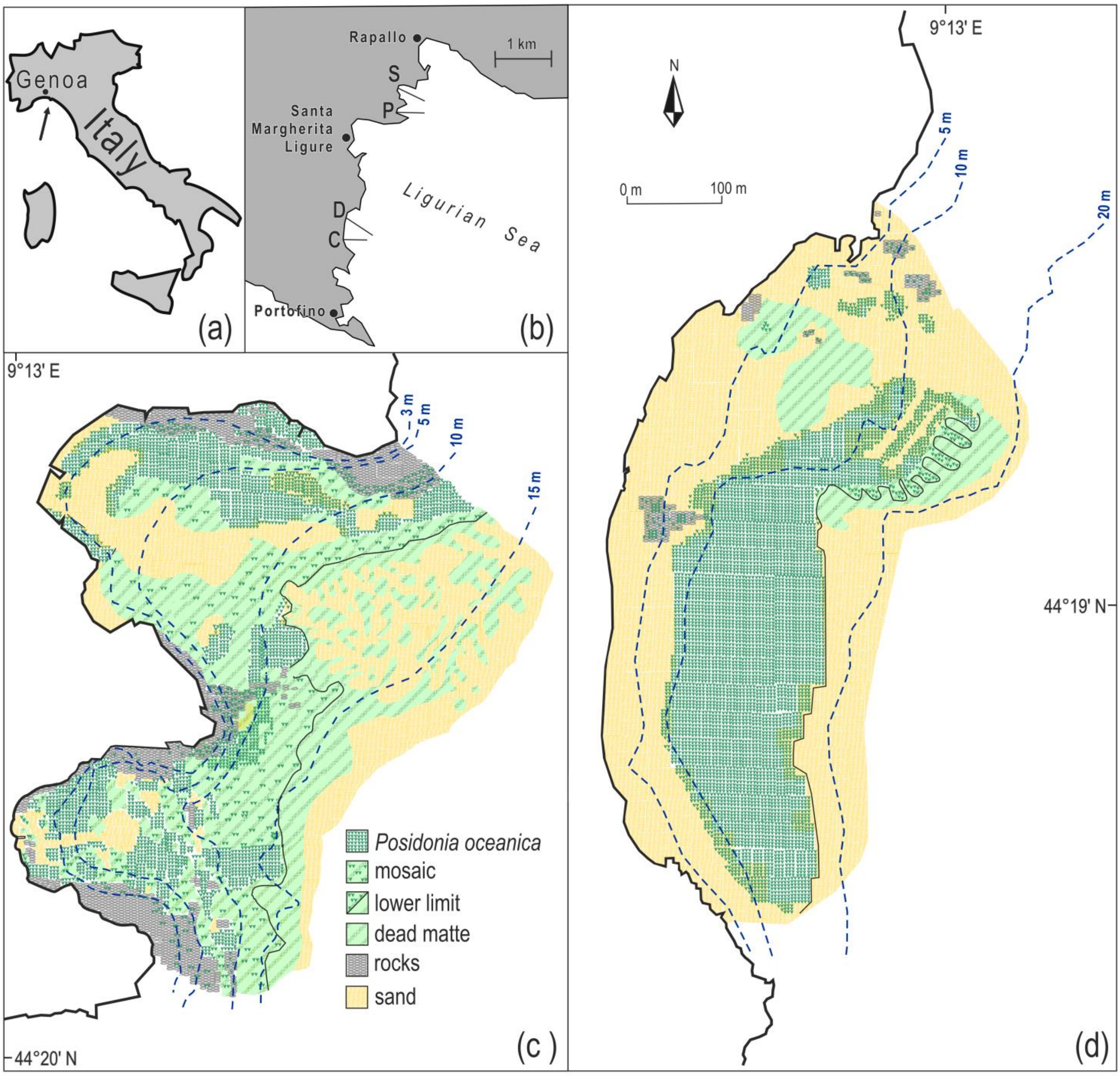

Fig. 1. Geographical situation of the study area in NW Italy (a); location of the four transects S, P, D, and C (b); detailed maps of the meadows of San Michele di Pagana (c) and Punta Pedale (d).

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2.3. Field methods and data collecting

In order to assess the immediate impact of the storm on *P. oceanica* comparing before and after data, meadows were investigated by scuba diving along four depth transects on November 2018, just few days after the storm. The same survey had been performed in 2017. Two transects were located in the meadow of San Michele di Pagana: S (44°20’25.55”N, 9°13’27.99”E) and P (44°20’12.97”N, 9°13’27.37”E); and two transects in the meadow of Punta Pedale: D (44°19’12.89”N, 9°12’47.44”) and C (44°19’5.17”N, 9°12’43.50”E) (Figure 1b). In each meadow, the two transects had different orientation: transects P and C were 90°N oriented, whilst transects S and D were 115-135°N (i.e., southeast) oriented, and thus highly exposed to Sirocco wind. Underwater visual surveys were used, where two experienced divers, swimming approximately 2 m above the meadow, collected data each 10 m along the transect line (Montefalcone et al., 2006b). Between the meadow lower limit (i.e., the lowest depth reached by the plant seaward) and the meadow upper limit (i.e., the meadow shallowest depth landward), cover data (expressed as the percentage of seafloor occupancy) of living *P. oceanica*, dead matte, sand, rock, and uprooted meadow (blocks of living shoots not anchored to the substrate) were recorded, and depth measured to detect change in the seabed profile (buried or eroded areas) along each transect.

2.4. Model chain

To assess the wave-induced bed shear stress (τ) taking place during the storm, the wave field in the area of interest was first computed. To this end, we employed SWAN (Simulating WAves Nearshore), a third generation model that resolves the wave action equation in shallow waters (Booij et al., 1999). A fine regular grid was developed in the area of investigation (Figure 2), with a resolution of 0.001° both in latitude and longitude (approximately 100 m at these latitudes).

Wave parameters were calculated, on an hourly base between 25 October 2018 and 31 December 2018 in two locations named P1 and P2 (Table 1 and Figure 2). The parameters extracted were the significant wave height (H_s), wave period (T), wave direction (θ), and wave length (L). For all parameters, both the peak and mean values were computed; henceforth, they were indicated with the subscripts p and m, respectively.

Table 1. Coordinates for the SWAN simulation. LC: lower corner of the grid; UC: upper corner of the grid. P1 and P2: locations where the wave parameters were calculated.

Points	Lon	Lat
LC	8.9980°	44.2200°
UC	9.3800°	44.4000°
P1	9.2583°	44.3132°
P2	9.2381°	44.3358°

SWAN was fed with the hindcast data developed by the Department of Civil, Chemical and Environmental Engineering of the University of Genoa (DiCCA, www.dicca.unige.it/meteocean/hindcast), with the WWIII numerical model (Tolman, 1989, 2009). The hindcast is defined all over the Mediterranean Sea from 1 January 1979 to 31 December 2018, with an approximate 0.1° resolution both in longitude and latitude (Mentaschi et al., 2013, 2015). The wave model was forced by a 10 m wind field obtained from the non-hydrostatic mesoscale model Weather Research and Forecast (WRF-ARW) version 3.3.1 (Skamarock and Klemp, 2008; Skamarock et al., 2008), based on NCEP Climate Forecast System Reanalysis (CFSR), for the period from January 1979 to December 2010 and CFSv2 (Climate Forecast System version 2) for the period from January 2011 to December 2019.

To evaluate bed shear stress (τ) along the profiles, XBeach 1D model was employed on the nearshore zone, using SWAN wave parameters output at 40 m depth as wave input at points P1 for profiles S and P, and at point P2 for profiles D and C. XBeach 1D is a numerical solver for coupled two-dimensional depth-averaged equations for short-wave envelope propagation and flow with spectral wave and flow boundary conditions (Roelvink et al., 2009), which allow computing and evaluating morphodynamic processes on sand and gravel beaches (Mucerino et al., 2019).

An irregular mesh for XBeach 1D simulation was employed to obtain a higher resolution across the surf zone and a lower resolution far from the coast. The grid size was about 0.5 m inshore and 10 m offshore. To simulate τ, the bed friction was computed using White-Colebrook formulation, which is based on the relation between the D_{90} (the particle diameter corresponding to 90% cumulative) of the top bed layer and the geometrical roughness of Nikuradse (1950). The grain size parameters adopted in the four transects (S, P, D, and C) were medium grain size (D_{50}) and D_{90} (Table 2).

Table 2. Grain size parameters D50 and D90 in the four transects investigated (S, P, D, and C).

Profile	D50 (mm)	D90 (mm)	Source
S	0.2	0.3	http://www.ambienteinliguria.it/eco3/DTS_GENERALE/20121015/
P	1.2	1.1	Lasagna et al. (2011)
D	0.7	0.8	http://www.ambienteinliguria.it/eco3/DTS_GENERALE/20121015/
C	0.7	0.8	http://www.ambienteinliguria.it/eco3/DTS_GENERALE/20121015/

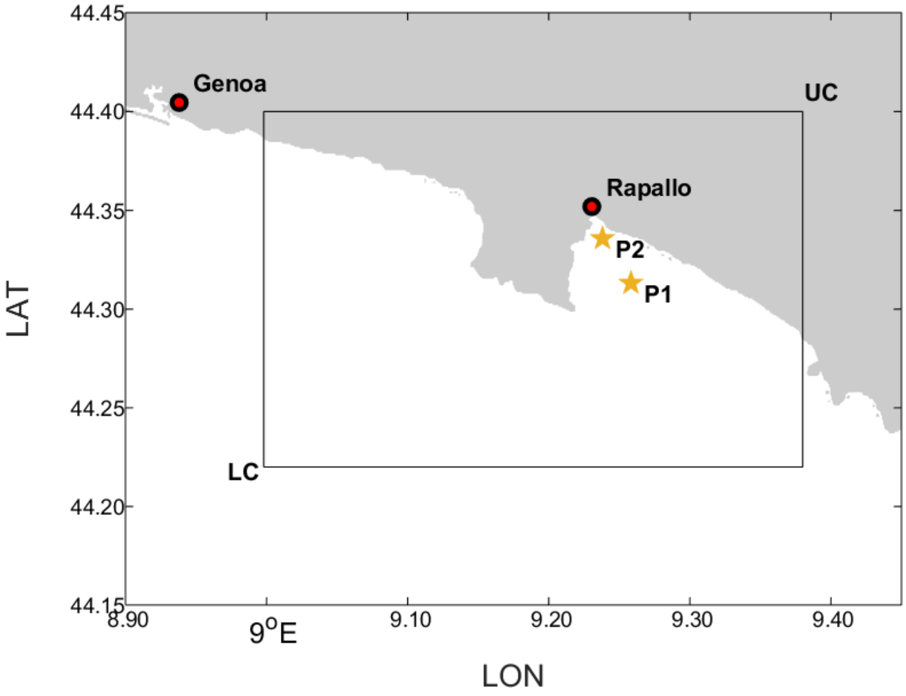

Fig. 2 Settings of the SWAN model; the codes on the boundaries refer to the hindcast points: LC: lower corner of the grid; UC: upper corner of the grid. P1 and P2: locations where the wave parameters were calculated. See Table 1 for points coordinates.

2.5. Data management

Transects have been analysed to detect the depth zones most influenced by the storm. Changes in meadow structure, seabed profile, and seagrass cover due to the event have been evaluated separately for the shallow (0 to 5 m depth), intermediate (5 to 10 m depth), and deep part (10 to 15 m depth) of each transect. Bathymetric differences in the seabed profiles before and after the storm have been averaged for the three depth zones to distinguish buried and eroded areas in each meadow. The loss of living *P. oceanica*, the increase of dead matte, and change in sand occurrence has been measured by comparing their percent cover before and after the storm. Significant differences have been evaluated by means of Student t-test.

Using seagrass cover data collected along transects, the Conservation Index (Moreno et al., 2001; Montefalcone, 2009) was calculated to assess the meadow health status before and after the storm, using the formula:

$$CI = P / (P + D)$$

where P is the percent cover of living *P. oceanica* and D is the percent cover of dead matte.

3. Results

3.1 Model chain

The beginning of the storm was characterized by waves propagating from southeast, typical of Sirocco wind (Figure 3). Due to the morphology of the coastline, no energy dissipation took place, and H_s and θ_m at P1 and P2 attained values similar to those at the boundary conditions. On the contrary, the peak of the storm showed south-west waves typical of Libeccio wind due to a shift in the sea storm direction, with H_s characterized by high intensities in deep waters (i.e., boundary conditions). However, the two points of interest lay in the shadow area behind the promontory with respect to the incoming wave direction. As such, there was a relevant energy dissipation of the waves, leading to a significant lowering of H_s and a rotation of θ_m (Figure 3). In particular, as regard P2, the majority of the waves were propagating from the south; this was due to the rotation induced by both the diffraction around the promontory and the refraction tending to orientate the waves normal to the shore.

The maximum values of bed shear stress (τ) in San Michele di Pagana meadow occurred in the shallow area (0-5 m depth), although they did not exceed +60 N•m^{-2} (Figure 6a, b). In the intermediate and deep areas, τ values were lower or negligible. In the meadow of Punta Pedale, maximum τ values were reached in the intermediate and shallow areas, showing τ greater than ±100 N•m^{-2} (Figure 6c, d). In the deep area, τ reached high values in transect C (Figure 6d). Similarly to τ, the significant wave height (H_s) was higher in the meadow of Punta Pedale (Figure 6c, d) than in that of San Michele di Pagana (Figure 6a, b).

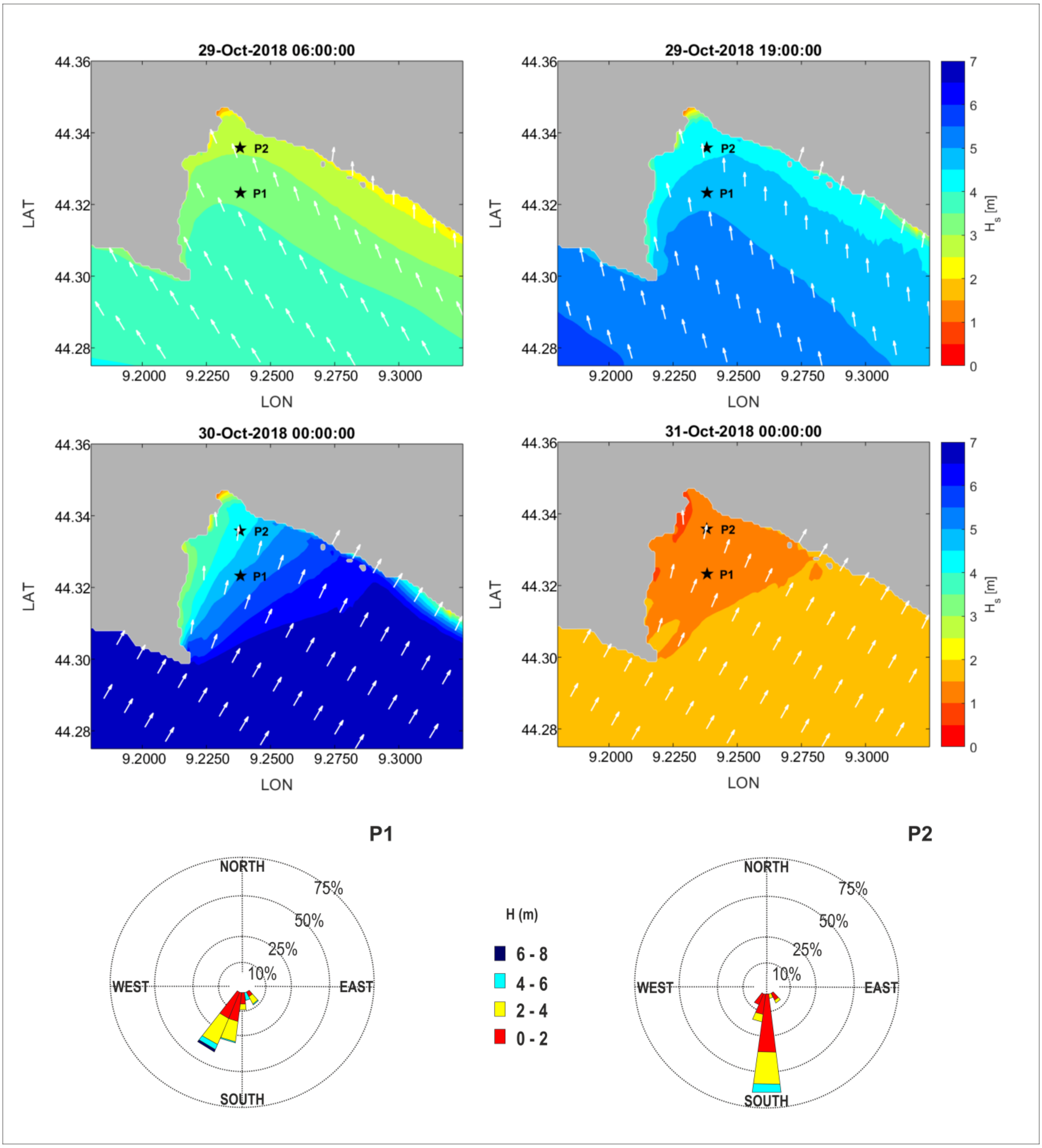

Fig. 3. Top: Computed SWAN wave propagation on the area investigated in four significant time steps during the storm of October 2018. Bottom: Wave polar plots referring to nested points through SWAN and XBeach 1D; the outcomes of H_s for the whole simulation are summarized with respect to θ_m through the polar plots in the locations P_1 and P_2.

3.2 Changes in seabed profile and *Posidonia oceanica* cover

After the storm, the seabed profile changed differently according to the exposure of transects. The southeast oriented transects (S and D) have been mainly eroded (Figure 4a, c) and their seabed profile decreased of about 0.3 m to 0.7 m in their deep areas (Figure 5). On the contrary, the east oriented transects (P and C) have been prevalently affected by burial (Figure 4b, d) and the seabed profile increased of up to 0.9 m in their deep areas (Figure 5). In both cases, major changes occurred in the deep parts of the meadows, between 10 m and 15 m depth. Apparently, the intensity of erosion and deposition phenomena mostly depended on the significant wave height and on the resulting bed shear stress (τ), since in transects S and P where τ was lower (Figure 6) changes in seabed profile were small as compared to those in transects D and C (Figure 5).

The transects S and P in San Michele di Pagana underwent smaller and more homogenous bed shear stress and lower maximum significant wave height (Figure 6a, b) as compared to the transects D and C in Punta Pedale (Figure 6c, d). However, more than bed shear stress and wave height, it was transect orientation that better correlated to the impact on the *P. oceanica* meadows: east oriented transects (P and C) experienced a more severe reduction in *P. oceanica* cover at virtually all the investigated depths (Table 3; Figure 6b, d), while southeast oriented transects (S and D) showed a significant cover decrease only in the intermediate and deep parts, respectively (Table 3; Figure 6a, c). The percent cover of living *P. oceanica* reduced dramatically after the storm, the total loss with respect to previous values averaging nearly 50% in all transects (Figure 8).

All transects exhibited a significant increase in dead matte cover after the storm (Table 3). However, in the east oriented transects (P and C) the increase was only in the shallow part (Figure 6b, d), while in the southeast oriented transects (S and D) the increase was in the intermediate and deep parts (Figure 6a, c). Sand cover also showed different trends according to transects orientation (Table 3): it increased significantly in the intermediate and deep parts of the east oriented transects P and C (Figure 6b, d), while it generally decreased in the southeast oriented transects S and D (Figure 6a, c). In transect S, the occurrence of uprooted *P. oceanica* ($p < 0.01$) after the storm was evident within 5 m depth (Figure 6a).

The health status of *P. oceanica* meadows described by the Conservation Index (CI) got worse after the storm in all transects (Table 4). Major change occurred in the shallow and intermediate parts of transects where the status passed from high to poor or even bad. The deep parts of the meadows showed a moderate or poor status already before the storm: in San Michele di Pagana did not change appreciably the status, whilst in Punta Pedale moved from a good to a moderate or bad status.

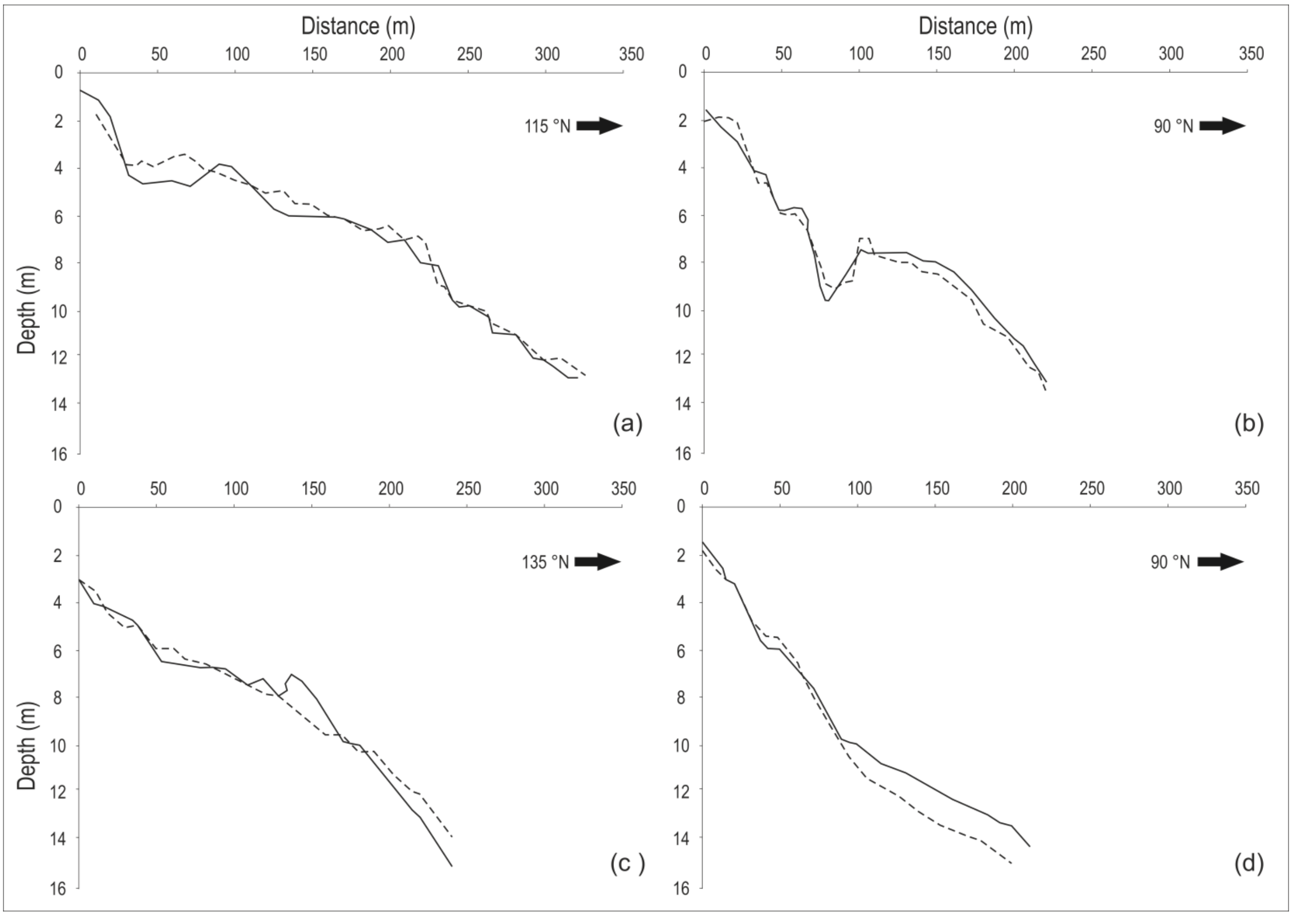

Fig.4. Seabed profiles before (dashed lines) and after the storm (full lines) for the transects S (a) and P (b) in the meadow of San Michele di Pagana, and for the transects D (c) and C (d) in the meadow of Punta Pedale.

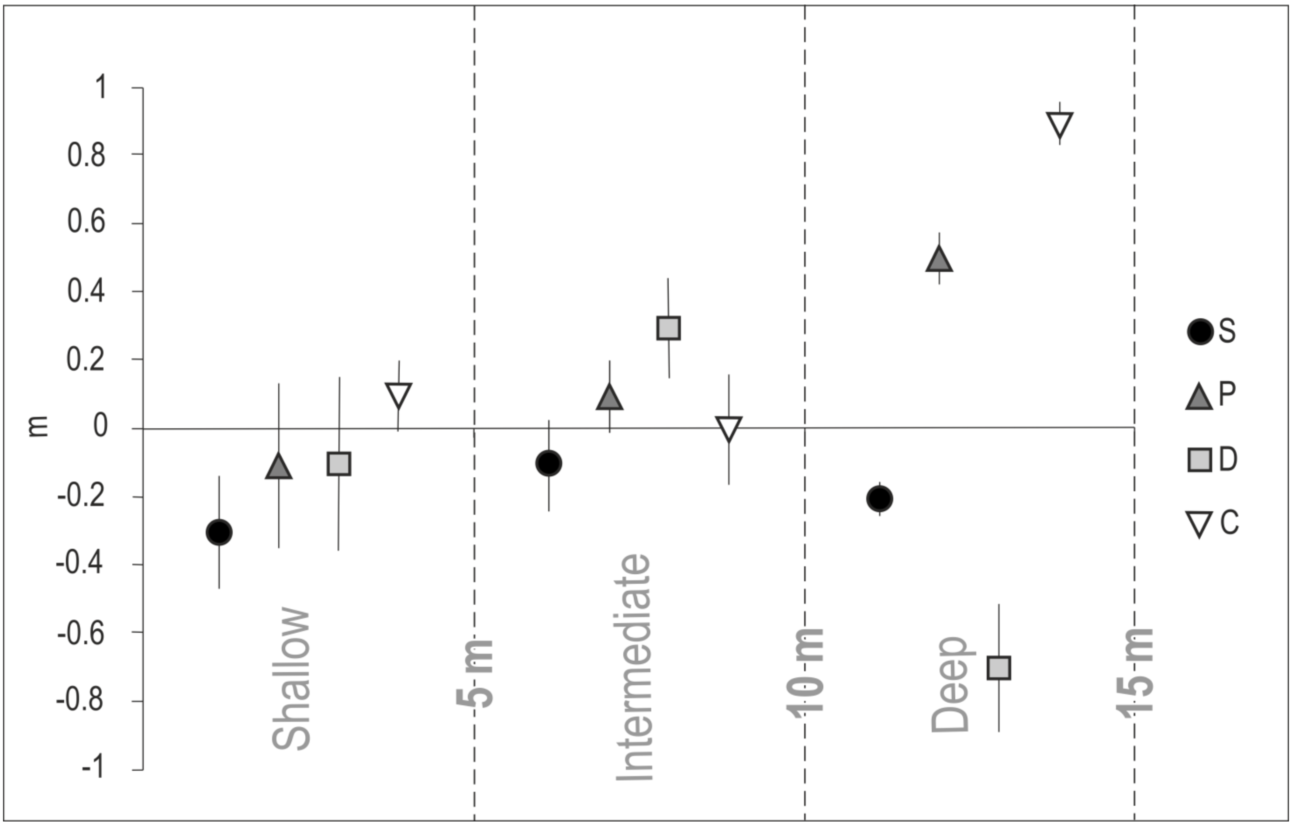

Fig. 5. Changes in the seabed profile for the shallow, intermediate and deep parts of the four transects S, P, D, and C.

Tab. 3. Summary of cover data before and after the storm in the four transects investigated (S, P, D, and C). Percentages refer to the mean (± s.e.) cover of each descriptor in the three parts of the transects (S = shallow, I = intermediate, D = deep).

		% cover before				% cover after				% cover differences (t test $^*p < 0.05$ $^{**}p < 0.01$)			
		P. oceanica (± s.e.)	dead matte (± s.e.)	sand (± s.e.)	Uprooted *P.oceanica* (± s.e.)	*P. oceanica* (± s.e.)	dead matte (± s.e.)	sand (± s.e.)	Uprooted *P.oceanica* (± s.e.)	*P. oceanica*	dead matte	sand	Uprooted *P.oceanica*
S	S	**3** ±1.5	**0** ± 0.0	**97** ±1.5	**0** ±0.0	**1** ±0.4	**4** ±2.9	**61** ±10.9	**34** ±11.0	-2	+4	**-36** **	**+34** **
	I	**58** ±14.9	**9** ±4.8	**33** ±14.8	**0** ±0.0	**19** ±6.0	**28** ±11.1	**53** ±15.9	**0** ±0.0	**-39** *	+19	+20	-
	D	**36** ±13.6	**19** ±9.8	**46** ±13.3	**0** ±0.0	**33** ±5.3	**53** ±10.5	**15** ±6.5	**0** ±0.0	-3	**+34** *	**-31** *	-
P	S	**98** ±2.9	**3** ±2.9	**0** ±0.0	**0** ±0.0	**30** ±12.5	**45** ±18.0	**25** ±28.9	**0** ±0.0	**-68** **	**+42** *	+25	-
	I	**78** ±11.1	**5** ±2.4	**17** ±9.7	**0** ±0.0	**25** ±6.3	**26** ±12.3	**50** ±9.7	**0** ±0.0	**-53** **	+21	**+33** *	-
	D	**32** ±13.5	**68** ±13.5	**0** ±0.0	**0** ±0.0	**33** ±9.5	**58** ±13.8	**9** ±6.2	**0** ±0.0	+1	-10	+9	-
D	S	**30** ±0.0	**10** ±0.0	**60** ±0.0	**0** ±0.0	**25** ±35.4	**0** ±0.0	**75** ±35.4	**0** ±0.0	-5	-10	+15	-
	I	**23** ±5.6	**6** ±0.0	**71** ±6.0	**0** ±0.0	**22** ±5.3	**37** ±7.7	**41** ±11.9	**0** ±0.0	-1	**+31** **	**-30** *	-
	D	**75** ±10.9	**20** ±11.7	**5** ±2.8	**0** ±0.0	**27** ±5.5	**72** ±5.8	**1** ±1.1	**0** ±0.0	**-48** **	**+52** **	-4	-
C	S	**73** ±14.8	**20** ±0.0	**7** ±4.1	**0** ±0.0	**8** ±2.0	**92** ±8.2	**0** ±0.0	**0** ±0.0	**-65** **	**+72** **	-7	-
	I	**82** ±3.4	**0** ±0.0	**18** ±3.4	**0** ±0.0	**34** ±10.4	**20** ±11.8	**46** ±10.0	**0** ±0.0	**-48** **	+20	**+28** *	-
	D	**88** ±7.8	**12** ±7.8	**0** ±0.0	**0** ±0.0	**53** ±4.5	**31** ±6.8	**16** ±5.7	**0** ±0.0	**-35** **	+19	**+16** **	-

Tab. 4. Health status of the three parts of the transects (S, P, D and C) before and after the storm according to the Conservation Index (CI).

	Shallow		Intermediate		Deep	
	Before	After	Before	After	Before	After
S	HIGH	BAD	GOOD	POOR	MODERATE	POOR
P	HIGH	POOR	HIGH	POOR	POOR	POOR
D	HIGH	HIGH	HIGH	POOR	GOOD	BAD
C	HIGH	BAD	HIGH	MODERATE	GOOD	MODERATE

4. Discussions

Published information documented how can strong extreme environmental events influence ecological dynamics (Gutschick and BassiriRad, 2003; Bailey and Pol, 2016; Batt et al., 2017). Similarly, the sea storm that hit Liguria in October 2018 affected considerably the submerged benthic habitats (Betti et al., 2020): *Posidonia oceanica* meadows, in particular, halved their living cover.

Damage due to extreme meteorological events is easily perceived on land, but due to lack of the perception of the marine environment (Bianchi et al., 2012) goes often unnoticed in the sea. In addition, it is rare to have updated information about the previous status of the ecosystems damaged. Our study represents a unique opportunity to improve the knowledge about the repercussions of extreme events on valuable habitats such as the *P. oceanica* meadows.

The storm had worse consequences in the east oriented transects, where the decrease in living *P. oceanica* cover was ascribable to the two combined effects of meadow burial and uprooting. In shallow water, the greater energy generated by waves crashing caused uprooting of a high number of seagrass shoots, resulting in a loss of more than 70% of meadow cover locally (Figure 7b, c, f). In the intermediate and deep parts of the meadows, the main cause of *P. oceanica* loss was sand burial (Figure 7a, d, e). Sediment burial and erosion are major impacts on seagrass (Cabaço et al., 2008). Gera et al. (2014) stated that areal loss due to uprooting was comparatively smaller than that lost by burial after a storm, and that burial levels above 9 cm resulted in the total mortality of *P. oceanica* shoots. In our study, burial occurred in patches, but this notwithstanding the comparison of seabed profiles before and after the storm allowed documenting an increase of seabed elevation between 10 cm and 90 cm, together with an increase in sand cover of 30%, which led to the near total mortality of shoots in the areas affected by burial. In the southeast oriented transect S of San Michele di Pagana, the decrease of *P. oceanica* cover was related to the uprooting caused by waves (Figure 7g, h); here, *P. oceanica* grows mainly on sand, not on matte, which could made plants weakly attached and more easily ripped off the substrate. Waves affected meadows also beyond the “closure depth”, i.e., the hydrodynamic boundary where waves are expected to have no more influence on the bottom (Vacchi et al., 2010). No sand deposition took place in southeast oriented transects; here, on the contrary, the removal of sediment particles made apparent dead matte once buried.

The Ligurian coastline is mainly exposed to winds blowing from the second and third quadrants (Vacchi et al., 2010). Southwest is the dominant wave direction, but thanks to the morphology of the coast, all the meadows investigated are sheltered. The storm of October 2018 showed a first phase characterized by unusual and powerful southeast waves, which later shifted to south: such a deviation in wave direction is likely to have caused the uprooting of large areas of the seagrass meadow of San Michele di Pagana.

Our results suggested that the meadow areas most adversely affected by the storm were those facing east. However, the southeast oriented transects were already poorly covered before the storm, and thus the loss of *P. oceanica* resulted paradoxically less severe. The Conservation Index (CI) evidenced little change in the health status of deep areas, where the meadows had already suffered the regression of their lower limit (Bianchi and Peirano, 1995). On the contrary, the greatest change occurred where the meadows exhibited a higher health status. Healthy meadows are known to withstand moderate and chronic stresses, but to easily succumb to high-intensity, pulse disturbances (Gera et al., 2014).

In tropical areas, seagrass beds periodically struck by hurricanes, like those of the northern Gulf of Mexico, exhibited high resistance to this kind of disturbances (Anton et al., 2009). However, other evidences suggest that the impact of extreme events on seagrass ecosystems may differ according to the hurricane intensity, the season and the specific location (Anton et al., 2009 and references therein). In the NW Mediterranean, the remarkable persistence of *P. oceanica*, the slowest-growing and longest-lived plant in existence (Arnaud-Haond et al., 2012), may suggest that it has the capacity to recover from extreme environmental events such as the storm of October 2018. Nevertheless, the high level of anthropogenic impact in the Ligurian Sea may have eroded the resilience capacity of coastal marine ecosystems (Bianchi et al., 2019), so that no prediction can be made about the recovery potential of the *P. oceanica* meadows investigated. Gera et al. (2014) found that 4 years after an intense storm only 20% of the meadows affected showed signs of recovery, and hypothesized that meadow restoration by clonal growth might require 30 years in absence of other disturbances.

Between the 1850s and the 2010s, the Liguria region experienced a loss of about 50% of the original extent of *P. oceanica* meadows due to anthropogenic pressures (Burgos-Juan et al., 2016). The amount of *P. oceanica* lost during the severe storm of October 2018 has been roughly the same. Thus, a single extreme event has caused in one day the same loss that anthropogenic pressures caused in more than one century.

Severe storms have historically affected Mediterranean coastlines, but the impact of each storm has been evaluated often using local socio-economic criteria (e.g. loss of lives and damage to property). Also the natural capital has a quantifiable value, which has been estimated at 1,720,000 €•ha^{-1}•a^{-1} in the case of *P. oceanica* meadows (Vassallo et al., 2013). This figure can be used for a first rough assessment of the natural capital loss after the coastal storm of October 2018. Considering that the total surface area of the meadows studied was 20.853 ha (http://srvcarto.regione.liguria.it/geoviewer/pages/apps/SICoast/Mappa.html?id=1224) and assuming a reduction of 50% of their extent (Figure 8), a total area of 10.427 ha must have been lost because of the storm, thus suggesting that the damage to the *P. oceanica* meadows under consideration could equate 17,934,440 €•a^{-1}.

The number of historical storms with major damages in Liguria has increased fivefold and their return time has more than halved between 1600 and 2000 (Garnier et al., 2018). Since climate change is likely to increase the magnitude and frequency of these extreme weather events (Easterling et al., 2000), the recovery capacity of coastal marine ecosystems will be reduced. Projected future wave climate in the NW Mediterranean Sea predict major alterations not in the significant wave height but rather in wave direction, with more frequent W-NW waves, especially during the winter season (Casas-Prat and Sierra, 2013). Although different studies (Lionello et al., 2008; Androulidakis et al., 2015) describe a decreasing trend in storminess under future climate scenario, the magnitude of sea surface elevation extremes may increase in several Mediterranean sub-regions.

The destructive effects of the storm of October 2018 on *P. oceanica* meadows may be due to the genesis of the event rather than to the magnitude of the storminess; it caused the convergence of two different sea storms coming from southeast and southwest that acted in synergy, amplifying the resultant impact on the coast. More importantly, a storm surge associated to intense winds and low pressure caused a significant sea level rise further intensifying the waves force (Onorato, 2018). Thus, considering future projections for wave climate, the storm of October 2018 can be seen as a warning model, anticipating the effects that should be expected under a predicted scenario of sea level rise.

5. Conclusions

This study provided new insights into the poorly known ability of *Posidonia oceanica* meadows to withstand natural disturbances extreme in size and intensity. Our approach, combining different fields of study (i.e. ecology, geomorphology, and modelling), made it possible to relate accurately the dynamics of the event with its effects on the meadows investigated. Being unable to predict how frequently these extreme events will recur in the future, we should ensure the protection of *P. oceanica* meadows by limiting the wide range of anthropogenic pressures affecting this habitat at least at the local scale. Coastal ecosystems, more than others, are threatened by multiple affectors that may overlap over a short time period reducing their resilience (Montefalcone et al., 2011). Such considerations claim at the importance of monitoring coastal habitats to guarantee always updated information on ecosystem status that may be useful in the case of unpredictable events. In this regard, the meadows affected by the storm of October 2018 should be regularly surveyed in the years to come to verify their potentiality of recovery.

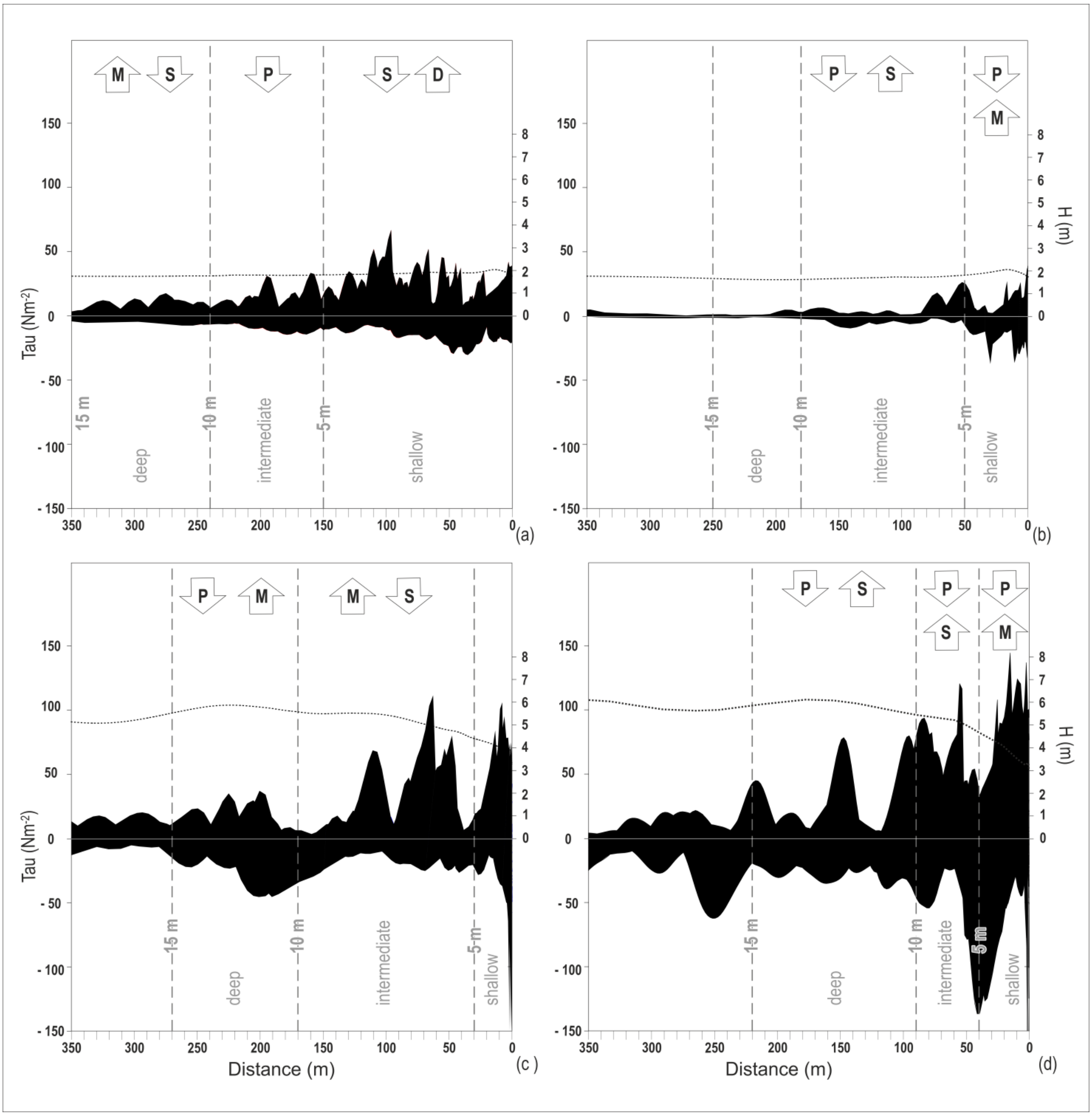

Fig. 6. Bed shear stress (τ) along the transects S (a) and P (b) in the meadow of San Michele di Pagana and along the transects D (c) and C (d) in the meadow of Punta Pedale. Dashed lines represent the maximum significant wave heights. Arrows indicate where *Posidonia oceanica* (P), dead matte (M), sand (S) and uprooted meadow (D) changed significantly.

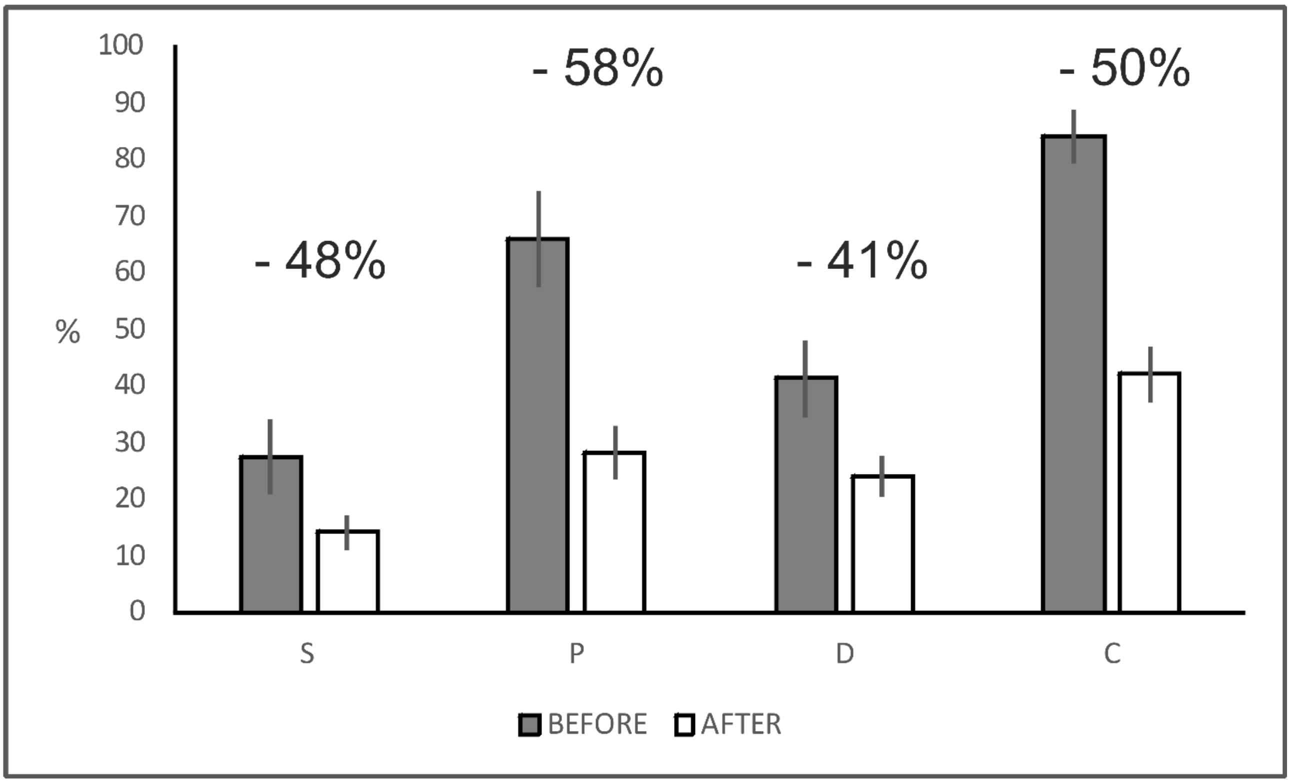

Fig. 8. Decrease of the living *Posidonia oceanica* cover in the four transects S, P, D, and C.

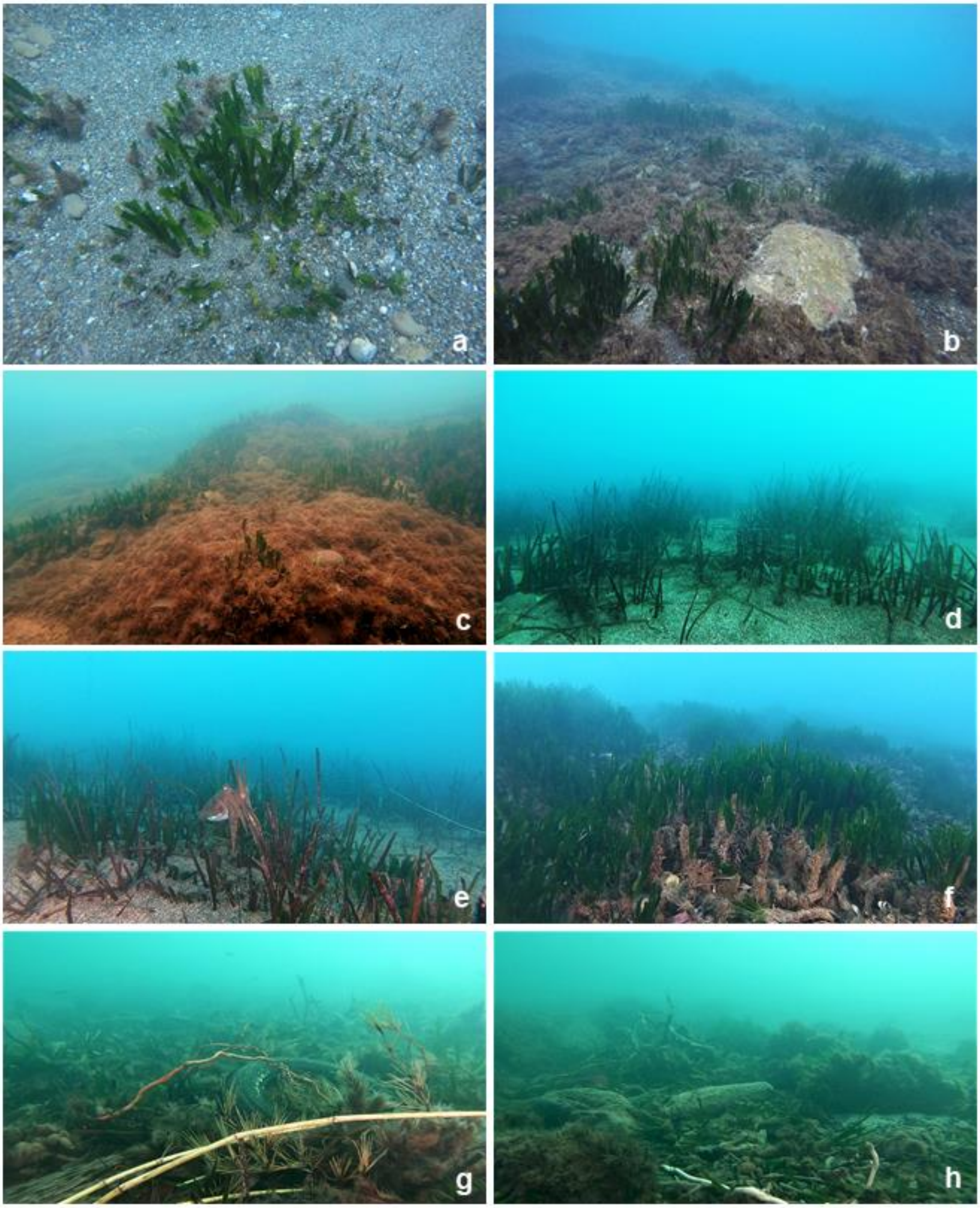

Fig. 7. Underwater photographs showing the impact of the severe storm of October 2018 on *Posidonia oceanica* meadows. Different areas affected by sediment burial in both the meadows of Punta Pedale (a) and San Michele di Pagana (d, e); rhizomes deprived of leaves and mown meadow in San Michele di Pagana (f); *P. oceanica* torn off the substrate in Punta Pedale (b) and San Michele di Pagana (c); uprooted *P. oceanica* shoots in San Michele di Pagana (g, h).

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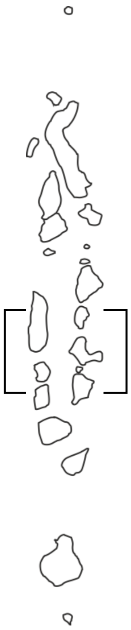
3°28'15.78"N	73° 33'4.47"E



1°45'3.75"N	125° 7'53.47"E
1°40'24.66"N	125° 8'4.17"E

PART TWO
CORAL REEFS

Coral reefs in tropical regions are renowned for their remarkable diversity (more than 3 million species) and the number of ecosystem services they provide to hundred million people living close by them (Woodhead et a. 2019). Fishing and tourism are the main commercial activities they support but their critical role is played in providing sea defences against storms, flooding, and land erosion. Ecological services from coral reefs are estimated at approximately 30 billion USD per year (Chen et al. 2015).

These peculiar habitats thrive in only a small percentage of global oceans. Covering less than 1 % of the ocean surface and living within 30° latitude of the equator, they are typically found in shallow waters, where they can grow optimally between 23° and 29°C (Spalding and Brown 2015).

Coral reefs are biogenic carbonate structures that accrete over decadal time scales. The three-dimensional architecture of this ecosystem is due to the active growth of living reef-building corals cemented together by the biological activities of other calcifying organisms (Spalding et al. 2001).

Developing in different shapes and sizes, coral reefs can be distinguished according to their geomorphological origin in: fringing reefs, barrier reefs and atolls.

Reefs are threatened worldwide by local impacts to large-scale temporally rare perturbations. The latter include physical disturbances such as storms and tsunamis, ecological imbalances caused by disease and predatory starfish outbreaks and oceanographic influences among which, increase in seawater temperature and pH reduction are those most alarming (Spalding and Brown 2015). The increasing temperature of the water surface is causing a widespread phenomenon of coral bleaching that results from the rupture of the symbiotic relationship between corals and their zooxanthellae. Although it can be reversible if it solves in few days, bleaching inevitably leads to coral death if the thermal anomaly persists for a long time. The first circumtropical coral bleaching was observed coupling to the El Niño Southern Oscillation (ENSO) in 1997–98 with temperature anomalies of + 3°C to 4°C and duration of 3-4 months. Up to 90% of mortality was recorded among corals and averagely 14 years were needed for a full recovery (Morri et al. 2015), although in many places, a phase shifts toward macroalgal and sponges dominance has been observed (Hughes 1994; Graham et al. 2015; De Bakker et al., 2017). Two following mass coral bleaching occurred at large scale in 2010 and 2014-2016 suggesting an increase in frequency and duration of these harmful events.

However, coral mortality after the 2016 bleaching was lower than in 1998, and the initial recovery occurred via a different trajectory than in 1998 (Montefalcone et al. 2018).

A further major threat to coral reefs is ocean acidification (OA) caused by the dissolution of the excess carbon dioxide produced by human activities into the ocean. The increasing acidity of seawater led to a drop of 0.1 pH units since the beginning of last century (from 8.2 to 8.1). Although it seems that the effects vary greatly from one species to another (Erez et al. 2011), OA may seriously affects the calcification rates of corals, and therefore reef growth (Pandolfi et al. 2011). Coral community has few ways to remedy to disturbances of such magnitude and recruitment is widely recognized as a fundamental process governing spatial patterns, dynamics, and maintenance of adult assemblages in marine invertebrate communities. Moreover, coral recruitment and juvenile survival are critical factors for successful recovery following disturbances and thus ensuring resilience of coral reef ecosystems (Adjeroud et al. 2017).

In this section, coral recruitment was investigated under the effect of thermal anomalies linked to El- Niño events across Maldivian atolls (Indian Ocean), one of the area most severely affected by repeated mass coral bleaching and mortality, thanks to a long-time series of data used to evaluate patterns of recovery over time (Chapter 5); and under conditions of reduced ph (Chapter 6), in shallow hydrothermal vents of North Sulawesi (Indonesia), considered as natural laboratories simulating climate and human impacts on marine habitats. In this latter area, the sponge dominated benthic community has also been investigated (Chapter 6).

Mediterranean Sea has no building corals comparable to those of tropical coral reefs; however, calcareous formations of biogenic origin also develop on the rocky substrates of temperate marine environments. The coralligenous habitat is one of the most important coastal ecosystems in the Mediterranean Sea considered as a “hot-spot” of biodiversity (Ballesteros, 2006). It grows in dim light conditions thanks to the delicate balance between bioconstruction, operated by calcareous red algae, and bioerosion processes (Piazzi et al. 2012). In this brief last section (Chapter 7), a trait-based approach (Gatti et al. 2012, 2015a; Montefalcone et al. 2017) is used to quantify the bioconstruction due to specific growth forms that constitute the basal layer of coralligenous assemblages in the rocky reefs of Portofino promontory MPA.

Chapter 5 Thermal Anomalies

5.1

Twenty-three years of coral recruitment in Maldives after repeated coral bleaching: the "Emergency spawning” hypothesis

Additional resources:
Unpublished data

Introduction

Coral reefs worldwide are facing the consequences of large-scale changes in the Earth’s climate. Ocean warming and particularly intense fluctuation in sea surface temperature have led to an increase in the severity, duration and frequency of coral bleaching events, which are threatening the long-term stability of coral reefs causing widespread mass mortality (Hughes et al., 2018).

Reefs in the world have recently been affected by three major global bleaching events, in 1997-1998, 2010, and 2014-2016. The 3-year duration of the 2014-2016 event was unprecedented, being the longest, the most widespread, and possibly the most damaging on record (Hughes et al., 2017). After the bleaching event of 1997-1998 Maldives has been among the most affected countries, with 60–100% coral mortality reported, depending on species and locality (Bianchi et al., 2003). A critical factor for successful recovery following disturbances and thus resilience of ecosystems is represented by recruitment. Coral recruitment is widely recognized as a fundamental process governing spatial patterns, dynamics, and maintenance of coral community (Adjeroud et al. 2017).

Following the bleaching event of 1997-1998, Loch et al (2002) speculated about several possible mechanisms by which corals realized the recolonization across the central atolls of Maldives.

According to the "emergency spawning hypothesis" (ESH), just before they died, corals released into the water a large number of larvae due to the high temperatures that forced gonad maturation. Coral larvae exhibited reduced sensitivity to bleaching than adults allowing reef recolonization.

An emergency sexual reproduction of survived scleractinian corals was also assumed. Although it was not fully corroborated, the emergency spawning hypothesis, suggested interesting insights on how coral community might face severe disturbance events. They would have two paradoxical strategies (Frontier 1999): firstly, they bleached to facilitate the renewal of their symbiotic algae (Baker 2001), then, they spent last energies to preserve their genetic pool through sexual reproduction.

A similar behaviour is well known in medicine and ecophysiology as "hormesis" (Stebbing, 1982) and it was already noticed in hydrozoan colonies under heat stress conditions, which showed an increase in goonozoids production, right before they died (Stebbing 1980; Piraino 1991).

Availability of twenty-three year series of data on coral recruitment in the Maldives (Fig. 1), encompassing severe and moderate bleaching events, provided the opportunity to compare the effects of heat anomalies testing the emergency spawning hypothesis and to define the general patterns of coral recovery of Maldivian coral reefs from bleaching events.

Material and methods

Between 1997 and 2019, 23 scientific cruises took place annually in April-May in the atolls of the Maldives Archipelago. Every year, eight to eleven sites were chosen randomly and surveyed, totalling 168 sites. Data were collected at reef sites located either on the ocean- or lagoon-facing sides of the atoll rims, or on lagoon patch reefs. Hard coral recruitment was quantified by counting small corals with approximately circular outlines in 12 replicated quadrats of 0.25 m^2, randomly placed at two depth zones: reef flat (5 m) and reef upper slope (10 m). Coral colonies smaller than 5 cm in diameter were called 'recruits', whereas the term 'juveniles' was used for colonies ranging between 5 and 15 cm

(Cardini et al., 2012). Both recruits and juveniles were divided into three categories: *Acropora*, *Pocillopora*, others (Bianchi et al., 2003, 2006).

A twenty-three year trend (1997-2019) of yearly maximum and mean sea surface temperature (SST) in the Maldives were plotted from data obtained from the US National Oceanic and Atmosphere Administration (NOAA) (data can be found at http://coralreefwatch.noaa.gov/vs/gauges/maldives.php), calibrated with discontinuous field data on sea surface temperature collected contemporaneously with the biological data (Fig. 2). Maximum SSTs were compared to the two known regional bleaching thresholds in the study area, corresponding to: i) 30.9°C for severe bleaching events that may cause widespread coral mortality; and ii) 30.5°C for moderate bleaching events that have no wide-scale effects on Maldivian coral reefs (Montefalcone et al., 2018). We identified two major bleaching events, in 1998 and 2016, and three minor moderate ones in 2003, 2007 and 2010 (Fig. 2).

To test the emergency spawning hypothesis we compared the two consecutive years after every bleaching event (Fig. 1). Lack of data for the year 2011 did not allow testing the ESH for the bleaching event of 2010. Significant differences have been evaluated by means of Student t-test for data pairs: 1999-2000, 2004-2005, 2008-2009, and 2017-2018.

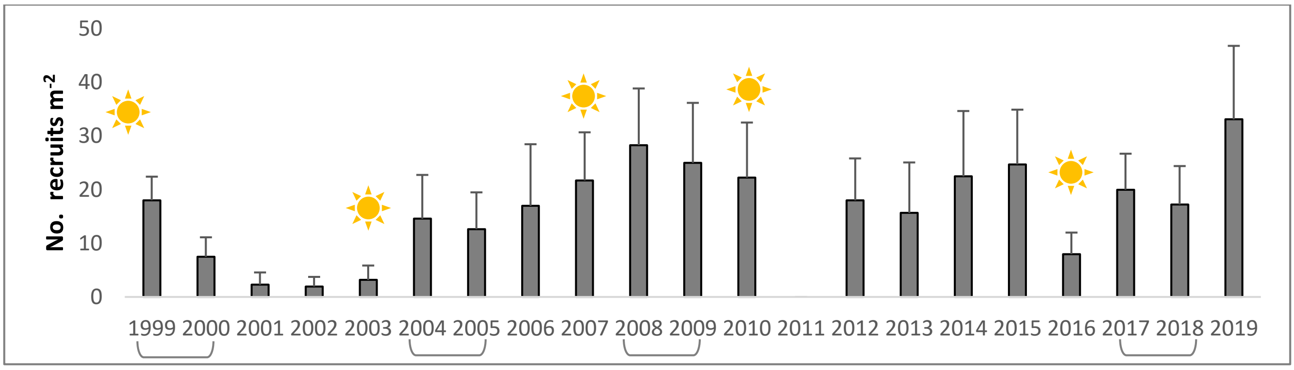


Fig 1. Long-time series of recruits in Maldives. Suns indicate bleaching events. Parentheses refer to the years compared.

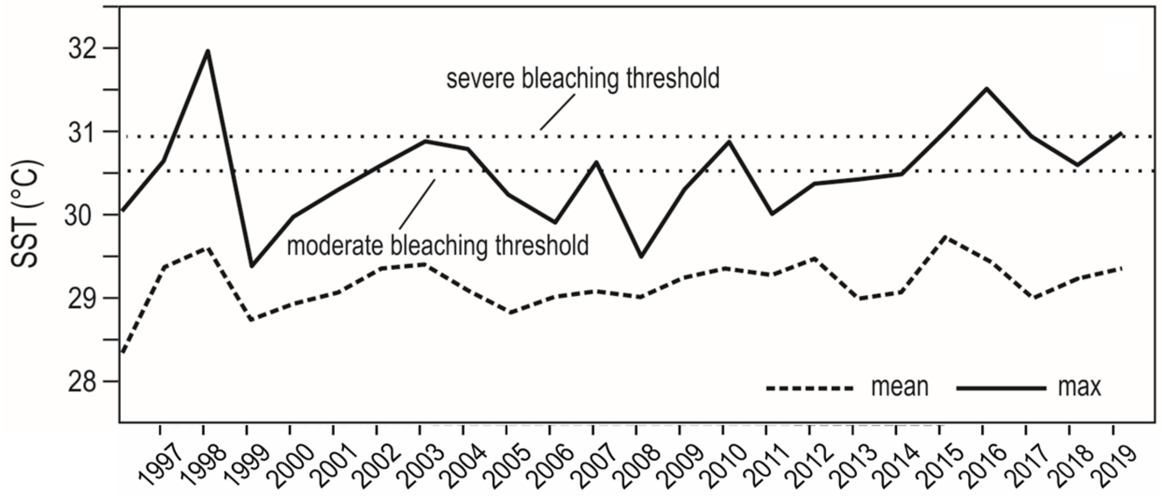


Fig. 2. Twenty-three year trends (1997-2019) of yearly maximum (continuous line) and mean (dotted line) sea surface temperature (SST) in the Maldives. The regional threshold temperatures triggering moderate and severe bleaching events are also reported (according to Montefalcone *et al.*, 2018).

Results

The general trend in coral recruitment following the severe coral bleaching of 1998 always showed a greater number of recruits one year after the event, confirming the emergency spawning hypothesis. Significant differences were evident also after the moderate bleaching events of 2003, only in lagoon sites, and 2007 only in ocean sites at 10 m depth.

Table 1. Total number of coral recruits one year and two years after the bleaching events. The student t–test highlights significant differences between the two years.

Total_Lagoon _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	14 ± 0.84	11 ± 0.39	**
Major - 2016	16 ± 2.31	17 ± 1.90	-
Moderate - 2003	21 ± 1.39	10 ± 1.34	**
Moderate - 2007	33 ± 3.12	28 ± 3.46	-

Total_Lagoon _ 10 m depth			
Bleaching event	1° year after	2° year after	t test *p < 0.05 **p < 0.01

	(mean ± s.e.)	(mean ± s.e.)	
Major - 1998	18 ± 0.82	7 ± 0.63	**
Major - 2016	18 ± 1.81	15 ± 1.28	-
Moderate - 2003	15 ± 1.68	9 ± 1.66	*
Moderate - 2007	27 ± 2.91	22 ± 3.34	-

Total_Ocean _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	23 ± 1.01	4 ± 0.45	**
Major - 2016	25 ± 1.93	19 ± 2.73	-
Moderate - 2003	19 ± 1.26	18 ± 2.16	-
Moderate - 2007	23 ± 1.69	29 ± 4.35	-

Total_Ocean _ 10 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	20 ± 1.34	13 ± 0.30	**
Major - 2016	23 ± 1.79	21 ± 2.37	-
Moderate - 2003	17 ± 1.39	15 ± 1.41	-
Moderate - 2007	35 ± 2.04	27 ± 3.20	*

Contrarily, for the genera *Acropora* most of the significant differences indicate a greater number of recruits the second year after the bleaching events.

Table 2. Number of *Acropora* recruits one year and two years after the bleaching events. The student t–test highlights significant differences between the two years.

***Acropora*_Lagoon _ 5 m depth**			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	0 ± 0.16	5 ± 0.30	**
Major - 2016	4 ± 0.64	3 ± 0.57	-
Moderate - 2003	3 ± 0.52	2 ± 0.56	-
Moderate - 2007	13 ± 1.73	21 ± 2.58	*

***Acropora*_Lagoon _ 10 m depth**			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	18 ± 0.82	7 ± 0.63	**
Major - 2016	18 ± 1.81	15 ± 1.28	-
Moderate - 2003	15 ± 1.68	9 ± 1.66	*
Moderate - 2007	27 ± 2.91	22 ± 3.34	-

***Acropora*_Ocean _ 5 m depth**			
Bleaching event	1° year after	2° year after	t test *p < 0.05 **p < 0.01

	(mean ± s.e.)	(mean ± s.e.)	
Major - 1998	2 ± 0.22	2 ± 0.20	-
Major - 2016	4 ± 1.21	2 ± 0.49	-
Moderate - 2003	4 ± 0.58	3 ± 0.64	*
Moderate - 2007	3 ± 0.59	15 ± 2.52	**

*Acropora*_Ocean _ 10 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	1 ± 0.19	4 ± 0.20	**
Major - 2016	3 ± 0.72	4 ± 0.92	-
Moderate - 2003	4 ± 0.48	3 ± 0.58	-
Moderate - 2007	4 ± 0.91	14 ± 1.40	**

The almost total lack of *Pocillopora* recruits after the bleaching event of 1998 do not allow making comparison between the following years. Significant differences occurred after 2003 and 2007 although no clear trends were evidenced.

Table 3. Number of *Pocillopora* recruits one year and two years after the bleaching events. The student t–test highlights significant differences between the two years.

*Pocillopora*_Lagoon _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	0 ± 0	0 ± 0.09	-
Major - 2016	2 ± 0.69	2 ± 0.52	-
Moderate - 2003	1 ± 0.37	0 ± 0.16	*
Moderate - 2007	2 ± 0.62	1 ± 0.26	*

*Pocillopora*_Lagoon _ 10 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	0 ± 0	0 ± 0	-
Major - 2016	2 ± 0.77	1 ± 0.34	-
Moderate - 2003	1 ± 0.20	1 ± 0.30	-
Moderate - 2007	2 ± 0.37	0 ± 0.27	*

*Pocillopora*_Ocean _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	1 ± 0.20	1 ± 0.24	-
Major - 2016	3 ± 1.39	2 ± 0.57	-
Moderate - 2003	1 ± 0.16	5 ± 0.66	**
Moderate - 2007	4 ± 0.79	7 ± 1.31	-

*Pocillopora*_Ocean _ 10 m depth

Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	0 ± 0	0 ± 0	-
Major - 2016	3 ± 0.83	2 ± 0.35	-
Moderate - 2003	1 ± 0.29	2 ± 0.67	-
Moderate - 2007	7 ± 0.71	5 ± 0.75	*

Others are the most representative category of the coral community. All the significant differences confirmed the Emergency spawning hypothesis.
We noticed that no significant differences were ever recorded following the major bleaching event of 2016.

Table 4. Number of Others recruits one year and two years after the bleaching events. The student t–test highlights significant differences between the two years.

Others_Lagoon _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	14 ± 0.83	6 ± 0.27	**
Major - 2016	10 ± 1.45	13 ± 1.44	-
Moderate - 2003	17 ± 1.35	8 ± 1.20	**
Moderate - 2007	18 ± 2.32	7 ± 1.34	**
Others_Lagoon _ 10 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	17 ± 0.82	5 ± 0.50	**
Major - 2016	12 ± 1.05	12 ± 0.96	-
Moderate - 2003	12 ± 1.55	5 ± 0.75	**
Moderate - 2007	15 ± 1.66	6 ± 1.08	**
Others_Ocean _ 5 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	21 ± 1.02	1 ± 0.24	**
Major - 2016	18 ± 1.95	16 ± 2.10	-
Moderate - 2003	14 ± 1.06	11 ± 1.65	-
Moderate - 2007	15 ± 1.27	8 ± 1.72	**
Others_Ocean _ 10 m depth			
Bleaching event	1° year after (mean ± s.e.)	2° year after (mean ± s.e.)	t test *p < 0.05 **p < 0.01
Major - 1998	19 ± 1.40	9 ± 0.37	**
Major - 2016	17 ± 1.48	15 ± 1.73	-
Moderate - 2003	12 ± 0.96	10 ± 1.26	-

Moderate - 2007	24 ± 2.08	8 ± 1.71	**

Conclusions

The validation of the emergency spawning hypothesis after the coral bleaching of 1998, confirmed the latter as one of the strongest bleaching event on record for the Maldivian coral reefs (Bianchi et al. 2003). In the same way, the lack of significant differences in recruits number between the two years following the 2016 coral bleaching is in accordance with the higher survival rates and the faster initial recovery recorded after the event (Montefalcone et al. 2018). Although 2016 has often been compared with 1998 event for the intensity, the following coral recovery occurred according to different trajectories than in the past (Montefalcone et al. 2018).

Acropora may have suffered the high temperatures effect on fecundation processes (Hoegh-Guldberg et al 1999) then corals that were able to survive to the bleaching event exhibited reduced recruitment, growth and calcification capacity (Goreau and Macfarlane 1990, Glynn 1993, Meersters and Bak 1993) provoking a greater number of *Acropora* recruits only two years after the bleaching.

Since *Pocillopora* are typically brooders, their abundance is strictly linked to the adults' persistence. The high mortality rates in adult colonies due to the thermal stress resulted proportional to the event intensity as it showed from the lack of recruits after 1998.

Others that followed a trend in accordance with the Loch's hypothesis dominated the coral community. The emergency spawning hypothesis was true even for the moderate bleaching event of 2007 and partly for the 2003 (only in lagoon sites).

Our results suggested that the emergency spawning did not depend on the intensity of the bleaching event but rather on the corals genera. Branching corals as *Acropora* and *Pocillopora* are more sensitive to thermal anomalies and apparently, they are not able to induce the ESH. Conversely, massive corals being the most representative corals of others might be able to implement this strategy having a better resistance and a higher survival rate to heat stress.

Frequency and severity of coral bleaching events is increasing (Heron *et al.*, 2017), and the long period needed for Maldivian coral reefs to recover from the severe bleaching event of 1998 (about 16 years) and the predicted frequency of two severe bleaching events per decade (Hughes *et al.*, 2018) would prevent future recovery of Maldivian reefs.

However, the recovery from the 2016 event is proceeding at a faster pace thanks to higher cover of survivors, and it is therefore foreseeable that a complete recovery will take place in a shorter time (within the next 4-5 years), thus giving greater hopes to Maldivian coral reefs. Continuing our long-term series of data will remain the most effective tool to validate these predictions and evaluate temporal patterns.

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Chapter 6 Hydrothermal Vents

6.1

Water circulation, and not ocean acidification, affects coral recruitment and survival at shallow hydrothermal vents

Additional resources:

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Abstract

Shallow hydrothermal vents emit warm water, carbon dioxide, toxic chemicals, nutrients and reduced compounds that altogether mimic climate and human impacts, and are therefore considered as ‘natural laboratories’ where to investigate the effects of these stressors on marine ecosystems. One of the effects more thoroughly investigated is the impact of reduced pH on marine biodiversity. Calcifying organisms, such as corals, are expected to be more affected, but their response to reduced pH values in seawater has been tackled mostly by laboratory studies. Here, we assessed coral recruitment and juveniles’ survival, two fundamental processes for coral reef maintenance and resilience, in shallow reefs of North Sulawesi (Indonesia) close to hydrothermal vents. Differences in abundance of coral recruits (< 5 cm in diameter) and juveniles (5 to 15 cm in diameter) were evaluated at vent sites and at control sites, on both reef flats and upper slopes. Recruits of *Acropora* and other broadcasting corals resulted more abundant near vents, while no difference in juveniles’ survival was observed between vent sites and controls. On the contrary, *Pocillopora*, which includes many brooders, showed low density of recruits and low survival rates at vent sites. Vents caused a typical closed water circulation that retained coral larvae on site, and this effect, rather than water acidification or emission of chemical compounds, was likely the responsible of increased recruitment of broadcasters.

1. Introduction

Volcanic systems giving rise to submarine hydrothermalism are widespread in the world ocean, in both deep and shallow water (Dando, 2010; Beaulieu, 2013). While deep-sea hydrothermal vents give rise to a distinct ecosystem fuelled by chemiolithosynthesis (Van Dover, 2000), those on the continental shelf induce change in ecosystems that are otherwise ‘normal’ (Cocito et al., 2000). Shallow-water hydrothermal vents emit warm water, carbon dioxide, toxic chemicals, nutrients and reduced compounds that altogether mimic climate and human impacts on shelf ecosystems (Bianchi et al., 2011), making them potential models for global change (Bianchi et al., 2012; Dahms et al., 2018).

Many field studies, for instance, used shallow-water vents and seeps emitting high quantity of CO_2 to investigate the effects of ocean acidification on the marine ecosystem (Hall-Spencer et al., 2008). Such studies are increasingly gaining value compared to laboratory experiments, as they take into account different environmental processes that cannot be simulated *ex situ* (Fabricius et al., 2011, 2017). Experimental studies indicate that calcifying organisms, such as corals, molluscs, sea urchins and coralline algae would be the most affected (Gazeau et al., 2007; Rodolfo-Metalpa et al., 2011; Jokiel et al., 2016; Barner et al., 2018), whilst non calcifying organisms would thrive little or no affected (Porzio et al., 2011; Suggett et al., 2012; Goodwin et al., 2014).

The effects of ocean acidification on hard corals, in particular, have been thoroughly investigated (Anthony et al., 2008; Ries et al., 2010; McCulloch et al., 2012). Individual assessments of ecological responses (calcification) to CO_2 levels are often contradicting (Kornder et al., 2018). In acidified sea water close to volcanic vent systems in Japan, hard corals were shown to be replaced by soft corals (Inoue et al., 2013). In volcanic seeps of Papua New Guinea, coral diversity was reduced in the vicinity of CO_2 emissions (Fabricius et al., 2011). However, corals have been shown to be able to regulate their internal chemistry in order to control their calcification and resist ocean acidification (Comeau et al., 2018). The symbiosis with zooxanthellae can help corals tolerate sea water warming and acidification (Rodolfo-Metalpa et al., 2011; Prada et al., 2017). In the central-west Gulf of California, the coral population of *Porites panamensis* living under the influence of a vent system tolerated extreme conditions thanks to high genetic plasticity of both the coral and its symbiotic zooxantelle (Oporto-Guerrero et al., 2018).

Compared to those describing adult corals response to high pCO_2, there are few studies investigating the effects of acidified seawater on the early life stage of corals (Cohen et al. 2009; Foster et al. 2015, 2016; Fabricius et al., 2017). Successful coral recruitment and high rates of juveniles' survival are widely recognized as fundamental processes to ensure coral reef maintenance and resilience (Adjeroud et al. 2017) and early post-settlement mortality of juvenile corals can thus influence future population structure (Penin et al. 2010).

In this paper we explored in the field coral recruitment patterns and juveniles' survival rates on natural substrata in shallow reefs of North Sulawesi (Indonesia), in the vicinity of hydrothermal vents and in control sites at two different distances ('near' and 'far') from vents.

2. Materials and methods

2.1 Study area

The study area is located in the equatorial Pacific Ocean, on the extreme tip of North Sulawesi and along the coast of Bangka Island (Indonesia), in the Minahasa province (Whitten & Henderson 2012). This area lies in the middle of the "Coral Triangle" (Fig. 1), which hosts 76% of all known coral species in the world (Hoegh-Guldberg 2009) and is considered the epicentre of marine biodiversity (Allen 2008; Whitten & Henderson 2012). In this area, ocean circulation is mainly driven by monsoon and tidal currents, with tidal amplitudes exceeding 2 m (Tomascik et al. 1997).

The North Sulawesi Peninsula is also characterized by the presence of a wide active volcanic system with many hydrothermal vents, responsible for gas emissions from the sea bottom in several coastal zones. The chemistry of vent fluids in the region has never been studied in detail, but some data can be found in a few biological papers (Manini et al. 2008; Zeppilli and Danovaro 2009; Januar et al., 2016). Close to the emissions, pH remain constantly around 7.8, with a pCO_2 of 500-700 µatm. Sulfide levels are normally below 2 ppm. Dissolved oxygen is about 7 mg L^{-1}, dissolved inorganic nitrogen is between 0.03 and 0.07 mg L^{-1}, whereas phosphate is always <0.4 mg L^{-1}. Gas flux intensity at vents is 809 L min^{-1} m^{-2}. In close vicinity of the vents, salinity is slightly reduced (33 psu), while water temperature passes from >90 °C at emission to 32-40 °C at 2 m from the vent. More recent investigation evidenced that vents fluids are also enriched in silica, up to 8.5 mg L^{-1} compared to <1 mg L^{-1} in normal sea water (Bertolino et al., 2017).

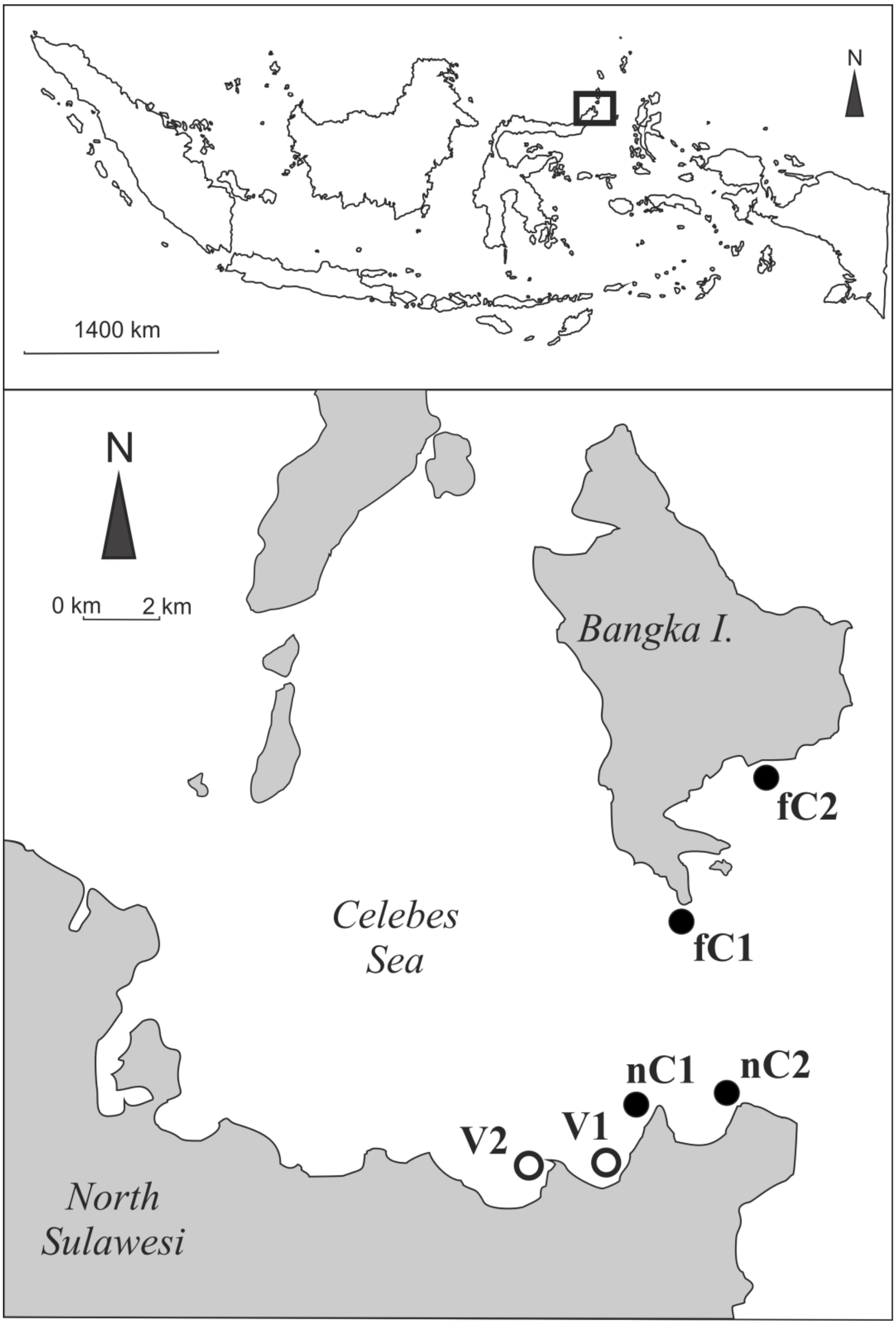

Figure 1. Sites location within the study area. Open dots represent the sites with hydrothermal vents: Yellow Coco (V1) and Paradise (V2); near control sites (nC) and far control sites (fC) are indicated by solid dots.

Reefs in this area are characterized by very high species richness (Tomascik et al., 1997). Our observations during field work showed that in the reef flat species diversity reached its peak and the coral community was dominated by large massive corals of the genera *Favites* and *Porites*; sheet corals and branching corals such as *Agaricia* spp. and *Acropora* spp., respectively, were common, whilst *Pocillopora* corals contributed little to total coral cover. Massive sponges, ascidians and algae also represented a considerable component of the reef community (Fig. 2).

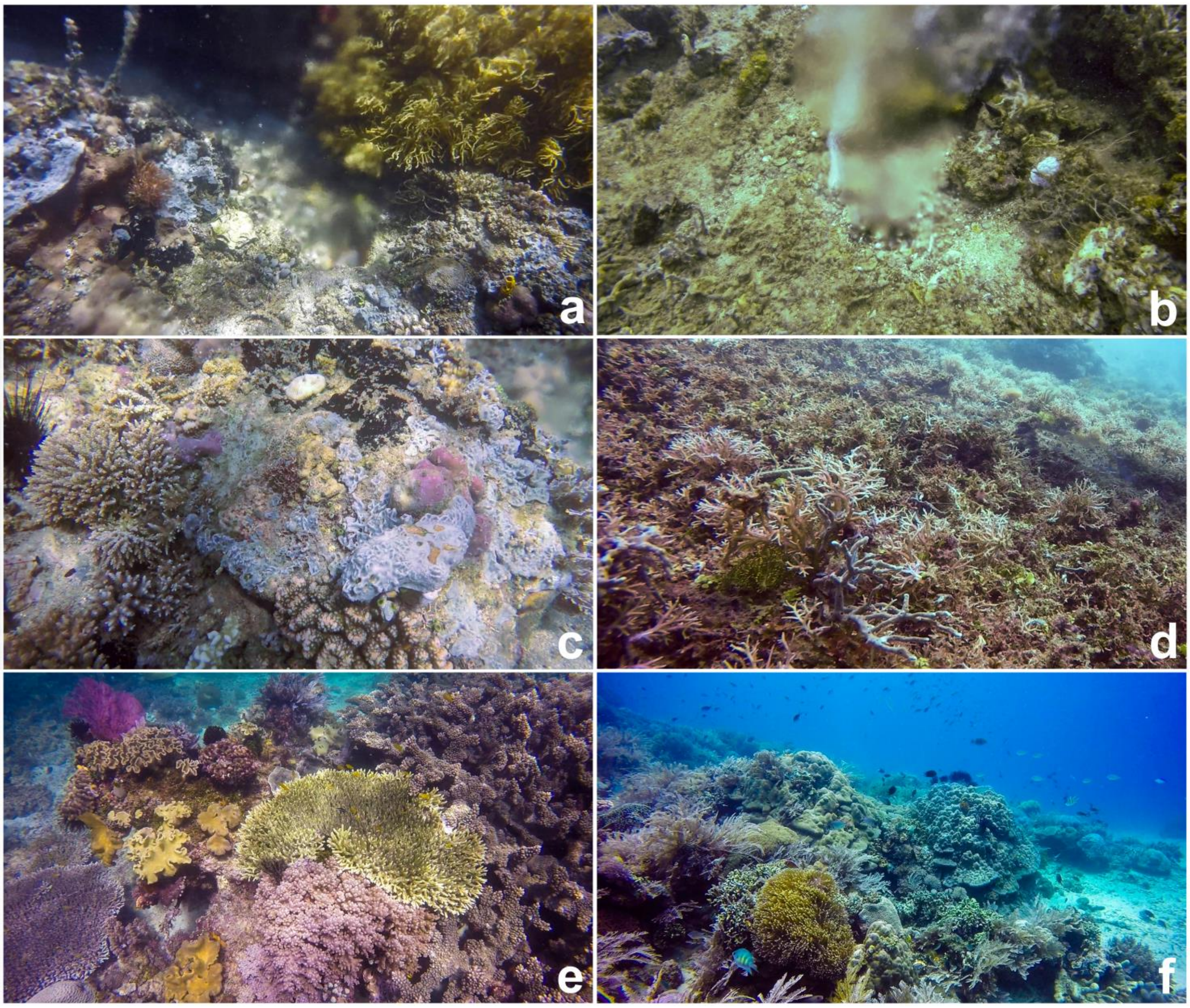

Figure 2. Some of the investigated coral reefs on the flat (left column) and on the upper slope (right column). (a) Paradise hydrothermal vent. (b) Yellow Coco hydrothermal vent. (c) Coral assemblages in proximity to the Paradise outflow. (d) Reef slope characterized by corals of the genus *Seriatopora* in close vicinity to Yellow Coco vent. (e) *Acropora* corals on the flat of a control site. (f) Massive corals on the reef slope of a control site.

2.2 Field activities

Our study concentrated on two hydrothermal sites: Yellow Coco (1°40.361' N, 125°8.112' E) and Paradise (1°40.457' N; 125°7.088' E). Vents were found on the reef flat at about 3 m depth and on the sandy bottom at the base of the reef slope at about 20 m depth. Data were collected in September and October 2015 in a total of six stations: the two vent sites of Yellow Coco (V1) and Paradise (V2), two near (< 5 km) control sites (nC1, nC2) located on the same coast of North Sulawesi but far enough to avoid the influence of vent fluids (pH = 8.2), and two far (> 7 km) control sites (fC1, fC2) on the facing island of Bangka (Fig. 1). At each site, surveys were carried out by SCUBA diving in two reef zones, the flat (3-5 m depth) and the slope (15 m depth). At vents sites, data were collected within 5-15 m from the actual venting.

For the purposes of this study, only colonies of scleractinian corals with a diameter smaller than 15 cm have been considered. Following Bianchi et al. (2006a, b), colonies still sexually immature with approximately circular outlines (larval settlement sign) and not exceeding the diameter of 5 cm were classified as recruits; colonies having a diameter ranging between 5 cm and 15 cm, potentially ready for sexual reproduction, were classified as juveniles. This terminology and these measures contrast with other studies that call recruits corals smaller than 2 mm in diameter (e.g., Salinas-de-Leon et al., 2013) or experiments with settlement tiles, where the term recruit is often applied to coral spat (e.g., Montoya-Maya et al., 2016).

Abundance of recruits and juveniles was counted within 12 quadrats covering a surface of 0.25 m^2, randomly placed on the reef at the two sampling depths in all sites, and following the method described by Cardini et al. (2012). Abundance data from 4 quadrats were randomly summed up to obtain densities per 1 m^2, with three replicates for each depth. Corals were distinguished in three categories: *Acropora*, *Pocillopora*, and Others.

2.3 Data analyses

Since the reef flat and the reef slope are different environments in terms of reef morphology, hydrodynamics and topography (Done 1982), the two hydrothermal vents investigated may have affected differently the coral community according to their position along the reef profile. Therefore, we decided to analyse separately coral recruitment and juveniles' survival at the two different sampling depths.

The complement to unity of the formula for the size-structure index (SsI%) of Cardini et al. (2012) has been used as a proxy for the survival of coral recruits:

$$1 - \text{SsI}\,\% = \left(1 - \frac{R}{R+J}\right) \cdot 100$$

where R is the density of recruits and J that of juveniles.

The whole "young" coral communities (recruits plus juveniles) in the reef flat and in the reef slope, were analysed with two nMDS based on Bray-Curtis coefficient on untransformed data.

2-way analyses of variance were performed to test differences in coral recruits' abundance and in recruits' survival. The analysis consisted of 2 factors: treatment with 3 levels (vent, near control, far control), and site with 2 levels, random and nested within treatment. Homogeneity of variance was tested by Cochran's C-test. Where significant p values occurred, the Student-Newman-Keuls test (SNK) was applied to detect significant differences.

3. Results

A total of 290 recruits and 428 juveniles of corals were counted during this study, with a mean density of $8.1 \pm 0.9 \cdot \text{m}^{-2}$ and $11.9 \pm 1.0 \cdot \text{m}^{-2}$, respectively. Others were always the dominant category, being six- to tenfold more abundant than *Acropora* and *Pocillopora.*

Whilst *Pocillopora* did not show any particular spatial pattern according to treatment (i.e., vent, near control, far control), density of *Acropora* recruits increased significantly moving toward the vent sites only on flat ($p < 0.01$). In the case of Others, density of recruits increased approaching the vent sites on both flat ($p < 0.05$) and slope ($p < 0.01$) (Table 1, Fig. 3 and Fig. 4).

Table 1. Results of significant 2-way ANOVAs on coral recruits' abundance and on recruits' survival (expressed as 1-SsI%). * = $p < 0.05$, ** = $p < 0.01$

		recruits ***Acropora*** **(flat)**		**recruits** **Others** **(flat)**		**recruits** **Others** **(slope)**		**1- SsI%** ***Pocillopora*** **(slope)**	
	df	MS	*p*	MS	*p*	MS	*p*	MS	*p*
Treatment	2	0.6667	0.0000	83.1667	0.0171	203.7222	0.0035	5088.7089	0.0460
Site	3	0.0000	1.0000	14.2778	0.6193	21.6667	0.0413	499.4311	0.3691
Residual	12	0.7222		23.2778		5.7778		434.6383	
Total	17								
Cochran's *C*-test		n.s. (C = 0.3077)		n.s. (C = 0.5752)		n.s. (C = 0.5481)		n.s. (C = 0.5278)	
Transformation		none		none		none		none	
SNK test		Vent > far Control **		Vent > far Control *		Vent > far Control ** Vent > near Control **		near Control > Vent * near Control > far Control *	

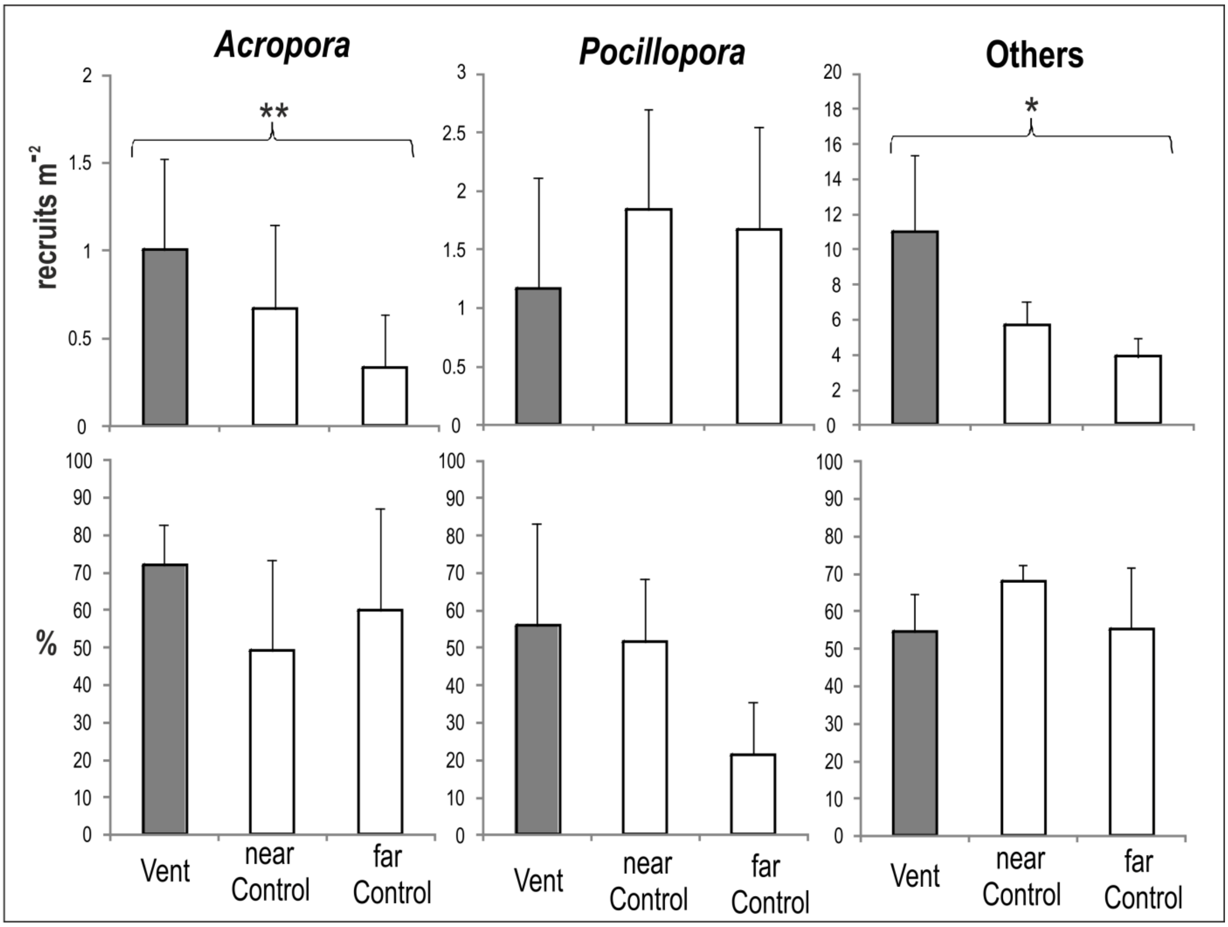

Figure 3. Average values (± se) of recruit density and recruit survival (expressed as 1-SsI%), on reef flat. Note that scales on Y axis are different.

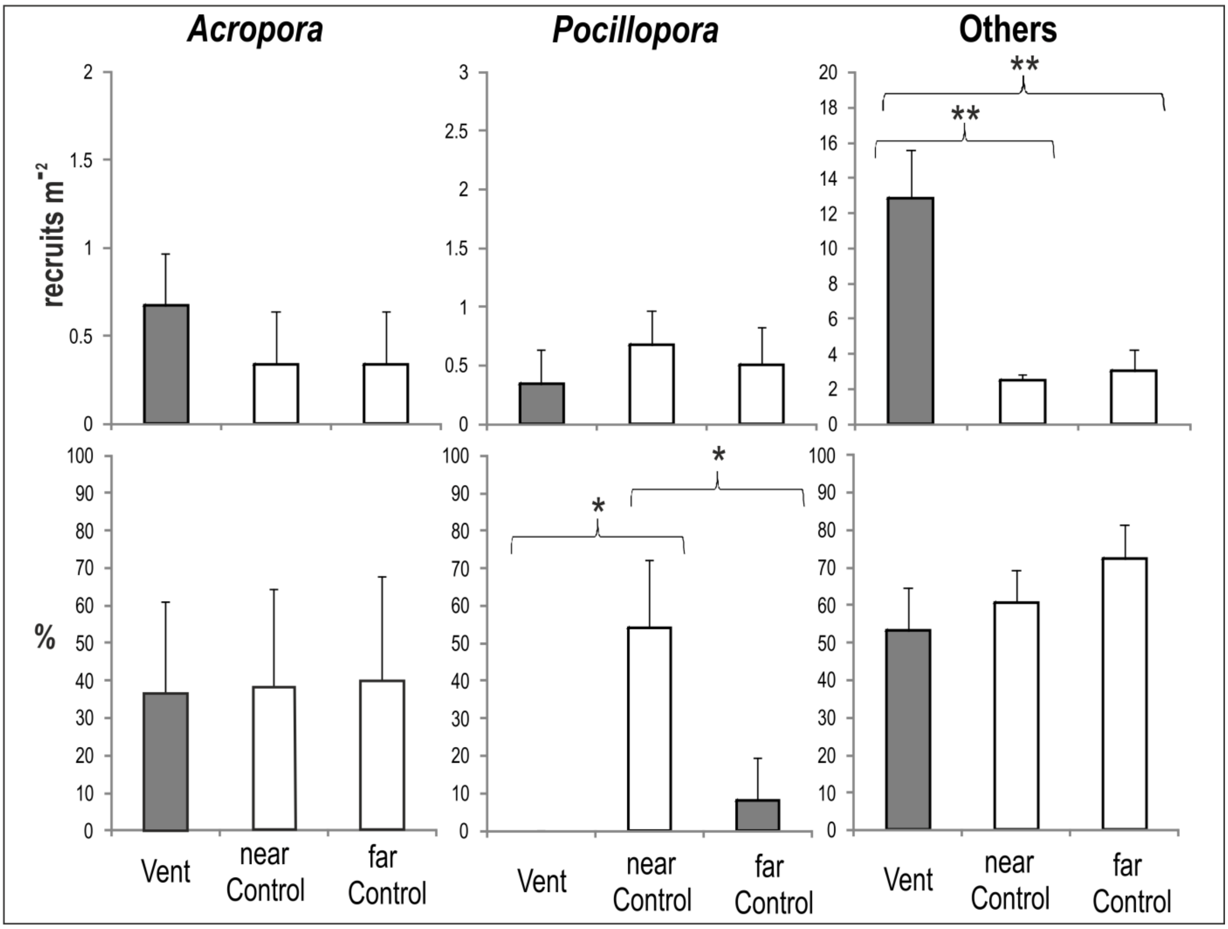

Figure 4. Average values (± se) of recruit density and recruit survival (expressed as 1-SsI%), on reef slope. Note that scales on Y axis are different.

On the reef slope the young coral community (recruits plus juveniles) showed a spatial segregation among site typologies (Fig. 5) and the vent sites resulted closer to the far control sites than to the near control sites. On reef flat, no evident spatial patterns were recognisable (Fig. 5).

Survival of coral recruits did not show any significant difference among site typologies on flat (Fig. 3). More than 50% of recruits survived, with *Acropora* and *Pocillopora* corals showing the highest rates of survival in the vent sites. On reef slope, *Acropora* never exceeded survival rates of 30-40% in all the sites, whilst Others showed higher survival rates (between 50% and 70%), especially in the far control sites (Fig. 4). *Pocillopora* showed a large variability of recruits survival among treatments, near control sites showing higher survival rates than far control and vent sites (p < 0.05, Table 1), the latter sites showing no survival of *Pocillopora* recruits at all.

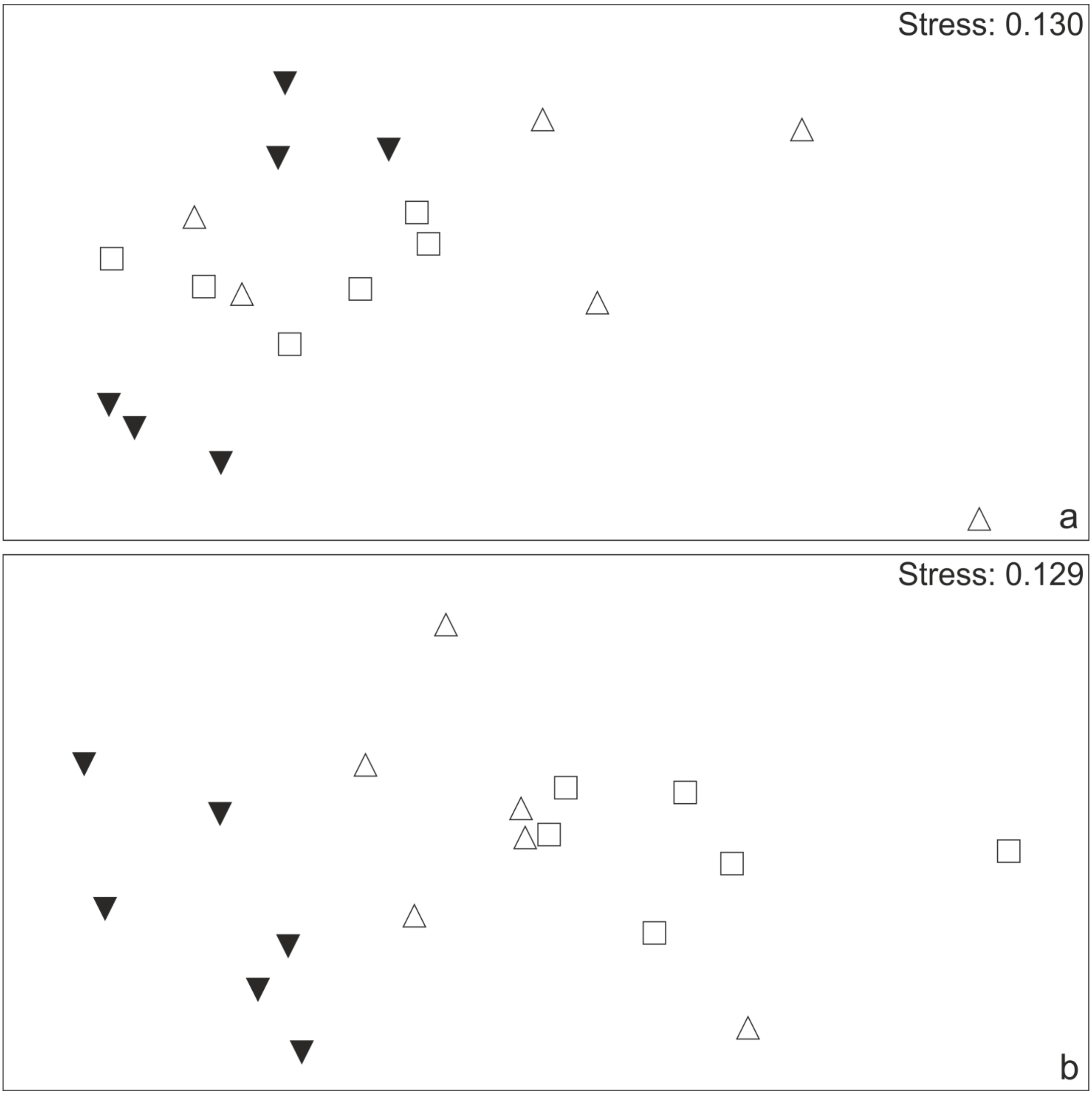

Figure 5. nMDS of young coral community on reef flat (a) and on reef slope (b). Solid triangles represent the vent sites, open squares the near control sites, and open triangles the far control sites.

4. Discussion

Results of this study revealed that coral recruitment and juveniles' survival were little affected by vent activity. Contrarily to what could be expected, proximity to the vents was not likely to compromise recruits' abundance; rather, it was indeed enhanced in vent sites compared to control sites. Greater abundance and diversity of other sessile epibenthic species living close to shallow hydrothermal vents has already been reported (Bianchi et al., 2011; Bertolino et al. 2017).

Increased recruitment in the vent sites was observed for all coral genera, except for *Pocillopora*. *Pocillopora* did not show any spatial pattern according to treatment (i.e., vent, near control, far control), and this result is likely to be due to the many brooding species included in this genus. Since their larvae are not dispersed far away from the natal colony, recruits number is strictly dependent on the abundances of adult colonies. Our observations are in line with previous studies (Ferrigno et al. 2016) and showed that adult *Pocillopora* corals were poorly represented on all the investigated reefs and their density was higher on the flat than on the slope. The null survival rates of *Pocillopora* found on the slope at the vent sites and the low values (<10%) found at the far control sites were thus likely to be due to the low number of adult colonies. In the high diversity reefs of North Sulawesi (Hoegh-Guldberg 2009), competition may be among the main causes of a general low recruitment, since space occupancy is high and brooding corals such as many *Pocillopora* species show double mortality rates than broadcast spawners (e.g. *Acropora*) at their earliest life stages (Doropoulos et al. 2015).

Although *Acropora* is among the main bioconstructors in North Sulawesi coral reefs (Ferrigno et al. 2016), their recruits were not abundant at all depths. Differences between adults and recruits densities already emerged in several studies on recruitment pattern (Harriott and Banks 1995; Hughes et al. 1999; Edmunds 2000; Adjeroud et al. 2007). Thanks to broadcast spawning corals, such as *Acropora*, locations that usually have small numbers of recruits may occasionally receive a much larger input. *Acropora* includes competitive corals displaying high aptitudes to fill all available space and low mortality, as the high survival rates demonstrated.

The young coral community in the investigated sites was mostly represented by the category Others, consistently with what has already been observed in South Sulawesi (Salinas-de-Leon et al. 2013). The most abundant taxa were represented by massive corals like *Porites* and *Favites*, for which the high number of recruits led to high abundance of juveniles and adults. Thanks to their life strategy (i.e. large colonies, slow growth rates), they usually show high survival rates (Penin et al. 2010; Kayal et al. 2015), as evidenced by the high survival (>50%) that we have encountered in all the sites. Due to their dominance on reefs, Others explained better than *Acropora* and *Pocillopora* the spatial pattern linked to hydrothermal vents. On both reef flat and upper slope, Others showed significant differences between vent sites and control sites, with more recruits being recorded on the slope.

A positive relationship between the abundance of recruits and adult colonies could also occur for broadcast spawning species in a closed system, where the pelagic larvae would be held close to the reef where they were born. Water circulation at hydrothermal vents could be explained according to McGinnis et al. (2004), who evaluated a steady state, horizontally averaged, bubble-plume model. A near-field torus of reduced stratification develops around the plume, so that the directly detrained water and fallback water are accumulated within tens of meters from the bubble plume. This leads to considerable short-circuiting of the return flow, limiting lateral transport and horizontal diffusion. We thus hypothesize that the “vent effect” was reflected into a closed water circulation, which increased recruitment by retaining coral larvae. This happened mostly at the reef slope, where such a closed circulation was less disturbed by local hydrodynamics. On the flat, on the contrary, water circulation was greatly influenced by wind-waves, tides and surface currents that made this portion of the reef open to exchanges from and to other portions of the reefs.

These dynamics could explain for the different abundances found in *Acropora* and Others recruits in vent sites at the two investigated depths (flat and slope). The former, a broadcast-spawner, was more abundant in the flat, where the vent effect was lower but little recruits from outside could enter; in the slope, the few *Acropora* larvae might be retained but no recruits from outside could enter because of the strong vent effect. The Others, mainly characterized by massive and broadcast-spawning corals, were naturally abundant in the slope. Even with little or no larval input from outside, they were able to maintain high coral densities by holding back their own recruits. In the flat, the larval input offset the output and the density remained high.

5. Conclusion

Our data do not allow any speculations about the possible effects of vent fluid chemistry on coral recruitment. While many studies indicate that coral communities are affected by water acidification near vents (Fabricius et al., 2011; Inoue et al., 2013; Oporto-Guerrero et al., 2018; among others), little literature information is available to date to discuss the putative influence of lowered pH at vents on coral recruitment and/or juvenile’ survival. The pH value (7.8) characterising the vent sites we investigated is known to be tolerated by corals (Fabricius et al,. 2011; Rodolfo-Metalpa et al., 2011; Januar et al., 2017), so that it may be sensible to assume that it is similarly ineffective on coral recruitment and survival, as our study might suggest. Under similarly ‘moderate’ conditions of acidification, Januar et al. (2016) affirmed that phosphate and dissolved inorganic nitrogen were more important than lowered pH value. However, our study showed different response of different coral taxa to venting, and we see no reason why the release of nutrients would benefit *Acropora* and not other corals. High content of silica in vent fluid have been said to favour sponges (Bertolino et al., 2017), which might outcompete massive corals but not the branching *Acropora* species. Silica is detrimental to the settlement of many hard substrate species (Bavestrello et al., 2000), which may indirectly favour coral spat survival (Tebben et al., 2014). In the lagoon of New Caledonia, where no venting exists, Adjeroud et al. (2010) found that water quality (including inorganic nitrogen, phosphate, and silica concentrations), had little effect on coral recruitment. At volcanic seeps in Papua New Guinea, Fabricius et al. (2017) observed that altered substrata rather than acidification was the primary responsible for low coral recruitment.

Unexpectedly, our study indicated that vent activity apparently promote coral recruitment, at least in some taxa. We hypothesize that in environments like the ones we studied, where pH values still do not compromise coral growth, an important role is played by the vent plume. Hydrothermal vent alters natural water circulation, in a way that may favour coral recruitment (Bianchi et al., 2011). In particular, broadcast-spawning corals (such as *Acropora* and most of the Others) seem to take some advantage.

Future research willing to use hydrothermal vents as natural laboratories where to study the effects of ocean acidification on coral reefs (Kleypas et al., 2006) should take in full account and clearly define all these alternative and related processes.

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6.2

Hydrothermal waters enriched in silica promote the development of a sponge community in North Sulawesi (Indonesia)

Additional resources:
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Abstract

Two shallow hydrothermal vents were investigated by SCUBA diving to evaluate their influence on the structure and diversity of a sponge community living close to the vent outflow, in the equatorial Pacific Ocean just off the coast of North Sulawesi, Indonesia (1°40.361′N, 125°8.112′E). No sponges identified were vent-obligate species, since they are found in the surrounding coral reefs too. The sponges were strongly attracted by the vent, concentrating in an area of a few meters around it, where they reached covering values up to 70% in the deeper vent and up to 42% in the shallower one. The high silica concentration, 8.5 mg L−1Si (deep vent) and 5 mg L−1Si (shallow vent), in hot spring water (90°C) was the putative environmental factor driving the sponge settlement and growth. These organisms take advantage of the increased silica availability that, facilitating skeleton formation, probably promotes sponge growth. This hypothesis is in agreement with the evidence that the spicules of the sponge specimens living around the hot springs have a thickness about double that of conspecific specimens present on the coral reefs at least 300 m away.

Introduction

Hydrothermal vents are peculiar habitats that offer a unique opportunity to investigate the effects of extreme environmental conditions on biodiversity (Amils et al. 2007). Despite the convenience of studying shallow-water structures, due to their easier accessibility, deep hydrothermal vents have always received more interest from the scientific community because they host peculiar, sometimes endemic faunas characterized by unusual physiological adaptations (Tarasov et al. 2005). Several studies have shown that shallow vents are, in general, colonized by communities that are subsets of the surrounding biota, where no vent-obligate species are recognized (Fricke et al. 1989; Pansini et al. 2000; Cardigos et al. 2005). However, there is evidence that biodiversity is proportionally higher at the sites closest to the hydrothermal vents and that vent proximity is more important than depth and distance from the shore (Morri et al. 1999; Pansini et al. 2000; Bianchi et al. 2011). These evidences are in contrast with the opinion that the total number of macrobenthic species reduces close to the vents (Fricke et al. 1989; Tarasov & Zhirmunsky 1989; Kamenev et al. 1993; Thiermann et al. 1997). Studies on communities associated with shallowwater hydrothermal vents date back to the beginning of the 20th century (Hinze 1903), but an exhaustive global inventory of these outflows is still lacking and information on these structures is fragmentary when compared with that on deep-sea hydrothermal springs (Tarasov et al. 2005). Shallow-water hydrothermal vents are recurrent in tectonically active areas of the West Pacific (Ferguson & Lambert 1972; Tarasov et al. 1986, 1988, 1990, 1991; Sarano et al. 1989; Sorokin 1991; Tarasov 1991; Hashimoto et al. 1993; Kamenev et al. 1993; Pichler & Dix 1996), the coasts of California (Vidal et al. 1978; Stein 1984), Iceland (Fricke et al. 1989; Olafsson et al. 1991) and the Azores (Cardigos et al. 2005). Even in the Mediterranean Sea, these habitats have been extensively studied (Bavestrello et al. 1995; Dando et al. 1995; Morri et al. 1999; Pansini et al. 2000; Bianchi et al. 2011). The influence on biodiversity of shallow-water hydrothermalism is variable according to the different examined groups (Bianchi et al. 2011). Sponges are among the most important components of these sessile communities (Fricke et al. 1989; Benedetti Cecchi et al. 1998; Tarasov et al. 1999), and a possible attractive effect due to the spring activity is still debated. Some authors have stated that in both the western and eastern Mediterranean, the proximity of hydrothermal vents had no influence on sponge distribution (Laborel 1960; Bavestrello et al. 1995). More detailed studies (Pansini et al. 2000) suggest a warm-water affinity of the sponge fauna associated with the vent sites. Moreover, Geodia cydonium in the vent community of Milos Island (Aegean Sea) might take advantage of increased silica availability around the outflows. In the same area closeness to vents seemed to have negligible effects on sponge cover, despite a primary effect on species diversity (Pansini et al. 2000). The abundant development of demosponges all over Matupi Harbor (Papua New Guinea), an area characterized by diffuse hydrothermalism, results in the accumulation of large amounts of sponge spicules in the sediment (Tarasov et al. 1999). Also in this area, it was suggested that sponge growth might have been stimulated by volcanic emissions eriche in silicon (Tarasov et al. 1999). In the Grotta Azzurra at Capo Palinuro (South Tyrrhenian Sea), the unusual large size of the specimens of G. cydonium living in the cave was related to the occurrence of warm sulfur-rich water springs (Morri et al. 1994) and to the abundant presence of sulfur-oxidizing bacteria associated with these emissions (Southward & Southward 1993; Morri et al. 1994). In this study, we investigate two shallow hydrothermal springs, located on a sandy bottom at 20 and 25 m depth, in the equatorial Pacific Ocean, just off the coast of the extreme tip of North Sulawesi (Indonesia). The aim of this work is to evaluate the influences of vent outflow on the structure and diversity of the sponge-dominated benthic community that thrives in this area.

Materials and methods

The studied hydrothermal vents are located in a popular dive site known as “Yellow coco” (1° 40.361′N, 125°8.112′E), along the coast of North Sulawesi facing Bangka Island (Figure 1).

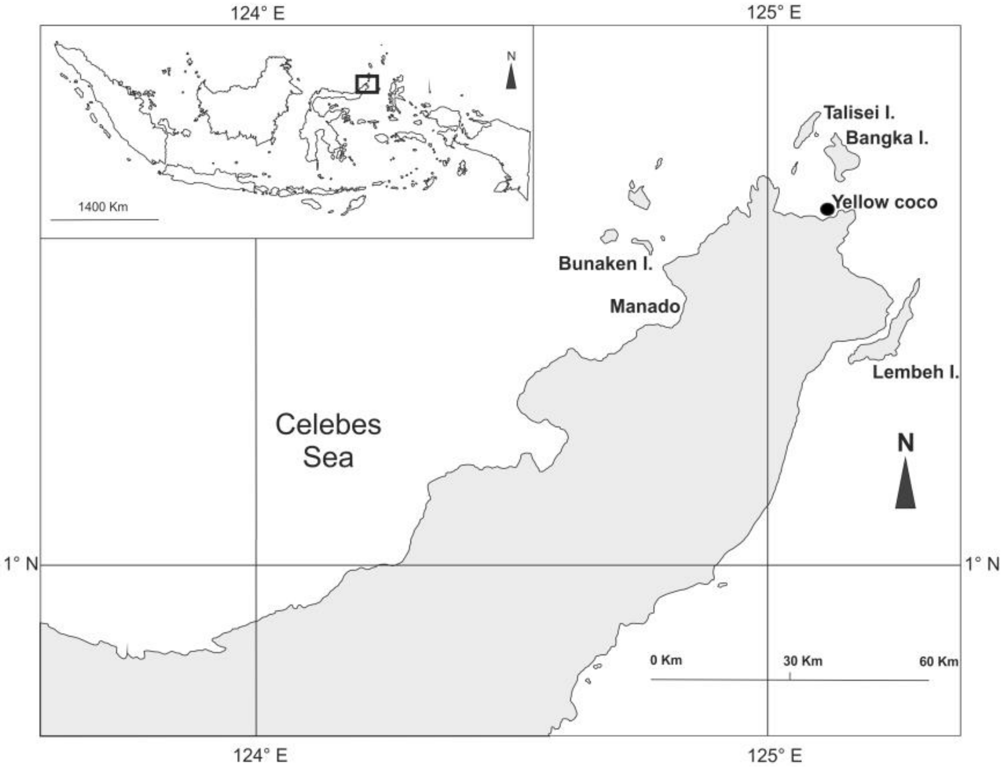

Figure 1. Study area and location of the Yellow coco diving site.

The North Sulawesi Peninsula is characterized by the presence of 129 volcanoes, responsible for gas emissions from the sea bottom in several coastal zones (Manini et al. 2008; Zeppilli & Danovaro 2009). In the studied site, the underwater seascape consists in a coral reef ending on a sandy ground at about 18 m depth. The two outflows arise from the sandy bottom at 20 (HV20) and 25 m (HV25) depth, 150 and 200 m off the coast, respectively. Sampling was carried out in October 2014 and all

field activities were performed by SCUBA diving. Sampling was carried out along four orthogonal line transects 10 m long, starting from the hot springs. In each transect photographic sampling, water sampling and temperature measurements were conducted at increasing distances (0, 1, 3, 5 and 10 m) from the vent. Photographic sampling involved the use of square frames with 50-cm sides (Bianchi et al. 2004). A total of 20 images for each vent were collected and analyzed to evaluate the sponge covering. Water sampling was performed always close to the bottom in order to measure the concentration of dissolved silica. The collected water was filtered using 0.45 µm pore size cellulose acetate filters (ø 47 mm) in order to eliminate any particulate matter, and frozen to await further laboratory analysis. The silicate concentrations were determined in 40 water samples (20 for each vent) following Hansen and Grasshoff (1983), using a Jasco V530 spectrophotometer. In both of the studied areas, temperatures inside the sediment were measured by SCUBA divers by means of a glass thermometer. In addition, sub-samples of the sponges found in the square frames were collected to allow their identification. Sponge specimens were fixed in alcohol 70%. The spicule complement of each sponge specimen was analyzed according to Rützler (1978). From 30 measurements for each spicule type, size range and mean were calculated. Whenever possible, skeletal architecture was examined under light microscopy. We followed the classification given by Hooper and van Soest (2002), and the updated nomenclature reported in the World Porifera Database (Van Soest et al. 2016). In Tedania (Tedania) dirhaphis Hentschel, 1912 and Xestospongia muta (Schmidt, 1870) (two of the most common species living close to the vents), the width of 500 spicules per type (100 spicules per five specimens) was measured and compared with that of five specimens living on the coral reef at least 300 m far away. Differences in the calculated averages (± standard error, SE) were tested by the Student's ttest.

Results

Both of the studied vents were characterized by a continuous outflow of hot water springing from the sandy bottom, easily detectable thanks to the opaque cloud caused by fresh water mixing with salt water (Figure 2a).

Visual observations indicated that HV25 had a flow rate approximately double that of HV20. At both vents, the temperature of the water flowing through the sediments is about 85–90°C. At HV20 the average temperature, 1 m from the center of the outflow, is around 82°C, while at HV25 it decreases, at the same distance, to 47°C. At a distance of 3 m from the source, the average temperature in both vents decreased to 32–34°C and remained quite constant for the entire length of the transects (Figure 3). One meter above both vents, the water temperature was about 40°C. The silicate concentration evaluated at the vent outflow, immediately over the sandy bottom, reached high values ranging from about 5 mg $L^{-1}Si$ at HV20 to 8.5 mg $L^{-1}Si$ at HV25. In both sites at 1 m from the vents, silicate concentrations dropped to 1–0.08 mg $L^{-1}Si$. At the HV25 site the silicate concentration increases again (2 mg $L^{-1}Si$) along the transect at a distance of 3 m from the vent, thus suggesting the presence of a secondary, smaller out flow (Figure 3). A visual survey of the bottom communities clearly showed a concentration of benthic macrofauna in proximity to the outflows (Figure 2).

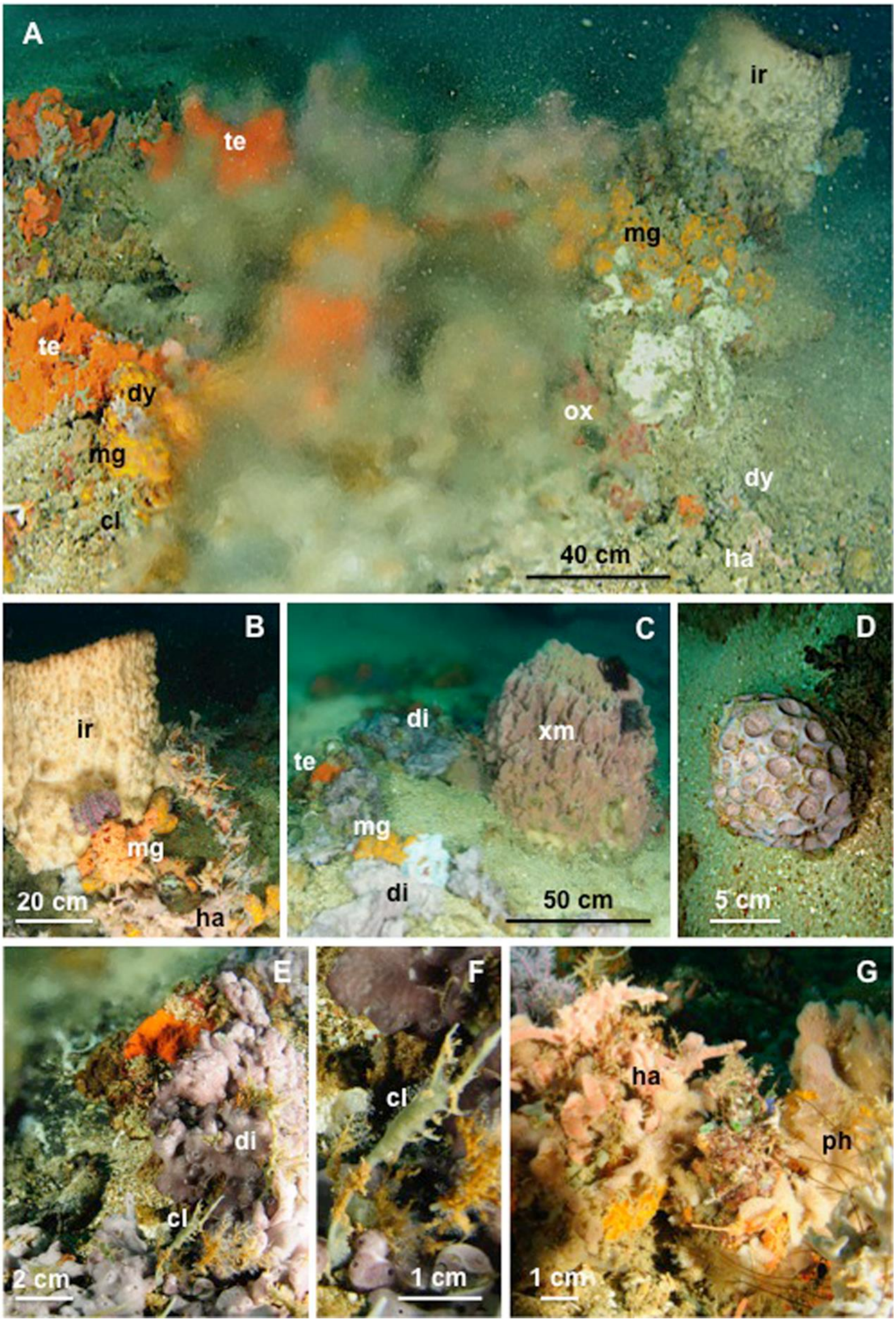

Figure 2. Main components of the benthic communities around the vents: (A) sponge specimens visible through the cloud caused by warm fresh water mixing with the surrounding marine water; (B) a large horny sponge surrounded by small-branched sponges and crinoids; (C) general view of the community characterized by large sponges and colonial ascidians. Vagile fauna is represented by crinoids; (D) Cinachyrella nuda; (E) a large colonial ascidian close to the water spring; (F) a sponge partially overgrowing a colonial hydroid; (G) dense coverage of branched sponges and hydrozoans. te: Tedania (Tedania) dirhaphis; mg: Mycale (Mycale) grandis; ir: Ircinia sp.; ha: Haliclona (Reniera) sp.; cl: Cladocroce cf. burapha; dy: Dysidea sp.; ox: Oxycorynia sp.; xm: Xestospongia muta; di: Didemnum sp.; ph: plumularid hydrozoans.

The second most representative taxa of benthic organisms in terms of abundance were solitary and colonial ascidians belonging to the genera Didemnum, Rhopalaea, Oxycorynia and Clavelina.Sertularellid and plumularid hydrozoans were widespread as epibionts of sponges and ascidians. At HV25, whip gorgonians of the genus Juncella were detected along the transect. Comatulid crinoids composed the vagile fauna. The quantitative study of the sponge covering showed in both sites the highest values in an area within 3–5 m of the vents. Around the outflow of HV20 the maximal covering reached 42%, while at HV25 the maximal covering reached values of 70% (Figure 3). In order to assess the influence of the water flow on the silica deposition, the average spicule width was measured in two specimens of Xestospongia muta (oxeas) and Tedania (Tedania) dirhaphis (styles and tylotes), respectively, which lived both close to the vents and at a distance of about 300 m from the outflows. In all cases, the thickness of the spicules coming from specimens living close to the vents was about double when compared with that of specimens living far from the water sources ($p < 0.01$; Figure 4).

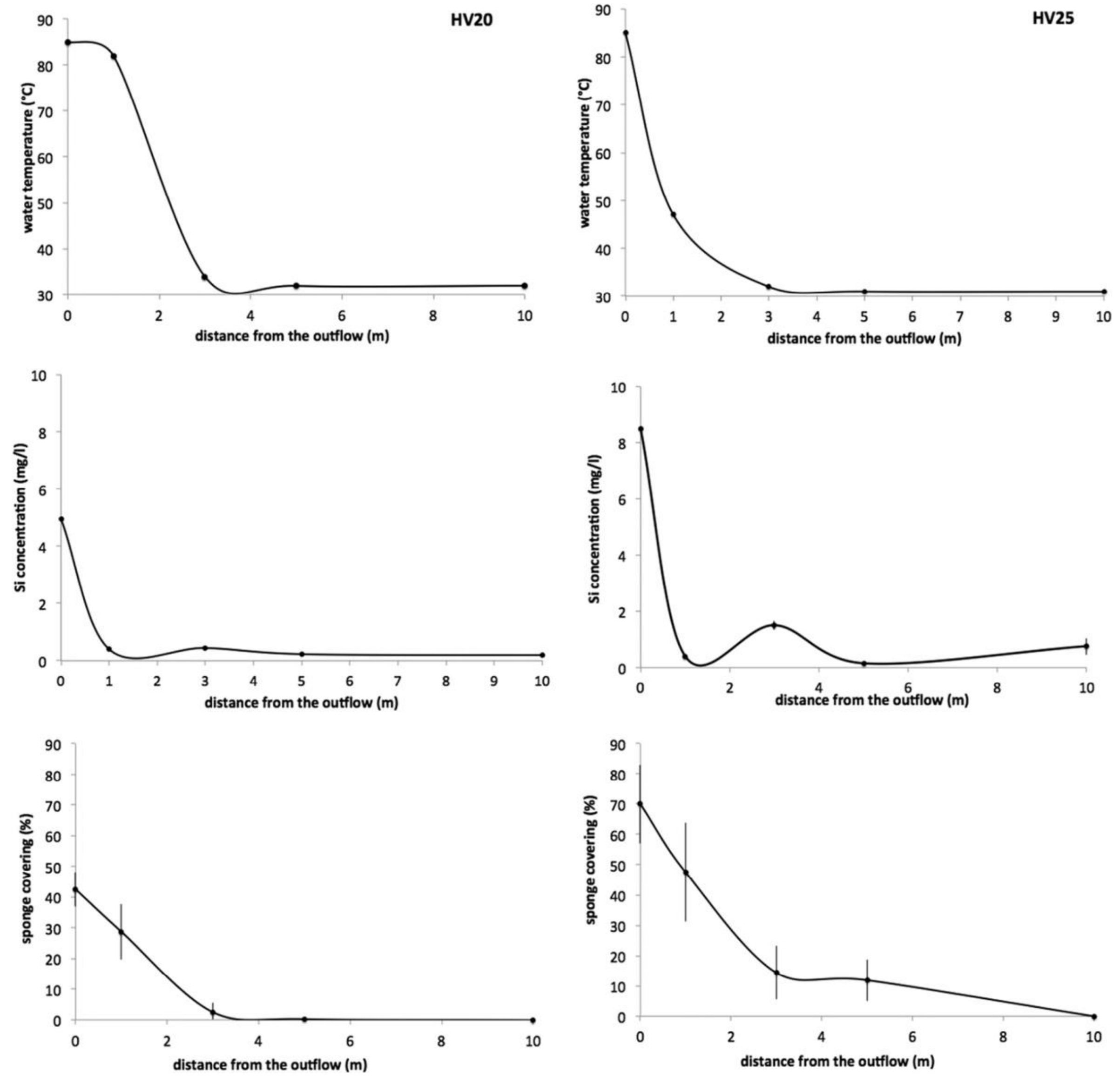

Figure 3. Trends of the average (± standard error, SE) water temperature, silica concentration in the water and percent sponge covering obtained along four 10-m-long transects starting from both vents (HV20 and HV25).

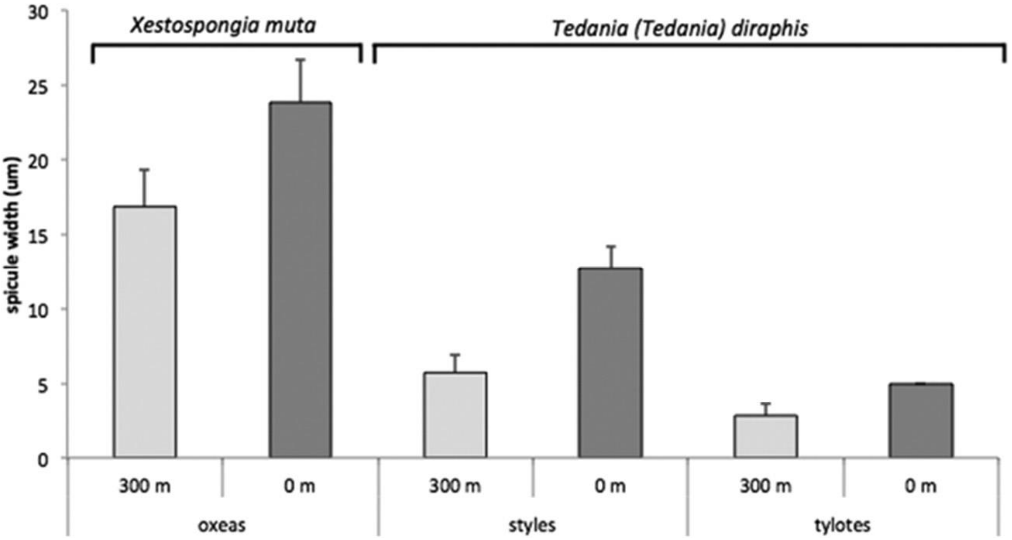

Figure 4. Average spicule width (+ standard error, SE) of Xestospongia muta (oxeas) and Tedania (Tedania) dirhaphis (styles, tylotes) collected close to the vent and 300 m away from it. All of the differences obtained were statistically significant (Student’s t-test).

Discussion

The studied community and particularly the sponge assemblage were formed by species commonly living on the neighboring coral reef, without any obligate species. This situation confirms the data already recorded around other shallow-water vents in different locations: Kolbeinsey, North Iceland (Fricke et al. 1989), Aegean Sea (Pansini et al. 2000) and the Azores (Cardigos et al. 2005). Nevertheless, our data suggest a strong attractiveness of hydrothermal vents for sponges, allowing them to bypass their usual requirement of a hard substratum for settling. In fact, the species recorded during this study generally settle on coral rocks and not on sand. The vents are indeed “islands” of hardbottom communities scattered on a wide extension of sandy bottoms. The role played by the hot springs in the sponge concentration is clarified by the quantitative transects showing how the maximal sponge abundance is centered close to the vent, with a rapid and steady reduction as the distance from it increases. This evidence confirms previous observations coming from Indonesian reefs (Tarasov et al. 1999), and the assumption of Grassle (1986) that members of phyla lacking a blood vascular system are able to live close to the hot springs. The ecological factors inducing sponges to settle close to the vents can be of different nature. In some situations, it was hypothesized that sponges are able to feed on the abundant sulfur-oxidizing bacteria recorded as associated with warm sulfur-rich water springs (Southward & Southward 1993; Morri et al. 1994). Almost all of the studies in the literature on shallow-water hydrothermal vents reveal high chemoautotrophic production (Tarasov 2006), which locally enhances trophic conditions (Southward 1989). However, it is not yet known to what extent the spring-associated sponges are able to use the high chemoautotrophic production of the vent bacteria (Fricke et al. 1989), although it is highly probable that they benefit from this enhanced food supply. Unfortunately, we have no data about the chemosynthetic production of the Yellow coco vents, notwithstanding the organoleptic characteristic of the vent outflows and the lack of colored bacterial mats, which leads us to consider the sulfur emission negligible. Given the awesome concentrations of silicates in the outflows, up to 10 times higher than in the surrounding water, we can assume that silica is one the main attractive factors promoting the settlement and growth of sponges in an area of a few meters around the vent. Past evidence emphasized the existing link between the high concentrations of silica in the vent fluids and the increased species richness of sessile epibenthic assemblages (Bianchi et al. 2011). Here we demonstrate that the sponge abundance also is remarkably enhanced by silicon-enriched emissions. The effect of high silica concentration on the vent sponge community is in agreement with the record of thicker spicules. It has been already stated that silica concentration drives spicule width, as demonstrated by both laboratory (Elvin 1971; Pè 1973) and field (Stone 1970; Bavestrello et al. 1993) studies. Moreover, other studies (Maldonado et al. 1999; Cárdenas & Rapp 2013) have demonstrated that variations in silica concentration are able to modulate the production of the different spicule kinds. Shallow hydrothermal vents were considered unstable in time and space (Desbruyeres et al. 2000), due to the presence of strong currents and rapid fluid dilution at the vent site (Cardigos et al. 2005). This is particularly true for a benthic community that draws nourishment from the outflow. In the Yellow coco vents, it is likely that is not the food supply but the silicon enrichment that mainly drives the community structure. This is highlighted by the presence of large specimens of Xestospongia muta, a sponge with a very slow growth rate, presumably with an age of tens of years (McMurray et al. 2008). The restricted amount of data on the presence of sponges in the biotic communities of hydrothermal vents (Fricke et al. 1989; Tarasov et al. 1999; Pansini et al. 2000) does not help in understanding how sponges can withstand the high temperature of sediment where they settle. However, damage resi stance and desiccation reduction, both improved by a toughened outer layer, have been observed in the sponge Cinachyrella voeltzkowii (Barnes 1999). Even though, at present, we have no evidence of the structural organization allowing sponges to withstand the excessive heat, it seems acceptable to hypothesize that, as occurs in C. voeltzkowii, the strengthening of the peripheral coating, at the cell/substratum interface, can act as a successful barrier.

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Chapter 7 Mediterranean Rocky Reef

7.1

Bioconstruction in the Marine Protected Area of Portofino (Ligurian Sea)

Additional resources:
A. Oprandi, M. Montefalcone, S. Musumeci, C. Morri, P. Povero, G. Bavestrello, C. N. Bianchi. *Biologia Marina Mediterranea (2016) 23 (1): 190- 193.*

Abstract

Mediterranean coralligenous reefs are considered indicators of sea-floor integrity. Coralline algae growing in dim light conditions are the main components contributing to the bioconstruction. We measured the bioconstruction potential, focusing on the basal layer (encrusting or with limited vertical growth organisms), of coralligenous reefs of the Marine Protected Area of Portofino under different levels of protection. The percent cover of builders was significantly lower in the zone C with respect to zones A and B. Sedimentation rate, rather than the level of protection, was apparently the major driver influencing bioconstruction, which however remains a largely unpredictable process.

Introduction

For the assessment of the “good environmental status” of the marine environment, the Marine Strategy Framework Directive (MSFD, 2008/56/EC) introduced the concept of “sea-floor integrity”, intending the integrity at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems are not adversely affected. Biogenic structures, such as the coralligenous reefs, should be adopted as indicators of sea-floor integrity (Rice *et al.*, 2012). Coralligenous concretions, the major calcareous formations of biogenic origin in the Mediterranean Sea, are produced by the accumulation of encrusting algae growing in dim light conditions and thriving in comparatively deep waters (20-120 m depth). Typically, coralligenous concretions develop on almost vertical walls, in grooves, or on overhangs, and occupy small surface areas (Ballesteros, 2006). All plants and animals growing in coralligenous habitats are thus sciaphilic but they can also be found in shallow waters if the required conditions are met, such as in the shadow of *Posidonia oceanica* (L) Delile leaves. Coralligenous reefs are a submerged seascape hosting a set of communities that result from the dynamic balance between the activity of building organisms and destroyers. The bioconstruction is mainly made of encrusting calcified rhodophyta under conditions of weak irradiance but still sufficient for the photosynthesis of sciaphilic algae, relatively low and steady temperature, uniform salinity, clean water and low hydrodynamics. The algal species most responsible for the bioconstruction belong to the genera *Lithophyllum*, *Lithothamnion*, *Mesophyllum*, *Neogoniolithon*, and *Peyssonnelia*. Several indexes have been recently proposed to assess the quality of the coralligenous but the only one that expressly gives attention to specific features of bioconstruction is the COARSE (COralligenous Assessment by ReefScape Estimation) (Gatti *et al.*, 2015). In addition to biotic cover and conspicuous species richness, the COARSE index takes into account the three-dimensional structure of coralligenous reefs, basing on the rapid visual assessment (RVA) approach proposed by Gatti *et al.* (2012). Three distinct layers, whose status is not necessarily correlated to each other, are considered: (1) basal layer, constituted by encrusting or with limited (<1 cm) vertical growth organisms; (2) intermediate layer, composed by organisms with moderate (1-10 cm) vertical growth; (3) upper layer, characterized by organisms with considerable (>10 cm) vertical growth. Here, we investigate the basal layer, which is the layer that best describes the bioconstruction, in nine underwater sites of the Marine Protected Area (MPA) of Portofino, distributed in the three different zones of protection, A (strict reserve, i.e. no take, no entry zone), B (partial reserve zone) and C (general reserve zone), to evaluate if and how the protection level affect the bioconstruction.

Materials and methods

The MPA of Portofino (Ligurian Sea) was established in 1999. Early studies on the benthic communities of this area date back to the late 1950s (Tortonese, 1958) but are still the object of several investigations because of their great biodiversity and richness. Between summer 2013 and autumn 2014 we collected data on coralligenous reefs (30-40 m depth) in three sites of A zone: Cala dell'Oro West 1 (A1), Cala dell'Oro West 2 (A2), Cala dell'Oro East (A3); three sites of B zone: Punta Altare (B1), Secca Gonzatti (B2), Punta Torretta (B3); and three sites of C zone: Punta Faro (C1), Punta Chiappa (C2), Aurora (C3) (Fig. 1). All field activities were performed by scuba diving using the RVA approach of Gatti *et al.* (2012). As for the basal layer, the percent cover of five benthic categories was visually estimated: encrusting calcified rhodophyta (ECR), non-calcified encrusting algae (NCEA), encrusting animals (AN), turf-forming algae (TURF) and sediment (SED). Thickness of the calcareous concretion was measured in millimeters with a hand-held penetrometer. Percent cover data were analysed after merging the 5 benthic categories in 3 guilds, according to their contribution to bioconstruction: builders (ECR), non builders (NCEA+AN), and sediment, including turf (TURF+ SED). Differences in bioconstruction among the three levels of protection were tested trough two-way ANOVAs: protection (3 levels: zone A, B, C) as fixed, sites (3 levels) as random and nested in protection, with n=3 observations per combination of factors levels.

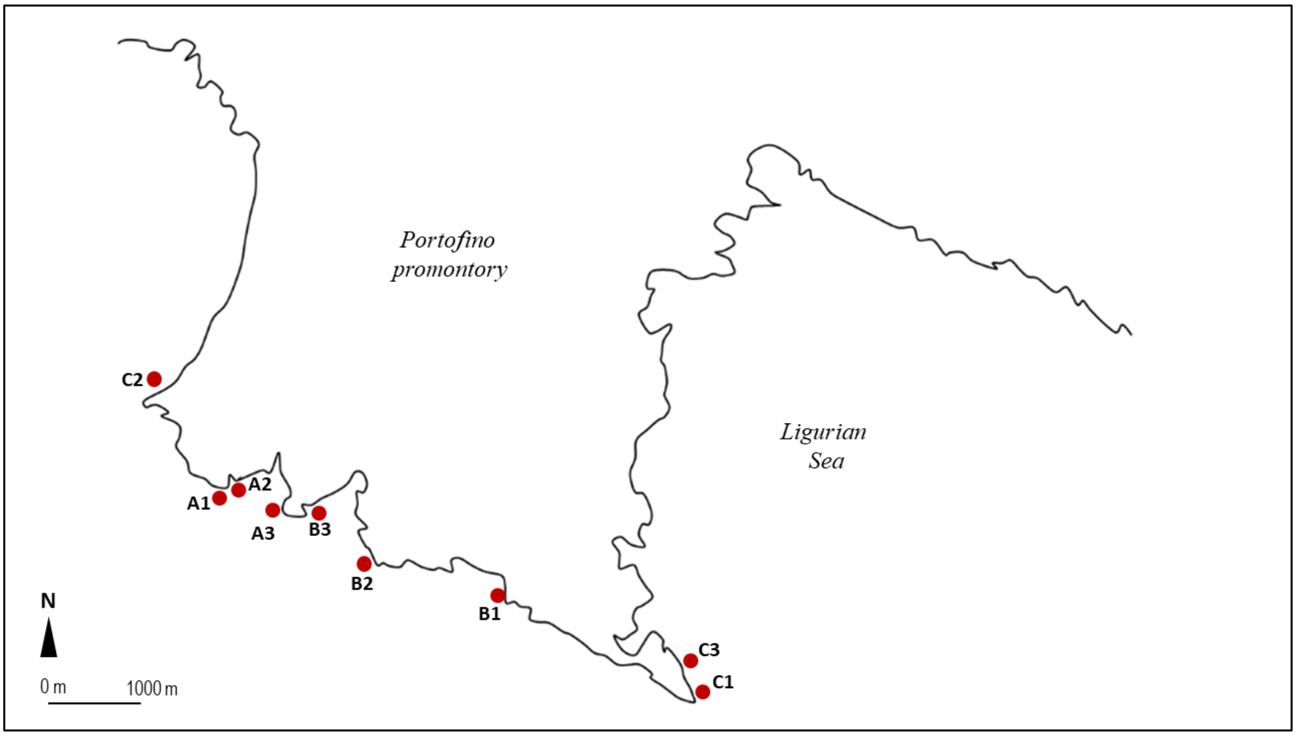


Fig. 1 - Marine Protected Area of Portofino: distribution of the nine study sites among the zones A, B and C.

Results

Little difference in bioconstruction exists among the sites located in zones A and B (Fig. 2). In the ternary diagram, the sites A1 (Cala dell'Oro West 1), A3 (Cala dell'Oro East), B1 (Punta Altare) and B2 (Secca Gonzatti) are located centrally, with approximately the same percent proportions of builders and non-builders.

In particular, the site B1 exhibits the greatest percent cover by encrusting calcified algae. A2 (Cala dell'Oro West 2) and B3 (Punta Torretta) form a separate group: the percent cover of builders remains similar to that in other sites of zones A and B, their points shifted to the right of the graph because of the comparatively high cover of turf and sediment (40%). All the sites of zone C, and especially site C1 (Punta Faro), exhibit high cover of turf and sediment and low cover of builders. The average values of thickness of the calcareous concretion were for the zone A: 0.5±0.06 cm; for the zone B: 0.7±0.3 cm; for the zone C: 0.1±0.1 cm. Cover of builders in zone C was lower than in zone A ($p<0.01$) and in zone B ($p<0.001$) (Tab. 1). Non-builders and turf+sediment showed no differences among the three levels of protection.

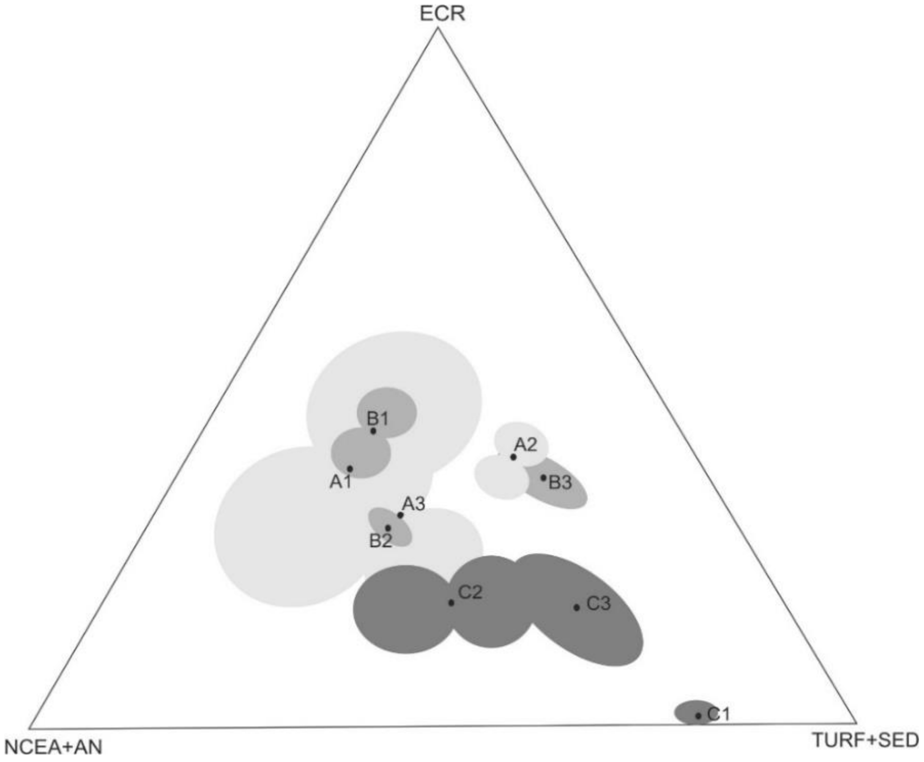
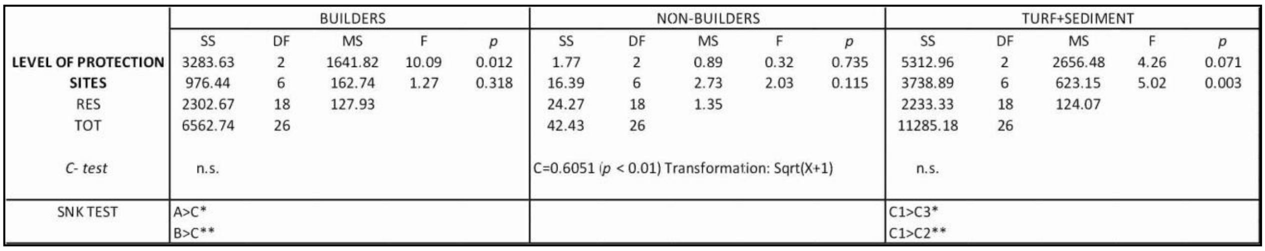


Fig. 2. Ternary diagram of the percent cover of three constructional guilds: ECR (encrusting calcified rhodophyta), NCEA+AN (non-calcified encrusting algae and encrusting animals), TURF+SED (turf-

forming algae and sediment). Shadowed areas depict standard errors: light grey for site A points, intermediate grey for site B points, and dark grey for site C points.

Tab. 1 - Two-way ANOVAs. **p<0.001; *p<0.01



	BUILDERS					NON-BUILDERS					TURF+SEDIMENT				
	SS	DF	MS	F	*p*	SS	DF	MS	F	*p*	SS	DF	MS	F	*p*
LEVEL OF PROTECTION	3283.63	2	1641.82	10.09	0.012	1.77	2	0.89	0.32	0.735	5312.96	2	2656.48	4.26	0.071
SITES	976.44	6	162.74	1.27	0.318	16.39	6	2.73	2.03	0.115	3738.89	6	623.15	5.02	0.003
RES	2302.67	18	127.93			24.27	18	1.35			2233.33	18	124.07		
TOT	6562.74	26				42.43	26				11285.18	26			
C- test	n.s.					C=0.6051 (*p* < 0.01) Transformation: Sqrt(X+1)					n.s.				
SNK TEST	A>C* B>C**										C1>C3* C1>C2**				

Conclusions

Results showed that zone C suffered from reduced bioconstruction compared to the rest of the MPA, as expressed by the lower coverage of encrusting algae and the small thickness of the biocarbonatic layer. However, this result should be considered context dependent. The percent cover of building organisms in the zone C never exceeded 20%; however, the ternary diagram shows two conditions, the site of Punta Chiappa (C2) with a low value of builders quite central in the diagram, and not so far from the sites of zone A and B, while the sites of Punta Faro (C1) and Aurora (C3) exhibit different results. This can be explained by their geographical position. C2 is on the western side of the Portofino promontory, while C1 and C3 are on the east side. Thus, the high values of sediment found in C1 and C3 may be due to the coastal dominant current that transports the load of the Entella River, located in the middle of the Tigullio Gulf (Morri *et al.*, 1986). Sediments travel towards the western part of the Gulf, from which they get out hitting the Promontory of Portofino and causing a reverse sedimentation gradient along the eastern side of the promontory, with deposition of silt inshore. It is difficult to predict what would be the situation in the absence of the Entella's sedimentation in the zone C: after all, water quality is affected by the impacts that come from outside the MPA (Parravicini *et al.*, 2013). Bioconstruction is a historical process, which implies randomness and self-organization and is therefore largely unpredictable knowing the local environmental conditions (Bianchi, 2001). Lack of difference between the strictly protected sites of zone A and those of zone B indicated that the present level of protection does not affect the constructional capacity of the coralligenous reefs of Portofino. Marine Protected Areas are primarily designed to manage biodiversity and also local artisanal fishery: as suggested by Parravicini *et al.*

(2013) further options of coastal management are needed to reach good environmental status and seafloor integrity of marine coastal ecosystems.

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“If you want to know your past life,
look at your present condition.
If you want to know your future life,
look at your present actions.”

Padmasambharva, the Tibetan Book of the Dead

Final remarks

The present work confirms the complexity of the interactions between stresses and disturbances, different in scale and intensity, operating on a same ecosystem. Benthic habitats responses to external agents depend on size, timing and location of the latter (Airoldi 1998).

A common driver of change in marine ecosystems, starting from the 1980-90s, can be identified by the increase in seawater temperature (Bianchi et al. 2019) that affected both seagrass meadows and coral reefs: the former, by facilitating the establishment of invasive alien species (e.g. *C. cylindracea*) under gradual and steady warming conditions, the latter, causing increasingly frequent and intense coral bleaching events due to comparatively brief thermal anomalies.

Even the rocky reefs of Portofino promontory have been affected in past and recent times by heat waves causing mass mortality events (Cerrano et al. 2000) and blooms of mucilage that entangled and suffocated benthic organisms (Bianchi et al. 2019), althought negative effects noticed on organisms with limited vertical growth of the coralligenous assemblages were due to local sediment stress (Oprandi et al. 2016).

Anthropic pressures, become a chronic stress, remain the primary causes of impact in *P. oceanica* meadows of the Liguria region, as also confirmed by retrospective analysis on sponge spicules. However, the severe storm of October 2018 demonstrated that a single natural disturbance can lead to the same loss of biomass generated by more than one century of chronic stresses due to human activities, since these latter have severely compromised the resilience capacity of *P. oceanica*. The erosion of ecosystems ability to absorb and recover from synergic stressors is an issue of primary interest that have to be taken into account in the studies on ecosystems change.

In the Maldivian coral reefs, the increased number of recruits detected after moderate and severe bleaching events confirmed that recruitment represents one of the best strategies to face such disturbance by corals. Although, patterns of bleaching and responses of corals are widely different as shown by the contrasting ability of branching and massive corals to realize the emergency spawning. Recent studies showed that some species seem to have gained tolerance to water temperature anomalies that possibly can be transferred to the next generations (Palumbi et al. 2014; Brown et al. 2015; Putnam and

Gates 2015). Regardless of the single ability of any coral species, concern remains about the capacity of the ecosystem as a whole to adjust quickly enough to address projected rates of temperature rise (Spalding and Brown 2015). Moreover, although coral cover needs approximately 14-16 years to return at the pre-bleaching values, the recovery of the original assemblages may take longer or may not occur at all (Johns et al. 2014). Long-term studies indeed confirm their importance to evaluate temporal patterns of change in marine ecosystems.

Juvenile corals and recruitment seemed not negatively affected by the chronic reduced pH condition at shallow hydrothermal vents (Oprandi et al. 2019). Nevertheless, the discovery of a sponge community that exhibits the unusual propensity to thrive in this environment (Bertolino et al. 2017), supports the concern about a possible future sponge and non-calcifying organisms dominance in reefs with enhanced-acidified conditions.

Some corals may adapt to warmer temperatures and lower pH, but there is not evidence that corals can face the enhancement of bioerosion due to water acidification. Reduced pH also compromise calcification rates of corals making reef accretion more expensive metabolically. Increased bioerosion coupled with reduced rates of reef accretion affects the reef rugosity and the ecological functioning of the ecosystem itself. Although a large diversity of corals survived in conditions of low pH, they did not produce extensive reefs anymore. Many species may not go extinct, but reef accretion will likely not counter bioerosion and rising sea level (Birkeland 2019).

Whether it is a tropical or a temperate ecosystem, it will be increasingly difficult to discern chronic stresses from disturbances as their effects will add up over time.

Data on benthic communities suggest that marine habitats are experiencing phase-shifts toward alternative and unknown states (Bianchi et al. 2019). These new conditions will be hardly reversible because of the dominance of different species that are more tolerant than those at present. Different species or groups of species dominate under different regimes of disturbance and stress since organisms capacity to withstand, tolerate, and compete under adversely conditions define the spatial distribution and stability of natural communities (Airoldi 1998). Consequently, future marine habitats will likely lose their original features acquiring a new different shape (Bianchi 2007).

Benthic ecosystems could develop a certain adjustment capacity to chronic stress to the detriment of an enhanced sensitivity towards disturbances but this is of concerns regarding the predicted increase of high intensity disturbances due to climate change.

Since examples of well-managed ecosystems as well as the most remote areas on earth, still report loss of species and effects of climate change, ecosystems resilience will require both local and global actions. Despite the efforts invested to date by scientists and stakeholders, threatened habitats are continuing to deteriorate. Disturbances are usually quicker than recovery, thus if disturbances become more frequent or stresses become chronic, their consequences can overlap in time, making them to shift from events to trends (Birkeland 2019).

Nevertheless, if the impacts will be prevent instead of treated a posteriori, providing to marine habitats the time required to recover by themselves, we will likely have more chances to face climate change successfully slowing down the ecosystem shifts.

Further change in marine ecosystems will continue to create major challenges and costs for the international scientific community and country policies.

In view of the findings and the amount of information coming from the several aspects investigated in this thesis, following issues are here suggested to be addressed in the future:

- Which aspects of marine ecosystem structure are most important for conferring resilience against stress and disturbance and how take them into account for management programs?

- How will the future ecosystem states with no analogue in the past influence our ability to forecast dynamics of marine ecosystems?

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Annexes

LIST OF PUBBLICATIONS

Oprandi A., Montefalcone M., Morri C., Benelli F., Bianchi C. N. 2019. Water circulation, and not ocean acidification, affects coral recruitment and survival at shallow hydrothermal vents. *Estuarine, Coastal and Shelf Science*. 217, 158-164. https://doi.org/10.1016/j.ecss.2018.11.017.

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