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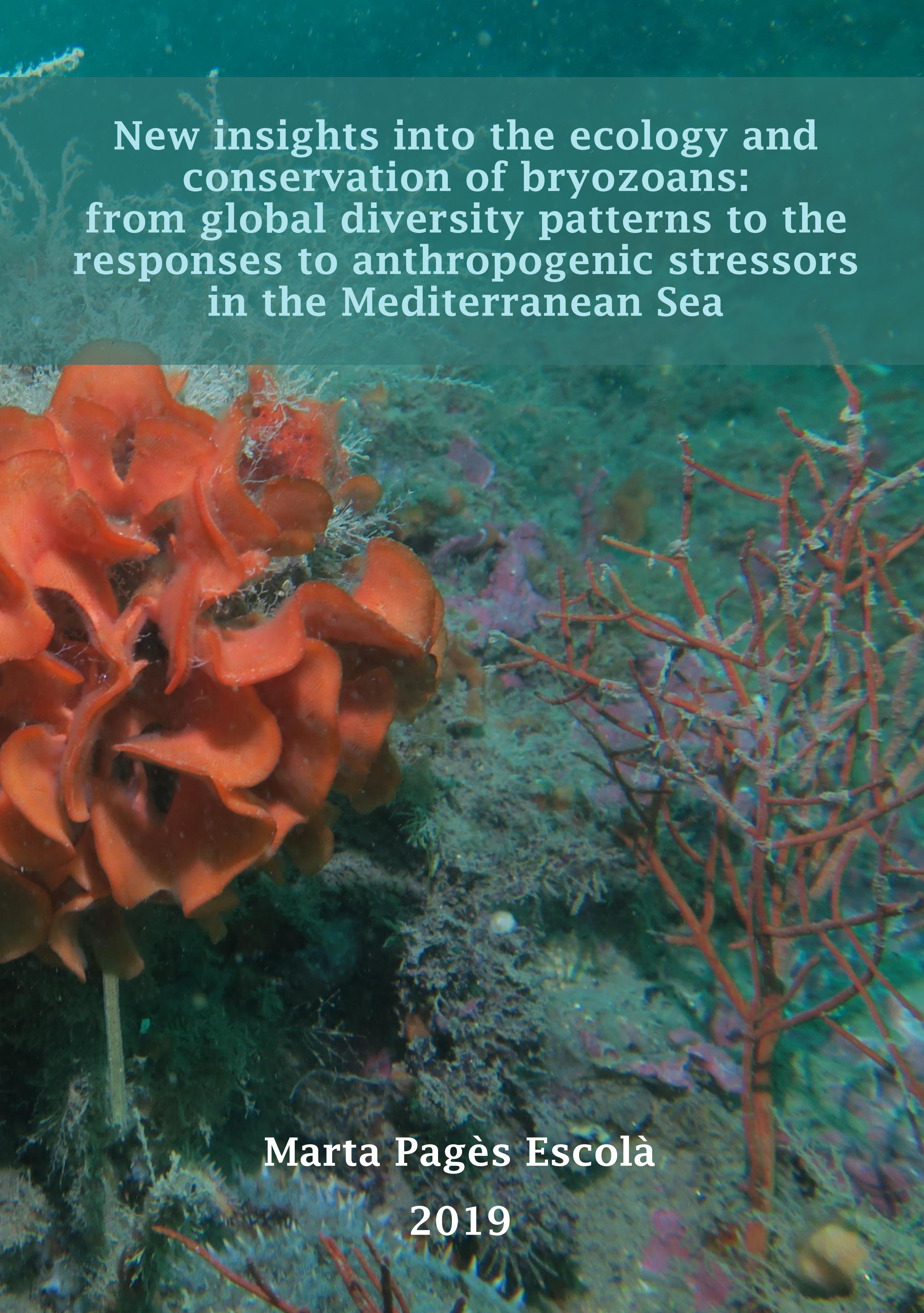
Marta Pagès Escolà



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TESI DOCTORAL

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals
Doctorat en Ecologia, Ciències Ambientals i Fisiologia Vegetal

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*Memòria presentada per **Marta Pagès Escolà** per optar*
al Grau de Doctora per la Universitat de Barcelona

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La directora de la tesis:
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Als meus pares, la Rosa Maria i el Jordi,

A tu Xavi, per continuar caminant plegats.

Mar blau,
que en el teu fons
escoltes el dolç remor de les teves aigües.

Les teves aigües,
abans cristal·lines,
grises s'estan tornant.

Rugeix ben fort,
fes que l'hom tremoli,
aixeca el teu onatge
en senyal de protesta.

A veure si l'home aprèn
a tenir cura de l'encant
que viu en el teu fons.

Rosa Maria Mestres i Tió, 1998

Agraïments

Agraeixo infinitament el suport de tota la gent que m'ha acompanyat i m'ha ajudat en aquest camí. Mirant enrere, recordaré els bons moments, però també els nombrosos obstacles i reptes als quals he hagut de fer front.

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A tots vosaltres, i a tots els altres que heu format part d'aquest camí,
Moltes gràcies.

Advisors' report

Dra. Cristina Linares and Dr. Bernat Hereu, professors at Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals (Universitat de Barcelona), advisors of the PhD thesis entitled "**New insights into the ecology and conservation of bryozoans: from global diversity patterns to the responses to anthropogenic stressors in the Mediterranean Sea**",

INFORM, that the research studies developed by Marta Pagès Escolà for her Doctoral Thesis have been organized in five chapters, which correspond to five scientific papers listed below: three of them are already published, one is under review, and the last one will be submitted in the next few months;

and CERTIFY, that the work has been carried out by Marta Pagès Escolà, participating actively in all the tasks: conceiving and setting the objectives, conceiving and performing the analyses, participating actively in the field work, carrying out the experiments and writing the manuscripts.

Finally, we certify that the co-authors of the publications listed below and that conform this doctoral thesis, will not use these manuscripts in another PhD thesis.

Barcelona, 18th October 2019

Adivsor:
Dra. Cristina Linares Prats
Universitat de Barcelona

Adivsor:
Dr. Bernat Hereu Fina
Universitat de Barcelona

List and publication status of the chapters of this thesis

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CHAPTER II: Pagès-Escolà, M.[1], Linares, C.[1], Montero-Serra, I.[1,6], Hereu, B.[1], and Costello, M.[5]. Global patterns and drivers of marine sessile biodiversity: novel insights focusing on the overlooked but abundant taxa of bryozoans. Under preparation. To be submitted at Global Change Biology. 5-year impact factor (2018): 10.171

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CHAPTER V: Pagès-Escolà, M.[1], Linares, C.[1], Goméz-Gras, D.[7], Medrano, A.[1], and Hereu, B.[1] (2019). Assessing the effectiveness of restoration actions for Bryozoans: the case of the Mediterranean *Pentapora fascialis*. Aquatic Conservation: Marine and Freshwater Ecosystems, accepted (In Press). 5-year impact factor (2018): 2.991.

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Summary

Marine ecosystems are directly threatened by multiple and interactive human stressors at global and local scales. Hence, it is vital to study biodiversity and ecological patterns through a multi-disciplinary approach, from understanding global diversity patterns to evaluating the ecological responses of species to different impacts in order to protect marine ecosystems. Until this moment most of related ecological studies have focused on charismatic and popular groups, such as gorgonians, corals, macroalgae or seagrasses. In this thesis, we focused on bryozoans, an abundant group of sessile marine invertebrates distributed worldwide, but generally understudied. Moreover, large bryozoans are considered habitat-forming species that can create bioconstructions enhancing the associated biodiversity and providing different ecological benefits. Bearing this in mind, the main aim of this thesis was to provide different approaches to understand discovery and macroecological patterns at global scales, and the response of species to different stressors at local scales, combining the use of open databases, the *in situ* monitoring of natural populations, experiments in aquaria and the development of restoration techniques. Furthermore, the present thesis aims to contribute to provide a general framework to identify and protect vulnerable populations in the context of increasing human threats.

In the first chapter, the discovery patterns of fossil and extant bryozoans revealed the highest number of fossil species described, highlighting that the current biodiversity represents only a small proportion of Earth's past biodiversity. Beyond these differences, both groups showed an increase in the taxonomic effort during the past century, reflecting the increase in the interest in the exploration of the marine environment, and the improvement of technological developments. Despite this progress, future projections of discovery patterns of both groups showed a large proportion of species remaining to be discovered by the end of this century, which corroborate the need to increase the effort to name and quantify marine biodiversity before hundreds of species become extinct due to human impacts.

In chapter 2, a comparative approach between marine sessile and bryozoan biodiversity patterns reported that the most of sessile groups presented higher diversity in the Southern ocean, displaying a non-unimodal latitudinal pattern with a dip in the number of species at the equator, contrary to the most traditionally accepted pattern in diversity studies. Moreover, this region will represent the less affected by global warming at the final of this century, suggesting that the high species richness recorded in this region may be explained by it has suffered lower temperature stress over evolutionary time. Related to biases in sampling effort, our analyses showed that the most sampled region for both marine sessile species and bryozoans was North Temperate Atlantic. To identify and quantify environmental drivers for both groups, we tested the effect of using the popular method of rarefaction to correct sampling effort biases *vs* the incorporation of a frequency index of sampling effort as co-variate in quantitative models. Despite we obtained the same best predictors for both approches (depth, nitrate, and SST), the models using the correction of sampling biases through frequency index showed better fitting, encouraging to incorporate this methodology in future studies.

Focusing on the Mediterranean Sea, in Chapter 3 we studied the responses of bryozoans to different stressors. First, we showed that two abundant and common bryozoans, *Pentapora fascialis* and *Myriapora truncata*, displayed different tolerances to warming. Through the combination of *in situ* monitoring and experiments in aquaria, we revealed that mass mortality event recorded of *Pentapora fascialis* populations during summer 2015 may be explained by its lower thermal tolerance ranks. Moreover, in Chapter 4 we take the advantage of the *in situ* monitoring of *Pentapora fascialis* natural populations increasing the spatial and temporal effort, revealing that the bryozoan *Pentapora fascialis* is characterized by fast population dynamics, with high recruitment and growth rates, and a high capacity of recovery. Accordingly, we observed an increase in the density of its populations in the Marine Reserve of Medes Island since the 1990s. However, we evidenced that in this Marine Protected Area, diving can impact on the density, recruitment, survival, and the size of the colonies, registering lower values in frequented localities. Our results highlight that although Marine Protected Areas have been recognized as effective management and conservation tools to protect coastal ecosystems, the over frequentation of divers compromises the future viability of populations, highlighting the need to explore other management strategies.

In this context, for the first time in Chapter 5, different restoration techniques for bryozoans were developed and tested, focusing on the recruitment enhancement through the installation of recruitment surfaces and the transplantation of adult colonies of *Pentapora fascialis*. Plastic grids represented the best substrate in terms of facilitating the recruitment of our model species. The most successful technique to transplant adult colonies was to fix the colonies to the substrate with a nylon thread attached to the colony *ex situ*. The successful results and the affordable and economic cost of tested techniques aim to encourage the managers of Marine Protected Areas to apply similar methodologies to restore and conserve bryozoan temperate bioconstructions and the ecological services that they provide.

The results presented in this thesis show the importance to combine different approaches to understand the global and local ecological patterns of understudied but abundant groups, such as bryozoans. Our findings enlarge the current ecological knowledge of bryozoans at different scales, and highlight that more effort is needed to protect vulnerable populations. Accordingly, adaptive management formal plans and restoration actions are required to promote the conservation of marine communities in the context of increasing local and global stressors.

Resum

Els ecosistemes marins estan sotmesos a múltiples impactes a escales locals i globals i que a més interaccionen entre ells. Per aquesta raó, és important estudiar els patrons de biodiversitat i ecològics a través d'una aproximació multidisciplinar, que pot anar des d'entendre els patrons de diversitat global fins a avaluar les respostes ecològiques de les espècies enfront diferents impactes, per així conservar i gestionar adequadament les comunitats marines. Fins aquest moment, la majoria d'estudis relacionat s'han centrat en grups carismatics i populars, com ara les gorgònies, els coralls, les macroalgues o les fanerògames marines. En canvi, aquesta tesis es centra en l'estudi dels briozous, un grup abundant de invertebrats sèssils marins distribuïts per tot el món, però generalment poc estudiats. La importància ecològica de moltes espècies de briozous, sobretot els de major talla, és elevada doncs es consideren espècies creadores d'hàbitat que poden formar grans bioconstruccions afavorint la biodiversitat associada i aportant diferents beneficis ecològics. Per aquesta raó, el principal objectiu d'aquesta tesis és utilitzar diferents aproximacions per entendre els patrons de descobriment i macro-ecològics a escala global, i la resposta a diferents impactes a escala local, combinant el ús de bases de dades globals, el seguiment *in situ* de les poblacions, experiments en aquaris i el desenvolupament de tècniques de restauració. A més, la present tesis vol proporcionar un marc de treball per identificar, gestionar i conservar les poblacions vulnerables en el context de l'augment de les activitats humanes que afecten els ecosistemes marins.

En el primer capítol, els patrons de descobriment dels briozous fòssils i actuals han revelat un major nombre d'espècies fòssils descrites, posant en relleu que l'actual biodiversitat només representa una petita part de la diversitat que habitava a la Terra en el passat. Més enllà d'aquestes diferències, en els dos grups s'ha observat un increment en el esforç taxonòmic durant el segle passat, reflectint l'augment en l'interès en l'exploració de l'ambient marí i la millora en el desenvolupament tecnològic. Tot i aquest progrés, les projeccions futures dels patrons de descobriment pels dos grups han mostrat una proporció molt gran de espècies que seran descrites al final d'aquest segle, posant de relleu la necessitat d'augmentar l'esforç per identificar i quantificar la biodiversitat abans que cents d'espècies s'extingeixen degut als impactes humans.

En el segon capítol, l'anàlisi comparatiu dels patrons de biodiversitat entre les espècies sèssils marins i els briozous ha demostrat que la majoria de grups marins sèssils presenten una major diversitat a l'Oceà Austral, mostrant un patró latitudinal no-unimodal amb una caiguda en el nombre d'espècies a l'equador, que contrasta

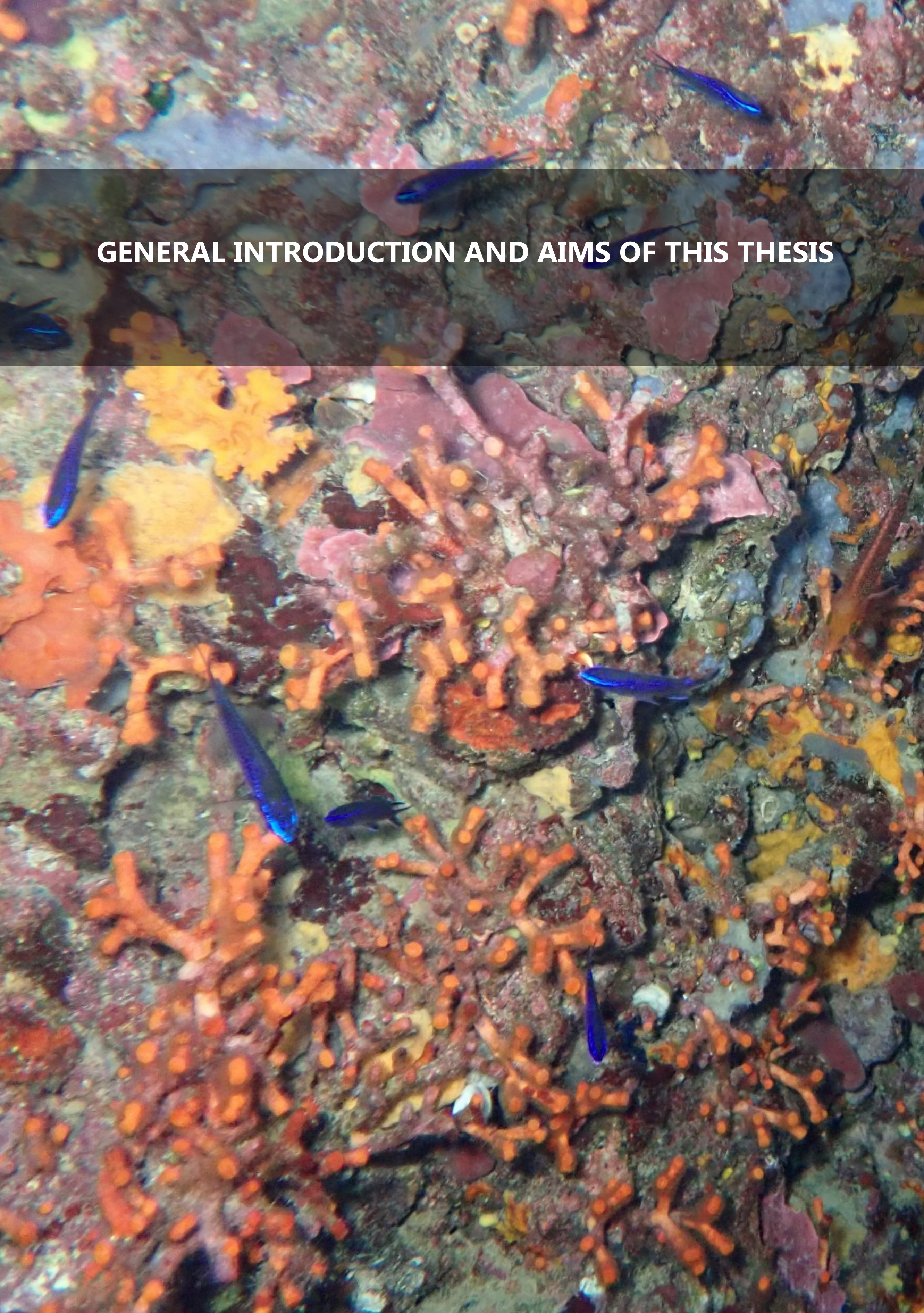
amb el patró tradicional més acceptat en els estudis de diversitat. A més, els anàlisis fets preveuen que aquesta regió estarà menys afectada pel escalfament global a finals de segle, suggerint que l'elevat nombre d'espècies observat en aquesta regió podria ser explicat pel fet que durant la història evolutiva ha patit un menor estrès tèrmic. Referent als biaixos en l'esforç mostral, els nostres anàlisis han mostrat que la regió més mostrejada per les espècies sèssils marins i els briozous és la zona Temperada Nord Atlàntica. Finalment, per identificar i quantificar els predictors dels patrons de diversitat en els dos grups, hem testat l'efecte d'utilitzar dos aproximacions diferents: en primer lloc, el popular mètode de la rarefacció per corregir biaixos en l'esforç mostral i en segon lloc, la incorporació de un índex de l'esforç mostral com a covariable en els models quantitatius. Tot i que s'han obtingut les mateixes variables per predir la diversitat en els dos tipus de models per les espècies sèssils i els briozous per separat (profunditat, nitrats, i temperatura superficial), aquells que incorporaven la correcció del biaix en l'esforç mostral a través de l'índex com a covariable van mostrar un millor ajust, mostrant que metodologies similars haurien de ser incorporades en futurs estudis.

Centrant-nos en el Mar Mediterrani, en el Capítol 3 s'ha estudiat la resposta dels briozous a diferents impactes. En primer lloc, els nostres resultat han mostrat que dues espècies abundants i comunes de briozous, *Pentapora fascialis* i *Myriapora truncata*, presenten diferents respostes a l'escalfament. A través de la combinació d'un seguiment in *situ* de les poblacions naturals i experiments en aquaris, s'ha demostrat que el esdeveniment de mortalitat massiva registrat en *Pentapora fascialis* l'estiu del 2015 podria estar explicat pels seus baixos nivells de termotolerància. A més aprofitant un seguiment més detallat en un major nombre de localitats i anys, el capítol 4 ha revelat que *Pentapora fascialis* està caracteritzada per una dinàmica de població ràpida, amb altes taxes de reclutament i creixement, i una alta capacitat de recuperació. Així mateix, s'ha registrat un augment notable en la densitat de les poblacions a la Reserva Marina de les Illes Medes des dels anys 90. Tot i així, els nostres resultats han evidenciat que en aquesta Àrea Marina Protegia, el busseig té un elevat impacte en la densitat, el reclutament, la supervivència i la mida de les colònies, observant valors més baixos a les localitat freqüentades. Els nostres resultats posen en èmfasi que tot i que les Àrees Marines Protegides han estat reconegudes com eines efectives de gestió i conservació per protegir els ecosistemes marines costaners, la sobre-freqüentació de bussejadors compromet la futura viabilitat de les poblacions, demostrant la necessitat d'incorporar noves estratègies de gestió.

En aquest sentit, per primera vegada, en el capítol 5 s'han desenvolupat diferents tècniques de restauració pels briozous, estudiant com millorar i facilitar el reclutament a través de la instal·lació de superfícies de reclutament i el trasplantament de colònies adultes de *Pentapora fascialis*. Les reixes de plàstic han sigut el millor substrat per facilitar el reclutament d'aquesta espècie. La millor tècnica per trasplantar colònies adultes ha consistit en fixar les colònies al substrat a través d'un fil de niló fixat a la colònia *ex situ*. Els bons resultats i el baix cost econòmic i logístic de les tècniques desenvolupades en el nostre estudi haurien d'animar als gestors de les Àrees Marines Protegides a aplicar metodologies similars per restaurar i conservar les bioconstruccions conformades per briozous en zones temperades i així preservar els serveis ecològics que ofereixen.

Els resultats obtinguts en aquesta tesis mostren la importància d'aplicar diferents aproximacions per entendre els patrons ecològics globals i locals de grups abundants però poc estudiats, com són els briozous. Els resultats obtinguts contribueixen a augmentar el coneixement dels patrons ecològics dels briozous a diferents escales, i mostren que cal més esforç per protegir les poblacions vulnerables. Així, mesures de gestió adaptativa i de restauració i són necessàries per promoure la conservació dels ecosistemes marins en un context de impactes creixents derivats de l'activitat humana tant a escales locals com globals.

GENERAL INTRODUCTION AND AIMS OF THIS THESIS



1. Marine biodiversity and biogeographical patterns

1.1 The importance of biodiversity

Biodiversity refers to the full variety of life on Earth, which is usually measured at different levels of complexity, from genes to species to ecosystems (Takacs, 1996; Sala and Knowlton, 2006). The most commonly used metric of biodiversity is species richness, or the number of species occurring in one site, habitat or region, which is traditionally measured through a variety of indices, most of which are related to the quantification of species abundance, composition and distribution (Magurran, 2005; Hamilton et al., 2010; Costello and Wilson, 2011; Laurila-Pant et al., 2015).

An increase in species richness may enhance ecosystem productivity and stability, providing a range of economic, socio-cultural and ecological benefits and services, such as the provision of food resources and clean water, carbon retention, or the regulation of climate and water flow (Loreau et al., 2001; Turner et al., 2007; Laurila-Pant et al., 2015). In this context, functional diversity, or the variety of different functional species (e.g., with different feeding niches or habitats), enhances the variety of responses of these communities, increasing their capacity to buffer the effects of environmental changes and making them less vulnerable to anthropogenic disturbances (Gray, 1997; Tilman, 2001; Morri, et al., 2013; Pearce and Moran, 2013).

In recent years, an increase in biodiversity loss has been documented due to human stressors, such as pollution, overexploitation of natural resources, habitat destruction, the introduction of exotic species and climate change, compromising the services and benefits that different species provide (Worm et al., 2006; Lotze et al., 2006; Halpern et al., 2008; Cardinale et al., 2012). In this context, it is vital to quantify and measure biodiversity through a multi-disciplinary approach, analysing the ecological responses of species and the cost of implementing management and conservation measures, in order to sustain the ecological, economic and social benefits of natural systems in a changing world (Laurila-Pant et al., 2015).

1.2 Quantification of marine biodiversity

Quantifying the number of species on the Earth has always been a focus of ecologists and biologists (Ødegaard, 2000). The first registers of early exploration of the seas were found from the first century B.C. when Aristotle began the classification and description of the marine biodiversity in the Mediterranean Sea (Coll et al., 2010). Nevertheless, the establishment of systematic collections of diversity started between the 1700s and 1800s, influenced by *Systema Naturae* from Linnaeus, who began the naming and classification of species based on a binomial system linked to their morphological relationships (Linnaeus, 1758). The history of marine species discovery can generally be divided into three periods: an initial period of exploratory studies that took place between the mid-1700s and the late 1800s in several regions, such as James Cook's voyages in the 1770s or the Challenger expedition in the 1870s; a second period of regional studies between the late 1800s and the mid-1900s, when there was an improvement of research resources in developing countries, an increase of taxonomists and specialists, and the beginnings of the establishment of research laboratories; and finally, a third period in the 1990s when large-scale multidisciplinary investigations began, which was characterized by the development and application of modern technologies (Costello et al., 2010).

Since the discovery of the first species, the interest in biodiversity has grown exponentially, and more than 1.2 million species have now been named and described; only ~200,000 being named in the ocean (Mora et al., 2011; Appeltans et al., 2012). However, recent projections of biodiversity estimates around ~8.7 million species globally, of which ~2.2 million are marine suggesting that the current knowledge of biodiversity is largely incomplete, comprising only a small fraction of all species on the land (~14%) and in the ocean (~9%), with a large proportion of species remaining to be discovered (Mora et al., 2011).

1.3 Marine versus terrestrial systems

Although marine diversity only represents a small proportion of the total named global species, life began in the sea, and many extant phyla originated during the Cambrian radiation more than 500 million years ago; later, most species started to invade the land during the Palaeozoic Era (approximately 200-400 million years ago) (Signor, 1994; Benton, 2016). The fossil record indicates that marine diversity was higher than terrestrial diversity 600 million years ago, with a high diversity of algae and animals in the oceans, such as molluscs, cnidarians, bivalves and fishes (Sepkoski, 1981; Benton, 2016). However, during the Cretaceous Terrestrial Revolution, the rise of angiosperms precipitated the explosion of the diversity of insects, mammals and lizards (Benton, 2016) (Fig. 1).

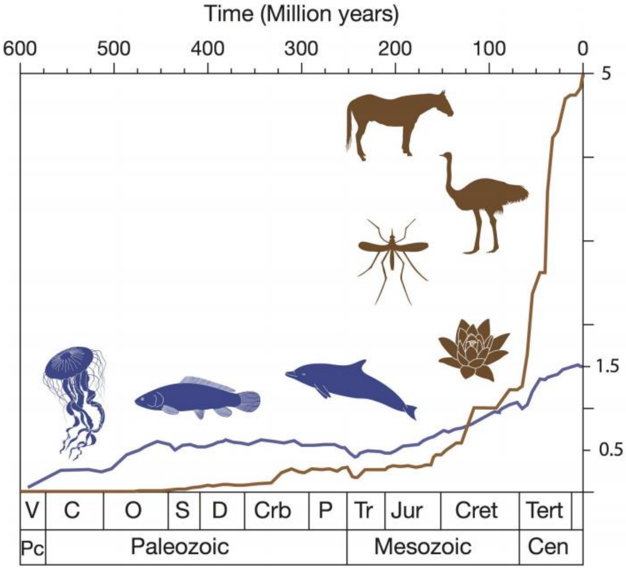


Figure 1. The history of biodiversity on land and in the sea (from Benton, 2016). Note the postulated cross-over 125 million years ago, when the life on land (brown line) became more diverse than the life in the sea (blue line).Abbreviations: C, Cambrian; Crb, Carboniferous; Cret, Cretaceous; D, Devonian; J, Jurassic; O, Ordovician; P, permian; S, Silurian; Tert, Tertiary; Tr, Triassic; V, Vendian. Drafted by Simon Powell (University of Bristol).

Despite the lower numbers of species in marine ecosystems, there was a greater variety of body plans and major groups, and a higher number of endemic species have been found compared to in terrestrial systems (64% of animal phyla inhabit only the sea, while only 5% of animal phyla live exclusively on land) (May, 1994). Accordingly, marine environments present higher functional and trophic diversity than terrestrial environments (Ray, 1988; Gray, 1997; Reaka-Kudla, 1997). Specifically, among all macroscopic organisms, 38 phyla are found in marine environments, with a high diversity of macroinvertebrates. In addition, some marine communities also contain higher species diversities than land systems, such as coral reefs or deep-sea ecosystems (Reaka-Kudla, 1997). Conversely, in terrestrial ecosystems, there are 11 phyla, which show the greatest diversity in insects and terrestrial plants (Barnes, 1989; Reaka-Kudla, 1997).

1.4 Global marine diversity patterns

Understanding the biodiversity patterns across the globe and their drivers has long been a focus of interest in ecology (Field et al., 2009). In recent decades, considerable progress has been made towards the combination of remote sensing, intensive field work, powerful databases, and improved statistical models, allowing the testing of the macroecological hypothesis and increasing the number of related works (Gaston, 2000; Smith et al., 2008). Specifically, environmental modelling constitutes a useful tool to underlie trends in the ecological processes determining macroecological patterns by statistically exploring the relationship between species richness and environmental gradients (Austin and Smith, 1990; Pykälä et al., 2005).

One of the most studied diversity patterns is the relationship between species richness and latitude, which has been traditionally assumed to be a unimodal latitudinal pattern with an increase in diversity from the polar to the tropical regions, where there are a high proportion of the terrestrial, freshwater and marine species (Gaston, 2000; Willig et al., 2003). During recent decades, this pattern has been explained by different theories such as the Rapoport's rule, which assumes that the geographic range of species increases with latitude and shows a decrease in diversity at high latitudes (Stevens, 1992), the *species-area hypothesis*, which suggests that larger areas in the tropics can support more individuals and reduce the extinction risk of populations (Rosenzweig, 1995; Chown and Gaston, 2000), or the *species–energy hypothesis*, which assumes that the higher numbers of species in the tropics results from the faster metabolic and speciation rates associated with warmer temperatures (Kaspari et al., 2004).

However, recent studies have challenged this pattern in marine ecosystems, suggesting that the latitudinal gradient of species diversity in marine environments is bimodal, with a dip in species richness in the tropics, which highlights the need to reformulate some traditionally accepted macroecological theories and to analyse the environmental and physical drivers of diversity patterns (Chaudhary et al., 2017; Saeedi et al., 2017; Menegotto and Rangel, 2018).

1.5 Differences in sampling effort between marine areas and groups

The sampling effort in marine ecosystems has not been evenly distributed across the globe, with fewer research efforts in some areas, such as the deep pelagic ocean, due to the difficulty of exploring them (Mora et al., 2007; Webb et al., 2010; Menegotto and Rangel, 2018) (Fig. 2A,B). Specifically, the mid-latitudes of both hemispheres have had the highest sampling intensity due to the higher funding of marine research provided by developed countries. Conversely, most developing countries, such as those located at tropical latitudes, have had less funding for marine research, causing higher spatial gaps in the completeness of taxonomic inventories (Costello et al., 2010; Menegotto and Rangel, 2018) (Fig. 2A,B). Moreover, the larger oceans in the tropics contribute to lower sampling efforts in these areas (Menegotto and Rangel, 2018).

Furthermore, the sampling effort vary among organisms, with large fishes displaying the highest levels of completeness and state of knowledge, followed by the angiosperms, macroalgae, and Echinodermata (Costello et al., 2010). Other abundant marine groups, such as Porifera or Bryozoa, have been less studied than the other taxa (Costello et al., 2010) (Fig. 2C).

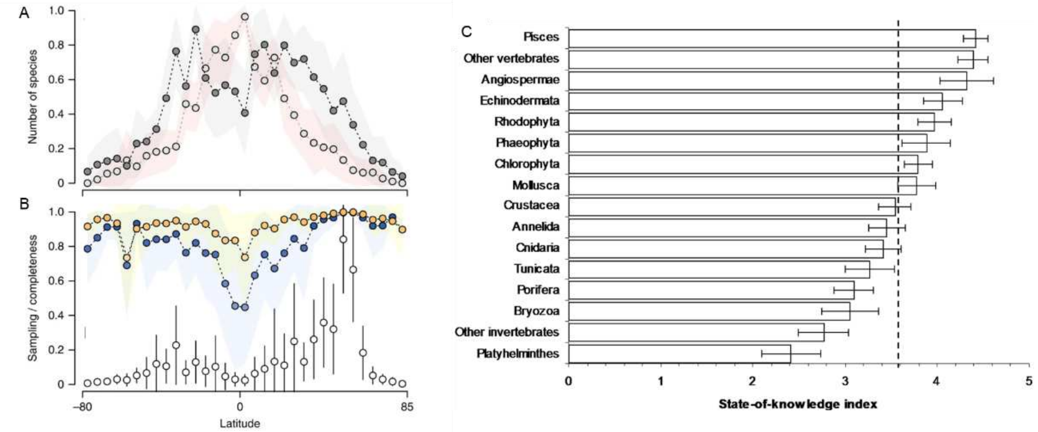


Figure 2. Patterns of latitudinal variation in species richness, spatial gaps and sampling efficiency for marine taxa. A) Mean (± s.d) latitudinal variation in the number of observed species (dark grey circles) and the number of missing species (light grey circles). B) Mean (± s. d) latitudinal variation in the sampling effort (number of unique sampling events; open circles) and two estimates of the inventory completeness (sample coverage: orange circles; species accumulation curve: dark blue circles) (extracted from Menegotto and Rangel, 2018). C) Marine taxonomic groups ranked by their state-of- knowledge index (mean ± s.d.) across taxa. Dashed lines represent the overall means (extracted from Costello et al., 2010). The state of knowledge it a measure of the sampling effort and it was classified from 1 to 5 (5 = very well known; 4 = well-known; 3 = poorly known; 2 = very poorly known; 1 = unknown.

1.6 Biogeographical regions and hotspots of marine diversity

The classification and mapping of global diversity have been important tools for the conservation and management of marine communities (Lourie and Vincent, 2004; Spalding et al., 2007). In recent years, an increasing number of studies have analysed biogeographical regions in accordance with the development of numerical methods (multivariate analyses) which have been used to classify biodiversity on clusters or groups of units of similar species, also allowing to include physical and biological characteristics (Ray and Hayden, 1993; Saeedi et al., 2017; Costello et al., 2017). Most of these studies have focused on terrestrial systems, being biogeographical regions usually defined by biomes, or ecological communities determined by their environment, and realms defined by continental plates (Udvardy and Udvardy, 1975; Olson et al., 2001). In contrast, fewer works explored biogeographical regions on the ocean due to the three-dimensional nature of marine habitats, their multitude dynamic processes which differ greatly depending on the communities, and the wide variety of life histories and species ranges in these ecosystems (Lourie and Vincent, 2004). Despite we can find some early works in the exploration of biogeographical regions and their boundaries in the marine environment (Ekman, 1953; Briggs, 1995), only in recent years some studies proposed consistent and standardized methods to identify biogeographical units in marine ecosystems. The most accepted system was proposed by Spalding and collaborators (2007), who reported a system of marine biogeographical regions for coastal zones based on different levels: 12 realms or large regions with unifying features of geography and diversity; 66 provinces or large areas defined by the presence of distinct biotas that have some cohesion over evolutionary time frames, and are driven by the different abiotic features such as geomorphological or hydrographic features; and 232 ecoregions, which present homogeneous species composition, and there are determined by isolation and other physical parameters (Fig. 3).

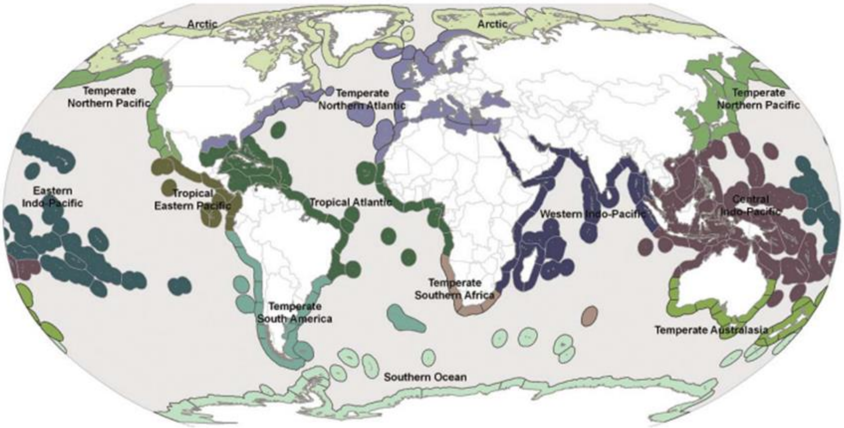


Figure 3. Biogeographic coastal realms with the ecoregions boundaries outlined (from Spalding et al., 2017).

In addition, the identification of "hotspots", or areas with high diversity is essential for effective conservation planning (Myers et al., 2000; Brooks et al., 2006). Moreover, these regions are known to present high concentrations of endemic species (species only found in those areas) (Kareiva and Marvier, 2003; Mittermeier et al., 2011). Previous studies have shown that most hotspot areas are distributed across coastal ecosystems due to the high diversity that they comprise, and they provide ecological and social services to the human populations (Costanza et al., 1997; Myers et al., 2000; Spalding et al., 2007) (Fig. 4A). Specifically, the regions with higher diversity in marine ecosystems have been documented in the Western Pacific for coastal taxa and in the North and South Atlantic for oceanic taxa (Tittensor et al., 2010) (Fig. 4B, C, D). Nonetheless, these hotspots usually occur in coastal areas that have been highly impacted by humans, highlighting the need to increase management and conservation efforts in these areas (Roberts et al., 2002; Tittensor et al., 2010).

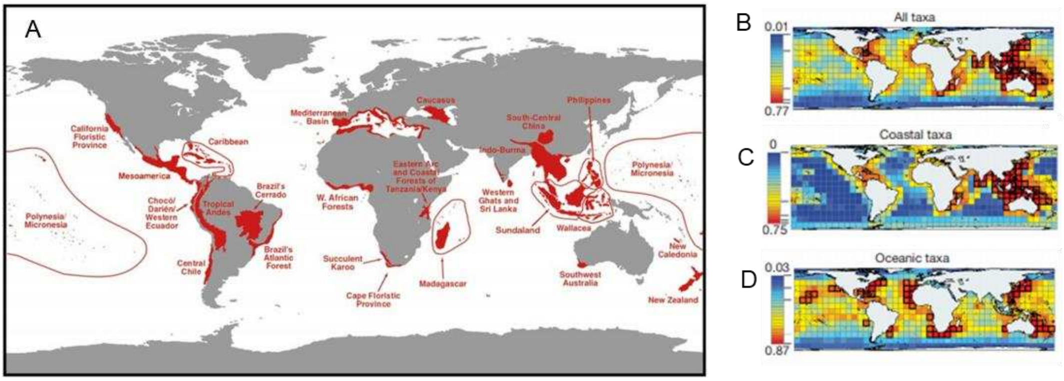


Figure 4. A) The 25 global hotspots (extracted from Myers et al., 2000). B, C, D) Marine species richness and hotspots across taxa (Global, coastal and oceanic respectively). Cells with the bold outline are hotspots (defined as the 10% of cells with the highest mean richness) (extracted from Tittensor et al., 2010).

2. Coastal ecosystems: threats to biodiversity

2.1 Multiple stressors affecting coastal ecosystems

As noted above, marine coastal ecosystems are characterized by high diversity rates and provide ecologically and socio-economic services to a large proportion of Earth's human populations (Costanza et al., 1997; Palumbi et al., 2009). Specifically, previous studies have estimated that the world's ecosystems provide an average of US $33 trillion dollars of services annually, with only US $10.6 trillion provided by the coastal systems (Costanza et al., 1997). However, these areas are highly affected by the cumulative effects of multiple stressors that drive biodiversity loss, resulting in compositional and structural changes in the communities, local extinctions, and destruction of marine communities (Jackson et al., 2001; Airoldi and Beck, 2007; Halpern et al., 2008). Specifically, previous studies have shown that most coastal areas are medium or highly impacted by humans, with areas such as the North Sea, the waters off of Eastern California and the Japanese waters being the most highly impacted, threatening marine communities such as coral reefs and the seagrasses of rocky reefs (Fig. 5) (Halpern et al., 2008).

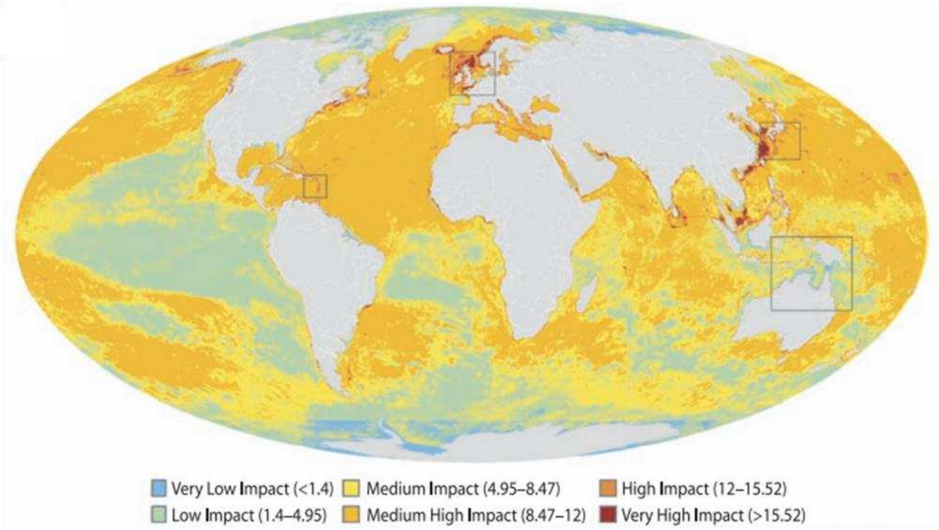


Figure 5. Global map of the cumulative human impacts across 20 ecosystem types. (Extracted from Halpern et al., 2008)

At local scale, multiple and interactive impacts are threatening coastal ecosystems as a result of human activities such destructive fishing practices, anchoring, diving, the overexploitation of natural resources and the eutrophication caused by environmental pollution, all of which drive biodiversity loss and cause subsequent changes in the structure and functioning of communities and even local extinctions (Jackson et al., 2001; Airoldi and Beck, 2007; Halpern et al., 2008). Moreover, at global scale, climate change is one of the most concerning threats to marine coastal ecosystems around the world.

2.2 Climate change, the most worrying threat

During recent decades, the increasingly high concentrations of carbon dioxide (CO_2) and the emissions of other gases into the atmosphere have changed the Earth’s climatic system, affecting different levels of biodiversity, from genes to ecosystems (Scheffers et al., 2016) (Fig. 6C). As a result, the global mean surface temperature has increased 0.74°C from 1906 to 2005 and is expected to increase between 1.8°C and 4°C during the twenty-first century, depending on the socio-economic Representative Concentration Pathway (RCP) emissions scenario, compromising the function and resilience of marine ecosystems (Hoegh-Guldberg and Bruno, 2010; IPCC, 2015) (Fig.6A, B).

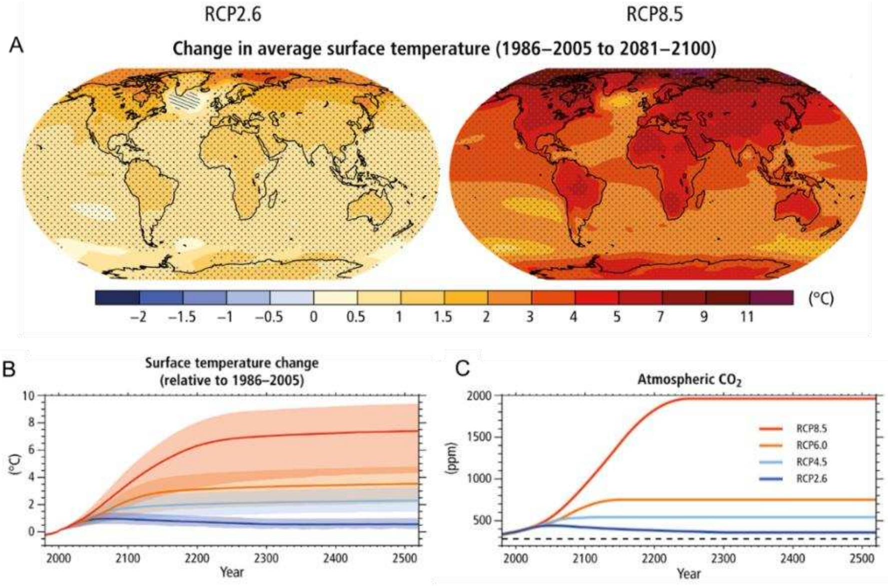


Figure 6. Projections of changes in the average surface temperatures (A, B) and atmospheric CO_2 (C) by the end of the 21st century under the different emission scenarios (extracted from IPCC, 2015)

In addition to warming, in recent years, there has been an increase in heatwaves or extreme events of warm sea surface temperature (SST) that persists for days to months, impacting the structure and functioning of marine ecosystems (Hobday, 2016). Moreover, these events may result in mass mortality events in benthic systems, such as those recorded on tropical coral reefs (Graham et al., 2008; Hughes et al., 2018) and also on temperate rocky reefs, affecting corals, gorgonians and bryozoans, among other organisms (Garrabou et al., 2009; Cocito and Sgorbini, 2014; Wernberg et al., 2016).

In addition to the increase in temperature, the increasing greenhouse gas concentrations will have other important impacts on the marine systems, such as the sea level rise or the decrease in pH due to the increased concentrations of CO_2 (Harley et al., 2006), affecting the physiological processes of marine benthic invertebrates and decreasing the calcification rates of those organisms made up of calcium carbonate skeletons, such as corals or bryozoans (Orr et al., 2005; Harley et al., 2006; Hoegh-Guldberg et al., 2007; Lombardi et al., 2011a, b, c).

2.3 Ecological responses to climate change and other threats

Climate change can impact marine populations directly at three different levels: at the species level, impacting different stages in the life history cycle of species, changing their physiologies, morphologies or behaviours; at the population level, affecting demographic processes such as recruitment; and at the community level, changing the relative abundances and interactions between species (Harley et al., 2006). Specifically, the vulnerability of marine species to warming is determined by their thermal tolerance preferences, and an increase in temperature can negatively affect their physiological and demographic processes, increasing the risk of the local extinction of species with limited thermoregulatory abilities (Hutchinson, 1957; Somero, 2002; O'Connor, 2008). Moreover, the increase in temperature can result in changes in the species distribution ranges. For example, during the recent decades, some marine species have been observed to respond to ocean warming by shifting the distributions of their latitudes and depth patterns (Perry et al., 2005; Pinsky et al., 2013). At a minimum, climate change can reduce the abundance and species richness of many marine species, having consequences on the communities and ecosystems such as changes in the habitat complexity and productivity currently observed in coral reefs and kelp forests (Harley et al., 2006; Hoegh-Guldberg and Bruno, 2010).

The ecological responses to climate change and other human threats can also be related to the species life history traits that determine their potential to mitigate environmental changes (Fields et al., 1993). Traditionally, ecologists have classified species life strategies between r- or K-selection (Parry, 1981). Later, species classification changed into a continuum of slow-fast gradient of species life history (Stearns, 1992; Jeschke and Kokko, 2009), founded on the idea that at one extreme are the species that growth quickly, which are highly reproductive but short-lived and are usually smaller-bodied and abundant; at the other extreme are the species that growth slowly, which have low reproductive rates but are long-lived, larger bodied and less abundant (Reynolds, 2003; Frisk, 2010). Previous studies have shown that in changing environments are successful those species that are short-lived due to earlier and higher growth and reproduction rates; conversely, in stable environments, the species that are successful are characterized by slow growth rates and long life spans (Cohen, 1966, 1968). Accordingly, in climate change scenarios, long-lived species are expected to have slow responses and lower capacity for recovery, decreasing their resilience and making them more vulnerable to environmental changes (Berteaux et al., 2004; Wiedmann et al., 2014; Quetglas et al., 2016). In this context, the ecological responses to climate change and multiple human stressors are complex, hindering the prediction of the long-term consequences on the benthic communities and highlighting the need for the understanding of the life history strategies and thermal tolerance preferences of species to manage and conserve populations in the context of increasing human stressors in marine ecosystems.

2.4 The Mediterranean Sea as a case study

The Mediterranean Sea is the largest and deepest enclosed sea on earth and represents a hotspot of terrestrial and marine biodiversity (Bianchi and Morri, 2000; Myers et al., 2000; Coll et al., 2010). Although it comprises only 0.82% of the global surface area, it is known to host more than 17,000 described marine species, holding 7% of the world's marine biodiversity as well as a high proportion of endemic species and several unique and endangered habitats, such as seagrass meadows (Boudouresque, 2004; Ballesteros, 2006; Coll et al., 2010). The high number of species observed in the Mediterranean Sea can be explained by its geological history, which is characterized by high rates of environmental change and speciation and a variety of climatic and hydrologic conditions, such as the annual seasonality recorded in the annual mean sea surface temperature, which shows varying gradients from the west to the east and the north to the south (Coll et al., 2010).

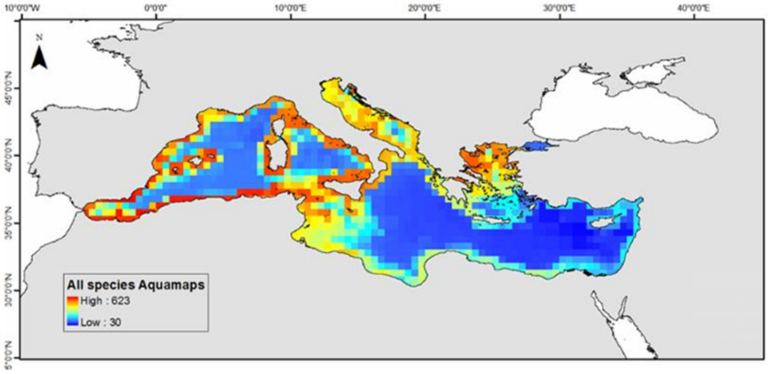


Figure 7. Species richness in the Mediterranean Sea (extracted from Coll et al., 2010).

The highest concentrations of species are found in the coastal waters of the western Mediterranean, the Adriatic and the Aegean Seas; conversely, the number of species decreases from the north-western to the south-eastern regions, following the gradient of productivity (Coll et al., 2010) (Fig. 7). The variety in these conditions enhances the variety of habitats that we can find in the Mediterranean Sea, comprised of assemblages of different species characterized by a wide range of life history strategies (Ballesteros, 2006; Coll et al., 2010). In the relatively shallow waters, we can find several unique and endangered habitats, such as the seagrass meadows of *Posidonia oceanica* and the coralligenous assemblages formed by the accumulation of encrusting algae growing in the dim light conditions, which are characterized by the presence of habitat-forming species such as the red gorgonian *Paramuricea clavata*, the red coral *Corallium rubrum*, and some bryozoan species such as *Pentapora fascialis* or *Myriapora truncata*, among multiple other species (Bianchi and Morri, 2000).

In addition, the Mediterranean coasts support a high density of inhabitants, providing ecosystem services to 143 million people distributed throughout 21 countries, and representing one of the top tourist destinations across the globe, with 200 million tourists per year (Coll et al., 2010). The main human drivers of historical biodiversity changes in the Mediterranean Sea have been identified as overexploitation and habitat destruction (Lotze et al., 2011). In recent years, the Mediterranean marine communities have been increasingly threatened by other interactive anthropogenic local stressors, such as fishing, pollution, eutrophication, invasive species, and global impacts, such as climate change, all of which are predicted to increase in the future and have greater impacts in coastal areas (Coll et al., 2010, 2012). In this region, climatic models predict an increase of 3.1 ºC in the mean surface temperature by the end of this century, compromising the viability of non-thermotolerant species in the long term (Coll et al., 2010). Accordingly, in this area in recent years, there has been an increment of species that are exposed to conditions over their thermotolerance limits due to global warming and an increase in heatwaves occurrence, resulting in mass mortality events of benthic organisms such as gorgonians, corals and bryozoans (Cerrano et al., 2000; Garrabou et al., 2009; Teixidó et al., 2013). Most of the affected species have been habitat-forming species that usually exhibit low population dynamics, slow growth and high longevity, which makes them more vulnerable to the cumulative effects of human perturbations with a low capacity for recovery (Garrabou et al., 2002; Linares et al., 2007; Linares and Doak, 2010; Teixidó et al., 2011; Kersting et al., 2014). At worst, the mortality of these habitat-forming species can impact the entire community, reducing the species richness and structural complexity of habitats and compromising the viability of these habitats in the long term (Hoegh-Guldberg and Bruno, 2010; Cahill, 2013).

3. Management and conservation tools in marine ecosystems

3.1 Marine protected areas

The creation of Marine Protected Areas (MPAs) has been recognized as an effective management and conservation tool for the protection and restoration of marine ecosystems and the mitigation of the multiple anthropogenic impacts (Milazzo et al., 2002; Harley et al., 2006). Due to an increase in interest in the conservation of biodiversity since the 1970s, there has been an increase in the establishment of marine protected areas around the world. However, this progress has been lower than that in terrestrial ecosystems, which have a higher proportion of protected areas than marine ecosystems (Watson et al., 2014) (Fig. 8). Specifically, in marine areas, by 2014, only 46 ecoregions (20%) had more than 10% protected coverage, and 107 ecoregions (46%) had less than 1% protected coverage (Fig. 8A). Conversely, terrestrial regions showed higher levels of protection, with 300 regions (36%) having more than 17% protected coverage, and only 68 (8%) having less than 1% protected coverage (Watson et al., 2014).

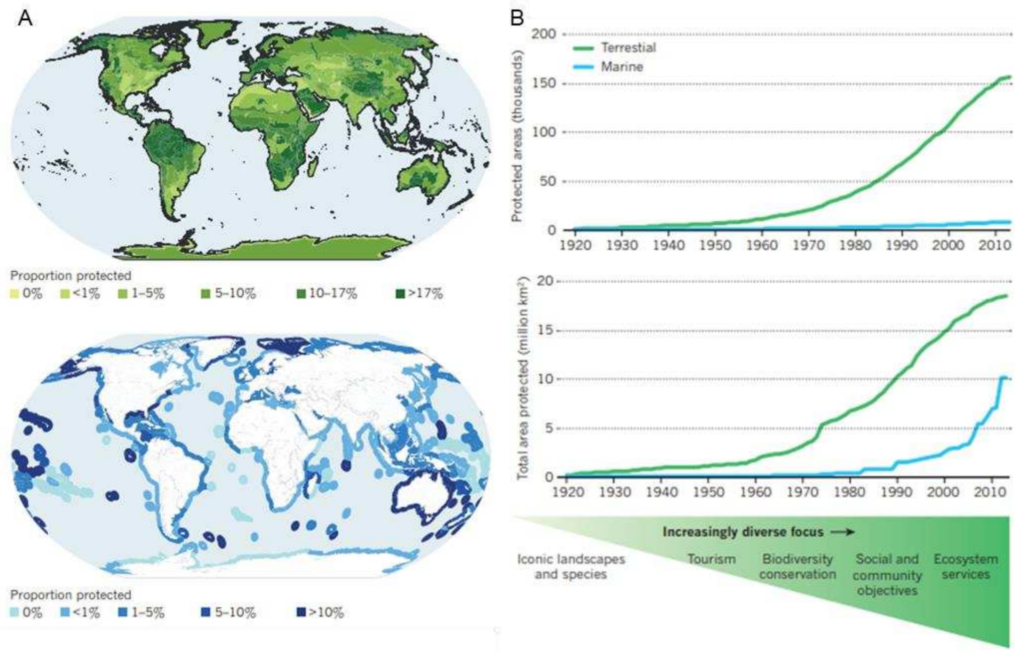


Figure 8. A) Proportion of each terrestrial and marine ecoregion protected by the year 2014. B) Growth of the modern terrestrial and marine protected areas. Note that the first formal protected area was established in 1864, and since this moment new and increasingly diverse focal objectives have been added to the objectives of protected areas (Extracted from Watson et al., 2014).

In 2004, the Convention on Biological Diversity (CBD), which had 193 parties, committed to protecting >10% of marine environments by 2020 (Secretariat of the Convention on Biological Diversity, 2010; Watson et al., 2014). This value was increased in the World Parks Congress in 2014, where the participants recommended the protection of 30% of the oceans by 2030. However, today's quantification of all marine protected areas showed that only 4.8% of the global ocean was protected. Moreover, of the total 11,805 MPAs around the world, 2622 have only been proposed but not implemented (Watson et al., 2014; Morgan et al., 2018; Sala et al., 2018).

MPAs may vary in design, maintenance, performance, and type of regulation because they integrate social and ecological attributes (Pollnac et al., 2010). MPAs were traditionally created to manage fisheries and to ensure the viability of fish stocks (Polunin, 1984; Mosquera et al., 2000). Accordingly, the most effective type of marine protected areas is the no-take marine reserve, where fishing is not allowed, which increases the size, density, biomass, and species richness of the fishes within the MPA boundaries, provides refuges for endangered and commercial species, and protect critical habitats from damage by destructive fishing practices and other human activities (Agardy, 2000; Mosquera et al., 2000; Sumaila et al., 2000; Micheli et al., 2004). Moreover, these areas enhance the local economy, providing human benefits through fishing and tourism activities (Sala et al., 2013).

Since the creation of MPAs, ecosystem-level benefits of the spatial protection have been documented (Hughes et al., 2007; Mumby and Harbone, 2010). Accordingly, they can increase the abundance of traditionally overfished species, restoring the ecosystem trophic cascades. For example, in the tropical coral reefs, it has been reported that enhanced herbivory within the MPAs facilitates new substrates for coral recruitment and recovery, which highlights that protection can also have benefits for benthic species (Mumby and Harborne, 2010; Selig and Bruno, 2010). However, although previous studies have registered an increase in the biomass, density, size and diversity of invertebrates and seaweeds within marine reserves (Lester et al., 2009), the direct effects of the protections on benthic ecosystems are unclear, with a high diversity of responses to the protection (Halpern, 2003; Micheli et al., 2004; Lester et al., 2009). In addition, due to the complexity of the organisms comprising the benthic communities, characterized by different life history strategies, their recovery and resilience normally occurs at longer temporal scales, hindering the effects of MPAs on benthic habitats (Linares et al., 2010a; Kaiser et al., 2018).

Conversely, the establishment of MPAs has contributed to an exponential increase in tourism attracted by the high biodiversity and ecological services, which can paradoxically negatively affect the marine ecosystems (Davis and Tisdell, 1995;

Badalamenti et al., 2000). Specifically, diving represents one of the major touristic activities in MPAs (Rouphael and Inglis, 2001; Hawkins et al., 2005; Parsons and Thur, 2008; Di Franco et al., 2009). In highly visited protected areas, scuba divers may affect the fragile sessile marine species in several ways, such as directly impacting the benthic organisms by breaking or damaging them, which results in a partial loss of the colonies (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández et al., 2014), or by indirectly affecting them by increasing sediment resuspension or creating air bubbles that might become trapped on marine caves (Lloret et al., 2006; Luna-Pérez et al., 2011).

One of the oldest and most popular Mediterranean MPAs is the Medes Islands reserve located in Montgrí, the Medes Islands, and the Baix Ter Natural Park in the northwestern Mediterranean Sea. This MPA represents one of the most frequently visited protected areas by divers across the Mediterranean Sea, with more than 50,000 dives per year in a small area of approximately 20 ha (Hereu and Quintana 2012; Sala et al., 2013; Hereu et al., 2017, 2018). Accordingly, the derived economic benefits of the protection of this area were estimated to be approximately 10 million euros annually (Merino et al., 2009; Capella, 2010; Sala et al., 2013). In this area, previous studies have highlighted the impacts of diving on benthic systems, causing fragmentation and decreasing the cover of corals, gorgonians and bryozoans (Sala et al., 1996; Garrabou et al., 1998; Linares et al., 2010b; Hereu et al., 2017, 2018).

3.2 Adaptive management plans are needed to ensure the optimal protection of natural populations

As noted above, despite MPAs have been recognized as effective management and conservation tools for protecting and restoring marine ecosystems, their establishment has contributed to an increase in recreational activities that can threaten marine benthic species (Milazzo et al., 2002; Harley et al., 2006). In this context, some studies have highlighted the need to implement adaptive management in MPAs, which consist of an iterative process of continuously improving decisions with changing management goals and methods based on the review and incorporation of new information and challenges (Walters and Hilborn, 1978). Specifically, the adaptive management strategies are based on the following steps: plan, implement, monitor, review, learn, revise, and repeat (Conservation Measures Partnership, 2007) (Fig. 9). In tropical regions, adaptive management programmes have been implemented successfully in developing nations where MPAs are usually small in size and decisions can be rapidly implemented (Cinner et al., 2006). However, in the developed countries, it has been more difficult to implement because the management tends to be centralized and the decision-making process is slower and more complex (Walters, 2007; McCook et al., 2010).

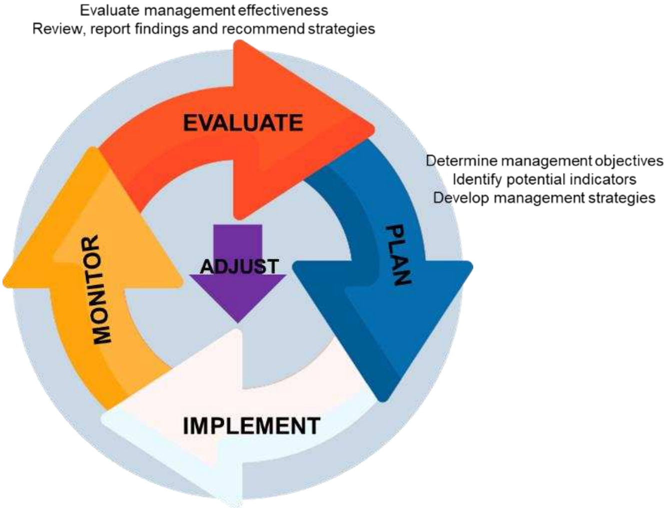


Figure 9. Conceptual diagram of adaptive management. Icon source: Flaticon (adapted from West, 2016).

Despite the debate about whether MPAs could mitigate and promote the resistance of species to climate change (Hughes et al., 2017a,b), effective adaptive management could help managers identify vulnerable communities and provide areas free of or with regulation of other local human perturbations, such as fishing, anchoring and diving. Several recommendations have been established to address the impacts of climate change in MPAs, such as a minimum MPA size (minimum 10-20 km diameters), which spreads the risk (replication of the MPAs with minimum representation of 20-30% of each habitat type), ensuring connectivity among the MPAs, and effective management of the frontiers of MPAs (McLeod et al., 2009). Moreover, effective management should consider socioecological parameters (Stringer et al., 2006; Armitage et al., 2009), such as the increase in tourism, which could greatly affect and degrade marine ecosystems (Wahab and Pigram, 1997). In addition, an effective management plan should include the identification and monitoring of potential indicator species. The sampling design (number of sites, temporal and spatial scale) of monitoring programmes should be based on the life history traits of the indicator species to detect changes in the structures and dynamics of the populations. Moreover, long-term programmes should be established to ensure the understanding of the dynamics and the functioning of the natural ecosystems and to evaluate their response to human threats (Lovett et al., 2007; Lindenmayer and Likens, 2009).

Due to the increasing number of local and global stressors in natural ecosystems, ecological indicators have been recognized as efficient tools for assessing the state and functionality of ecosystems (Salas et al., 2006). They are components of the ecosystems that can be used to assess the traits, characteristics and qualities of an ecosystem, which facilitates the assessment of the responses of natural communities and helps in development planning and decision-making (Salas et al., 2006; Mellin et al., 2011). Salas et al., (2006) proposed the following characteristics that define a good ecological indicator: "handling easiness, sensibility to small variations of environmental stress, independence of reference and control samples, applicability to extensive geographical areas and in the greatest number of communities or ecological environments, and relevance to policy and management's needs". In benthic systems, previous works have focused on the presence/absence of the indicator species and on the identification of different ecological strategies, diversities, or energy variations in the system (Salas et al., 2006). Following the previous criteria, some benthic species have been used as ecological indicators of human threats, such as species of the genera *Cystoseira*, the seagrass *Posidonia oceanica* or sponges as indicators of good water quality (Pergent-Martini, 1998; Pinedo et al., 2007; Juanes et al., 2008; Selvin, 2009), and gorgonians, sponges or bryozoans as indicators of the impacts of diving (Linares et al., 2010b; Luna-Pérez et al., 2010; De la Nuez-Hernández et al., 2014).

3.3 Restoration actions are needed when only protection is not adequate to enhance the recovery of degraded ecosystems

The rapid degradation of most ecosystems highlights the urgency of applying active management actions, which implies that direct human interventions are needed in addition to the establishment of protected areas to enhance biodiversity and restore ecosystem services (Holl and Aide, 2011; Possingham et al., 2015). Ecosystem restoration has been defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2004). While passive restoration is focused on protecting and removing the impacts of environmental stressors, such as through the creation of MPAs, active restoration is based on human management techniques applied directly to the environment, such as transplanting, planting seeds, deploying artificial surfaces in the natural habitat to enhance the recruitment of model species, and the construction of artificial reefs (Abelson, 2006; Bayraktarov et al., 2016). The decision about whether we should restore or protect depends on several ecological and social factors, such as the ecosystem to be restored, the economy of the country and the techniques to be applied (Bayraktarov et al., 2016).

Until now, most of the active marine restoration actions on benthic species have focused on charismatic groups such as gorgonians or corals (Linares et al., 2008; Benedetti et al., 2011: Montero-Serra et al., 2018), ignoring other abundant and vulnerable habitat-forming groups such as bryozoans.

4. Bryozoans: an abundant and common group but generally understudied in biogeographic and conservation studies

4.1 Biology and ecology of bryozoans

To date, most global marine conservation studies have focused on charismatic taxa such as mammals, fishes, corals or seagrasses (Tittensor et al., 2010), with fewer examples of traditionally understudied but very abundant taxa in marine ecosystems such as bryozoans, bivalves or molluscs (Chaudhary et al., 2016; Saeedi et al., 2017). Bryozoans are a phylum of aquatic invertebrates containing almost 6000 described species (Bock and Gordon, 2013) and are one of the most common and most abundant marine invertebrates in the benthic ecosystems (Bock, 1982; Ballesteros, 2006; Wood et al., 2012). They are suspension-feeding colonial invertebrates that are widely distributed across the globe, inhabiting most types of marine ecosystems (Ballesteros, 2006; Wood et al., 2012). Some previous works have shown a high diversity of bryozoans in the Southern Ocean, in contrast with other groups such as corals (Barnes and Griffiths, 2008; Tittensor et al., 2010). However, bryozoans have traditionally been overlooked in macroecological studies, leading to a lack of knowledge about their global diversity patterns and the environmental drivers behind these patterns.

These organisms are composed of functional units called zooids, which can differentiate functionally and structurally, and that are separated by walls constructed of skeletal material and organic cuticle. The communication between the zooids is through a funicular system of pores located in the dividing body walls. Feeding zooids or autozooids have a lophophore, or a ring of tentacles, at their distal end, on which cilia can create water flow into the mouth providing tiny particles of food (Fig. 10A). The mouth opens to the digestive tract that is divided into several regions and terminates in an anus that is located near the tentacles, which is why bryozoans are also known as Ectoprocta (Fig. 10A). Some species present zooid polymorphisms, such as the presence of avicularias, which are thought to be involved in keeping the colony free from particles and epizooties (McKinney and Jackson, 1991; Zabala, 1986;

Ryland, 2005) (Fig. 10A). The zooidal nervous system of the bryozoans consists of a small ganglion positioned between the mouth and the anus that supplies nerves to the various organs. The respiratory, circulatory and excretory systems are absent in bryozoans (Bock, 1982; Zabala, 1986; Ryland, 2005). The skeleton is external and calcified, giving bryozoans a rich fossil record that dates from the Ordovician (~500 My ago) (Ryland, 2005; Taylor and Waeschenbach, 2015).

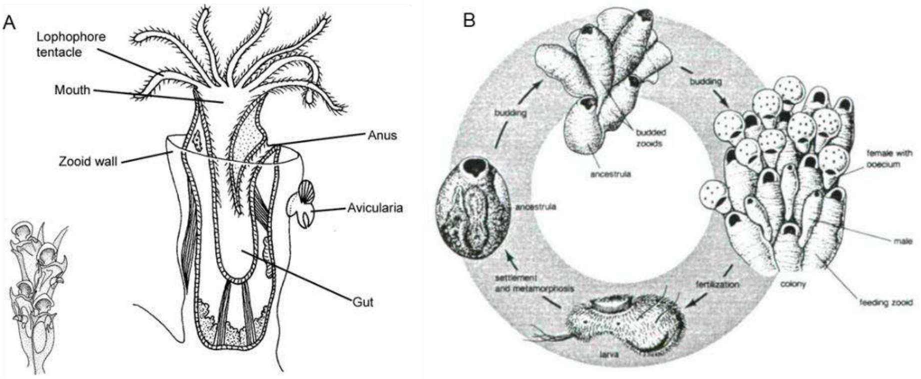


Figure 10. A) Morphological structure of a bryozoan (Illustrations from Ivy Livingston, BIODIDAC, extracted from sciencematey.com). B) Life cycle of *Cellepora* spp., representing the sexual phase, showing the larva that settles and metamorphoses, and creates the ancenstrula, and then through asexual growth by budding, creates the whole colony, which can be formed by sexual zooids (males, and ovicellate females or gonozooids) (extracted from Ryland, 2005).

Their life cycle is characterized by periods of sexual and asexual reproduction. Bryozoans produce pelagic larvae through sexual reproduction, and after a short time, these larvae settle and forms a primary zooid (ancestrula) that starts to grow through asexual reproduction by budding, producing new zooids (Fig. 10B). In this growth process, some zooids can become sexually mature, producing eggs and spermatozoa. The reproductive organs (ovary, testes) are situated on the lining of the body wall or on the funicula, a cord of tissue that links the stomach to the lining of the body wall. Although some species have differentiated male and female zooids, the majority of them have hermaphroditic zooids. The process of fertilization also depends on the species; some present external fertilization (in the sea); and other species show internal and, in most cases, cross-fertilization occurs in specialized zooids called gonozooids derived from the enlarging of female zooids, which are formed by a sac or a brood chamber called the ooecium, and skeletal protection called the ovicell (Bock, 1982; Zabala, 1986). Moreover, asexual reproduction may also occur by fission or fragmentation processes, producing identical progeny or clones (Zabala, 1986; McKinney and Jackson, 1991; Ryland, 2005).

Bryozoan species present great variability in colony sizes and forms, finding small colonies that can create crusts measuring only a few centimetres in contrast to other large and rigid colonies (Zabala, 1986) (Fig. 11). Large erect bryozoans are considered frame-builders and are characterized by presenting well-skeletonized structures that provide most of the volume and rigidity to the framework (Cocito, 2004; Lombardi et al., 2014). Bryozoan bioconstructions are widely distributed in coastal ecosystems across temperate environments (Wood et al., 2012). Specifically, the surfaces of bryozoan bioconstructions can provide several functions and ecological services, such as enhancing the settlement and recruitment of other benthic organisms by providing new substrates for colonization (Cocito, 2004; Wood et al., 2012; Lombardi et al., 2014), facilitating colonization by other bryozoan species (Cocito, 2004; Lombardi et al., 2014), offering protection and refuges from predation and competition, wave scour and high light irradiance (Buss and Jackson, 1979; Bradstock and Gordon, 1983; Lombardi et al., 2014), increasing carbon sequestration (Cocito and Ferdeghini, 2001; Wood, 2014), decreasing sedimentation rates, increasing the sediment that is incorporated into the benthic framework (Laubier, 1966), and increasing the variability of hydrodynamic and microtopographic conditions, which increases the variety of suitable feeding sources for different organisms (Cocito and Sgorbini, 2014). However, these structures are threatened by several local and global stressors and can produce the consequent loss of biodiversity, compromising the ecological services provided by these frame-builders (Gray, 1997; Moberg and Folke, 1999; Cadotte et al., 2011).

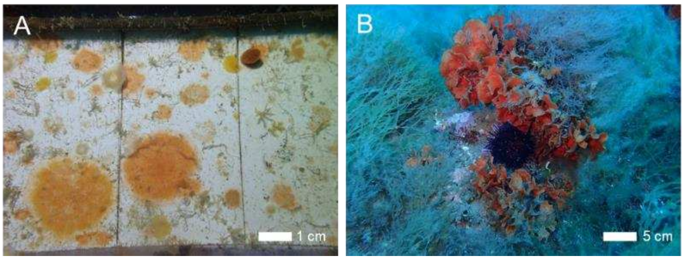


Figure 11. Diversity of sizes and forms of bryozoans from: A) Small colonies of different Mediterranean bryozoans species that create crusts, such as *Chorizopora brogniartii, Puellina hincksi or Disporella hispida*, to B) large colonies of the Mediterranean bryozoan *Pentapora fascialis* that can reach diameters up to 1 meter.

4.2 Current knowledge of bryozoans at global and local scales

Most bryozoan works have focused on the study of their zoology, followed by environmental sciences, ecology and palaeontology, as shown by a search of the Web of Science until August 2019 (Fig. 12). Moreover, we found a high proportion of bryozoan studies in the field of biomedicine (Fig. 12). Like other benthic organisms, some bryozoans produce bioactive compounds or metabolites, such as alkaloids, which have been investigated for the development of pharmacological products, such as the bryostatins produced by *Bugula neritina*, which have been identified as a potential anticancer compound (Jha and Zi-rong, 2004).

Approximately 17,000 bryozoan studies were found and the most published document types have been articles in scientific journals (16,298), followed by books (1523). This contrasts with the other benthic groups such as corals (68,892 articles) or sponges (77,834 articles), highlighting the lower level of knowledge and the fewer research efforts made in bryozoan research areas. On the other hand, the most productive bryozoan authors have been Paul D. Taylor (700 works), an ecologist focused in palaeontology and systematics of bryozoans; Dennis P. Gordon (266 works), an ecologist focused on the study of marine biodiversity, taxonomy and systematics of bryozoans; and Beth Okamura (117 works), an ecologist focused on the study of the ecology and evolution of bryozoans, which highlights that until now, the major efforts in bryozoan studies have been made in taxonomic and systematic areas. Accordingly, the Journal of Palaeontology (324), which is focused on the systematics, phylogeny, paleoecology, paleogeography and evolution of fossil organisms, represents the journal with the highest number of published bryozoan studies.

The first recorded studies were focused on bryozoan taxonomy and palaeontology showing a high interest in the description of new species and the study of fossil recording during the 1700s and 1800s (Costello et al., 2010). However, in recent years, there has been an increase in bryozoan works in other research areas. On the other hand, most of the studies have been carried out in North American or the United Kingdom, with fewer efforts made in other areas (Fig. 12), reflecting the need for an increase in the effort in these regions. Some other research areas, such as diversity and distribution patterns, have been less studied in bryozoan works; only location-specific studies were found, such as the studies in the North Atlantic or the Southern Ocean (Clarke and Lidgard, 2000; Barnes and Griffiths, 2008; Griffiths et al., 2009). Although ecologists have always been interested in macroecology, this field was named and formally described in 1989, when it became an emergent and rapidly growing field presenting many opportunities and challenges, which is why we found few related studies until this moment (Brown and Mauner, 1989; McGill, 2019).

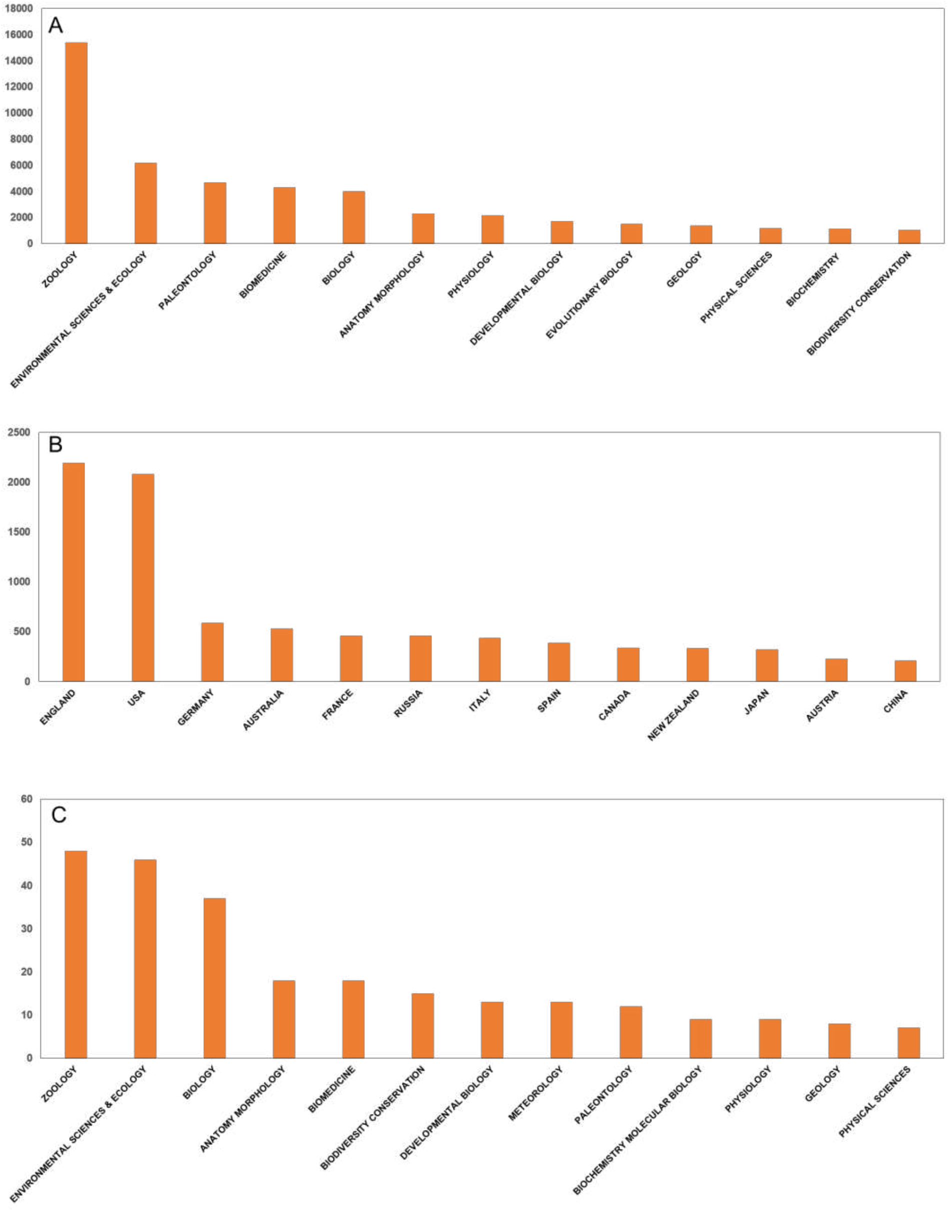


Figure 12. Bryozoan results from the ISI Web of Knowledge. A) Number of works for the 12 most researched areas. B) The number of works for the 12 most researched countries. C) The number of works in the Mediterranean Sea for the 12 most researched areas.

In contrast, several ecological works have focused on the study of skeletal minerology, growth rates and carbonate production (Lombardi et al., 2006; Rodolfo-Metalpa et al., 2010; Smith, 2014). Bryozoans have a calcified skeleton that can be formed by calcite, aragonite or both (Smith, 2014), making them particularly sensitive to acidification, which has gained the attention of ecologists. Specifically, some works have focused on the study of the effects of these environmental variables on the growth bands sometimes presented in bryozoan species such as *Pentapora fascialis* or on other parameters such as zooid size of other species (Menon, 1975; Okamura, 1992; Bader and Schäfer, 2004; Cocito, 2006; Lombardi et al., 2008a).

Despite the lower frequency of works on bryozoan population dynamics, we found the first demographic studies during the latest 1900s, when Stebbing (1971a) studied the growth of *Flustra foliacea*, Keough (1989) studied the growth rate and reproduction of *Bugula neritina* and showed a plastic response of colonies to environmental variations, and Hughes (1990) made the first explorations to unravel the population dynamics of the bryozoan *Celleporra pumicosa*, investigating the recruitment limitations, mortality and population regulation. Other first efforts were made by Harvell et al., (1990), who explored through matrix demographic models the effects of the density of the bryozoan *Membranipora membranacea* on its population dynamics, accounting for growth, reproduction and death. Later, other matrix population analyses were focused on *Mucropetraliealla elleri* and the study of the effects of fragmentation on its demography, highlighting the importance of considering the bryozoan asexual reproduction on the study of population dynamics (Linacre and Keough, 2003). Accordingly, other works have focused on the study of the asexual propagation and fragmentation of the marine bryozoan *Cupuladria exfragminis*, showing that autofragmentation was stimulated by cold waters (O'Dea, 2006) and the study of the partial and whole-colony mortality patterns in *Membranipora membranacea* (Denley and Metaxas, 2016). Recent efforts have analysed other aspects, such as the effects of size, age and damage on the demography of *Watersipora subtorquata* (Hart and Keough, 2009), the effects of dispersal and abundance on the *Bugula neritina* population dynamics (Burgess and Marshall, 2011), and the variation in settlement, recruitment and colony cover in *Membranipora membranacea* (Caignes and Gagnon, 2012). Beyond the differences among these works, all of them showed great variability in the demographic parameters between species and between the studied locations, highlighting the need to perform site-specific studies and making more difficult to understand bryozoan population dynamics and their life history traits.

In the Mediterranean Sea, we found 1036 bryozoan studies, in contrast with other benthic groups such as corals (2516 studies) or sponges (2669 studies). The differences were smaller than those observed at the global scale, which suggests that they are more studied in this area in comparison with the areas. Again, zoology has been the most studied research area, followed by environmental science/ecology. The most productive authors have been Jean-Georges Harmelin (89 works), an ecologist focused on benthic taxonomy and systematics; Antonietta Rosso (46 works), focused on paleobiology, systematics and marine biology; and Silvia Cocito (32 works), an ecologist focused on the biodiversity and conservation of the Mediterranean benthic assemblages and particularly on the study of the bryozoan *Pentapora fascialis*. As in global studies, we found the first bryozoan works in the Mediterranean Sea during the latest 1800s, according to the taxonomic and systematic works describing the Mediterranean bryozoan fauna, which rapidly increased the number of studies about other research areas since the 2000s.

4.3 The Mediterranean bryozoan *Pentapora fascialis* as model species

In the Mediterranean Sea, bryozoans constitute a common and abundant group recognized as bioconstructional framework builders and have been used widely as indicators of physical impacts such as diving or storms due to their high abundance and fragility (Sala et al., 1996; Garrabou et al., 1998; Ballesteros, 2006; Garrabou et al., 2009; Lombardi et al., 2013; Teixidó et al., 2013; De la Nuez-Hernández et al., 2014).

The Mediterranean benthic fauna contains approximately 480 species of bryozoans (Rosso, 2003), most of which form large colonies with calcareous skeletons conformed by encrusting multilaminar sheets that are able to form dome-like colonies and erect arborescent colonies contributing to bioconstructions (Lombardi et al., 2014). In contrast to the most of Mediterranean habitat-forming species, the preliminary studies on the growth rates for bryozoans showed higher values than those for other benthic groups (Cocito et al., 1998b), suggesting that they may display faster population dynamics and a higher capacity for recovery to environmental changes than other slow-growing species.

Specifically, this thesis is focused on *Pentapora fascialis*, which is known as the largest erect bryozoan; colonies can reach up to 1 m in diameter, and it is considered a frame-building and habitat-forming species due to its biogenic constructions (Cocito, 2004; Wood et al., 2012, Lombardi et al., 2014) (Fig. 13). It is distributed along the Mediterranean Sea, where its preferred substrates are rock bottoms exposed to strong currents, which are not subjected to heavy sediment accumulation, from 15 to 100 m depth (Zabala, 1986; Cocito et al., 1998b) (Fig. 13).

Moreover, on vertical walls, it can be found in exposed epibiotic positions on the gorgonian branches where water flow is more active, enhancing the prey capture (Sala et al., 1998; Lombardi et al., 2008b) (Fig. 13). It has bright orange calcified erect colonies and an encrusting base with bilaminar branches showing a globular shape (Zabala, 1986; Sala et al., 1996; Cocito, 2004). The habitat generated by *P. fascialis* enhances the associated marine biodiversity, providing new substrates for colonization by other organisms, such as small bryozoans, and offering refugee and protection from predation and competition for other organisms, such as crustaceans, bivalves, and fishes (Ferdeghini and Cocito, 1999; Cocito, 2004; Wood et al., 2012). Moreover, *P. fascialis* has to be considered one of the major contributors to the carbonate budget in the Mediterranean Sea due to its complex structures incrementing the carbon standing stocks (Cocito and Ferdeghini, 2001), and like other benthic filter-feeding species, it maintains the levels of phytoplankton by active filtering and decreases the sedimentation of particulate materials (Laubier, 1966; Officer, et al., 1982). Due to the fragility of its physical structure, this species may be threatened by severe storms and several perturbations, such as diving, warming, severe storms, pollution and siltation (Sala et al., 1996; Cocito et al., 1998a; Garrabou et al., 1998; Cocito and Sgorbini, 2001; Harmelin and Capo, 2001; Cocito and Sgorbini, 2014). Despite the importance and abundance of the species, its population dynamics, thermotolerance and recovery patterns remain unknown, compromising the proper management of this species in the context of increasing human stressors. For this reason, the present thesis aims to contribute to the improvement of the knowledge of the biology and ecology of this species.

In addition, in this thesis, we also analysed thermotolerance preferences and the effects of warming on demographic parameters of another abundant bryozoan on the Mediterranean Sea, *Myriapora truncata*. This species is also considered a forming-habitat species, presenting bright orange arborescent colonies, with a small incrusting base and bilaminar truncate branches showing tree-like growth, usually called "false coral" to their physical similarity to the red coral *Corallium rubrum* (Zabala, 1986). It is distributed along the Mediterranean Sea, occupying cryptic positions from 1 m depth in marine caves to 60 m in coralligenous bottoms and walls reaching 130 m in Tunisian area (Zabala, 1986) (Fig. 13). Due to its fragility and abundance, it has been used as an indicator of climatic change and sea acidity indicator (Berning, 2007; Lombardi et al., 2011a,b,c). There is little information about its life cycle and colony growth. However, previous studies suggested that due to their physical similarity and distribution as other slow-growing species, it may have lower population dynamics than other Mediterranean bryozoans, such as *P. fascialis* (Zabala, 1986).

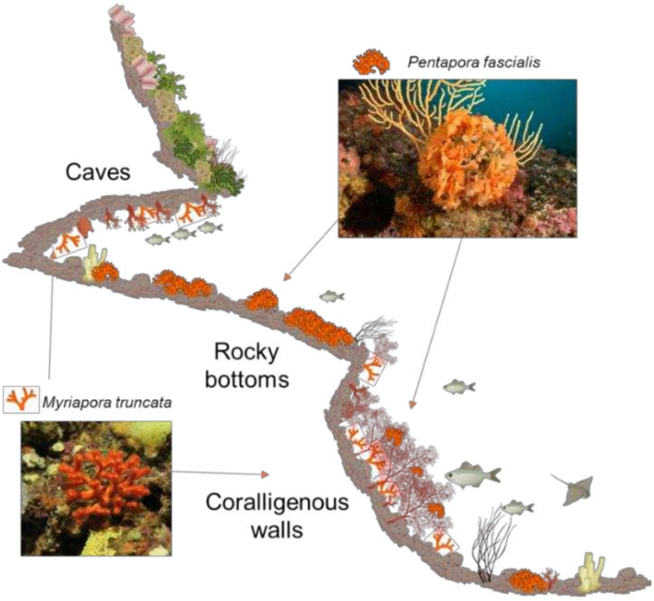


Figure 13. Benthic habitat of the Mediterranean bryozoans *Pentapora fascialis* and *Myriapora truncata* in a typical benthic Mediterranean system. Source: IAN Symbols Library, M. Pagès-Escolà, Medrecover group.

Aims of this thesis

The main aim of this doctoral thesis is to enlarge our knowledge about different ecological aspects of bryozoans, such as unravelling their discovery and biodiversity patterns at the global scale and to investigate the responses to local and global stressors, their thermal tolerances, and developing restoration actions to properly manage and conserve these organisms face increasing human impacts on coastal ecosystems.

At a global scale, we analysed discovery trends on extant and fossil bryozoans, and we estimated future projections of bryozoan discoveries to analyse the completeness of bryozoan inventories (Chapter 1). In addition, we analysed the bryozoan diversity patterns by comparing them with those of other sessile marine species, accounting for their latitudinal diversity patterns and hotspot areas. Moreover, we identified the environmental drivers of diversity patterns through environmental modelling accounting for the differences in the sampling effort (Chapter 2).

At a local scale, several studies have used bryozoan species as indicators of diving, storms or climate change but unfortunately without exploring these effects at the demographic level. Focusing on the Mediterranean Sea, we compared the vulnerability of two abundant and common bryozoan species*, P. fascialis* and *M. truncata*, which showed the importance of exploring the physiological differences between co-occurring species (Chapter 3). Moreover, we explored the impact of diving on the *P. fascialis* population dynamics, accounting for the survival, recruitment and growth rates, which have important implications for the recovery and management of these populations (Chapter 4). Finally, we explored restoration techniques for *P. fascialis*, testing for the first time on bryozoans the effective methodologies that have been previously performed on other benthic species, such as gorgonians or corals (Chapter 5).

The five chapters of this PhD combine open source data analyses (Chapters 1 and 2), modelling techniques (all chapters), field studies and manipulative experiments (Chapters 3, 4, and 5) and controlled experiments in the laboratory (Chapter 3).

The specific objectives of this PhD are as follows:

Chapter I: Progress in the discovery of extant and fossil bryozoans

The number of species that exist on Earth is an intriguing question in ecology and evolution. Previous studies have analysed trends in the discovery of marine extant species without comparing them to the fossil record. In this chapter, we compared the rates of description between extant and fossil species of bryozoans. Specifically, we analysed the trends in the description of new species, number of authors, and their relative productivities. In addition, we projected the future descriptions of both groups by the end of this century.

Chapter II: Global patterns and drivers of marine sessile biodiversity: novel insights focusing on the overlooked but abundant group of bryozoans

One of the major goals of ecology is to understand the biodiversity patterns at global spatial scales. The recent rise of open data availability and computational power has led to major advances in biogeography and macroecology. However, benthic marine ecosystems remain largely unexplored, and the highly heterogeneous sampling effort can result in biased conclusions about diversity patterns and their drivers. We analysed global diversity patterns in benthic habitats with a comparative approach focusing on bryozoans, a traditionally overlooked but highly diverse and abundant taxa. Moreover, we analysed the potential biases in the sampling efforts between marine regions, and we performed two types of generalized linear models to unravel environmental drivers of diversity patterns, comparing the use of the widely used rarefied species richness (ES50) method *versus* the incorporation of a new sampling effort correction using non-rarefied species richness. Finally, we accounted for the increase in SST under different RCP emissions scenarios in hotspot areas of marine sessile species and bryozoans to unravel the vulnerability of highly diverse regions to climate change.

Chapter III: Divergent responses to warming of two common co-occurring Mediterranean bryozoans

Climate change threatens the structure and function of marine ecosystems, highlighting the importance of understanding the response of species to changing environmental conditions. Despite thermal tolerance determines the vulnerability to warming of many abundant marine species, it is still poorly understood. In this study, we quantified in the field the effects of a temperature anomaly in the Mediterranean Sea during the summer of 2015 on the populations of two common sympatric bryozoans, *M. truncata* and *P. fascialis*. Then, we experimentally assessed their thermal tolerances in aquaria as well as their different sublethal responses to warming.

Chapter IV: Unravelling the population dynamics of the Mediterranean bryozoan Pentapora fascialis to assess its role as an indicator of recreational diving for adaptive management of marine protected areas

Marine protected areas have been recognized as effective management and conservation tools to protect marine coastal ecosystems. However, due to an increasing interest in marine ecosystems, recreational activities such as scuba diving are rapidly growing in these areas, highlighting the need for adaptive management strategies based on continuous monitoring and evaluation. To date, several studies have quantified the impacts of diving using benthic species, such as bryozoans, as indicators, but these studies have usually ignored their population dynamics. In this chapter, we studied the population dynamics of the abundant and common bryozoan *P. fascialis* in a Mediterranean MPA with high levels of diving activity, accounting for the density and size of the colonies, partial mortality, recruitment, survival, and growth and compared them between frequented and non-frequented locations. Moreover, we compared the densities observed in this study to those from previous studies performed in the same area during the 1990s.

Chapter V: Assessing the effectiveness of restoration actions for bryozoans: the case of the Mediterranean species Pentapora fascialis

Marine ecosystems are highly affected by several human stressors. Beyond passive restoration such as the establishment of marine protected areas, it is urgent to explore active restoration actions to ensure the recovery and long-term viability of the vulnerable marine sessile species. Despite their commonness and abundance, restoration actions for bryozoans have rarely been explored to date. In this study, we focused on two types of methodologies: recruitment enhancement and transplantation of adult colonies using the Mediterranean bryozoan *Pentapora fascialis* as a model species. First, we installed different types of artificial surfaces to test the effectiveness of the enhancement of recruitment. Then, we tested different methodologies for adult transplantation, and using the most successful method, we performed a restoration action by transplanting adult colonies collected from a ghost fishing net.

CHAPTER I: Progress in the discovery of extant and fossil bryozoans

Abstract

The number of species that exist on Earth has been an intriguing question in ecology and evolution. For marine species, previous works analysed trends in the discovery of extant species, without comparison with the fossil record. In this work, we have compared the rate of description between extant and fossil species of the same group of marine invertebrates, Bryozoa. There are nearly three times as many described fossil species as there are extant species. This indicates that current biodiversity represents only a small proportion of Earth's past biodiversity, at least for Bryozoa. Despite these differences, our results showed similar trends in the description of new species between extant and fossil groups. There has been an increase in taxonomic effort during the past century characterized by an increase of the number of taxonomists, and no change in their relative productivity (i.e., similar proportions of authors described most species). The 20th century had the most species described per author, reflecting increased effort in exploration and technological developments. Despite this progress, future projections in the discovery of bryozoan species predict around 10% and 20% more fossil and extant species than named species, respectively, will be discovered by 2100, representing 2430 and 1350 more fossil and extant species respectively. This highlights the continued need for both new species descriptions and taxonomic revisions, as well as ecological and biogeographic research, to better understand the biodiversity of Bryozoa.

1. Introduction

Assessing the number of species existing on the planet has been a focus of interest of biologists and ecologists for centuries (Ødegaard, 2000). The decade 2000-2010 saw more marine species named than any decade earlier, and over five times more people naming species than before (Benton, 2008; Appeltans et al., 2012; Costello et al., 2012). However, while there are more scientists working in taxonomy, there has been a decrease in the number of species described per author in terrestrial, freshwater and marine groups (Costello et al., 2012), parasites (Costello, 2016), and other taxa suggesting a declining rate in the discovery of new species in relation to taxonomic effort (Joppa et al., 2011; Appeltans et al., 2012).

Quantifying and understanding biodiversity is vital to biological and ecosystem sciences, management of natural resources and to predict which species may become extinct (Costello et al., 2013a). In this context, the commonest measure of biodiversity is species richness (Hamilton et al., 2010; Costello and Wilson, 2011). The most recent inventory of named marine species listed 243,000 out of an estimated total of 300,000 (Costello and Chaudhary, 2017).

In the last 600 million years the fossil record indicates that in addition to background extinctions, around 65–95% of marine species disappeared during five mass extinctions (Raup, 1986; Wake and Vredenburg, 2008; De Vos et al., 2015). Accordingly, related work has calculated that present-day biodiversity constitutes only 2–5 % of all species that ever existed (May, 1994) suggesting that c. 10–32 million marine species became extinct (Costello et al., 2012). Paleontological research provides the only avenue of inquiry in estimating past biodiversity and reconstructing past ecosystems and extinctions (Cooper et al., 2006; Wang and Dodson, 2006; Harnik et al., 2012). However, the fossil record is taxonomically biased and incomplete. Small organisms are underrepresented compared to original extant populations (size bias) (Kidwell, 2001; Jablonski et al., 2003; Cooper et al., 2006), macroevolutionary patterns are correlated with variability in the sedimentary rock record (Raup, 1972; Crampton et al., 2003; Peters, 2005), and preservation varies amongst taxonomic groups (Foote and Sepkoski, 1999). Despite these limitations, there are some taxa that are well preserved in fine-grained, originally soft sediments, particularly marine invertebrates with mineralized skeletons (Thayer, 1979; Smith and McGowan, 2011).

In many benthic ecosystems, bryozoans are among the commonest and most abundant invertebrates, sometimes forming complex habitats for other species (Ballesteros, 2006; Wood et al., 2012). They are suspension-feeding colonial invertebrates, widely distributed, inhabiting most types of aquatic ecosystems.

Because they are predominantly calcifying organisms, bryozoans are well preserved in the fossil record. There are three classes: Phylactolaemata are freshwater species with a very limited fossil record; Stenolaemata are exclusively marine and widely represented in the fossil record; and Gymnolaemata are predominantly marine and comprise the majority of extant species (Bock and Gordon, 2013).

The earliest bryozoan records are from the Early Ordovician (500–430 Myr ago), with peaks of Stenolaemata diversity in the Ordovician, Devonian, Carboniferous and Permian, before being hit hard by the Permo-Triassic extinction event (McKinney and Jackson, 1991; Knoll, 2003; Taylor and James, 2013; Taylor and Waeschenbach, 2015). The Mesozoic was a time of recovery for Stenolaemata, with only the order Cyclostomatida surviving into and beyond the Jurassic, and it continued to radiate into the Cretaceous (Ryland, 2005). Following its origination in the Late Jurassic, the order Cheilostomatida (class Gymnolaemata) exhibited competitive interactions with cyclostomes during the Late Cretaceous, when cheilostomes underwent explosive radiation developing most of the complex skeletal structures that characterize today's species (Sepkoski et al., 2000; Ostrovsky and Taylor, 2005; Ryland, 2005; Taylor et al., 2015). Accordingly, bryozoans constitute an excellent group for studying the fossil record.

In this paper, we provide the first comparison of trends in the description of fossil and extant species in bryozoans. In addition, we examined changes in numbers of authors of species descriptions as an indicator of taxonomic effort over time. Finally, we modeled the rate of species description to predict how many, and what proportions of named, species will be discovered this century.

2. Materials and Methods

2.1 Data Sources

For our analyses, we used the bryozoan list from the World Register of Marine Species (WoRMs), an open-access online database which includes all taxonomically accepted bryozoans and distinguishes marine, freshwater and fossil species (Costello et al., 2013a; Horton et al., 2018). Although data were downloaded in December 2017, the marine data were last updated in 2014. Fossil data were collated from the literature by author PEB, and were current to 2017. Additional freshwater data to some already in WoRMS were collated by author DPG, also current to 2017. To avoid over-estimation of the number of species, we analysed only species with formally accepted nomenclatural status. We thus excluded species' names that were classified as 'unaccepted' or 'alternate representation' to avoid invalid, synonymous names, as validated by the corresponding taxonomic editor (PEB). We thus excluded 1429 extant and ~25,000 fossil species names considered invalid.

2.2 Number of species and taxonomic effort

All analyses were adjusted to account for the most recent decade being incomplete: i. e., for freshwater and fossil species 2017, only 7 of 10 years; for marine species the last year of available data was 2014, representing only 4 of 10 years.

We analysed trends in the number of newly named species per year for freshwater, marine and fossil species from the earliest descriptions until the present day following previous methodologies (Costello et al., 2012; Arfianti et al., 2018). The ratio of the number of species named in a decade to the number of authors in the same decade was used as an indicator of taxonomic effort or the rate of finding and describing new species (Gray and Cavers, 2013). Only the first author of a species name was considered, in order to minimize estimates in effort and avoid any bias due to increasing multiple authorships per species in recent decades, as in other studies (Costello et al., 2012; Arfianti et al., 2018; Pamungkas et al., 2019). Spelling variants were corrected and counted as the same author. Previous studies have found that the number of species named per author rises in the early history stages of discovery and decreases when it becomes harder to find new species (e.g., Costello, 2016). To find when this tipping point occurred, we performed piecewise linear segmented regressions, and to test the significance of the change of the slopes of these regressions we performed Davies Tests (Muggeo, 2008).

Trends in taxonomic effort might be biased by the relative productivity of authors (Arfianti et al., 2018). For instance, if relatively more authors described only one species over time, then it may require more authors to describe the same number of species. Whether this is the case could be analysed by plotting the trend in the number of authors who described many or few species over time. Here, we analysed the proportion of one-species authors over time (decades) through linear Spearman rank correlations (Wilcox, 2003).

We compared the trends between the first and last years of species named by particular authors to see if 'publication lifetimes' decreased over time using Spearman rank correlations. A generalized linear model (GLM) with a Poisson distribution was used to analyse the relation between the number of species described per authors and their publications lifetimes.

2.3 Rates of description

A popular method to estimate the number of species yet to be named is by modelling the cumulative species number as a function of the year of description (Steyskal, 1965; White, 1975). Thus, we used the logistic nonhomogeneous renewal process (NHRP) which is composed of trend and variation components (Wilson and Costello, 2005), to analyse the proportion of the present named species relative to the overall number of all bryozoan species which will be named by 2050 and 2100 respectively. This model has been shown to fit the shape of species description rate curves across many taxa (Costello and Wilson, 2011; Costello et al., 2012; Arfianti et al., 2018; Pamungkas et al., 2019). Moreover, recent studies highlighted the better fitting of this model to cumulative species curves than others not tested in this study and widely popular in biodiversity studies (Woodley et al., 2019). Specifically, this model does not underestimate the amount of error as do other models such as the Poisson process which normally considers the variance equal to the mean and can therefore incorrectly estimate the amount of error (Costello and Wilson, 2011). We limited extrapolation to 2100 to avoid large uncertainties in the longer term, as in previous studies (Costello and Wilson, 2011; DeWalt and Ower, 2019; Pamungkas et al., 2019). Finally, we analysed the proportion of the present named species relative to the overall number of all bryozoan species which will be named by 2050 and 2100 respectively.

All analyses were conducted using R version 3.1.2 (R Core Developer Team, 2014).

3. Results

3.1 Species discovery

There were nearly three times more fossil (17,867) than extant bryozoan species (6135) described (Table 1). Among extant taxa, the number of marine species was far higher (6063) than in fresh water (108). The number of recognized Families was also higher for fossil than extant species (Table 1, Tables S1-S3).

Table 1. The number of classes, orders, families, genera, and species for each group of bryozoans.

Bryozoan Group	Class	Order	Family	Genus	Species
Extant species	3	3	218	812	6135
Marine	3	3	218	812	6063
Freshwater	2	2	13	26	108
Fossil species	2	11	331	NA	17,867

Formal descriptions of bryozoans began with the publication of the tenth edition of Linnaeus' *Systema Naturae* in 1758 (Fig. 1). For marine bryozoans, the decades with most species described were the 1890s, 1930s, and 1980s; in freshwater species the 1910s, 1980s, and 2010s; and in fossil species 1930s and 1970s (Fig. 1). Over the past two decades, there has been a decrease in descriptions of new fossil species, not seen in extant species. Although the 2010-2020 decade for marine species appeared to have fewer species compared to previous decades, data were only available until 2014, and this means the sample size was small (three years) and sensitive to delays in capturing new species in the database (Fig. 1).

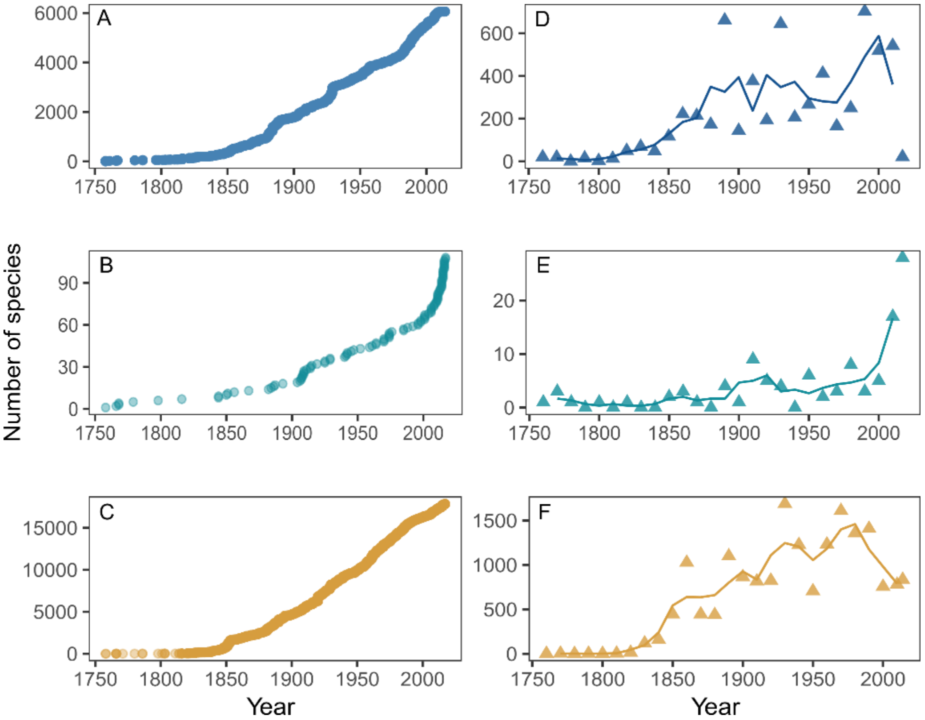


Figure 1. The cumulative per year (A-C), and actual per decade (D-F), number of species described for marine (A, D), freshwater (B, E) and fossil (C, F) bryozoans. The trend lines are three-year moving averages.

3.2 Number of authors

The number of authors of marine and fossil species increased over time and was highest between the 1970-2010s (Fig. S1). In contrast, in freshwater species, the number of authors was highest at the beginning of the 1900s (Fig. S1). The number of first authors describing species in a decade changed from increasing to decreasing species (Fig. 2). The significant breakpoints were the 1930s for marine and fossil species. Due to the small samples sizes, the breakpoints for freshwater species were not statistically significant. We similarly did not attribute any significance to the breakpoints in the 1800s for fossil and 1810s for marine species because of the few authors and high variability in description rates in these early years of description. Thus, the number of new species has been fewer in proportion to the number of authors since the 1930s for marine and fossil species (Fig. 2, Fig. S1).

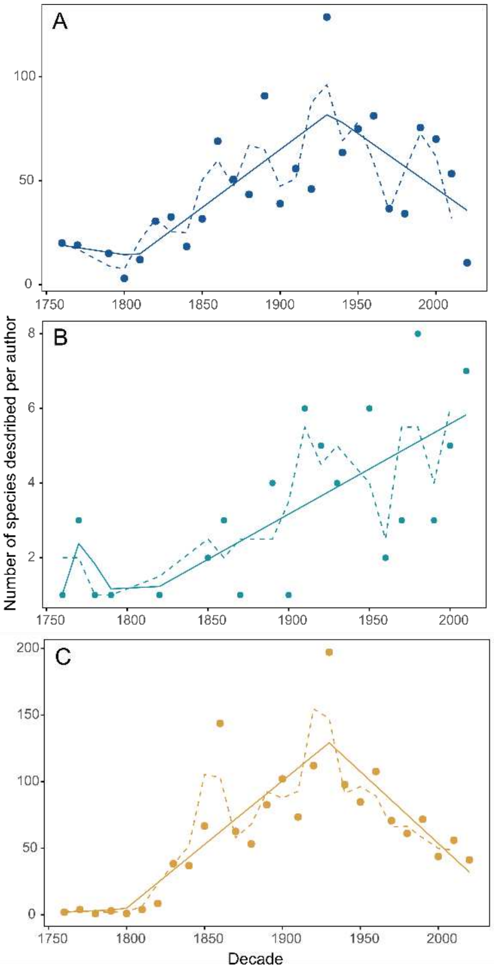


Figure 2. Breakpoint analyses using segmented linear regression models on the ratio of species described per authors in a decade: (A) two breakpoints for marine (1810, 1930) (p<.001); (B) three for freshwater (1760, 1790,1820) (p=0.883); and (C) two for fossil species (1800,1930) (p<0.001). P-value is refereed to Davies test.

There was no significant trend in the proportion of authors who described only one bryozoan species through time (Fig. 3A, B, C). The correlations were close to zero for marine (R = -0.17), freshwater (R = -0.28) and fossil (R = -0.24) species. The higher proportion of one-species authors in marine and fossil species in the 18th and early 19th centuries is attributed to the small sample size, and it became lower in subsequent years. Thus there is no indication that the change in the number of authors is due to relatively more describing very few species. As expected, generalized linear models showed an increase in the number of species described by authors with longer publication lifetimes for marine ($p<0.001$), freshwater ($p<0.001$) and fossil species ($p<0.001$) (Fig. S2). Although we did not find any trends in the authors' publication lifetime against the year of their first species description for marine and freshwater species (Fig. 3D, E), for fossil species we found a positive correlation between them (Fig. 3F, R = 0.73, $p<0.001$), showing an increase of author's lifetime productivity over time (Tables S4-S6).

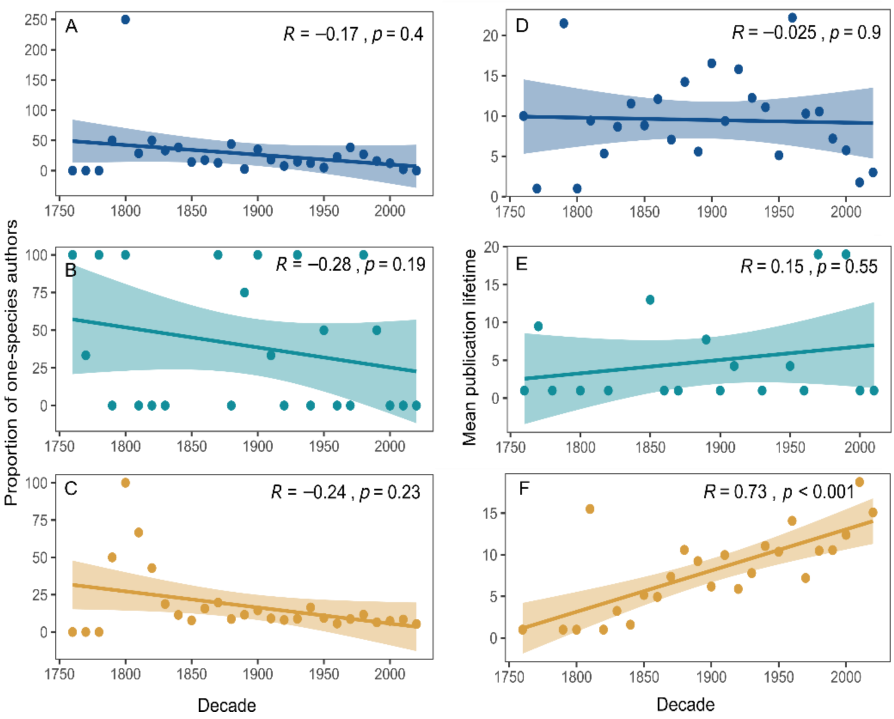


Figure 3. Spearman rank correlations of the percentage of one-species authors over time for (A) marine, (B) freshwater, and (C) fossil bryozoans, and of the mean publication lifetime of authors against the decade of their first species description for (D) marine, (E) freshwater and (F) fossil bryozoans. Each plot shows the regression line with 95% CI, Spearman rank correlation coefficient (R), and P-value (p).

3.3 Future rates of discovery

For the 6135 named extant bryozoans, the median predicted additional species to be described were 780 by 2050 and 1350 by 2100 (Table 2) (Fig. 4A). For the 17,678 named fossil bryozoans, the median predictions were 1530 and 2430 respectively (Fig. 4B). The high upper confidence limit for extant species, in contrast to fossil species, indicates the greater uncertainty in prediction because the rate of description is still relatively high (Table 2). Thus, our predictions showed that the present number of named species represents 89% for extant, and 92% for fossil taxa of named species by 2050, and 82% for extant and 88% for fossil taxa by 2100.

Table 2. Median predicted species to be discovered by 2050 and 2100 with their lower and upper 95% probability interval (CI).

Bryozoan group	**By 2050**				**By 2100**		
	n	**Median**	**95% CI**		**Median**	**95 % CI**	
			lower	upper		lower	upper
All extant species	6135	780	680	890	1350	1180	1569
Fossil species	17,678	1530	1410	1640	2430	2250	2610

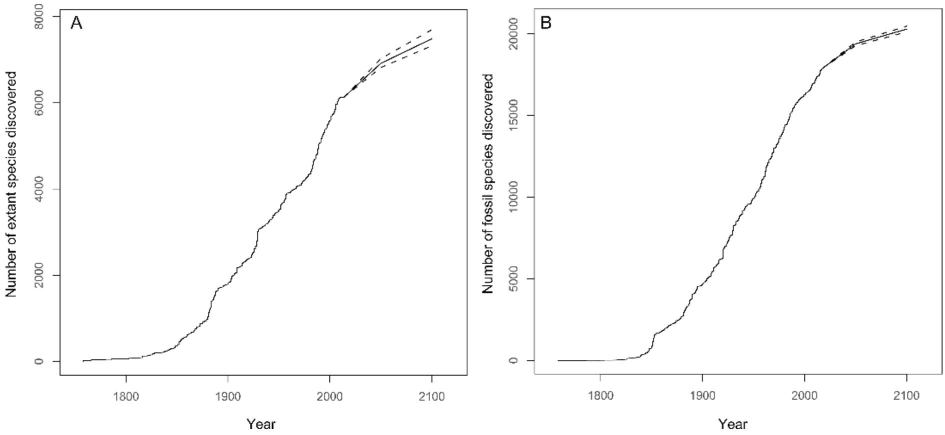


Figure 4. The cumulative number of (A) extant and (B) fossil bryozoan species over time, showing the number of species predicted to be described by 2050 and 2100. Dashed lines show 95% confidence intervals. Note scales for number of species discovered differ.

4. Discussion

Recent decades have seen an increase in the number of taxonomists describing new species of bryozoans, as noticed for other marine and terrestrial taxa (Appeltans et al., 2012; Costello et al., 2012), including fossil mammals (Alroy, 2002). Our analyses found that there were three times more fossil than extant bryozoans, supporting the unsurprising previous findings that extant species represent only a small proportion of past biodiversity (May, 1994).

By the early 1900s, 30% of marine, 25% of freshwater and 26% of fossil species currently named had been described. Thus the relative rates of discovery were similar across the three groups. This time period was the beginning of the exploration of the seas worldwide characterized by the first large campaigns such as the 1873–

1876 *Challenger* expedition (National Research Council, 2003; Deacon et al., 2013). The most productive decades in all groups were around the 1930s and 1970s–1980s. Our results reflect the increased interest in ocean discovery during the 20th century (Deacon et al., 2013) as well as the temporary declines in taxonomic publications during the two World Wars, as observed for other taxa (e.g. Alroy, 2002; Costello et al., 2012). Since the 1950s, exploration of new marine locations and habitats has become easier, owing to the growth of marine science internationally, with an increase in the number of species described per decade (Appeltans et al., 2012; Costello et al., 2013a). Furthermore, in recent decades, the use of scanning electron microscopy and other advanced methodologies have enhanced the description of new species thanks to the better resolution of skeletal structures and optimal preservation of the organisms (Taylor, 1990; Benton, 2008; Taylor et al., 2015).

The 20th century saw both the most species described and most authors. However, our results highlighted that the number of species described per author in a decade has been declining since the 1930s. The proportion of single-species authors did not increase over time, suggesting that for bryozoans the change in the number of species per author is not because of changing proportions of specialists as proposed by Bouchet et al., (2005). Moreover, we found a positive trend between the publication lifetime of authors and the number of species described. Other authors have reached the same conclusions for terrestrial and marine groups (Costello et al., 2012) and recently for amphipod crustaceans (Arfianti et al., 2018) or polychaete worms (Pamungkas et al., 2019). The increasing numbers of authors and the decrease of authors'productivity (the number of species described per author) thus appear a reasonable indicator of taxonomic effort suggesting that at the beginning of bryozoan discovery it was easier to describe new species, with more taxonomic effort and more workers required subsequently.

Future projections of description rates for bryozoans estimate that around 20% of extant and 10% of fossil bryozoan species relative to the overall number of actual bryozoan named species remain to be discovered by 2100. Thus the fossil fauna, despite having three times more species, appears better described than extant species in relative terms. The decline in new fossil species being described since the 1970s possibly supports this prediction. However, because there are more fossil species, 64 % of the species likely to be described by 2100 will be fossils (2430 vs 1350 extant). That about 80% of Bryozoa may now be described relative to the total number of species that will be described by the end of this century places them amongst the better-known taxa on Earth, as the average for all taxa is about two-thirds (Costello and Chaudhary, 2017).

One caveat in our findings is that some currently recognized species will be identified as synonyms in the future (Alroy, 2002). A review of all extant marine taxa suggested that 20% of present species names may turn out to be synonyms (Appeltans et al., 2012). If this proves true for bryozoans, then the number of new species that may remain to described will be offset by synonymization, and the actual number of species will change little in the future, despite perhaps thousands of new species being described. This highlights the importance of taxonomic revisions and species identification guides to facilitate the study of bryozoans by the wider community.

Acknowledgements

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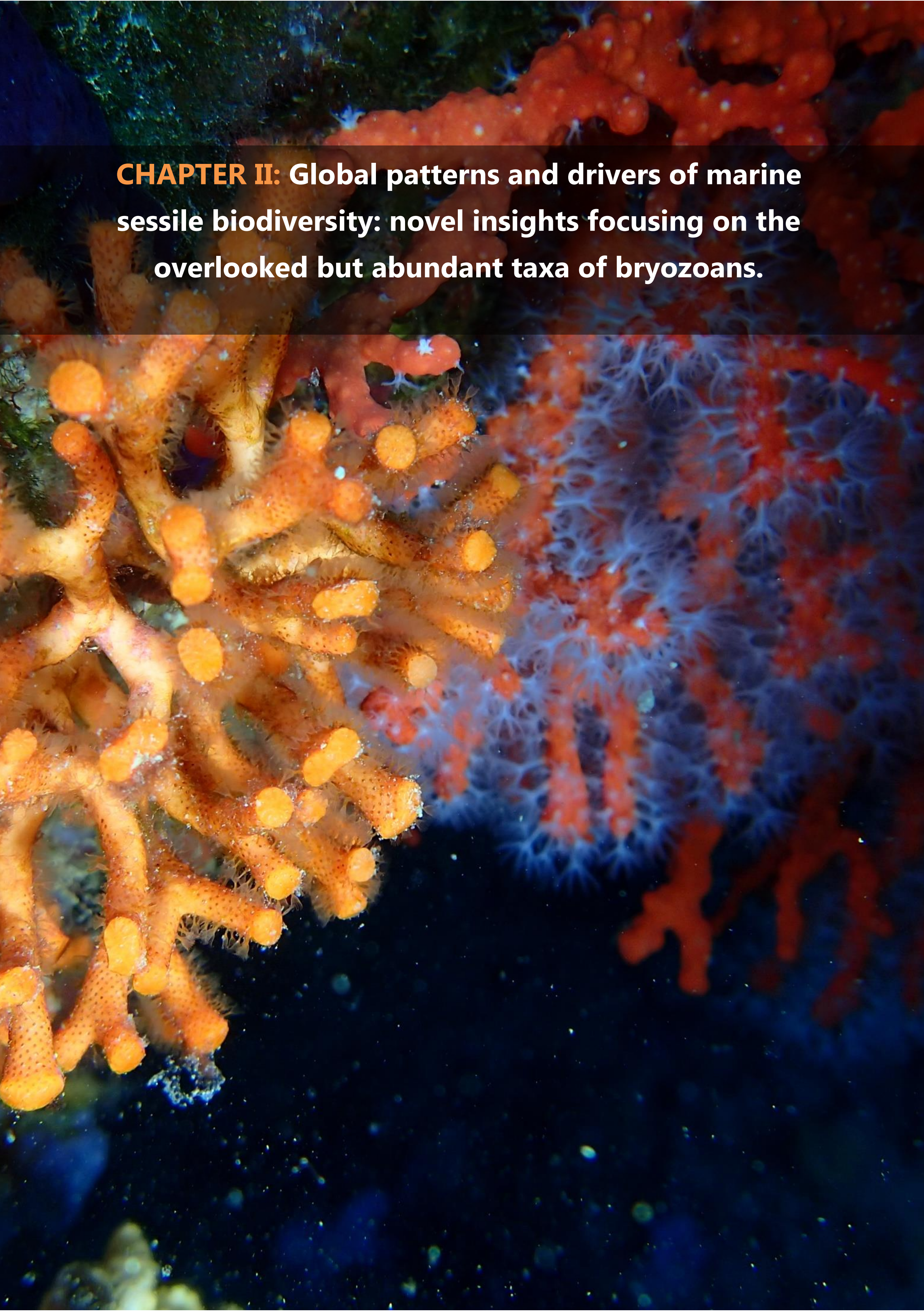

CHAPTER II: Global patterns and drivers of marine sessile biodiversity: novel insights focusing on the overlooked but abundant taxa of bryozoans.

Abstract

One of the major goals of ecology is to understand biodiversity patterns at global spatial scales. The recent increase in data availability and computational power has led to major advances in macroecology providing unprecedented opportunities to test biogeographic hypothesis using field observations. Accordingly, the most accepted diversity pattern is the increase in species richness from high latitudes towards the tropics. However, recent studies suggested that the highly heterogeneous sampling effort can result in biased conclusions about diversity patterns highlighting the need to account for its differences in biogeographical studies. Here, we analyzed global diversity patterns of marine sessile species, with a comparative approach focusing on bryozoans, a traditionally overlooked but highly diverse and abundant group of marine benthic invertebrates. Bryozoans showed higher species richness in temperate regions, being the Southern Ocean the most diverse area. Accordingly, most of latitudinal patterns of marine sessile groups showed a dip in the number of species at the equator, and an increase of diversity at Southern Ocean, and particularly, at Antarctic shelf. Conversely, potential biases in the sampling effort of marine sessile species and bryozoans showed that regions have not been equally sampled, with higher efforts on North Temperate Atlantic. Related to this, to unravel environmental drivers of diversity patterns, we performed two types of models comparing the use of the widely used rarified species richness (ES50) *vs* the incorporation of a sampling effort correction. Despite both models obtained depth, nitrate, and SST as the best predictors for bryozoan and marine sessile diversity, the models using our sampling effort correction showed higher levels of deviance explained. Finally, we accounted for the increase on SST under different emission scenarios on hotspot areas for marine sessile species and bryozoans, obtaining that the major impacts will be predicted in the northern hotspot areas, suggesting a high spatial heterogeneity of potential warming impacts. Contrary, Southern Ocean will be the least impacted area by ocean warming, suggesting that the high species richness of most marine sessile groups is related to the fact that this area has suffered lower temperature stress over evolutionary time than other areas. Our study provides new insights in the global diversity patterns of marine sessile species, with a special emphasis on bryozoans, also providing a more comprehensive understanding of the potential effects of climate change on Earth’s biodiversity.

1. Introduction

Since Darwin, ecologists have been interested in the study of large-scale patterns of species richness and their underlying mechanisms (Ricklefs, 2004; Field et al., 2009). In the last decades, considerable progress has been made towards the integration of environmental and field observations in large and open databases, combined with improved computational power, facilitating more complex modeling approaches and allowing to test macroecological hypothesis (Smith et al., 2008; Costello et al., 2017). Despite most of related studies have focused on terrestrial systems (Blackburn and Gaston, 2006; Grenyer et al., 2006; Jenkins et al., 2013), the study of marine organisms have received less attention, with an increase of global studies in the last recent years (Tittensor et al., 2010; Chaudhary et al., 2017; Costello et al., 2017).

Traditionally, macroecological studies have examined different causal hypotheses to explain diversity patterns in relation to environmental factors, such as latitude, temperature, and productivity (Waide et al., 1999; Allen et al., 2002; Willig et al., 2003; Chaudhary et al., 2017). One of the oldest accepted biogeographic pattern is the increase in species richness from high latitudes towards the tropics, generally assumed to reach a single (unimodal) peak at the equator (Rosenzweig, 1995; Willig, 2001; Hillebrand, 2004). However, this unimodal pattern has been challenged by recent works on marine ecosystems, where some taxa present a divergent bimodal pattern with a dip in species richness at the equator (Chaudhary et al., 2016; Saeedi et al., 2017). Moreover, the sampling effort in the ocean is not evenly distributed across all the regions and depths (Costello et al., 2015; Menegotto and Rangel, 2018). For this reason, recent studies suggested that the registered reduction in some marine species in tropical latitudes may be driven by an overlooked spatial bias in the sampling effort highlighting the importance to use properly rarefaction methods to correct related biases and explore the differences in the sampling effort between regions on macroecological studies (Menegotto and Rangel, 2018).

Environmental modeling constitutes a useful tool to underlie the ecological processes determining macroecological patterns, exploring statistically the relationship between species richness and environmental gradients (Austin and Smith, 1990; Pykälä et al., 2005). Moreover, species distributions are strongly correlated to environmental factors (Macpherson, 2002) and warming is causing important shifts in species geographic patterns over latitude and depth (Parmesan, 2006; Cheung et al., 2008). Hence, a better understanding of diversity patterns along environmental gradients and the mapping of biodiversity hotspots would allow us to identify the most vulnerable areas in the face to climate change, and to establish management and conservation priorities of marine ecosystems (Reid, 1998; Myers et al., 2000; Orme et al., 2005; Jenkins et al., 2013). In this context, the classification and mapping of global biodiversity are essential for prioritizing conservation and management efforts (Wallace, 1876; Lourie and Vincent, 2004; Spalding et al., 2007).

To date, most of global marine macroecological works have focused on charismatic taxa such as mammals, fishes, corals or seagrasses (Tittensor et al., 2010), with fewer recent examples of other traditionally understudied groups but very abundant in benthic habitats (Chaudhary et al., 2016; Saeedi et al., 2017). For this reason, the main aim of this work was to provide a comprehensive macroecological study of marine sessile groups, focusing in bryozoans, an abundant and widely distributed group of suspension-feeding colonial invertebrates in marine benthic ecosystems, which has been traditionally overlooked in global biodiversity patterns works (Wood et al., 2012). Moreover, due to their rigid skeleton, large bryozoans are considered habitat-forming species enhancing the associated marine biodiversity (Cocito, 2004; Wood et al., 2012; Lombardi et al., 2014). However, most of these species are threatened by several human impacts, such climate change, and a change in the distribution and diversity of this group may decrease the associated biodiversity compromising the ecological benefits and services that they provide (Gray, 1997; Moberg and Folke, 1999; Cadotte et al., 2011).

Specifically, in this study we mapped and plotted global diversity patterns of marine sessile species richness with a particular approach in bryozoans, and modelled their potential environmental drivers, testing alternative methods to account for biases on the sampling effort. Moreover, we analyzed latitudinal diversity patterns of marine sessile groups to unravel if they display an increase of species in the equator. Finally, hotspot areas for bryozoans and marine sessile species were identified and overlapped projected warming trends under different Representative Concentration Pathways (RCP) emission scenarios to predict potential future impacts of climate change on these marine communities. Our study represents the first attempt to assess global diversity patterns of traditionally overlooked taxa in macroecological studies, bryozoans, comparing them with marine sessile species diversity patterns, providing a more comprehensive understanding of global biodiversity patterns in the context of loss of biodiversity due to human threats.

2. Material and methods

2.1 Species data

We obtained the species data from two different open databases: the Ocean Biogeographic Information Systems (OBIS, 2018, http://www.iobis.org) and The Global Biodiversity Information Facility (GBIF, 2018). Specifically, we downloaded about 4,181,712 (OBIS, 2018) and 4,694,656 (GBIF, 2018) records of the following sessile marine groups inhabiting benthic habitats: Anthozoa, Ascideacea, Bivalvia, Bryozoa, Cirripedia, macroalgae, Porifera, Polychaeta Sedentaria and seagrasses. Like recent studies, we cross-referenced OBIS and GBIF data to avoid duplication of records (Saeedi et al., 2017). Specifically, to compile and integrate all available data of both sources, we carried out a specific search in each data source to avoid errors and limitations. In some cases, when we search for the global of the phyla (p. e., Cirripedia), there were not available information in the open databases, and we have to perform a more focalized search, searching for other minor taxonomic levels, such as Class or Orders. Moreover, this specific search allowed us to exclude the non-sessile groups of each studied phyla. Accordingly, for cnidarians, we searched Anthozoa class on OBIS and GBIF; for ascidians we searched Ascideacea phylum on OBIS and GBIF; for bivalves, we searched Bivalvia phylum on OBIS and GBIF; for bryozoans we searched Bryozoa phylum on OBIS and GBIF; for cirripeds, we searched Cirripedia phylum on OBIS, and Sessilia, Pedunculata, orders on GBIF (we excluded from the analyses parasitic groups); for macroalgae, we searched Phaeophyceae, Rhodophyta and Ulvophyceae classes on GBIF and OBIS; for sponges, we searched Porifera phylum on OBIS and GBIF; for polychaetes, we searched Sendentaria subclass on OBIS, and Sabellida and Terebellida orders on GBIF; and for seagrasses, we searched families Posidoniaceae, Zosteraceae, and Cymodoceaceae on GBIF and OBIS (Table S1).

After compiling all data, we removed occurrences with incomplete information (data without coordinates or equal to zero and non-species level data), land records and duplicates using *plyr* and *dplyr* packages in R (Wickham, 2009; Wickham et al., 2015). Moreover, we deleted non-accepted or wrongly named species using the *worms* package in R (Holstein, 2017). After data evaluation, we merged all databases obtaining a total of 3,068,301 records for marine sessile species, and specifically 146,149 for bryozoans (Table S1).

2.2 Global species richness patterns

To estimate abundance patterns we computed the occurrence or the total number of species in a grid of 5° cells for the total of marine sessile groups and bryozoans. In each case, following previous methodologies, we analysed the number of species in each cell correcting by the sampling effort using the popular method of rarefaction using the *vegan* package in R (Oksanen et al., 2018), which consists in correcting species richness by only considering a specific and random subset of samples (the most popular and effective method in diversity studies is to consider only 50 samples (ES50)) (Chaudhary et al., 2017).

Furthermore, to analyze diversity latitudinal patterns of marine sessile species, we divided our data into latitudinal bands (between 2.5ºC), and we measured the mean value of rarefied species richness on each band (ES50) (Chaudhary et al., 2017). Specifically, we carried out this analyses not only for bryozoans but also for all other marine sessile groups, to analyse if they follow the most traditional accepted pattern which posits an increase in species richness in the tropics. In each case, to test the relationship between species richness and latitude we performed Generalized Linear Models (GLMs) (McCullagh and Nelder, 1989) using the *MASS* package in R (Ripley et al., 2013) fitting the family of the response variable (species richness) as binomial negative, as other studies pointed that species richness data is like (Lopatin et al., 2016).

2.3 Differences in the sampling effort

To quantify biases on the sampling effort on marine sessile species and bryozoan data, in each case we used the incidence (or occurrence) of records to create a frequency index (0-1) giving a different value in each 5° cell depending on the abundance of their records (0 was the value for no sampled cells; conversely, 1 was the value for the most sampled cells). Using this index, we analysed sampling effort latitudinal patterns for marine sessile species and bryozoans, dividing our data into latitudinal bands and measuring the mean value of the sampling effort on each band.

Moreover, to compare the sampling effort between biogeographical regions, we compiled our 5° cells into realms following previous works (Spalding et al., 2007) and also more accurately in IHO regions (Flanders Marine Institute, 2018), accounting for the mean value of the sampling effort in each of these (based on the sampling effort frequency index measured on the previous section).

2.4 Environmental drivers of marine diversity

To identify potential drivers of diversity patterns for both studied groups we downloaded a set of 10 environmental variables traditionally tested on macroecological works, from BioOracle v2.0 using the *SDMpredictors* package in R (Bosch et al., 2018) (Table S2). First, we carried out data preparation detecting and eliminating extreme values or outliers, and we standardized our explanatory variables using the *z* method transformation, recalculating our values to achieve a mean = 0 and standard deviation (SD) = 1 for each variable (Grueber et al., 2011). In ecological modeling, the best model selection has to be implemented with correct explanatory variables selection studying the collinearity between them (Feld et al., 2016). For this reason, we used Spearman's Rank correlations to quantify the correlation between each pair of selected environmental variables, obtaining the following non-collinear variables: maximum depth, nitrate, mean SST, range SST and maximum chlorophyll (Table S3).

After data preparation and variable selection, as previous studies conducted (McCullagh and Nelder, 1989; Edgar et al., 2017), we fitted a set of Generalized Linear Models (GLMs) using the *mgcv* package in R (Wood and Wood, 2018), modelling species richness as the response variable and environmental variables as predictor variables for the total of marine sessile groups and bryozoans (Lopatin et al., 2016). In both cases, we compared the effect of considering rarefied species richness (ES50) *vs* including the sampling effort frequency index as an interaction on the models of non-rarefied species richness. Specifically, we fitted two types of GLMs: First, we explored the relation of rarefied species richness (ES50) (response variable) to each environmental variable (predictors); Second, we explored the relationship between non-corrected species richness to each environmental variable, incorporating the sampling effort frequency index (measured in the first part of this work) as an interacting variable on each model. In both cases, we also fitted a more complex set of models including more than one predictor to determine the best environmental predictors of observed diversity patterns. To assess model performance, we used Aikeke's Information Criteria (AIC; Akaike, 1973), and deviance explained (D), which has been used as a measure of a model's goodness-of-fit (e.g., Mellin et al., 2012), to decide the best model in both cases. Finally, we analysed the marginal effects of these models to explore visually the relationship between species richness and each selected environmental variable, using the *sjplot* package in R, following previous methodologies (Mellin et al., 2012; Sperling et al., 2016; Greenwell, 2017) (Fig. S1).

2.5 Impact of climate change on diversity hotspots

We identified hotspots of species richness defined as the 10% of cells with the highest species richness for the total of marine sessile species and bryozoans, as did Tittensor et al., 2010. Then, to assess the future vulnerability of these highly diverse areas, we computed for each cell the expected increases in SST mean under two different emission scenarios (RCP 4.5 and RCP 8.5) by 2100, obtained from BioOracle v2.0 (Assis et al., 2018). In each case, to analyse the patterns between expected increases in SST mean and latitude, we also measured the mean expected increase in SST for each latitudinal band. To compare differences between expected increases and latitude, we computed a set of Generalized Linear Models (GLMs) fitting the family of the response variable (increase in SST mean) as Poisson.

All statistical analysis and graphics were produced using R version 3.1.2 (R Core Developer Team, 2014).

3. Results

3.1 Global diversity patterns and differences on the sampling effort

Marine sessile groups are widely distributed across continental-shelves of all realms, being more abundant on Temperate North Atlantic, Temperate Australasia, and Northern Pacific in terms of number of records (Fig. 1A). Higher values of rarefied species richness (ES50) were also found across different continental-shelves, with high concentration of species on Southern Ocean, North and Central Atlantic, Indo-pacific, Australia and South America (Fig. 1B). In contrast, bryozoans were widely distributed across temperate continental-shelves with a high abundance in Temperate North Atlantic, and other areas such as Australasia, Southern Ocean, and Northern Pacific. However, they were less abundant in other tropical areas such as Northern and Central Pacific, and Tropical Atlantic (Fig. 1D). Southern Ocean and some areas of New Zealand, Australia and Temperate North Atlantic represent the regions with highest values on rarefied species richness (ES50) (Fig. 1E).

Sampling effort differed with latitude in both studied groups, being higher in Northern latitudes (Fig. 1C, F). Specifically, for both groups the most sampled region was Temperate Northern Atlantic, specifically for marine species presenting a high sampling effort in Baltic, Celtic and North Sea, followed by Temperate Northern Pacific, being the Coast of Alaska the most sampled area inside this region. Similarly, Temperate North Atlantic represents the most sampled region for bryozoans, with highest effort on North Atlantic Ocean, followed by Celtic and Baltic Sea, and also West Mediterranean Sea. Conversely, for both groups, other regions presented low values of sampling effort such as Southern Ocean, Arctic Sea, Temperate South America and Western Indo-Pacific, being the areas with the lowest value in the sampling effort the Siberian Sea for marine sessile species, and the Siberian Sea, The Northwestern Passages (Arctic Sea) and Sea of Okhotsk (Temperate Northern Pacific) for bryozoans (Table S4).

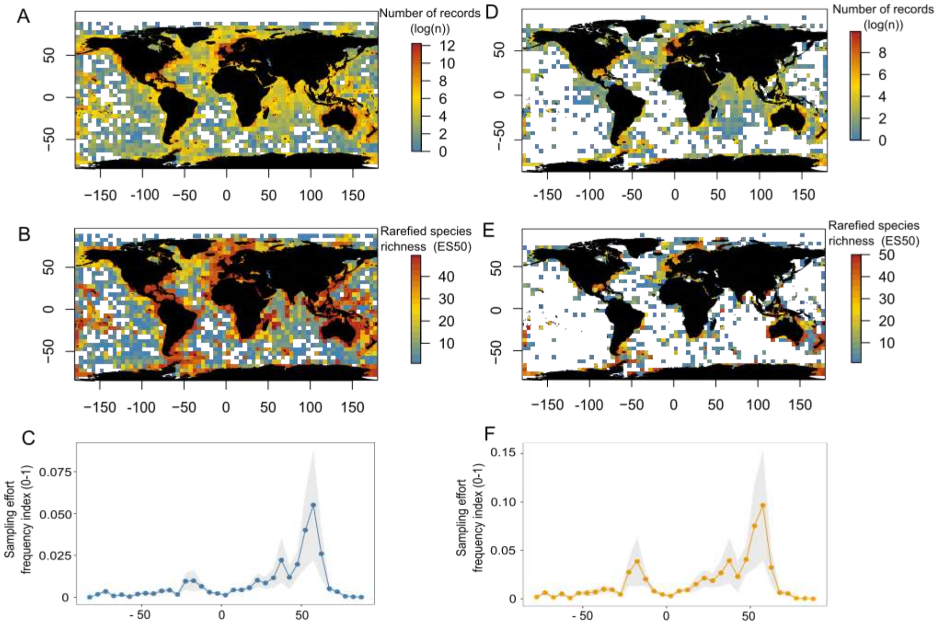

Figure 1. Abundance or number of records per cell (5º) in logarithmic adjustment for marine sessile species (A) and bryozoans (D). Rarefied species richness (ES50) for marine sessile species (B) and bryozoans (E). White cells represents no data. Mean sampling effort frequency index (0-1) on each latitudinal band for marine sessile species (C) and bryozoans (F).

3.2 Latitudinal diversity patterns of marine sessile groups

Marine sessile groups had most species richness (highest ES50) on the Antarctic shelf (between 70ºS and 80ºS) (Fig. 2A), a pronounced depression in the deep Southern Ocean (between 50ºS and 60ºS), and relatively high and similar species richness from 25ºS to 75ºN (Fig. 2A). Accordingly, we did not obtain significant differences between marine sessile species richness and latitude (Table S5). Conversely, we observed a wide range of different patterns when we analysed the latitudinal diversity of each marine sessile group separately, and only anthozoans displayed an increase in species richness at the equator (Fig. 2). Moreover, only seagrasses, macroalgae, and cirripeds lacked on the Antarctic diversity. Thus, most taxa had a non-unimodal latitude pattern, with peaks in Antarctica and low to mid-latitudes of both hemispheres.

Specifically, bryozoans showed a significant latitudinal pattern with a pick on the number of species in Southern latitudes (between 60ºS and 90ºS) corresponding to the Southern Ocean, and less evident but also a high diversity in temperate regions

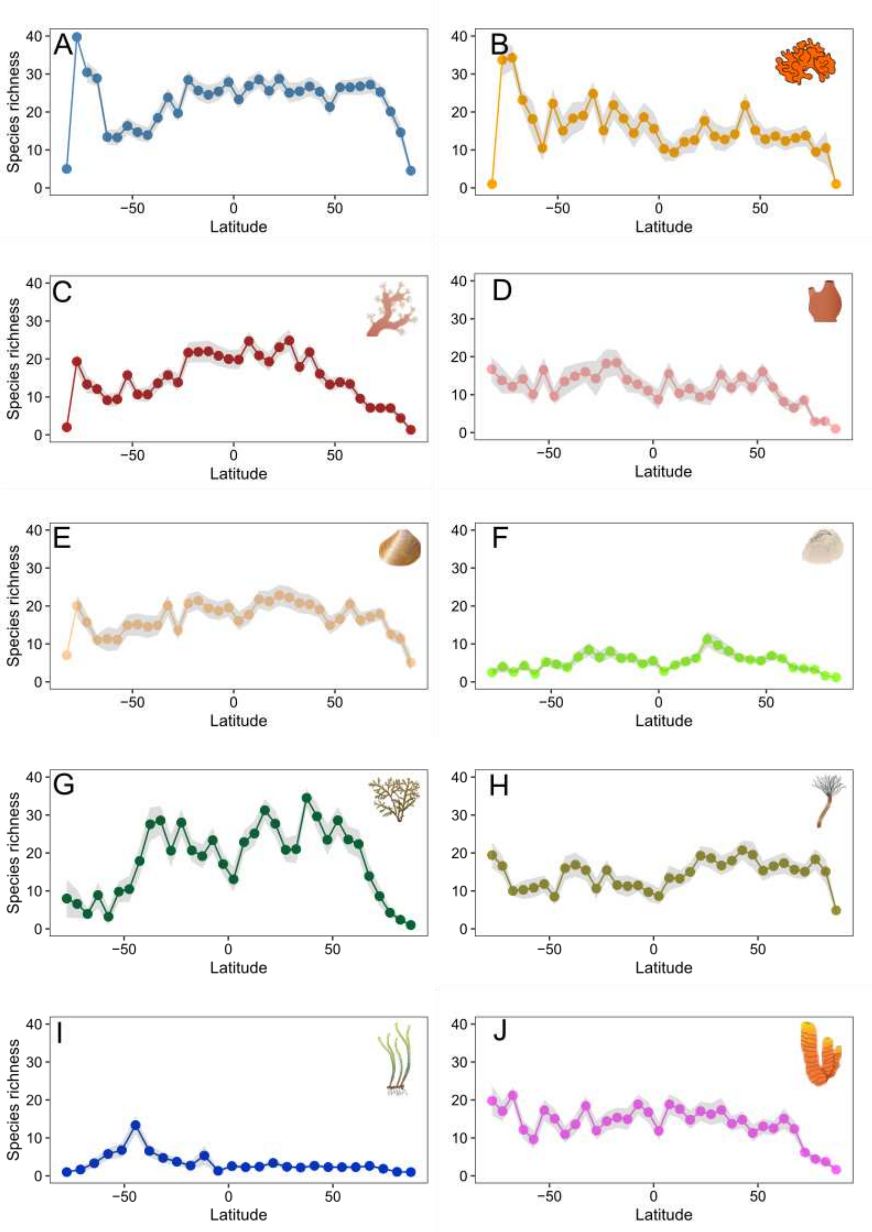

Figure 2. Latitudinal diversity patterns for marine sessile species in terms of mean rarefied species richness (ES50 ± SE) on each latitudinal band (A), distinguishing for each marine group: bryozoans (B), anthozoans (C), ascidians (D), bivalves (E), cirripeds (F), macroalgae (G), polychaetes (H), seagrasses (I) and sponges (J).

of Southern and Northern hemisphere (between 50ºS-20ºS and 20ºN-50ºN respectively) corresponding to Temperate South America and Australasia, and Temperate Northern Atlantic. Conversely, bryozoan species richness was low in the deep Southern Ocean (between 50ºS and 60ºS) and other tropical regions, showing a dip in the number of species in the equator (Fig. 2B, Table S5). Despite the fact that we did not found significant differences, anthozoans are the most highly diverse group in the tropics, with lower richness in medium-high latitudes of Northern Hemisphere (between 50ºN and 90ºN), but with also a diversity peak in the Antarctic shelf (70ºS-80ºS) (Fig. 2C, Table S5). Ascidians, bivalves, and sponges displayed a similar pattern, being significantly more abundant in low-medium than in higher latitudes with a dip in species richness in the equator, and also presenting the Antarctic shelf peak (Fig. 2D, E, J, Table S5). Similarly, we also observed the dip at the Equator in polychaetes, with high species richness in medium-high latitudes, such as the Antarctic shelf, but also in other high latitudes of North Hemisphere (Fig. 2H, Table S5). Conversely, other groups such as Cirripedia or macroalgae presented a dip at the equator, with higher levels of species richness in mid-latitudes and low species richness at high latitudes (Fig. 2F, G, Table S5). Finally, seagrasses showed lower species richness across all latitudes with the exception of the southern hemisphere between 20ºS and -40º SC corresponding to tropical regions of Indo-Pacific (Fig. 2I).

3.3 Environmental drivers of diversity

On both studied groups, quantitative models showed no differences on the best environmental predictors between using rarefied species richness (ES50) and the models using non-rarefied species richness corrected by sampling frequency index, identifying maximum depth, nitrate and mean SST as the best ones for both groups (Table 1). However, deviance explained by the models was very low when we used rarefied species richness (ES50) (between 1-10%, Table 1). In contrast, models using non-rarefied species richness corrected by sampling frequency index showed two to five times higher levels of deviance explained (between 20-50%, Table 1).

For marine sessile species, our models found a significant decrease in species richness with depth and nitrate, and a significant increase with mean and range SST and with maximum chlorophyll (Fig. 3). These relationships also held for bryozoans, although we found a significant decrease of bryozoan species richness with range SST, and the relation between species richness and mean SST was not statistically significant (Fig. 3).

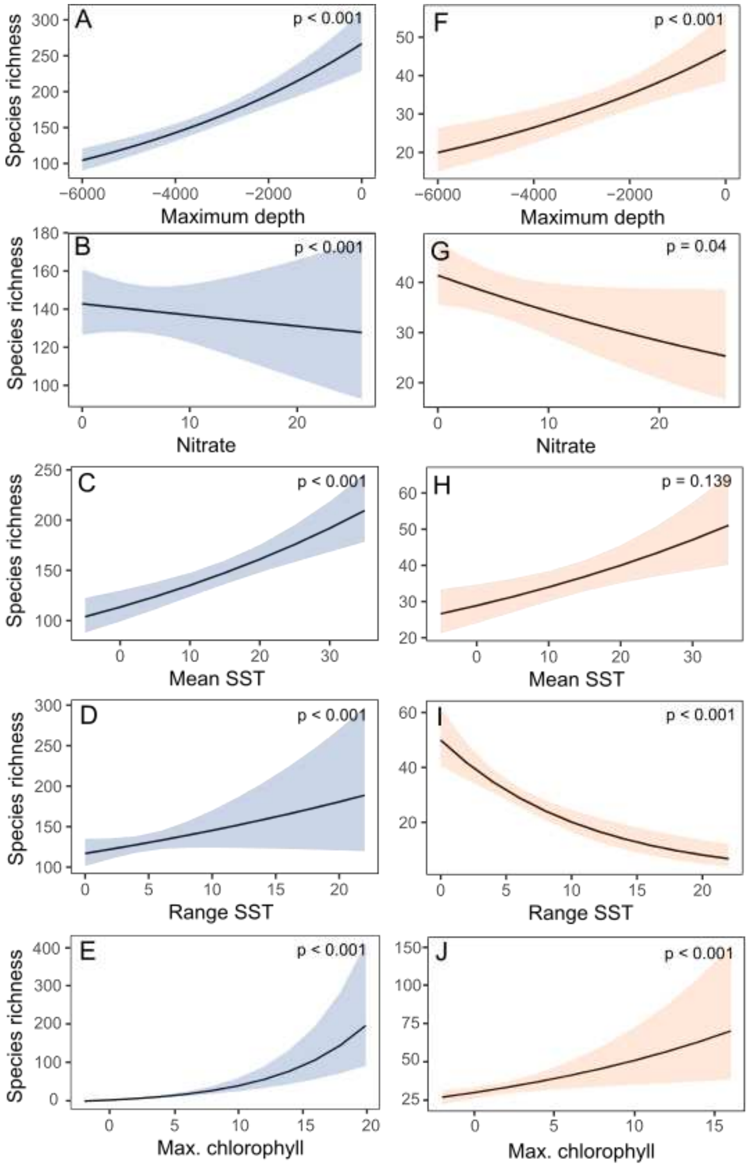

Figure 3. Marginal effects of predictors of Generalized Linear Models (GLM) of non-rarefied species richness against each environmental predictor corrected by the sampling effort index for best fitted model of the data (Table 2). Individual curves with P-value represented species richness against maximum depth (A, F) and nitrate (B, G), mean SST (C, H), range SST (D, I), and maximum chlorophyll (E, J) for marine sessile species (A-E; blue) and bryozoans (F-J; orange).

Table 1. Generalized linear models of bryozoan and marine sessile diversity with respect to selected environmental variables (maximum depth, mean SST, range SST, and nitrate). Analyses were run performing two types of models: the first one, considering rarefied species richness (ES50) as the variable response; the second, considering non-rarefied species richness and correcting the model by the sampling effort frequency index. For each analysis, deviance explained (D) and AIC are shown. For the details of the models see Supplementary Tables S6 and S7.

		Bryozoans		**Marine sessile species**	
Response	Predictors	D	AIC	D	AIC
Rarefied species richness (ES50)	Maximum depth	0.06	4289	0.09	11,414
	Mean SST	0.001	4328	0.006	11,553
	Range SST	0.001	4329	0.003	11,558
	Nitrate	0.01	4321	0.009	11,549
	Max. chlorophyll	0.002	4328	0.01	11,542
	Nitrate + Range SST	0.01	4323.3	0.01	11,549
	Nitrate + Mean SST	0.01	4320.9	0.01	11,550
	Nitrate + Max. chlorophyll	0.01	4322.3	0.04	11,493
	Maximum depth+ Max. chlorophyll	0.06	4289.8	0.02	11,527
	Maximum depth + Mean SST	0.06	4290.6	0.11	11,369
	Maximum depth + Range SST	0.06	4286.8	0.09	11,416
	Maximum depth + Nitrate	0.07	4283.3	0.10	11,399
	Maximum depth +Range SST + Nitrate	0.07	4284.5	0.10	11,401
	Maximum depth + Mean SST + Nitrate	0.09	4270.9	0.12	11,367
Non-rarified species richness corrected by sampling frequency index	Maximum depth*Sampling effort	0.23	4892.5	0.46	14,957
	Mean SST *Sampling effort	0.17	4941.7	0.29	15,430
	Max. chlorophyll *Sampling effort	0.16	4950.6	0.29	15,418
	Range SST *Sampling effort	0.18	4930.8	0.31	15,385
	Nitrate*Sampling effort	0.21	4903.5	0.30	15,404
	Nitrate + Range SST *Sampling effort	0.24	4887.3	0.34	15,318
	Nitrate + Mean SST *Sampling effort	0.24	4887.8	0.32	15,371
	Nitrate + Max. chlor. *Sampling effort	0.23	4894.8	0.43	15,499
	Maximum depth+ Max. chlor. *Sampling effort	0.23	4895.7	0.46	14,960
	Maximum depth + Mean SST *Sampling effort	0.24	4882.1	0.50	14,850
	Maximum depth + Range SST *Sampling effort	0.26	4865	0.47	14,937
	Maximum depth + Nitrate *Sampling effort	0.29	4834.9	0.49	14,866
	Maximum depth + Range SST + Nitrate *Sampling effort	0.30	4829.2	0.50	14,849
	Maximum depth + Mean SST + Nitrate *Sampling effort	0.32	4816.2	0.51	14,838

3.4 Climate change effects on hotspot areas

Hotspots for marine sessile species were distributed across continental-shelves of different regions, showing a great concentration in Temperate Australia, Central Indo-Pacific, and Temperate Northern Atlantic. Moreover, there was also a high concentration of marine sessile species in South America, Tropical Atlantic, and Central Indo-Pacific and there were few hotspot areas in the Southern Ocean (Fig. 4 A, B). In contrast, the majority of hotspot areas for bryozoans were located in the Southern Ocean and Temperate Australasia. However, there were also fewer areas in Central Indo-Pacific and the Mediterranean (Fig. 4 C, D).

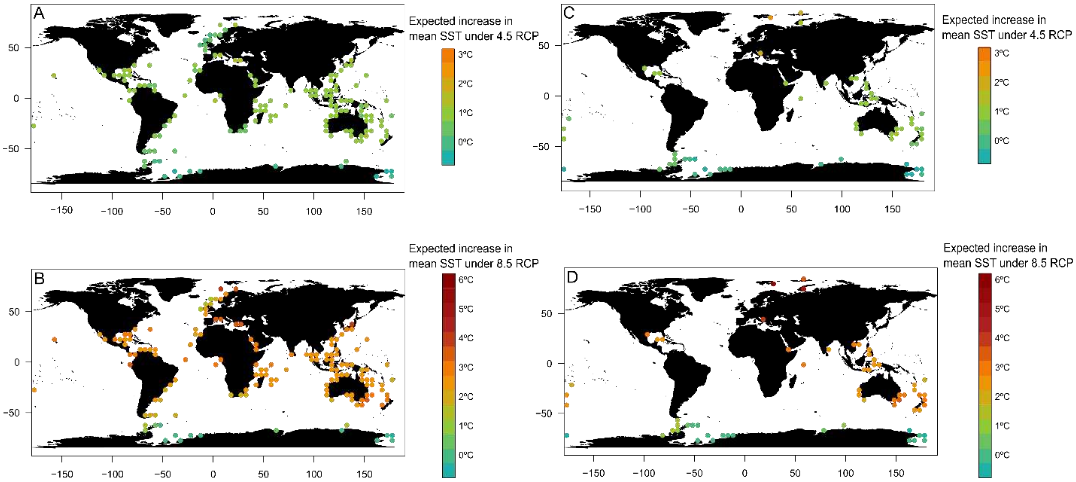

Figure 4. Predicted increase in mean SST in hotspot areas (measured as 10% of the grids with mean highest species richness) for marine sessile species (A, B) and bryozoans (C, D) under two different emission scenarios (RCP's 4.5 (A, C); and 8.5 (B, D)).

Our results showed differences in expected mean SST by 2100 between different RCP scenarios for both studied groups (Table S8, Fig. S1). Under 4.5 RCP emission scenario, in most of the marine sessile species and bryozoan hotspots, the mean expected increase will be around 1°C in mean SST, reaching maxima of 2°C in some northern latitudes, such as the Arctic Sea. However, in Southern regions, mean SST is not expected to reach these values with a maximum increase between 0-1 °C (Fig. 4A, C, Fig. S1). As expected, under RCP 8.5 the mean increase of SST is expected to be around 2.5 to 3°C, affecting most of marine sessile and bryozoan hotspots, but not those ones located on the Southern Ocean. Maximum temperature increases between 4-6°C are predicted to occur in some northern latitudes affecting areas such as the Mediterranean and Arctic Sea, with a less impact on Southern regions with expected increases between 0-1.5°C (Fig. 4B, C, Fig. S1).

4. Discussion

Understanding global patterns of diversity and their environmental drivers is a major challenge of macroecology gaining importance in the last years to anticipate the vulnerability of different organisms and regions in the face of climate change (Tittensor et al., 2010). Here, we provided a comprehensive approach to the global patterns of sessile biodiversity and a detailed analysis of an abundant but traditionally overlooked phylum of bryozoans with important implications for the conservation of vulnerable marine communities under climate change scenario.

4.1 Latitudinal diversity gradient

The Tropics represent a high diversity area traditionally assumed to be characterized by higher diversification rates due to a larger historically and geological time than temperate regions, larger areas with greater energy inputs supporting more individuals and populations, and faster metabolic and speciation rates associated with warmer temperatures (Rosenzweig 1995; Mittelbach et al., 2007). Despite previous studies on the latitudinal patterns of marine species have reported as unimodal with a tropical peak (Rosenzweig, 1995; Willig, 2001; Hillebrand, 2004), our study agrees with recent findings on marine benthic diversity reflecting a non-unimodal pattern for bryozoans and the most of marine sessile groups with a dip in the number of species in the equator (Saeedi et al., 2017; Chaudhary et al., 2017). This highlights the need to challenge the most traditionally accepted hypothesis for the latitudinal pattern such as Rapoport's rule, as it assumes unimodal diversity pattern of species with a tropical peak (Gray, 2001).

To explain the lower diversity richness in the tropics registered in the most of marine groups, a recent study suggested that this pattern may be due to a lower sampling effort in these regions (Menegotto and Rangel, 2018). However, bryozoans have been characterized as one of the best benthic sampled groups (Lidgard, 1990), suggesting that the lower species richness in tropical regions of this group may be explained by other biological and physiological factors such as competition rates among species, habitat suitability or thermal tolerances (Bowen et al., 2013; Chaudhary et al., 2017; Rabosky et al., 2018). Moreover, previous studies suggested that the increase in species richness on high latitudes may be due to latitudinal differences in the colonization rates, disturbances or productivity, showing these latitudes more available substrates to be colonized, less competitive levels and reduced pool sizes permitting to support a greater regional diversity, which also may be valid to explain the highest species richness of the other marine sessile groups (Witman et al., 2004).

Moreover, the diversity latitudinal peak of bryozoans and other benthic groups found in the Southern hemisphere is in accordance with previous works (Griffiths et al., 2009; Downey et al., 2012). Differences in the glacial and climatic history are major factors underlying the contrasting patterns of marine diversity between both hemispheres (Dunton, 1992; Clarke and Crame, 1997). In contrast with the terrestrial environment, the Southern Ocean marine shallow-fauna is abundant and diverse, characterized by dense hard substrata communities dominated by suspension feeders (Clarke and Crame, 1992). Accordingly, high diversity patterns on Southern Hemisphere temperate and polar continental shelves of some marine benthic groups, such as bryozoans, coupled with their strong fossil record (Moyano, 1983). All these facts suggest that the longer period of isolation of Antarctica may be derived in higher speciation rates and contribute to a higher diversity of some benthic groups such as bryozoans or sponges (Dayton et al., 1994; Downey et al., 2012). The high diversity of many groups found in the Southern Ocean recorded in this study pointed out Antarctica as an important center of origin for many marine invertebrate taxa due to a more shallow-water habitat was available at these higher latitudes (Clarke and Crame, 1992). Moreover, in contrast with tropical regions, Southern ocean is characterized by relatively uniform water temperatures and physical conditions due to the homogenizing effect of the Antarctic Circumpolar Current (ACC) facilitating the colonization into the deep sea from the adjacent shelf of many benthic species (e.g. Arntz et al., 1994; Brandt et al., 2007).

4.2 Accounting for sampling biases

Recent estimates of catalog all known species are about two-thirds of all marine species (Appeltans et al., 2012; Costello and Chaudhary, 2017). However, these efforts traditionally differed between biogeographical regions, most works focusing on the temperate regions such as European seas (Costello and Wilson, 2011). Accordingly to previous studies, Temperate North Atlantic correspond to the highest sampled biogeographic region for marine sessile species and bryozoans (Costello and Wilson 2011; Chaudhary et al., 2016; Menegotto and Rangel, 2018), followed by Temperate Northern Pacific only for marine sessile species, suggesting that until this moment it has been a higher funding for marine research provided by developed countries at temperate latitudes. Otherwise, low sampling efforts were made in tropical regions such as Tropical Atlantic or Central Indo Pacific, and also in other remote areas of the Arctic Sea and the Southern Ocean, highlighting the need to increase the sampling effort at low latitudes and in developing countries on future works to explore if the patterns recorded on this work and the dip in species richness registered for the most of the groups at the equator is naturally-driven or it is biased by differences in the sampling effort (Menegotto and Rangel, 2018).

4.3 Environmental drivers of marine diversity patterns

To date, most of the studies in quantitative modeling of diversity drivers have focused on the study of rarefied diversity by ES50 method (Beck and Chey, 2008; Chaudhary et al., 2017). In contrast, our study explored differences in the methodology between using this popular method and a new methodology incorporating sampling frequency index as an interaction in quantitative models. Despite we obtained the same environmental drivers on the best-fitted model between two methodologies (depth, nitrate, and mean SST), deviance explained was higher when we used non-rarefied species richness corrected by the sampling effort index, suggesting that the use of rarefied species richness implies worst fits due to it not account for all the amount of the data. Deviance explained is a measure of the goodness of fit for statistical models and a major proportion of it represents a high explanatory power of models conforming better predictions of our data (McCullagh and Nelder, 1989; Luoto et al., 2007). Accordingly, our results suggested that including a measure of the total sampling effort as a covariate in biogeographical analyses improve the robustness of the underlying drivers and may have higher accurately predictions when projecting present and future diversity patterns. However, other global studies in diversity patterns ranged deviance explained values from 30-50 % on their performed models (Leprieur et al., 2008; Pasquaud et al., 2015) highlighting the difficulty to predict diversity patterns at global scales and the need to consider other factors such as isolation and continental drift in future studies to obtain better predictions of our models.

Large-scale patterns of species diversity are often strongly correlated with key environmental variables despite the mechanisms behind them remain in most cases are still unknown (Ricklefs, 2004). Specifically, our results showed a decrease in diversity of both studied groups through depth suggesting that the expanse of deep water decreases the number of possible habitats also affecting the number of potential species, previously registered for other taxa (Tittensor et al., 2010; Costello et al., 2018). Moreover, we showed that species diversity is negatively correlated with nitrate according to previous works (Macpherson, 2002; Edgar et al., 2017), and positively correlated with chlorophyll which is an indicator of total phytoplankton abundance and also of energy inputs into the system (Dolan, 2000; Kent et al., 2004; Edgar et al., 2017).

Finally, SST was identified as one of the best predictors of benthic diversity showing a positive relationship between temperature and species richness supporting the kinetic energy or temperature hypothesis which suggests that higher temperatures increase metabolic rates promoting rates of speciation causing a high number of species (Mapherson, 2002; Titttensor et al., 2010; Saeedi et al., 2017). Despite we obtained a positive relationship between marine sessile diversity and SST predictors, a negative pattern was registered between bryozoan diversity and range SST which accords with their lower diversity on the tropics and may be explained by other factors such as their biogeographic affinity or their physiological preferences.

Furthermore, patterns and mechanisms behind changes in species composition among areas have generally received less attention on macroecological scales (McKnight et al., 2007; Buckley and Jetz, 2008). Few studies at a global scale have tested the niche limitation theory (Gaston et al., 2007; Buckley and Jetz, 2008), which posits that areas with contrasting environments would present different sets of species. This study was focused to test the main environmental drivers of global diversity without the aim of considering sites or habitats or analyzing the differences in the species composition between them (beta-diversity). Futures studies should explore the role of other factors such as biological interactions or speciation, extinction, and dispersal processes, and also explore differences between local and site-specific richness, which have been highlighted as important factors determining species richness patterns (Wiens et al., 2010; Edgar et al., 2017).

4.4 Hotspot areas under climate change scenarios

Terrestrial hotspots have been identified across the entire globe, with a large representation of tropical areas and the absence of high diversity areas on high latitudes (Myers et al., 2000). In contrast, many of bryozoan hotspots were located in high latitudes, with a high number in Antarctica, and fewer on tropical areas, differing from previous studies (Roberts et al., 2002; Tittensor et al., 2010). Despite we also identified hotspots of marine sessile diversity on high latitudes, such as the Southern Ocean, many of them were located in temperate and tropical ecosystems, such as Temperate Australasia, Temperate North Atlantic, and Central Indo-Pacific, as other studies found previously for coastal and oceanic taxa (Tittensor et al., 2010).

Marine ecosystems are being increasingly affected by climate change, with steady increases in global sea surface temperatures and more frequent and intense marine heatwaves impacting on marine communities causing regime shifts and local extinctions (Perry et al., 2005; Hughes et al., 2010). In the face of climate change, identifying warming hotspots and potential climatic refugees is vital to address effective conservation measures (McLeod et al., 2009). In line with previous studies, our results showed that the stronger impacts on marine communities derived from climate change will be under "business as usual" RCP 8.5 scenario (Lenton et al., 2015). Specifically, northern regions such as the Arctic and Mediterranean hotspots will suffer the highest increase in temperature. However, some regions of the Southern Ocean will be less impacted, suggesting a minor vulnerability than other tropical and temperate regions (Pugh and Convey, 2008). Moreover, this fact suggests that this area could represent a "climatic refugee" for many species in the future years in comparison to other areas. However, this must be taken cautiously considered given that the threats to Antarctic biodiversity are escalating, despite its remoteness and protection (Wauchope et al., 2019) A possible reason to explain the high marine benthic diversity recorded in the Antarctic shelf and the surrounding areas could be that these areas have suffered less temperature stress than other areas over evolutionary time such as the interglacial periods (Thatje et al., 2005). Despite previous works in terrestrial areas suggested that the terrestrial diversity could be related to the historical climatic variability, such as the highest recorded diversity rates of the Amazon forest or the Mediterranean area (Hewitt, 1996; Malhi et al., 2008), few studies explored this pattern in the marine environment, highlighting to explore it in future works.

Finally, global diversity patterns presented here need to be interpreted cautiously bearing in mind different limitations. First, despite open species databases are a powerful tool for macroecological studies incrementing significantly the amount of data available to be analysed, they present different possible error sources as wrong identification of species or potential temporal biases (Costello et al., 2013a). In addition, other difficulties such as the study of deep-sea species are usually not well represented in open databases (Tittensor et al., 2010). Nevertheless, this study provides new insights into the global patterns of benthic marine biodiversity focusing on traditionally understudied taxa accounting for its latitudinal diversity patterns, and differences in the sampling effort between regions, with important implications for the management and conservation of marine communities under a global warming scenario.

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CHAPTER III: Divergent responses to warming of two common co-occurring Mediterranean bryozoans

Abstract

Climate change threatens the structure and function of marine ecosystems, highlighting the importance of understanding the response of species to changing environmental conditions. However, thermal tolerance determining the vulnerability to warming of many abundant marine species is still poorly understood. In this study, we quantified in the field the effects of a temperature anomaly recorded in the Mediterranean Sea during the summer of 2015 on populations of two common sympatric bryozoans, *Myriapora truncata* and *Pentapora fascialis*. Then, we experimentally assessed their thermal tolerances in aquaria as well as different sublethal responses to warming. Differences between species were found in survival patterns in natural populations*, P. fascialis* showing significantly lower survival rates than *M. truncata*. The thermotolerance experiments supported field observations: *P. fascialis* started to show signs of necrosis when the temperature was raised to 25-26ºC and completely died between 28-29ºC, coinciding with the temperature when we observed first signs of necrosis in *M. truncata*. The results from this study reflect different responses to warming between these two co-occurring species, highlighting the importance of combining multiple approaches to assess the vulnerability of benthic species in a changing climate world.

1. Introduction

Marine ecosystems are highly affected by climate change, with impacts predicted to increase in the coming years (Halpern et al., 2008; Hoegh-Guldberg and Bruno, 2010; Hughes et al., 2017b). Specifically, climatic projections of global sea surface temperature predict 0.3–4.8ºC increase by the end of the 21st century, depending on the CO_2 emissions scenario (IPCC, 2015). In addition to the expected steady increase in temperature, in recent years there has been an increase in the frequency of heat waves, causing mass mortality events in marine ecosystems and affecting a wide variety of species such as gorgonians, sponges, algae and fishes in temperate and tropical seas (Cerrano et al., 2000; Garrabou et al., 2009; Wernberg et al., 2013; Hughes et al., 2017b). Increases in recurrence of these mortalities can lead to population declines and widespread shifts in species distributions, which are currently occurring in all ecosystems as a consequence of environmental changes (Perry et al., 2005; Chen et al., 2011).

The fundamental niche of marine species is determined by their thermal tolerances, where their functional traits raise the optimal values, and an increase of temperature can affect negatively their physiological and demographic processes (Hutchinson, 1957; Somero, 2002; O'Connor, 2008). Due to climate change, in recent years there has been an increment of species that are frequently exposed to conditions over their thermotolerance limits, as the case of coral bleaching events (Hughes et al., 2003; Donner et al., 2017) or mass mortalities of Mediterranean populations of gorgonians (Cerrano et al., 2000; Garrabou et al., 2009). As a result, species with low tolerance to warming are at the greatest risk of local extinction because of their limited thermoregulatory ability (Somero, 2010; Cahill et al., 2013). Related to this, the mortality of non-thermotolerant habitat-forming or key species can have serious consequences on the entire community, reducing species richness and structural complexity of prominent habitats such as kelp forests or coral reefs (Worm et al., 2006; Hoegh-Guldberg and Bruno, 2010).

The Mediterranean Sea is a biodiversity hotspot, highly threatened by climate change (Ballesteros, 2006; Lejeusne et al., 2010). To understand the response of Mediterranean marine species to global warming, several studies have performed thermotolerance experiments in multiple co-occurring Mediterranean benthic species, such as anthozoans, revealing highly divergent levels of sensitivity (Linares et al., 2013; Kersting et al., 2015; Crisci et al., 2017). In some cases, these divergences occur at population level, as in shallow populations of the red coral *Corallium rubrum* (Linnaeus, 1758), where some populations can be more tolerant to an increase of temperature (Torrents et al., 2008). However, while most of the thermotolerance preference studies have focused on charismatic taxa, such as gorgonians or corals, there is a lack of knowledge about other abundant benthic organisms.

In this study, we focused on bryozoans, abundant colonial filter-feeding invertebrates that inhabit many types of benthic ecosystems, being absent or rare on muddy seabeds. In the Mediterranean Sea, bryozoans are prominent organisms on hard rocky benthic ecosystems, where their colonies can significantly increase the habitat complexity and provide shelter and microhabitats for other organisms (Cocito, 2004; Ballesteros, 2006; Wood et al., 2012). Because of the fragility of some erect species to physical disturbances, some bryozoans are known as excellent ecological indicators for different stressors, such as storms or physical stress from recreational diving (Sala et al., 1996; Teixidó et al., 2013; De la Nuez-Hernández, 2014). In this study, we selected two model co-occurring species of common and abundant Mediterranean bryozoans, *Myriapora truncata* (Pallas, 1766) and *Pentapora fascialis* (Pallas, 1766), with different distribution patterns at local and regional scales. Despite these two erect calcified species inhabiting similar hard rocky habitats across the Mediterranean, *M. truncata* populations are found from 1 m depth in marine caves to 60 m in coralligenous bottoms, reaching 130 m in Tunisian area. In contrast, populations of *P. fascialis* are found between 15–100 m depth in rocky bottoms (Zabala, 1986) (Fig. 1). Despite previous field and experimental studies that have studied the effects of warming on Mediterranean bryozoans, most studies have focused on mineralogical, physiological and structural parameters (Lombardi et al., 2006; Rodolfo-Metalpa et al., 2010). To date, there is a lack of knowledge about the effects of temperature anomalies on demographic parameters of bryozoan populations and our study represents the first attempt to combine results from field and laboratory. Specifically, we combined field data of two erect heavily calcified species during a temperature anomaly in the Mediterranean in the summer of 2015, and the experimental study of the lethal and sublethal effects of thermal stress on both species in aquaria under controlled conditions.

2. Methods

2.1 Study species and study area

Populations of both species were monitored in 7 locations at 18–25 m depth in the Montgrí, Medes Islands and Baix Ter Natural Park in the North-Western Mediterranean (Fig. 1, Fig. S3). We monitored all the locations every 6-months through one year (October 2014, April 2015 and October 2015) to describe bryozoan population dynamics between the summer and winter periods. Selected locations were classified by protection level (unfrequented *versus* highly frequented by recreational SCUBA divers) and by type of habitat (hard rock bottoms or coralligenous walls). In each location, we installed a permanent transect of 10 m^2 where colonies of *P. fascialis* and *M. truncata* were individually identified, and their heights, diameters, and degrees of exposure were measured *in situ* by SCUBA diving following similar procedures (Sala et al., 1996). Moreover, we photographed all the colonies to obtain other parameters such as colony area through image analyses (Photoshop CC2017). Through demographic analyses, we obtained parameters such as survival and recruitment between the studied periods (winter 2014: October 2014 – April 2015; summer 2015: April 2015 – October 2015). In modular marine species, the age of individual colonies is hard to assess and life-history traits as survival or growth are often modeled as a function of colony size (Hughes and Connell, 1987). Thus, we fitted a set of regression models of survival and colony size data to explore the potential effects of multiple factors (season, habitat type, etc.).

On the other hand, local thermal regimes during the monitoring period were quantified by high-resolution hourly temperature recordings at 20 m depth obtained from the T-MedNet platform (http://www.t-mednet.org/).

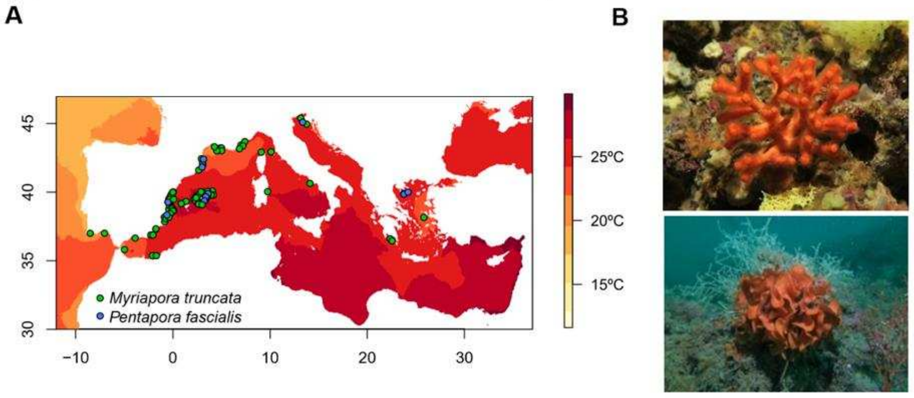

Figure 1. (A) The Mediterranean Sea and the study area (arrow) with maximum temperatures of the warmest month (August) represented by a color gradient and the distribution of studied species (occurrence data downloaded from OBIS and GBIF) represented by green and blue dots. (B) Model species: *Myriapora truncata* (top) and *Pentapora fascialis* (bottom).

2.2 Experimental thermal stress study

2.2.1 Sample collection and experimental design

To explore differential responses to thermal stress between the two bryozoan species, we studied them under experimentally controlled conditions. One fragment of 3-5 cm height from 90 healthy colonies of each species were sampled at the same depth (approximately 20 m) in Medes Islands during October 2016 and transported in aerated seawater to the Experimental Aquarium Facilities of the Institute of Marine Sciences in Barcelona (in less than 24 hours). All the colonies were set in aquaria tanks (approximately 48 l volume), continuously supplied with seawater (salinity 38 ppm) and a current of flow rate around 60 l h^{-1} generated by a submersible pump and were subjected to an acclimation period of 7 days at 18ºC (Arizmendi-Mejía et al., 2015; Kersting et al., 2015). The colonies were fed three times per week with 3 ml of a liquid mixture of particles between 10 to 450 µm in size (Benthos Nutrition Marine Active Supplement, Maim, Vic, Spain) in each aquarium.

We designed 3 different treatments, one control, and 2 different temperature treatments; each utilized of three tanks (replicates) containing 10 colonies from each species. In the control treatment, seawater temperature was maintained by a continuous flow-through of new water at 18ºC. In the temperature treatments, the seawater was heated with submersible resistance heaters regulated by temperature controllers (Aqua Medic T controllers). The first temperature treatment simulated a relatively large period of high temperatures subjecting the colonies to 25ºC for a period of 44 days. This temperature has been recorded in several mass mortality events and identified as a critical threshold for several Mediterranean invertebrate species (Garrabou and Team, 2003; Arizmendi-Mejía et al., 2015; Crisci et al., 2017). In contrast, the second temperature treatment was subjected to a sequential increase of temperature from 25ºC to 30ºC, to investigate thermotolerance features of both species and detect the maximum critical temperature. Specifically, the temperature was increased firstly to 25ºC and, from there it was increased 1ºC every 5-7 days until reaching 30ºC when the experiment finished after 72 days. This methodology was previously used in several studies and demonstrated to be effective to study thermotolerance ranks in benthic species (Linares et al., 2013; Kersting et al., 2015).

2.2.2 Variables studied

We carried out photographic monitoring of all the colonies at regular intervals of 3–6 days and we quantified the proportion of necrosis (dead tissue) expressed as % of the total area through image analysis (Photoshop CC2017). Necrosis was expressed as the proportion of the areas presenting a loss of colony coloration derived from the partial or total lost of living tissue covering the skeleton (Rodolfo-Metalpa et al., 2005;

Cocito et al., 2006; Garrabou et al., 2009), following previous studies on corals or gorgonians (Linares et al., 2013; Kersting et al., 2015; Cau et al., 2018). Necrosis rates were estimated in 10% intervals, and we considered a colony to be affected by partial mortality when it showed recent necrosis over 10% of tissue (Kersting et al., 2015). On the other hand, to obtain the mean growth of the colonies, all of them were weighted at the beginning and at the end of the experiment using the buoyant weight technique (Davies, 1989).

We also tested whether thermal stress may drive physiological non-lethal effects by comparing respiration rates between the temperature treatment at 25ºC and the control. To achieve this, 6 healthy specimens for each treatment and species were incubated for 12 hours in individual chambers (130 ml in volume) that were completely filled with 50 µm pre-filtered seawater (without any air space) and hermetically closed, according to the standardized protocol (Naumann et al., 2011). Moreover, 6 chambers, filled with pre-filtered sea water without any bryozoan, were used as controls. Chambers were maintained at a constant temperature in a water bath (18 and 25 ºC, respectively), and a Teflon-coated magnetic stirrer ensured water movement inside each incubation chamber. Oxygen concentration in each chamber was recorded at the beginning and end of the incubation, using an optode sensor (YSI ProODO Optical Dissolved Oxygen meter, precision 0.2 mg L^{-1}). Variation in the oxygen concentration measured from the control chambers was subtracted from those measured in the bryozoan chambers, and oxygen consumptions were derived from the dissolved oxygen over the incubation and were normalized by colony weight.

To perform skeletal structure and mineralogical analysis, at the end of the experiment we collected from all treatments different fragments from two colony areas (proximal and distal zones) from each specimen in both species. The samples were stored and prepared to be observed with a Scanning Electron Microscope (SEM). Specifically, we selected 3 replicates of 1x1 mm^2 per colony and zone, and we registered structural variables such as the density of zooids, ovicells, avicularia, damaged or broken zooids, and the mean area of the primary orifice (Zabala, 1986; Lombardi et al., 2011b). Moreover, to evaluate the non-lethal effects in the skeletal content, we quantified calcite and Mg content of the calcite (type 1: low-magnesium calcite; type 2: high-magnesium calcite) (Smith et al., 2006) and aragonite on colonies subjected to thermal stress experiment (25ºC) at the end of the experiment. We performed mineralogical analyses cutting 3 replicates (2x2 mm^2) from the growing edge following previously described methodologies (Figuerola et al., 2015). The pieces with 10 grains of pure halite (NaCl) as an internal standard were powdered using a quartz pestle and mortar. The samples were sandwiched between films of polyester of 3.6 microns of thickness. X-ray powder diffraction (XRD) was performed on PANalytical X'Pert PRO MPD powder diffractometer (240 mm goniometer radius) equipped with a PIXcel detector and operating with a Cu Kα (λ = 1.5418 Å) radiation source generated at a voltage of 45 kV and a current of 40 mA at the Scientific and Technological Centers of the UB (CCiT-UB). An angular range of 4 to 65° 2θ was measured with a step size of 0.026° and a 200 s counting time per step. Soller and incident slits were set to 0.04 rad and 0.7 mm, respectively. To determine the proportions of aragonite and calcite, peak intensities were fitted to standard patterns generated from 100% aragonite and 100% calcite. The wt% $MgCO_3$ in calcite was calculated by measuring the position of the d104 peak, assuming a linear interpolation between $CaCO_3$ and $MgCO_3$ (Chave, 1952) and recalibrated for the specific machine used. A linear trend of d104 versus mol% $MgCO_3$ can be observed in the range between 0 and 17 mol% $MgCO_3$ (Mackenzie et al., 1982). All data of this study fall into this range.

2.3 Statistical analysis

To reveal differences between maximum temperatures between our study period and the previous years we used Linear Models (LM). Moreover, to analyze the results of field study we used General mixed models (GLM) fitting binomial distributions of the errors to test the relation between the survival and census period (time), locality, protection level, habitat type, and colony-size (colony area). On the other hand, we used LM's to test for differences between aquaria treatments and species in several parameters that indicate lethal and sub-lethal physiological effects: percentage of necrosis, growth rate, respiration rates, skeletal structure (as density of zooids, ovicells, avicularia, damaged or broken zooids, and the medium area of primary orifice) and mineralogy (Mg content, calcite and aragonite). All statistical analysis and graphics were produced using R version 3.1.2 (R Core Developer Team, 2014).

3. Results

3.1 Field study

3.1.1 Thermal regime in study area

Our results revealed a thermal anomaly in Medes islands during the summer of 2015 when the sea water temperature was higher than the average of the previous years (2005–2014) (19.32±0.22ºC versus 18.99±0.24ºC). Despite this difference was not significant, the maximum temperature reached during summer 2015 was higher than the previous years (24.5ºC versus 22.7ºC), with significantly more days of high temperatures (>22ºC) ($p<0.001$) (Fig. 2).

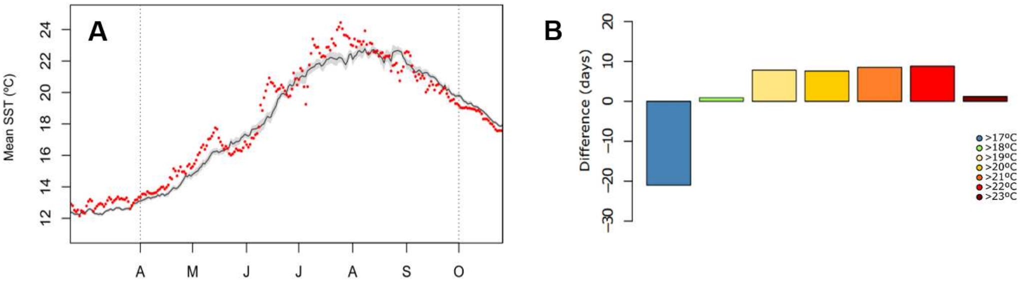

Figure 2. (A) Mean annual sea temperature recorded in 2015 (red dots) and the mean temperature recorded from 2005 to 2014 (gray line). (B) Difference in the number of days with high temperatures recorded in 2015 and those recorded from the mean of the previous years (2005-2014).

3.1.2 Thermal anomaly effects in natural populations

We found differences in the survival between the two species in the field after the summer of 2015 (Table S1). All colonies of *Myriapora truncata* showed a similar high survival in both studied periods (winter 2014: October 2014 – April 2015; summer 2015: April 2015 – October 2015). In contrast, survival of *Pentapora fascialis* colonies significantly decreased in summer 2015 at all localities ($p<0.001$), independently of the protection level and habitat type (Fig. 3, Table S2). In this period, most *P. fascialis* colonies died or were affected by necrosis (Fig. S1). Survival rates were positively related to colony size ($p<0.001$, Fig. 3, Table S2).

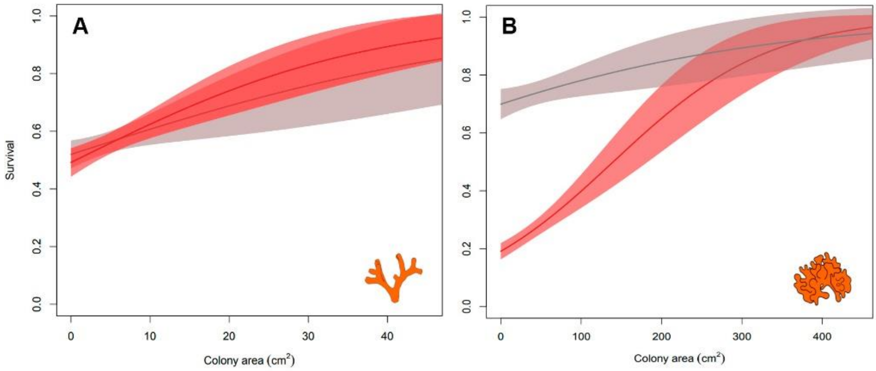

Figure 3. Survival of colonies of *Myriapora truncata* (A) and *Pentapora fascialis* (B) during winter 2014 (grey) and summer 2015 (red).

3.2 Thermal stress under laboratory conditions

3.2.1 Patterns of necrosis

There were significant differences between the response of species to thermal stress at 25ºC ($p<0.001$) (Figs. 4 and 5, Table S3 and Fig. S2), while in control treatments no sign of mortality was detected for either species. Specifically, colonies of *M. truncata* did not show any signals of necrosis until the end of the experiment (44 days), when the colonies started to show small percentages of partial mortality (seen as a loss of coloration, see methodology). In contrast, colonies of *P. fascialis* started to exhibit necrosis around day 15. At the end of the experiment, all colonies showed around 50% partial mortality (Figs. 4 and 5, Table S4).

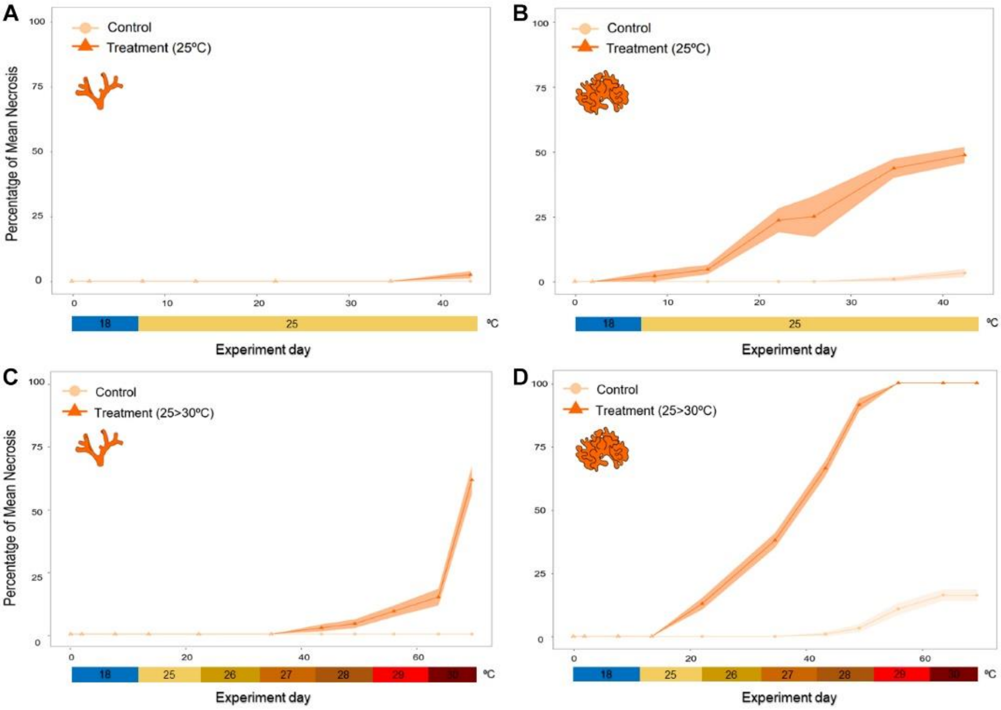

Figure 4. Partial mortality of both species (*Myriapora truncata* (A, C): *Pentapora fascialis* (B, D)) during thermal stress at 25ºC treatment (A, B) and increasing temperature treatment (from 25ºC to 30ºC treatment (C, D).

In the increasing temperature treatment, there were also differences between the responses of the two species to temperature ($p<0.001$) (Figs. 4 i 5, Table S3 and Fig. S2). Colonies of *M. truncata* started to show necrosis only after 45–50 days when the temperature was 28ºC, and necrosis increased rapidly to 70% when the temperature was raised to 30ºC. In contrast, signs of partial mortality in *P. fascialis* colonies were observed after 15-20 days at 25-26ºC, about 20 days earlier and with 2ºC cooler temperature treatment than *M. truncata*. After this period, necrosis increased gradually with temperature, showing a 100% of mortality of all colonies when the temperature reached 28ºC after 45 days from the beginning of the experiment (Figs. 4 and 5, Table S5).

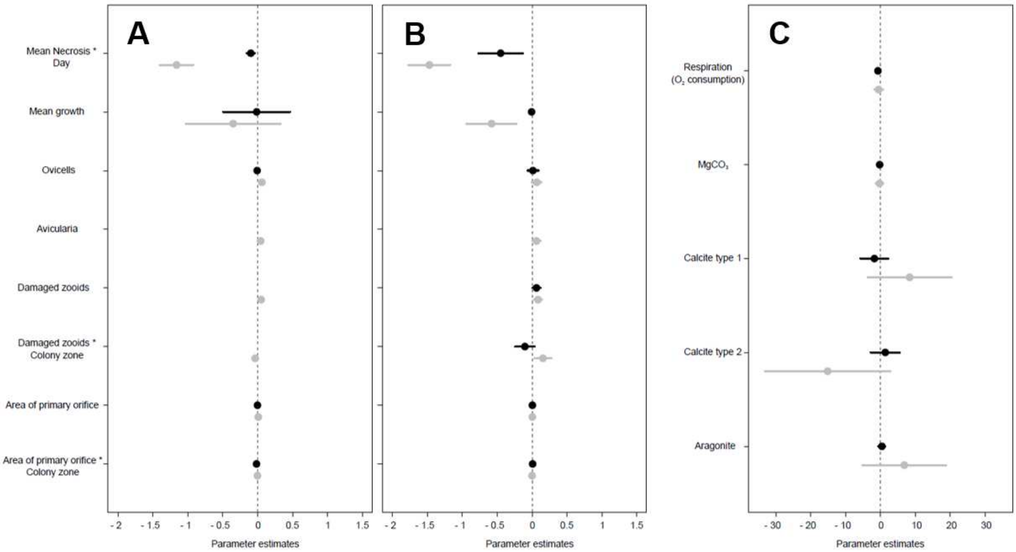

Figure 5. Summary of LM's parameter coefficients and 95% confidence intervals of studied species (in black, *Myriapora truncata*: in grey, *Pentapora fascialis*) for variables responses between treatments in thermal stress at 25 ºC (A), increasing temperature experiment (B) (see Tables S4, S5) and non-lethal effects variables on thermal stress at 25ºC (C).

3.2.2 Growth rates

Colonies of both species showed higher growth rates in control than in both stress treatments, the differences being larger in *P. fascialis* rather than in *M. truncata,* but only significant for *P. fascialis* in the increasing temperature treatment ($p<0.01$) (Figs. 5 and 6, Table S5).

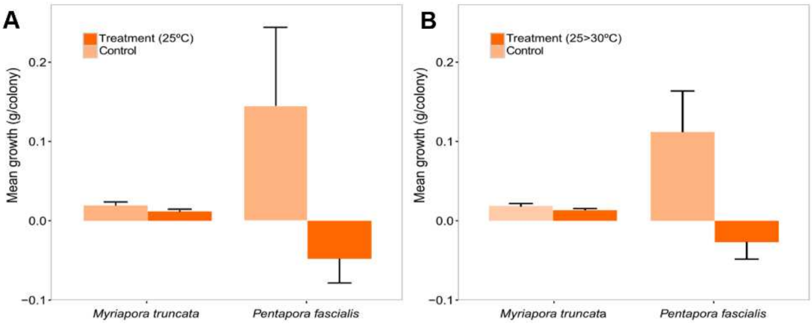

Figure 6. Mean growth (g/colony) between the beginning and the final in thermal stress (25ºC) experiment (A) and increasing temperature experiment (B) in both species.

3.2.3 Respiration rates

A decrease in oxygen consumption was found in all colonies of both species exposed to temperature treatments. However, this was not significant in both species or between them (Fig. 5, Tables S4 and S7).

3.2.4 Structural and mineralogical analyses

Signs of skeletal damage in the temperature treatments were clearly observed in *P. fascialis* but were less evident in *M. truncata*. In the first treatment (25°C), while colonies of *M. truncata* showed no signs of damaged zooids, colonies of *P. fascialis* showed some damaged zooids (*p*=0.010) (Figs. 5 and 7, Tables S3 and S4). Moreover, the mean area of the primary orifice in *P. fascialis* was higher in colonies under thermal stress treatment (*p*=0.010) (Table S6).

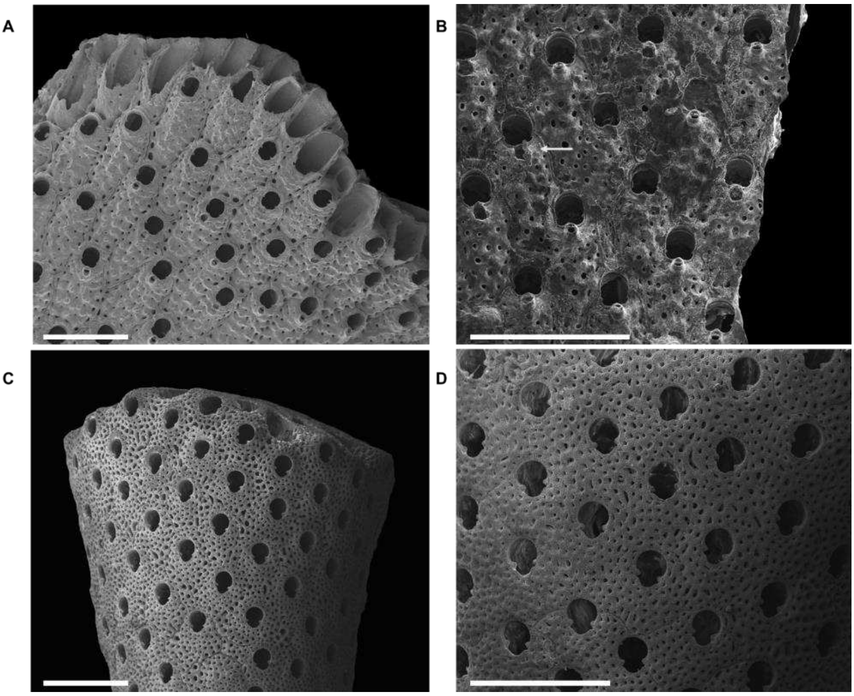

Figure 7. SEM images of *Pentapora fascialis* (A, B) and *Myriapora truncata* (C, D). (A, C)Growing colony edges under control treatment. (B) Group of autozooids with some suboral avicularia (arrowed) broken of *P. fascialis* under thermal stress treatment. **D** Portion of healthy colony of *M. truncata* under thermal stress treatment. *Scale bar* 1 mm.

In the increasing temperature treatment, despite colonies of *M. truncata* showed some damaged zooids, there were no significant differences between treatments. In contrast, *P. fascialis* also showed damaged zooids in colonies under the increasing temperature treatment, zooids at the distal growth tips of the colonies being most affected (*p*=0.010) (Fig. 5, Table S5). Moreover, as in thermal stress experiment, colonies of this species showed higher values for the mean area of the primary orifice (*p*=0.044) (Table S6). The other structural variables showed no trends between treatments and experiments (Tables S3 and S4).

Mineralogical analyses did not show clear differences between treatments; however, we observed higher values of Mg in both species and of aragonite in *P. fascialis* when the colonies were exposed to high temperatures (Fig. 5, Tables S4 and S7).

4. Discussion

Assessing the thermal vulnerability of under-studied but abundant groups of organisms which are important members of many benthic communities such as bryozoans is vital to better understand how the distribution and structure of benthic communities will change under a warming ocean. Our results provide novel insights into the contrasting thermal vulnerability of two abundant and sympatric bryozoan species, highlighting the importance of studying species-specific responses.

Survival patterns in the field revealed a clearly contrasting vulnerability of each species to a thermal anomaly that occurred during summer 2015, showing a clear impact on populations of *Pentapora fascialis* (mainly affecting small-sized colonies), and negligible effects on *Myriapora truncata.* This result agrees with data from previous mass mortality events in the Mediterranean, which revealed *P. fascialis* to be among the affected species together with gorgonians, corals or sponges (Cerrano et al., 2000; Coma et al., 2006; Garrabou et al., 2009). However, these previous studies did not detect differences between these two co-occurring bryozoan species. In agreement with field observations, aquarium experiments revealed differences in the vulnerability to thermal stress between the studied species, where *M. truncata* displayed a higher resistance to a wide range of thermal stress conditions. The maximum registered temperatures in our study area are 23–24ºC and an increment of 1-2ºC is predicted for the end of this century (IPCC, 2015), suggesting that the ongoing warming trend may be critical for populations of *P. fascialis* in the future. Our findings also showed the importance of linking observational and experimental studies to understand the effects of climate change and its consequences for marine species inhabiting in similar habitats.

Beyond the lethal effects of thermal stress, our study also demonstrates other non-lethal effects of warming in *P. fascialis*, and in *M. truncata* to a less extent. On one hand, our results showed a decrease of growth caused by warming, which has been described in other studies focused on bryozoans (Lombardi et al., 2006; Amui-Vedel et al., 2007; Saunders and Metaxas, 2009). On the other hand, in both species we registered a decreasing trend of respiration rates in colonies submitted to thermal stress, which suggest sublethal effects on their metabolic activity under thermal stress, in spite of the absence of necrosis in *M. truncata*. Moreover, structural analyses confirmed the negative effects of temperature on *P. fascialis*. In particular, analyses on Scanning Electron Microscope (SEM) showed a major proportion of damaged zooids in colonies exposed to temperature treatments in this species. Similarly, mean area of primary orifices was higher in temperature treatments, which may indicate that this orifice was broken and was registered as damaged zooids. These results suggest a dissolution or removing of the skeleton around the orifice increasing its area. Previous studies showed that temperature has effects on zooid size, skeletal growth, biomineral deposition and carbonate production on many species of bryozoans (Smith and Key, 2004; Lombardi et al., 2008a). However, some of them showed that only a positive interaction between temperature and pH caused the corrosion of the *M. truncata* skeleton (Rodolfo-Metalpa et al., 2010; Lombardi et al., 2011b) highlighting the need to improve our understanding of the mechanisms behind the physiological responses of *P. fascialis* to thermal stress. On the other way, although the differences were not significant, we observed higher values of Mg in both species and of aragonite in *P. fascialis* respectively when the colonies were exposed to high temperatures. These findings agree with previous studies in other groups and other bryozoan species (Davis et al., 2000; Taylor et al., 2015). However, our results should be taken cautiously given the reduced sample size and the short-term exposures to these conditions.

Life history traits may also influence the response of species under climate change scenario (Adrian et al., 2006). Despite a general lack of information about the life history traits and population dynamics of bryozoans, there is evidence that *P. fascialis* grows faster than *M. truncata* (Zabala, 1986; Cocito et al., 2006). The high vulnerability showed by *P. fascialis* is in accordance with the idea that species with faster dynamics are more vulnerable to environmental changes (Morris et al., 2008). Future studies should explore the relationship between life-history traits and vulnerability in bryozoans and other temperate invertebrates.

The distributional patterns of species reflect their realized niche and environmental tolerances (Parmesan and Yohe, 2003). Both bryozoan species inhabit similar habitats across the Mediterranean, from shallow hard-rocky bottoms to coralligenous assemblages, however it is known that populations of *M. truncata* can be shallower than *P. fascialis* (Zabala, 1986). In this way, we hypothesize that in the areas where the temperature is warmer, *P. fascialis* may habit deeper where the temperature is not so high, contrary to populations of *M. truncata*. Accordingly, many studies showed that the coexistence of similar species involves divergences in some ecological aspect, as temperature tolerance, to adapt to different parts of the environmental gradient (Kraft et al., 2007; Losos, 2008) which agrees with our results. Nevertheless, it is crucial to explore the relationship between distribution patterns and environmental variables to accurately model their ecological niches. However, it is important to take into account the limitations of working with open databases. In our study, we found that due to the actual disagreement about whether *P. fascialis* and *P. foliacea* are separate species, all registers in north-Atlantic bryozoan *P. foliacea* were recorded as*. P. fascialis* (Lombardi et al., 2010). This highlights the importance to complement the use of open databases such as OBIS or GBIF with the taxonomic and ecological knowledge of the target species to avoid errors in the interpretation of distributional patterns.

To sum up, to understand the future of ectotherms under climate change it is necessary a better understanding of how species diverge in climatic niches to forecast the response of species to warmer conditions and which are in risk of local extinction (Somero, 2010). Future studies should integrate a better knowledge of ecological niches, demographic processes and physiological responses to predict the future of vulnerable populations in a changing world.

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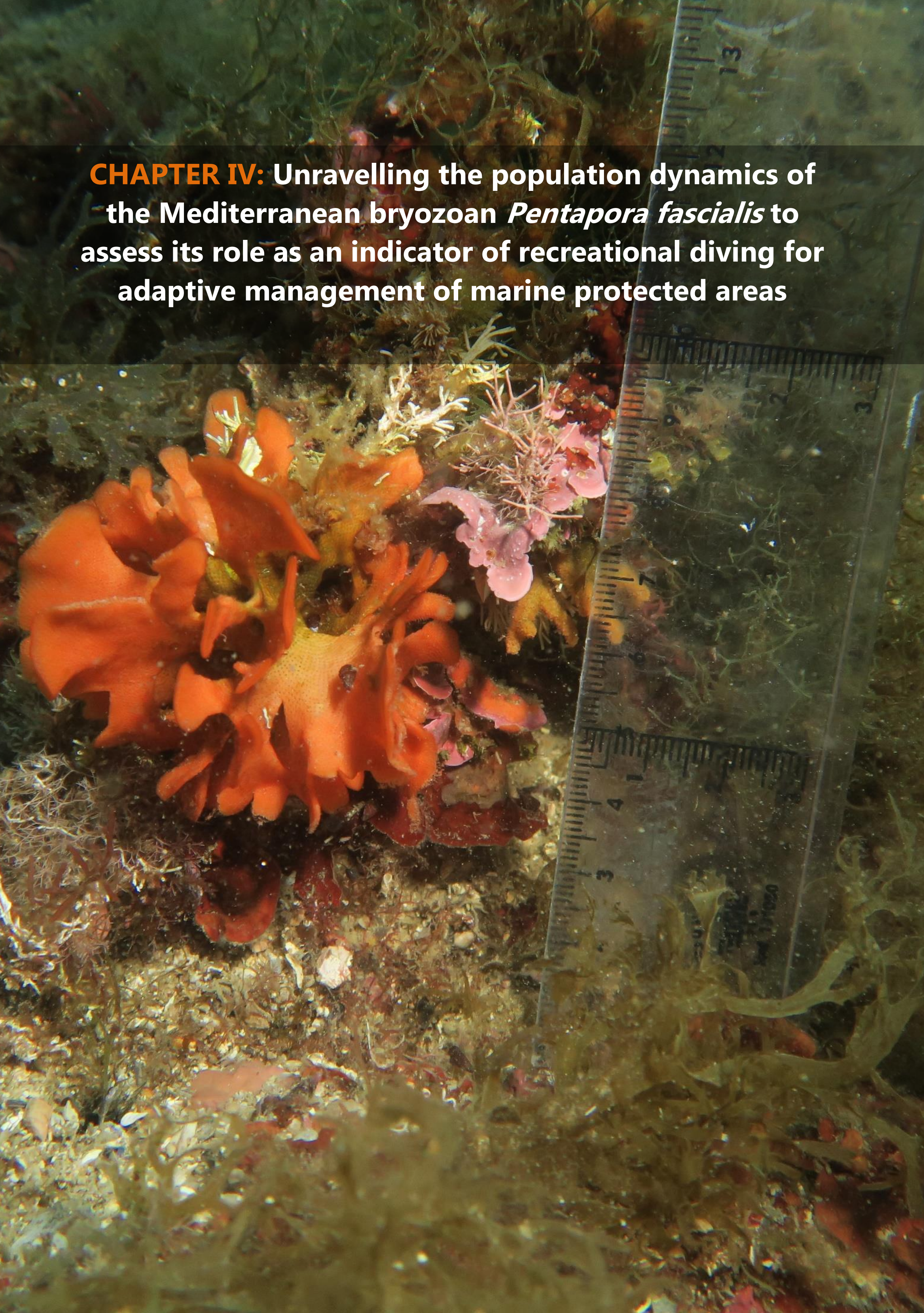
CHAPTER IV: Unravelling the population dynamics of the Mediterranean bryozoan *Pentapora fascialis* to assess its role as an indicator of recreational diving for adaptive management of marine protected areas



Abstract

Marine Protected Areas (MPAs) have been recognized as effective management and conservation tools to protect marine coastal ecosystems. However, due to an increasing interest in marine ecosystems, recreational activities such as scuba diving are rapidly growing in these areas, highlighting the need to implement adaptive management strategies based on continuous monitoring and evaluation of protected areas. To date, several studies have quantified the impact of diving using benthic species as indicators, such as bryozoans, but usually ignoring their population dynamics. Here, we studied the population dynamics of the abundant and common bryozoan *Pentapora fascialis* on a Mediterranean MPA with high levels of diving activity. Specifically, we monitored eight different localities with two different levels of diving frequentation (non-frequented *versus* frequented) from October 2015 to October 2018, accounting for the demographic parameters before and after the summer. Our results showed the impact of diving on the density, recruitment, survival, and size of colonies, reaching higher values on non-frequented localities. In addition, we detected two peaks of recruitment during July 2016 and July 2018, suggesting that bryozoan recruitment events are stochastic, with a high inter-annual variation. Contrastingly, regardless of the diver frequentation level, we found higher growth rates during the colder months and higher necrosis rates after the summer in all the studied localities. Besides the aforementioned differences, the densities observed in this study were much higher compared to previous studies performed in the same area during the 1990s. Taken together, these results suggested rapid population dynamics of *P. fascialis*, with fast growth rates and a high capacity to recover from perturbations. Despite the quantified effects of diving on our studied species, their abundance in frequented sites remained very low over the whole study period, compromising the use of *P. fascialis* as an optimal indicator of diving impact for adaptive management of temperate benthic populations. Overall, our results highlight the importance of continuous monitoring programs to unravel the population dynamics of indicator species to effectively manage marine populations and evaluate the impact of human activities on marine protected areas.

1. Introduction

Over the last decades, marine coastal ecosystems have been increasingly impacted by multiple and interacting anthropogenic stressors, such as habitat destruction or climate change, resulting in a biodiversity loss and an alteration of the ecosystem functioning (Halpern et al., 2008; Cardinale et al., 2012). The creation of Marine Protected Areas (MPAs) has been recognized as an effective management and conservation action to protect and restore marine ecosystems (Milazzo et al., 2002; Harley et al., 2006). However, the establishment of new MPAs worldwide has contributed to an exponential increment of tourism attracted by the high biodiversity and ecological services that they provide (Davis and Tisdell, 1995; Badalamenti et al., 2000). In this context, effective management of MPAs requires linking social-ecological considerations through adaptive management strategies, based on continuous monitoring and evaluation, to assess the protection goals in the context of increasing anthropic perturbations (Agardy et al., 2011; Ban et al., 2012).

MPAs can provide economic benefits through fishing and tourism activities such as diving or snorkeling, among others (Sala et al., 2013). Specifically, economic benefits of tourism in marine protected areas contribute significantly to their local economy, ranging from US$2 million per year for some Caribbean Islands (Fernandes and Van't Hof, 1995) to ~US$5 billion gained in 2006-2007 in the Great Barrier Reef, Australia (McCook et al., 2010). In these areas, diving has become popular worldwide and nowadays it represents one of the major touristic activities in MPAs (Rouphael and Inglis, 2001; Hawkins et al., 2005; Parsons and Thur, 2008; Di Franco et al., 2009). At local scale, previous studies have documented the high interest of divers to visit MPAs, such as the case of the small but popular Medes Islands marine reserve located in the NW Mediterranean Sea (Spain), where around 67,000 divers were annually registered, which generate direct benefits of €235,000 coming only from diving fees (Sala et al., 2013). The total benefit of the protection of this area is estimated around €10 million annually, considering all the economic benefits derived from the tourism sector (i.e., hotels, restaurants) and the creation of working places that grew in association with diving activity (Merino et al., 2009; Capella, 2010).

Despite the conservation and economic benefits of MPAs, the over-frequentation of divers in these areas can have negative consequences for marine benthic communities (contrasting with their ecological values). Some studies have demonstrated that scuba divers may affect marine organisms in several ways, both intentionally and unintentionally, increasing the degradation of marine ecosystems (Davis and Tisdell, 1995; Hawkins et al., 1999; Milazzo et al., 2002; Uyarra and Côté, 2007). Specifically, they may impact directly to benthic organisms, breaking or damaging them, resulting in a partial or total loss of colonies (Garrabou et al., 1998) and negative population growth rates (Linares and Doak, 2010), or indirectly, increasing sediment resuspension or creating air bubbles that might remain trapped on marine caves (Lloret et al., 2006; Luna-Pérez et al., 2010). Accordingly, these impacts may result in high partial mortality rates, decreasing the cover of benthic invertebrates such as hard corals, gorgonians, or sponges (Milazzo et al., 2002; Zakai and Chadwick-Furman, 2002; Luna-Pérez et al., 2010).

To unravel the impact of diving on benthic organisms, some works have studied diver behavior directly (Zakai and Chadwick-Furman, 2002; Di Franco et al., 2009; Luna et al., 2009), but the majority of works have focused on the study of indicator species (Garrabou et al., 1998; Linares et al., 2010b; De la Nuez-Hernández et al., 2014). Adequate indicator species should have some key characteristics, such as a high abundance and a wide distribution to ensure sampling repeatability. In this regard, gorgonians and hard corals are considered optimal indicators of human perturbations (Linares et al., 2010b). Up to now, most of the previous studies have focused on tropical seas (Hawkins et al., 1999; Barker and Roberts, 2004; Dearden et al., 2010), with few examples in other areas, such as the Mediterranean Sea (Sala et al., 1996; Coma et al., 2004; De la Nuez-Hernández et al., 2014). In this area, bryozoans, among other organisms, have been widely used as indicators of diving impact due to their high abundance and fragility (Ballesteros, 2006). Despite the fact that previous works have registered the impact of diving on these organisms (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández, 2014), there is a lack of knowledge about their population dynamics, compromising the use of these organisms as optimal indicators of physical impacts.

The main goal of this study was to unravel the effect of diving on the common Mediterranean bryozoan *Pentapora fascialis* (Pallas, 1766), analyzing its population dynamics through an in situ monitoring. The study was carried between 2015 and 2018, monitoring eight different locations within a Mediterranean MPA characterized by different levels of diving frequentation. On each location, we installed one fixed transect which was monitored annually before and after the summer, identifying individually all the colonies and registering the density, size, and partial mortality of the colonies. Moreover, we analyzed demographic parameters between monitoring periods, such as survival, recruitment, and growth, to unravel differences between frequented and non-frequented locations. Our study represents the first attempt to study the population dynamics of the bryozoan *P. fascialis*, with important direct applications for the adaptive management of benthic communities in MPAs.

2. Materials and Methods

2.1 Study Area

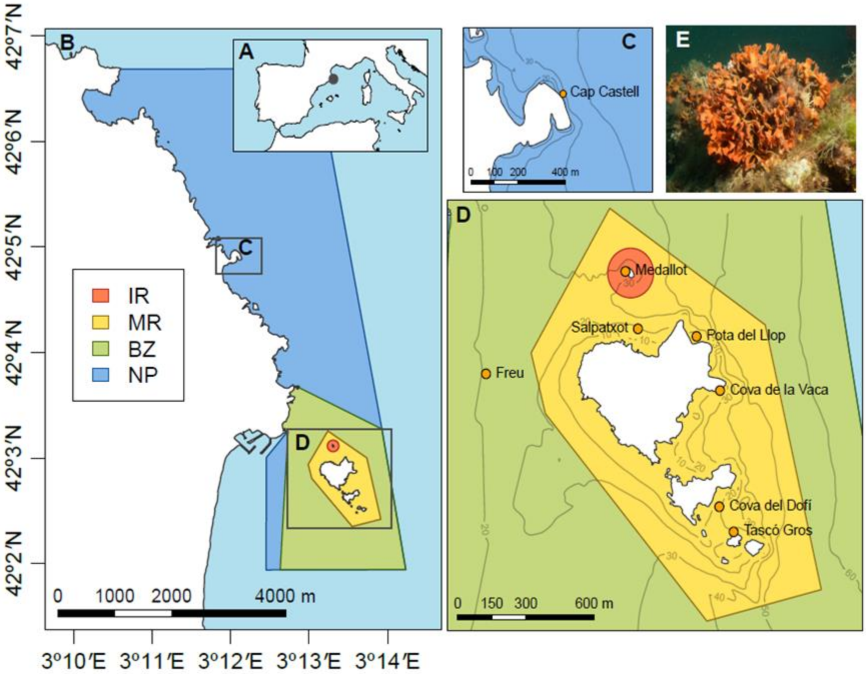


Figure 1. Map of the study site and image of the species monitored. General location of the study area in the NW Mediterranean (A). Location of The Montgrí, The Medes Islands and The Baix Ter Natural Park (B). Detail of the Cap Castell location (C) and the Medes Islands (D). Colors represent different levels of protection: Integral Reserve (IR), Marine Reserve (MR), Buffer Zone (BZ) and Natural Park (NP). Image of the monitored species, the bryozoan *Pentapora fascialis* (E)

Our study was performed in the Montgrí, the Medes Islands and the Baix Ter Natural Park (Catalonia, Spain) in the Northwestern Mediterranean Sea (Fig. 1A). In this protected area, the Medes Islands Marine Reserve represents one of the protected areas most frequented by divers in the Mediterranean Sea (Sala et al., 2013). This MPA is characterized by different levels of protection: a Marine Reserve (MR), where diving is allowed but regulated by buoys with a maximum number of divers per year, anchoring is forbidden, and navigation is regulated; a Buffer Zone (BZ), where diving, artisanal fishing, and angling are allowed; and a Natural Park (NP), which comprises the remaining coast of Montgrí, where diving, anchoring, artisanal fishing, and spearfishing are allowed without restrictions (Fig. 1) (Hereu and Quintana, 2012; Sala et al., 2013). Recently, in 2015, one of the study locations (Medallot) inside the Marine

Reserve (MR) was declared as an Integral Reserve (IR), and all the activities inside this area were forbidden except scientific diving (Hereu et al., 2017).

2.2 Monitored species

Pentapora fascialis is a common bryozoan in the Mediterranean benthic communities, distributed from 15 to 100 m depth on hard rocky bottoms (Zabala, 1986) (Fig. 1E). Adult erect colonies reach up to 30 cm in diameter and 20 cm in height, with a high mean growth of 9.8 ± 4 cm/year (Zabala, 1986; Cocito et al., 2006). Due to its physical structure, it is considered a habitat-forming species that increases the associated biodiversity (Cocito, 2004). Previous studies concluded that this species is a good indicator of the impact of diving and other physical perturbations, such as storms, due to the fragility of its skeleton and its lack of commercial value (Sala et al., 1996; Garrabou et al., 1998) (Table S1). However, there is a lack of basic knowledge about its population dynamics, and only a few previous studies explored demographic aspects, such as mean annual growth (Cocito et al., 2006).

2.3 Sampling sites and data collection

This study was carried out at eight different locations of the MPA where we identified populations of *P. fascialis* at similar depth range (between 17-22 m depth) (Fig. 1). Localities were selected according to its protection level, recreational diving activity and the presence of *P. fascialis* populations. Study locations were classified by the diving frequentation level (unfrequented versus frequented by divers), classifying the locations inside the Marine Reserve as Frequented (Cova del Dofí, Cova de la Vaca, Pota del Llop, Salpatxot and Tascó Gros) and the locations outside the Marine Reserve or in the Integral Reserve as Non-Frequented (Cap Castell, Freu and Medallot) (Fig. 1). Despite outside the Marine Reserve diving is allowed and can be performed by anchoring, it is basically performed from buoys which identify the suitable sites to dive and facilitates their access to the divers. For this reason, the two studied locations outside the Marine Reserve (Cap Castell and Freu) were placed in remote areas without diving buoys, which ensures that they are not frequented by divers, and if diving occurs, it is very rare as demonstrated by the fact that during all the study no divers have been observed in these locations. Specifically, no divers were registered in the non-frequented locations in the period 2016-2018; in contrast, between 1600 and 5500 divers were registered annually at frequented locations. Detailed information on the divers registered per year during the whole study period at each locality is available (Table S2).

In each location, we installed a permanent transect of 6 m length and 2 m width marked with plastic screws attached to the substrate with epoxy glue (Fig. S1). The size of the transects was selected in order to have a representative number of bryozoans. We installed the permanent transects in six of our eight study locations between October 2015 (Medallot and Tascó Gros) and July 2016 (Cova de la Vaca, Cova del Dofí, Pota del Llop, and Salpatxot), and in the two other localities were installed in October 2017 (Freu and Cap Castell). To monitor each transect, we used plastic quadrats of 0.5 x 0.5 m (0.25 m^2), being four quadrats in one line of each transect, and hence, 48 quadrats in each total transect (12m^2). All quadrats were surveyed during all the monitoring. In each of these quadrats, we identified and registered individually all the colonies to follow them during the whole study period, measuring their maximum height (with a plastic ruler) and visually estimating the percentage of affected surface (necrosis). This parameter was expressed as the proportion of the area presenting a loss of colony coloration derived from the partial or total loss of living tissue covering the skeleton, following previous methodologies (Sala et al., 1996; Pagès-Escolà et al., 2018).

To quantify the impact of diving, we monitored all the locations before (July) and after the summer (October), following previous studies (De la Nuez-Hernández et al., 2014). For each location and survey period, we estimated the following demographic parameters: (i) survival, as the ratio between the number of remaining colonies and the total colonies at the beginning of each period, considering as dead the colonies with 100% of necrosis; (ii) recruitment, as the number of new colonies that appeared after each monitoring; (iii) and growth, as the difference of size (height) between surveys. Finally, we analyzed the number of total colonies, recruits and adults (estimated as the colonies that were not identified as recruits) on each quadrat and we extrapolated to the number of colonies/m^2 on each studied location (Sala et al., 1996).

2.4 Data analysis

In order to evaluate the diving impact on *P. fascialis* populations, we performed a set of Generalized Linear Mixed Models (GLMMs) (Bolker et al., 2009). The total, adult and recruit densities of *P. fascialis*, height, necrosis, survival, and growth were fitted as the dependent variables. The explanatory variables year, month (before/after the summer), and diving frequentation (frequented/non-frequented) were included as fixed factors, and the sampled location, nested to the frequentation level, was included as a random effect. For each model, the data distribution of the response variable was inspected and fitted to the most likely distribution (binomial, negative binomial, poisson or gaussian). The analyses were conducted using the package "lme4" for R (Bates et al., 2014).

To test the relation between the survival and necrosis with the initial size of the colonies, we performed Generalized Linear Models (GLMs) (McCullagh and Nelder, 1989) considering the level of frequentation to analyze if there were statistical differences between frequented and non-frequented zones. Moreover, to analyze the growth of the colonies, we fitted the same model testing the relation between the initial size vs the posterior size of the colonies. As noted above, the data distribution of each response variable was inspected for each model and fitted to the most likely distribution.

According to previous studies, to detect changes in *P. fascialis* populations, population size structure was calculated by pooling colonies in size classes of 1.5 cm (Sala et al., 1996). Differences among locations, years and months were tested using the non-parametric two-sample Kolmogorov-Smirnov (K-S test; Legendre and Legendre, 1998).

All statistical analyses were performed with the software R, version 3.3.3 (R Core Development Team, 2017).

3. Results

3.1 Density

Our results showed higher densities in non-frequented locations compared to the frequented ones, reaching the highest values of 6.2 ± 0.28 colonies/m^2 (mean ± SE) in the location of Freu and 9.75 ± 0.39 colonies/m^2 in the location of Cap Castell, both in July 2018 (Fig. 2A, Table 1). Despite the fact that most of the frequented locations presented lower densities, reaching values from 0 to 1.91 ± 0.29 colonies/m^2, the location of Tascó Gros (2.41 ± 0.29 colonies/m^2) showed similar densities to the non-frequented location of Medallot (2.45 ± 0.34 colonies/m^2) in July 2018 (Fig. 2A). We found statistically significant differences between years, showing higher densities in July 2016 and 2018 (GLMM, z= -4.52, $p<0.001$; Table 1). Similarly, we found significant differences between months, showing higher values of density in July and a significant decrease in the number of colonies in October (GLMM, z=-4.79, $p<0.001$; Table 1).

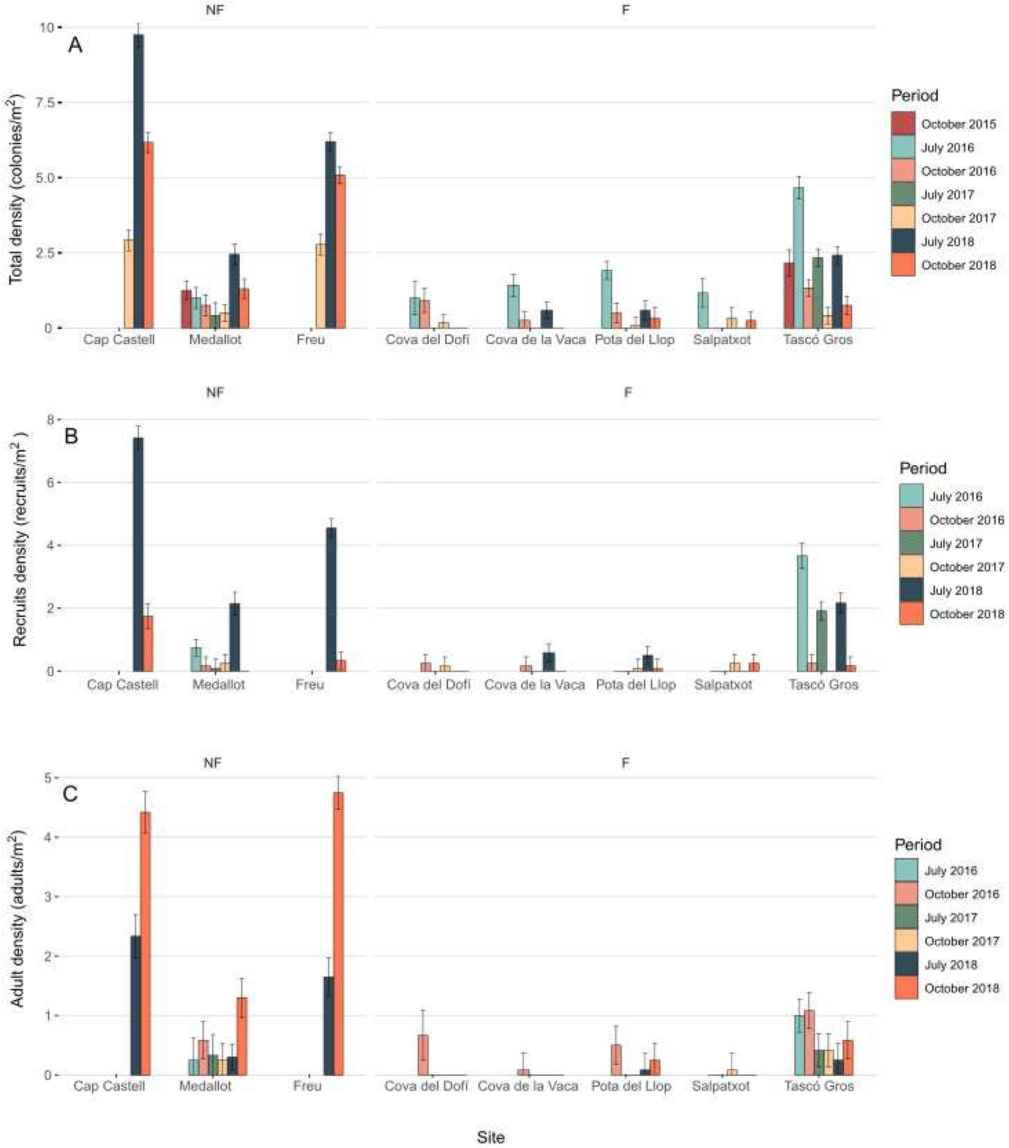


Figure 2. A) Total density of colonies (mean ± SE), B) recruits density (mean ± SE), and C) adult density (mean ± SE) for each location grouped according to the diving frequentation (NF, non-frequented; F, frequented) and for each monitoring period. Note that the scale of the figures is different. For figures B and C, the first monitoring was not represented since the data from the previous year is required to differentiate between adult colonies and recruits

Table 1. Generalized linear mixed models (GLMM) between response variables (density colonies, density recruits, size, survival, and necrosis) and the fixed factors (protection, year, and month) and the random factor (locality), following the model formula "*Response variable* ~ Protection*(Year + Month) + (1|Protection: Locality)". In each case, we fitted the model accordingly with the distribution of the response variables (Negative binomial for total, recruit and adult densities and necrosis; Poisson for size; Binomial for survival; Gaussian for growth). For each model, we presented the statistics and the marginal and conditional R^2 to estimate the importance of the random variable. Significant analyses were indicated in bold (<0.05).

Response variable	Predictors (Fixed factors)	Estimate	Std. Error	Z value	*p*	Marginal R^2	Conditional R^2
Density Colonies	Intercept	-1.84	0.58	-3.16	**<0.001**	0.26	0.34
	Protection	1.47	0.39	3.69	**<0.001**		
	Year	-0.90	0.19	-4.52	**<0.001**		
	Month	-0.97	0.20	-4.79	**<0.001**		
	Protection*Year	0.54	0.13	4.04	**<0.001**		
	Protection*Month	0.41	0.13	3.02	**<0.01**		
Density Recruits	Intercept	-3.09	0.72	-4.27	**<0.001**	0.34	0.45
	Protection	0.88	0.49	1.8	0.06		
	Year	-0.01	0.27	-0.06	0.95		
	Month	-0.58	0.24	-2.35	**0.01**		
	Protection*Year	0.24	0.19	1.24	0.21		
	Protection*Month	-0.19	0.15	-1.22	0.22		
Density Adults	Intercept	-4.18	1.02	-4.08	**<0.001**	0.30	0.34
	Protection	2.04	0.68	2.98	**<0.01**		
	Year	-1.54	0.38	-3.98	**<0.001**		
	Month	0.49	0.36	1.37	0.16		
	Protection*Year	1.20	0.26	4.55	**<0.001**		
	Protection*Month	-0.10	0.22	-0.49	0.62		
Size (height)	Intercept	0.98	0.21	4.54	**<0.001**	0.092	0.149
	Protection	0.37	0.13	2.74	**<0.01**		
	Year	-0.11	0.12	-0.92	0.35		
	Month	0.07	0.12	0.59	0.55		
	Protection*Year	0.11	0.08	1.42	0.15		
	Protection*Month	0.1	0.08	0.13	0.89		
Growth	Intercept	1.72	0.56	3.07	**0.002**	0.16	0.16
	Protection	0.44	0.32	1.39	0.16		
	Year	0.74	0.59	1.25	0.20		
	Month	-0.47	0.52	-0.91	0.37		
	Protection*Year	-0.4	0.37	-1.08	0.27		
	Protection*Month	-0.61	0.29	-2.04	**0.04**		
Survival	Intercept	-2.72	0.55	-4.91	**<0.001**	0.113	0.133
	Protection	1.37	0.33	4.18	**<0.001**		
	Year	-0.55	0.38	-1.47	0.14		
	Month	-0.04	0.36	-0.12	0.90		
	Protection*Year	0.37	0.22	1.71	0.08		
	Protection*Month	0.05	0.22	0.27	0.78		
Necrosis	Intercept	1.01	3.34	0.30	0.76	0.390	0.828
	Protection	-0.13	2.17	-0.06	0.95		
	Year	2.30	0.89	2.56	**0.01**		
	Month	2.17	0.94	2.29	**0.02**		
	Protection*Year	-1.51	0.51	-2.95	**<0.01**		
	Protection*Month	0.12	0.51	0.24	0.81		

Similarly, we found higher levels of recruitment in non-frequented locations, reaching 7.42 ± 0.38 recruits/m^2 in the location of Cap Castell and 4.55±0.29 recruits/m^2 in the location of Freu, both in July 2018 (Fig. 2B). We found lower numbers of recruits on frequented locations during all the monitoring, with the exception of the location of Tascó Gros, where, during July 2016 and 2017, we registered higher numbers of recruits (3.66 ± 0.40 recruits/m^2 and 1.91 ± 0.280 recruits/m^2 respectively) than in non-frequented location of Medallot (0.75 ± 0.26 recruits/m^2 and 0.08 ± 0.28 recruits/m^2 respectively). However, the number of recruits were similar in the two locations in July 2018 (Tascó Gros reaching 2.16 ± 0.32 recruits/m^2 *vs* Medallot reaching 2.15 ± 0.36 recruits/m^2) (Fig. 2B). Accordingly, we also found statistical differences between months, reflected in the higher recruitment peaks of July in non-frequented locations and the frequented location of Tascó Gros (GLMM, z=-2.35, p=0.01; Table 1). Despite the high peak of recruitment in 2016 and 2018, we did not find statistically significant differences between years due to the high variability (Table 1).

Like for recruit densities, we observed higher adult densities in non-frequented locations, reaching 4.42 ± 0.35 adults/m^2 and 4.75 ± 0.32 adults/m^2 in the locations of Cap Castell and Freu, respectively, in October 2018 (Fig. 2C). Although we found lower levels of adults in frequented locations, the location of Tascó Gros showed similar levels of adults than the non-frequented location of Medallot during the monitoring period (Fig. 2C). However, in October 2018 the location of Medallot showed higher levels of adults (1.3 ± 0.32 adults/m^2) than the frequented Tascó Gros (0.58 ± 0.31 adults/m^2). We obtained significant differences in the adult densities between years (GLMM, z=-3.98, p<0.001; Table 1), but we did not find them between months (Table 1).

3.2 Size structure

Despite the fact that we did not find any pattern on the population size structure between different frequentation levels (Table S3), we accounted the higher proportion of larger colonies in non-frequented locations together with the frequented locations of Tascó Gros and Cova del Dofí, reaching large class sizes (10-12 cm height, Fig. 3). In fact, we found significant differences in the mean size between levels of frequentation, being higher in non-frequented sites (Table 1). Moreover, we did not observe any differences in the mean size between years and months regardless of the registered increase of recruitment density in July 2016 and July 2018. Conversely, we registered statistical differences between July and October 2018 in most of the locations, independently of their level of frequentation, highlighting the decrease in the number of colonies during this period (Table S3).

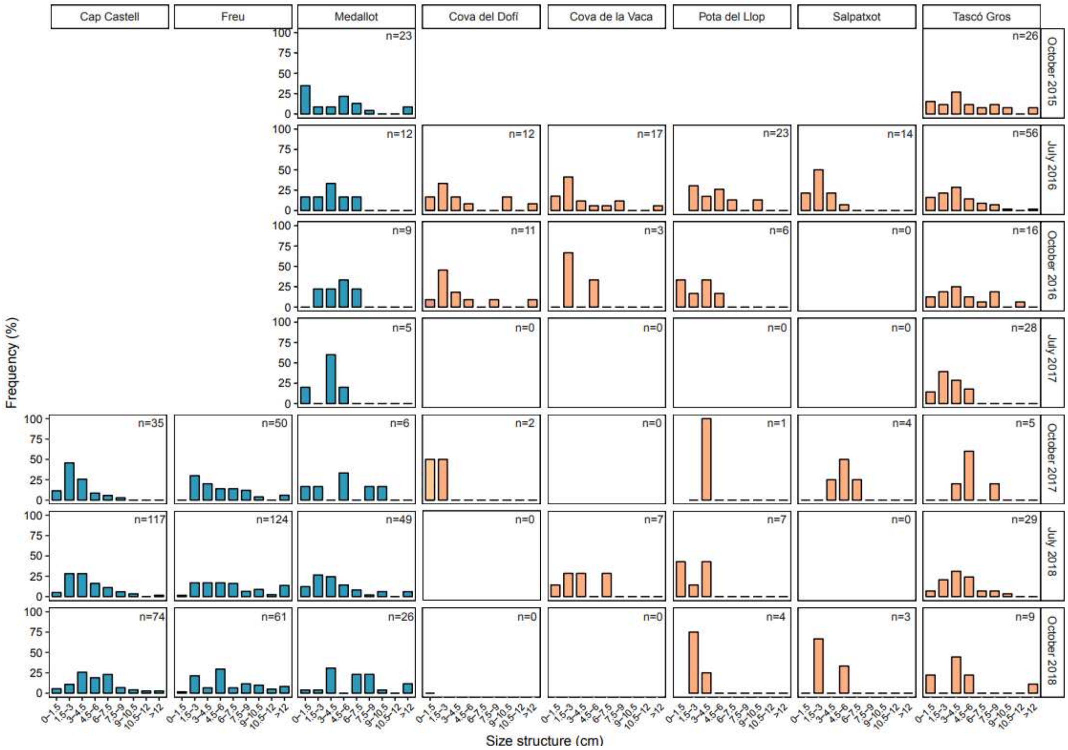


Figure 3. Temporal evolution of size structure (height, cm) of the colonies at each sampling location. The non-frequented locations are presented in blue and the frequented locations are presented in orange. The number of colonies registered (n) is indicated for each location and sampling

3.3 Survival

The highest survival rates were found in non-frequented locations, reaching the highest mean survival values of 1 in the location of Medallot, 0.7 ± 0.06 in the location of Freu, and 0.62 ± 0.08 in the location of Cap Castell in July 2018 (Table 1, Fig. 4A). However, we also found a high survival in the frequented location of Tascó Gros in July 2018 (0.6 ± 0.25). Despite the fact that we did not find any patterns between years and months, locations with a large sample size of colonies (non-frequented: Cap Castell, Freu, Medallot; and frequented: Tascó Gros) showed lower levels of survival after the summer, decreasing between July 2018 and October 2018. The survival of the colonies increased with their initial size (GLM, z=2.28, *p*=0.02; Fig. 5A, Table S4), without showing differences between levels of frequentation. However, our results suggested that the survival of the small-sized colonies was higher in non-frequented sites (Fig. 5A).

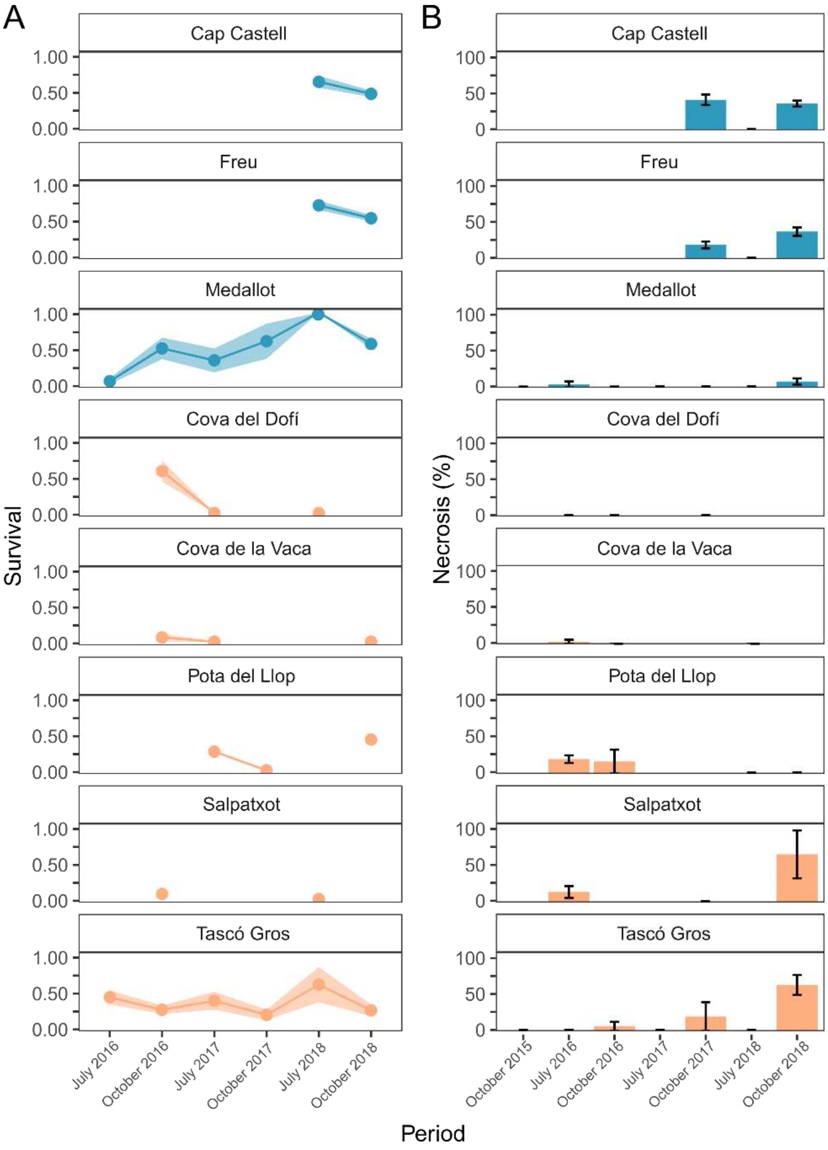


Figure 4. A) Survival (mean ± SE) and B) Partial mortality (necrosis) considered as proportion of affected surface (mean ± SE) for each study period and at each sampling site in the non-frequented (blue) and frequented (orange) locations

3.4 Necrosis

We did not find statistically significant differences between non-frequented and frequented locations, both showing higher levels of necrosis in October than in July (GLMM, z=2.29, *p*=0.02; Table 1, Fig. 4B). Moreover, we observed significant differences in necrosis between years, showing higher levels of mortality in 2017 and 2018 (GLMM, z=2.56, *p*=0.01; Table 1, Fig. 4B).

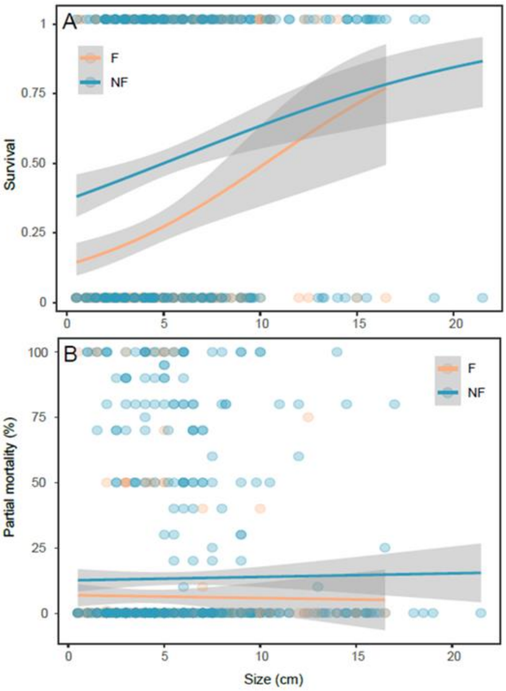


Figure 5. Relation between the survival (A) and partial mortality (B) with the initial size of the colonies accounting for the level of frequentation, with non-frequented locations (NF) in blue and frequented locations (F) in orange. The lines represent the generalized linear model fitted between the response variable and the predictor. For each model the data distribution of the response variable was fitted to the most likely distribution (binomial distribution for survival, and negative binomial distribution for necrosis)

The necrosis did not show any relation with the initial size of the colonies (Fig. 5B, Table S4), showing non-significant differences between levels of frequentation (Fig. 5B, Table S4).

3.5 Growth

We did not find significant differences in growth rates between levels of frequentation and between years and months; however, we observed higher growth rates in July reaching the highest mean growth values of 5.25 ± 0.35 cm in the location of Freu in July 2018 (Table 1, Fig. 6).

There was a positive relationship between the initial size of the colonies (t0) and the size observed on the next monitoring period (t1) (GLM, z=3.59, *p*<0.001; Table S4), without differences in the level of frequentation (Fig. 7, Table S4).

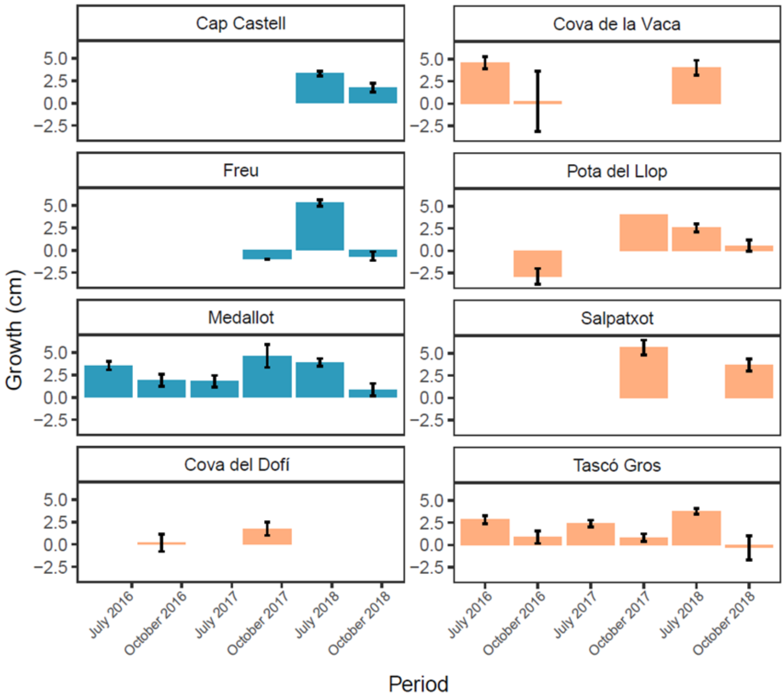


Figure 6. Mean growth (mean ± SE) (cm) of colonies for each studied period at each non-frequented (blue) and frequented (orange) location

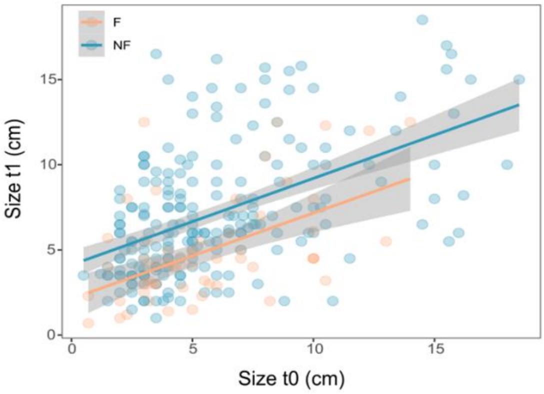


Figure 7. Relation between the posterior size (t1) and the initial size (t0) of the colonies, accounting for the level of frequentation, with non-frequented locations (NF) in blue and frequented locations (F) in orange. The lines represent the generalized linear model fitted between the response variable and the predictor. Data distribution of the response variable was fitted to the most likely distribution (Poisson distribution)

4. Discussion

This work represents the first attempt to study the population dynamics of the common Mediterranean bryozoan *P. fascialis* in order to elucidate its suitability as an indicator of recreational diving impact. In accordance to previous studies on the same species (Sala et al., 1996; Garrabou et al., 1998), our results evidence the impact of diving on the abundance and size of the colonies. However, we did not register differences in partial mortality and growth rates between frequented and non-frequented sites.

Like in previous works, our study found a higher abundance of *P. fascialis* in non-frequented locations, highlighting the diving pressure in frequented areas, which presented lower densities of bryozoans (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández et al., 2014). However, the location of Medallot showed the lowest levels of density among the non-frequented locations, which may be explained by the fact that in this area diving was allowed until 2015 when this location was declared an Integral Reserve and only scientific diving has been allowed since then (Hereu et al., 2017). Although we did not find records of previous abundances of *P. fascialis* before the full protection of this location, its higher density than frequented locations may indicate the recovery of this population against the recent impact of diving and suggest a possible continued increase in its density in the future years.

Density values registered in our study differ from those reported on previous works performed in the same study area. In non-frequented locations, we found a maximum number of colonies of 9.75 colonies/m^2 contrasting with the 3.6 colonies/m^2 registered in the same area during July 1992 (Sala et al., 1996). In frequented locations, we found maximum values of 4.6 colonies/m^2 differing from the 0.6 colonies/m^2, respectively. Since both studies applied similar methodologies, this fact suggests that the abundance of bryozoan populations has increased in non-frequented locations since the 1990s, as well as in some frequented locations such as Tascó Gros, potentially explained by the high recruitment rates registered in this study. However, in the other frequented locations, densities have remained very low since the 1990s, suggesting that the high levels of diving have not allowed the development of abundant and well size-structured populations (Garrabou et al., 1998). Apart from diving impact, it is important to bear in mind other factors such as local differences on habitat, currents or nutrients, which also may affect the abundance and distribution of benthic organisms (Ballesteros, 2006). These factors may explain the high density observed in the frequented location of Tascó Gros, highlighting the need to account for other factors in future studies.

The recruitment of new individuals is a key ecological process for the maintenance, resilience, and recovery of natural populations (Richmond, 1997; Hughes and Tanner, 2000). In the same line as density levels, we found high recruitment rates in non-frequented locations and the frequented location of Tascó Gros, which might be explained by other factors that were not considered in this study. Accordingly, previous studies have demonstrated that the spatial variations of recruitment patterns might be explained by abiotic factors, such as the orientation of the substratum, current regime, or temperature, among others (Hughes et al., 1999; Perkol-Finkel and Benayahu, 2007; Caines and Gagnon, 2012).

Recruitment of most of benthic invertebrates is characterized by irregular annual variations and stochastic peaks (Gotelli, 1988; Caley et al., 1996; Garrabou and Harmelin, 2002). We registered higher levels of recruits in non-frequented locations and Tascó Gros in July compared to October, suggesting that the optimal season for recruitment for *P. fascialis* takes place between winter and spring, when temperatures are lower, accordingly with its thermotolerance preferences (Pagès-Escolà et al., 2018). Our study found higher recruitment rates in 2016 and 2018 than in 2017, suggesting for the first time that recruitment of *P. fascialis* is characterized by biannual pulses. These results suggest that our species model displays faster population dynamics than other benthic species with longer temporal intervals between recruitment peaks, such as corals or gorgonians (Garrabou and Harmelin, 2002; Linares et al., 2007; Montero-Serra et al., 2019).

Despite the occurrence of recruitments peaks, we did not find evidence of the incorporation of small recruits in size-structure analyses. Such lack of changes in size structure suggests that the new colonies registered as recruits were characterized by relatively large sizes, which might be explained by two possibilities. First, the high growth rates of new colonies incorporated to the population during winter, which allows the colonies to reach large sizes by spring, could difficult the detection of small-sized colonies. Another possibility could reside in the fact that a proportion of large recruits could come from asexual reproduction processes such as fragmentation, which might break bryozoan colonies into smaller ones (fragments) that can survive, grow and reproduce (Hawkins and Roberts, 1994; Linacre and Keough, 2003). We suggest that future works should explore in more detail the recruitment process of this species at large spatial and temporal scales, given its importance for population dynamics.

Physical damage caused by direct contact from scuba divers has been well documented in sessile species (Sala et al., 1996; Linares et al., 2010b; De la Nuez-Hernández et al., 2014). According to Zakai and Chadwick-Furman (2002), the level of damage to the contacted hard corals by divers may depend on their morphology. Massive structural species are damaged more often, as they tend to suffer breakage and separation of individuals if they are colonial. Our study finds higher values in the mean size of colonies in non-frequented locations. However, we did not find differences in growth rates between frequentation levels, suggesting that the smaller sizes recorded in frequented locations were related to the fragmentation of colonies by divers (Garrabou et al., 1998). Moreover, the survival of colonies incremented with the size of the colonies, being this trend more pronounced in frequented localities, suggesting that the larger colonies tend to resist better the physical impacts such as fragmentation.

In contrast, our study did not show any differences in the partial mortality patterns between frequentation levels, suggesting that other factors might be involved. Previous studies documented extensive mass mortality events affecting Mediterranean benthic macroinvertebrates, such as gorgonians, sponges, and bryozoans, caused by anomalous warming temperatures, highlighting the vulnerability of temperate sessile invertebrates to climate change (Cerrano et al., 2000; Garrabou et al., 2009). Similarly, we observed higher partial mortality (necrosis) and lower survival rates after summers, when temperatures were higher (Nykjaer, 2009). Our results are aligned with the vulnerability of *P. fascialis* to high temperatures (Pagès-Escolà et al., 2018), suggesting future decreases of their Mediterranean populations in a warming scenario, regardless the level of protection.

Nevertheless, our study finds that *P. fascialis* is characterized by higher growth rates during the colder months, as other studies pointed out previously (Cocito et al., 2006). We did not find any related impact of diving on growth rates, unlike other previous studies that observed that the slow growth rates of impacted populations did not allow colonies to recover from year to year (Sala et al., 1996; Cocito et al., 1998a; Coma et al., 2004). Despite the vulnerability of our model species to warming and diving (Sala et al., 1996; Garrabou et al., 1998; Pagès-Escolà et al., 2018), the high growth and recruitment rates registered in this study highlight the capacity of bryozoan populations to recover rapidly from anthropic perturbations, which may explain the high densities observed in non-frequented locations. Moreover, our results suggest a possible recovery of bryozoan populations in frequented locations if diving pressure decrease in the future.

During the last decades, the creation of effective MPAs has been considered a good option to conserve marine ecosystems (Agardy, 1997; Edgar et al., 2014; Costello and Ballantine, 2015). This work demonstrates that diving activities can have a strong impact on benthic communities, contrasting with the conservation and protection goals of MPAs. The sustainability of diving activity depends on the number of divers accessing the sites and the capacity of the ecosystem to recover from perturbations (Harriott et al., 1997). Therefore, to manage recreational scuba diving it is vital to estimate the carrying capacity of benthic communities and establish diving quotas to ensure that natural resources are not destroyed (Salm et al., 2000; Barker and Roberts, 2004). Although previous studies have suggested different tolerable levels of diving, ranging from 500 to 15,000 divers per year (Dixon, 1993; Zakai and Chadwick-Furman, 2002), it is complex to determine a scientifically defendable limit of diving effect due to the different life-history traits of the organisms and the interaction with other perturbations, such as climate change (Linares et al., 2010b). Our results showed the difficulty to estimate a non-critical level of divers for marine communities; in fact, one of the most frequented locations (Tascó Gros) showed similar levels of density than the non-frequented location of Medallot. This fact highlights the importance of considering other environmental factors rather than diving pressure, as well as the difficulty of estimating diving quotas to adapt the conservation criteria to our changing era in adaptive management strategies.

5. Conclusions

Continuous monitoring programs, like the presented study, need to be formally established to detect changes in natural populations before the impact of diving becomes critical (Luna et al., 2009). Specifically, our work provides evidence that the populations of *P. fascialis* in Medes Islands Marine Reserve are directly impacted by a high-frequentation of divers. However, most of the frequented populations in this area showed critical abundances compromising the use of our model species as an optimal indicator of the long-term adaptive management. In addition, our results evidenced the fast population dynamics of our model species with a high capacity to recover from anthropic perturbations, such as diving or climate change. Nevertheless, in order to enhance the recovery of impacted populations, it is recommended to reduce the pressure of divers in frequented areas, reevaluate the carrying capacity of these communities, and establish educational programs such as eco-briefings before the dives to increase the environmental awareness (Luna et al., 2009). Our work highlighted the need to implement continuous monitoring actions to properly manage anthropic activities in marine protected areas to preserve and protect marine benthic communities.

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CHAPTER V: Assessing the effectiveness of restoration actions for Bryozoans: the case of the Mediterranean *Pentapora fascialis*

Abstract

Marine ecosystems are highly affected by several human stressors. In this context, beyond passive restoration measures such as the creation of marine protected areas, it is urgent that we explore active restoration actions to enhance and accelerate the recovery of sessile marine species. Bryozoans are among the most common sessile invertebrates in rocky bottom ecosystems and are considered habitat-forming species that are highly vulnerable to physical disturbances such as recreational diving, ghost fishing nets, and global warming, which makes them highly vulnerable to other impacts. However, despite their ecological importance and vulnerability, restoration actions for bryozoans have rarely been explored to date. In this study, different restoration techniques were developed and tested, with a focus on two types of effective methodologies previously applied to other marine invertebrates: recruitment enhancement and the transplantation of adult colonies, using in both cases the Mediterranean bryozoan *Pentapora fascialis* as a model species. First, different types of artificial surfaces were installed in different coralligenous habitats to test the enhancement of recruitment, concluding that plastic grids are the best substrate in terms of facilitating the recruitment of new bryozoan colonies. Second, different methodologies were tested for adult transplantation. The most successful was to fix colonies to a suitable substrate with a nylon thread attached to the colony *ex situ* (i.e. on the boat). Using this technique, a trial restoration programme was undertaken involving transplanting adult colonies collected from a ghost fishing net trapped on the bottom, which showed a high survival rate of ~50% after 6 months. The low economic cost of the implementation of the proposed techniques as well as the successful results obtained highlight the viability of restoring bryozoan populations at long temporal and spatial scales.

1. Introduction

Marine coastal ecosystems are directly impacted by multiple and interacting anthropogenic stressors, such as habitat destruction, eutrophication, pollution and climate change, resulting in biodiversity loss and the alteration of ecosystem functioning (Halpern et al., 2008; Cardinale et al., 2012). In this context, ecological restoration is increasingly implemented worldwide to address the dramatic loss of biodiversity and the associated ecosystems services that such biodiversity provides (Young, 2000; Perring et al., 2015).

The final aim of ecological restoration is to recover ecosystems that have been degraded, damaged, or destroyed (SER, 2004). Traditionally, conservation efforts have focused on passive restoration to enhance the natural recovery of ecosystems by removing the impact of stressors in their habitats through the creation of protected areas (DellaSala et al., 2013). However, the current rapid degradation of many ecosystems highlights the urgency to apply active management measures that involve direct human interventions together with the establishment of protected areas to enhance biodiversity and restore ecosystem services (Holl and Aide, 2011; Possingham et al., 2015).

In recent decades, there has been an increase in studies showing the effectiveness of restoration actions in a wide array of terrestrial systems (Benayas et al., 2009; Perring et al., 2015). In marine ecosystems, restoration actions have mainly focused on charismatic taxa, such as corals and seagrasses, by transplanting fragments of adult colonies, planting seaweeds, and/or deploying artificial surfaces in the natural habitat to enhance the recruitment of the target species (Bayraktarov et al., 2016) as well as by installing artificial reefs to rehabilitate and enhance the ecological functions of degraded habitats (Pratt, 1994; Abelson, 2006). Most actions have been applied at a small scale and over short time scales, however, thus presenting many challenges when estimating the cost effectiveness of the efforts involved and the temporal scales needed, and because of the poor understanding of the life-history traits of most benthic marine species, which determine suitable restoration methodologies (Montero-Serra et al., 2018).

Marine habitat-forming species are generally considered key species because they provide refuge habitat for many other species. Bryozoans are one of the most common structural organisms in marine benthic ecosystems, increasing ecosystem complexity and providing shelter and microhabitats for other species (Hong, 1982; Cocito, 2004; Wood et al., 2012). Moreover, they have been used as ecological indicators for different stressors due to their sensitivity to physical disturbances, such as storms or recreational diving (Sala et al., 1996; Di Franco et al., 2009; Teixidó et al., 2013), and to environmental stressors, such as warming (Pagès-Escolà et al., 2018). Despite their importance and vulnerability, restoration actions have not been previously explored.

In this study, for the first time, different restoration techniques were tested for the common Mediterranean bryozoan *Pentapora fascialis* using methodologies shown to be effective for other invertebrates, such as gorgonians and hard corals, based on the installation of recruitment surfaces and the transplantation of adult colonies (Linares et al., 2008; Benedetti et al., 2011; Montero-Serra et al., 2018). First, the suitability of two different types of artificial surfaces to enhance recruitment in the natural habitat of the target species was tested. Second, five different methodologies for adult *P. fascialis* colony transplantation were undertaken to identify the most suitable technique for attaching adult colonies to the substrate. Finally, using the most successful methodology, a restoration action was carried out by transplanting *P. fascialis* adult colonies retrieved from a ghost fishing net. Our study provides for the first time new insights into the restoration of bryozoans, understudied but common marine benthic invertebrates.

2. Methods

2.1 Study area and model species

The present study was carried out in four different locations within the marine reserve of the Montgrí, Medes Islands and Baix Ter Natural Park in the north-western Mediterranean Sea at 15-20 m depth (Fig. 1A, B). Restoration actions were focused on *Pentapora fascialis* (Pallas, 1766) (Fig. 1C), a common and dominant Mediterranean bryozoan in rocky benthic communities distributed in the Mediterranean Sea from 15 to 100 metres depth on hard bottoms exposed to strong currents, which are not subjected to heavy sediment accumulation (Zabala, 1986; Cocito et al., 1998b). This species is one of the largest living bryozoans, with bright orange calcified erect colonies and an encrusting base with bilaminar branches showing a globular shape, measuring 30 cm in diameter and 20 cm in height in the shallower areas (12-20 depth) of Medes Islands Reserve, but reaching 1 m in diameter in other areas (Sala et al., 1996; Cocito, 2004). Previous studies showed a mean growth rate of 9.8 ± 4 cm per year, with higher values during the relatively cold months (Cocito et al., 2006; Pagès-Escolà et al., 2020). Its colony development starts from an encrusting patch or a first phase of planar growth, and when the colony area reaches 2 cm^2, it grows in height, forming bifurcating branches (Cocito et al., 1998b). It is considered a habitat-forming species that increases the associated biodiversity (Cocito, 2004; Wood et al., 2012).

Due to the fragility of its physical structure, it has been used as an indicator of physical perturbations such as diving (Sala et al., 1996; Garrabou et al., 1998). Despite its importance and abundance, its population dynamics are poorly understood.

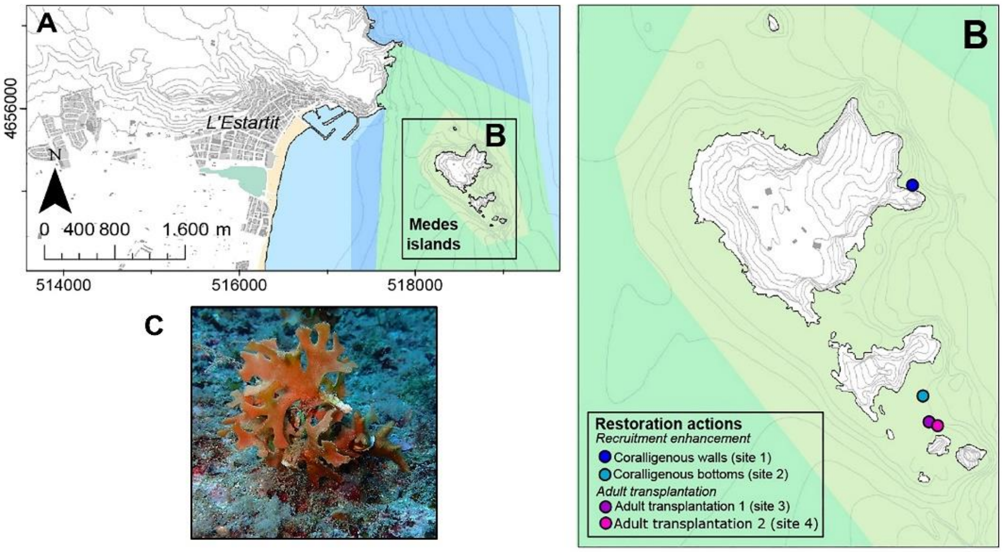

Figure 1. (A, B) Study area and model species *P. fascialis* (C). Different levels of protection were represented by the Montgrí, Medes Islands and Baix Ter Natural Park: marine reserve (light green), a buffer zone (dark green) and natural park (dark blue). All tested restoration methodologies were performed in different locations within the marine reserve: installation of artificial substrates to enhance the recruitment of *P. fascialis* on coralligenous walls (site 1) and bottoms (site 2); transplantation of adult colonies of *P. fascialis* on coralligenous bottoms (site 3) and adult colony transplants obtained from a ghost fishing net (site 4).

2.2 Recruitment surfaces

To test the suitability of different surfaces for the enhancement of the recruitment of *P. fascialis*, in October 2016, two different types of recruitment surfaces were installed on coralligenous habitat at two different sites: coralligenous vertical walls (site 1) and boulder bottoms (site 2), within the marine reserve between 15 and 20 m depth (Fig. 1). The first type of recruitment surface consisted of 5 x 5 cm plain-surface plates composed of natural rocks, selected for their similarity to biogenic substrate, attached directly to the substrate using two-component epoxy putty. The second type of recruitment surface consisted of 10 x 10 cm plastic grids, each one attached with a zip tie to a stainless steel bar fixed to the substrate and identified with a colour code (Fig. S1). Fifteen plates of each type were installed at each study site. Initially, not only the recruitment of *P. fascialis* but also that of other Mediterranean bryozoan species (such as *Myriapora truncata*) was planned to be tested. For this reason, recruitment surfaces of different sizes were installed on both habitats. However, this work was focused on *P. fascialis*, as it was the most abundant species on the recruitment surfaces.

After the installation, the recruitment surfaces at each location were photographically monitored in February, April, July, and October of 2017 and in July and October of 2018, recording the total number of *P. fascialis* colonies (identified *in situ* and from close-up photographs with the help of a taxonomic bryozoan specialist), identifying individual colonies in the photographs (recording their position), and measuring the size (area (mm^2) of each colony) and percentage of dead tissue (partial mortality) using Photoshop (Photoshop CC2017) (Fig. 2). Photographic monitoring was performed perpendicular to the grid to facilitate the measurement of the growth of the colonies, accounting for the two-dimensional area of the substratum covered. Partial mortality was expressed as the proportion of the area presenting a loss of colony coloration caused by the partial or total loss of living tissue covering the skeleton, following previous methodologies (Sala et al., 1996; Pagès-Escolà et al., 2018) (Fig. S2). The following demographic parameters were estimated between monitoring periods: survival, recruitment, growth and shrinkage. Survival was estimated as the ratio of the number of remaining colonies to the number of colonies at the beginning of the period considering dead colonies to be those with 100% necrosis (Linares et al., 2005; Cebrian et al., 2012). Recruitment was analysed as the number of newly visible colonies that appeared after each monitoring event (Linares et al., 2005). Growth was measured as a positive difference in size between surveys, and shrinkage was considered as negative growth between surveys, and both were standardized according to the growth/shrinkage per month (mm^2/month).

To test the effectiveness of the recruitment surfaces, a set of generalized linear models (GLMs) was used to model the response variables (density, survival, size, recruitment, necrosis, growth, shrinkage) through predictor variables (monitoring period). Moreover, growth, necrosis, and shrinkage (response variables) were modelled as a function of the initial size of the colonies (predictor variable). Finally, survival was modelled as a function of the initial value of the studied variables (size, recruitment, necrosis, growth, shrinkage).

Figure 2. *P. fascialis* recruitment enhancement experiment. Detail of one of the recruitment grids located on a coralligenous bottom during monitoring: (A) April, (B) July and (C) October 2017 and (D) July and (E) October 2018, showing the recruitment and growth of a *P. fascialis* colony.

2.3 Adult transplants

2.3.1 Study of the best methodology to perform adult transplants

To identify the best methodology for adult transplantation, in July 2017, a pilot action was carried out using different methodologies to attach adult colonies to the substrate (Fig. 3A). Specifically, a total of 50 adult colonies of *P. fascialis* were collected from a rocky bottom between 15 and 20 m depth and transplanted into the same location at the Medes Islands Marine Reserve (Fig. 1B site 3, Fig. S3A). Two-component epoxy putty was used as glue to paste a colony or a plastic screw to the substrate depending on the tested methodology, transplanting 10 adult colonies for each tested methodology (Fig. S3):

a) Gluing *in situ* the colony to the bottom using two-component epoxy putty (Fig. 3Aa, Fig. S3B, F).

b) In a first dive, a plastic screw was inserted into the epoxy putty glued to the bottom and, when the epoxy putty had hardened, in a second dive the base of the colony was manually tied *in situ* to the plastic screw using a flange (Fig. 3Ab, Fig. S3G).

c) In a first dive, a plastic screw was inserted into the epoxy putty glued to the bottom and, when the epoxy putty had hardened, in a second dive the base of the colony was manually tied *in situ* to the plastic screw using a nylon thread (Fig. 3Ac, Fig. S3H).

d) In a first dive, adult colonies were collected and the base of each colony was manually attached *ex situ* (i.e. on the boat) to a plastic screw using a flange, and in a second dive, the screw was fixed to the bottom using two-component epoxy putty (Fig. 3Ad, Fig. S3C, D, E, F).

e) In a first dive, adult colonies were collected and the base of each colony was manually attached *ex situ* (i.e. on the boat) to a plastic screw using a nylon thread, and in a second dive, the screw was fixed to the bottom using a two-component epoxy putty (Fig. 3Ae, Fig. S3C, D, E, G).

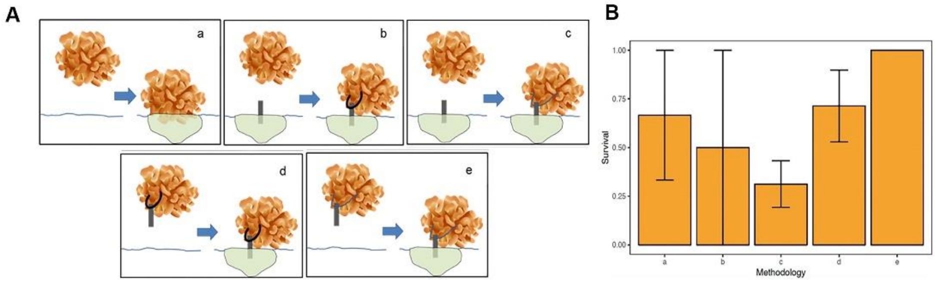

Figure 3. (A) Different tested techniques used to attach adult *P. fascialis* colonies to the substrata: a) directly with epoxy putty; b) with a flange tied to a plastic screw placed *in situ*; c) with a nylon thread tied to a plastic screw placed *in situ*; d) with a flange attaching the colony to a plastic screw *ex situ* (in the boat) and then placed on the bottom and e) with a nylon thread attaching to the colony to a plastic screw *ex situ* (in the boat) and then placed on the bottom (n=50, 10 per methodology). (B) Mean survival of the transplanted colonies after 6 months of restoration action.

The first technique (a) was the only case where installation could be performed within a single regular dive. A minimum of two dives were required to set up the rest of the tested techniques (from b to e) in accordance with the epoxy putty drying time (b, c) and the *ex situ* attachment techniques (d and e).

For each of the methodologies tested, all the colonies were individually identified in the space, their position recorded and marked with a colour-coded flange, and were photographed in July 2017 and in September 2017. The survival of the colonies was measured as the ratio of the number of remaining colonies to the number of colonies at the beginning of the period considering dead colonies to be those with 100% necrosis; shrinkage was considered as negative growth between surveys (Linares et al., 2005; Cebrian et al., 2012). Generalized linear models were used to find significant differences among methodologies.

2.3.2 Transplantation action

After establishing the best methodology to transplant *P. fascialis* adults, a restoration action was performed in October 2017 at the same depth near the site where the different transplant methodologies were tested. Thirty adult colonies attached to a ghost fishing net trapped on a coralligenous bottom were collected and transplanted in the same location where the ghost fishing net was found to ensure that the habitat was suitable for them (Fig. 1B, site 4). All colonies were individually identified and measured (maximum height) in October 2017 and April 2018 to measure their survival and growth. A set of generalized linear models was developed to study the relationship between survival and the initial size of the transplanted colonies.

All statistical analyses and graphics were produced using R version 3.1.2 (R Core Developer Team, 2014).

2.4 Costs of active restoration actions

The cost of restoring a bryozoan population was analysed considering an area of 10 m^2 using the best methodologies identified in the present study. Specifically, the analyses accounted for the transportation, materials, and personnel comprising two divers and one boatmaster needed to implement the described restoration actions following the methods of previous studies (Bayraktarov et al., 2016; Verdura et al., 2018). The personnel salaries were established according to the guidelines established for monitoring protocols in marine protected areas (Generalitat de Catalunya, 2017). Transport costs vary depending on the country, although these costs were estimated for our study area these values can be considered as a reference for those other locations.

3. Results

3.1 Recruitment surfaces

High recruitment rates of *Pentapora fascialis* were observed on the second recruitment surface type (plastic grids) located on coralligenous bottoms (Figs. 2, 3A). In contrast, no *P. fascialis* recruits were observed on the plain-surface settlement plates nor on both recruitment surfaces types located on coralligenous vertical walls during the entire study.

After the installation of the plastic grids (October 2016), a high recruitment event of *P. fascialis* was observed in February 2017 (48 recruits), with the number of recruits significantly decreasing over time (Figs. 4A, B, Table S1). Despite this trend, in July 2018, a new peak of recruitment was recorded (Fig. 4A).

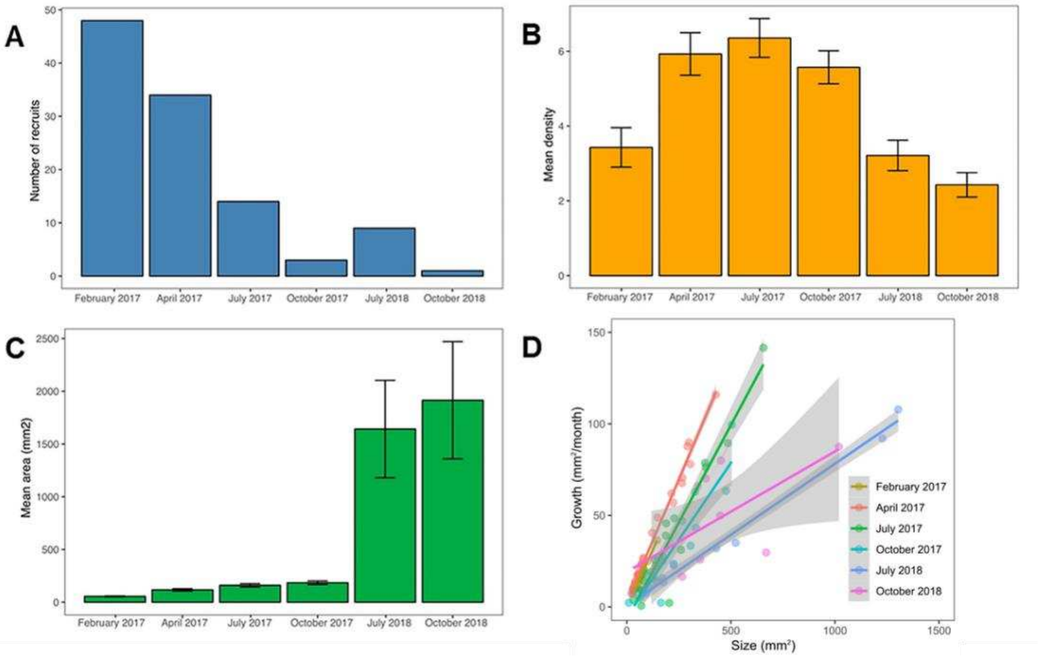

Figure 4. Results from the *P. fascialis* recruitment enhancement experiment: (A) total number of recruits, (B) mean density/grid, (C) mean area of recruits (mm^2) and (D) GLM of growth (mm^2/month) and initial size of the colonies (of the previous monitoring action) for each monitoring action.

The mean density of all colonies (new recruits and already established colonies) differed among the studied periods, being highest in July 2017, reaching 6.35 ± 0.52 colonies/grid, and decreasing in regard to the number of colonies after that time (Fig. 4B, Table S1). This contrasts with the temporal trend in the colony size (mean area), which was lowest during 2017 (i.e. 184.7 mm^2 in October 2017) and significantly higher after summer 2018 (1915.4 ± 555.6 mm^2 in October 2018), coinciding with the lowest density of colonies (2.42 ± 0.32 mm^2/grid in October 2018) (Figs. 4C, D). A positive relationship was found between growth and the initial size of the colonies (Fig. 4D, Table S2). In terms of the size of the colonies, the highest growth rates per month were observed in the winter and spring surveys (April and July) (Fig. 4D), with the highest growth rate per colony recorded in July 2017, reaching 141.60 mm^2/month.

After October 2017, the number of colonies decreased significantly, coinciding with higher rates of partial mortality in the already established colonies (Fig. 5, Table S1). In this way, the survival of the colonies decreased with an increase in partial mortality, reaching the highest partial mortality of 69.85 ± 6.41% necrosis/colony in October 2018 (Fig. 5, Table S3). Moreover, no relationship was found between necrosis and the initial size of the colonies (Table S2). Despite no significant differences were recorded in shrinkage rates between the studied periods (Table S1), the highest mean shrinkage values were recorded after the warmest periods, reaching -114.32 ± 39.09 mm^2/month in October 2017 and -233.13 ± 85.03 mm^2/month in October 2018 (Fig. S4). In addition, a negative relationship was found between shrinkage and the initial size of the colonies, indicating the largest colonies have the highest shrinkage values (Fig. S4, Table S2).

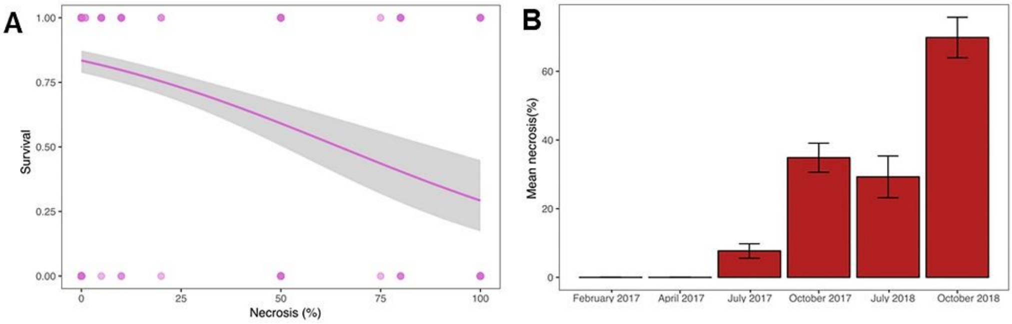

Figure 5. Results from the *P. fascialis* recruitment enhancement experiment: (A) GLM of survival and necrosis for all the established colonies on the plastic grids across the experiment and (B) mean percentage of necrosis (% of damaged area) of the established colonies over time.

3.2 Adult transplants

Significant differences in the survival of transplants were found among tested methodologies (Table S4). The technique with the highest survival rates consisted of the attachment of the colony to a plastic screw on the boat (*ex situ*) using a nylon thread and then fixing the screw to the substrate with epoxy. Lower survival rates were obtained with the other methodologies, especially with those ones which involve the *in situ* manipulation of colonies (Fig. 3B). Specifically, when a nylon thread was used to attach the colony to a plastic screw on the boat (Fig. 3Ae), all the transplanted colonies survived (Fig. 3B), highlighting that this methodology is the best one for transplanting adult colonies of *P. fascialis*. A mean survival rate of 0.72±0.18 (Fig. 3B) was recorded when the colony was attached to a plastic screw using a flange on the boat (Fig. 3Ad), suggesting that this material is not as suitable for carrying out transplantation actions. In contrast, for the *in situ* methodologies, the mean survival of transplanted colonies was 0.66±0.33 for those that were directly attached to the bottom using two-component epoxy putty (Fig. 3Aa) and 0.5±0.5 for those that were attached to the bottom with a plastic screw tied to the colony *in situ* with a flange (Fig. 3Ab), and the lowest survival of 0.31±0.12 was found among those that were attached to the bottom with a plastic screw tied to the colony *in situ* with a nylon thread (Fig. 3Ac).

After 6 months using the best technique to transplant adult colonies (e), the mean survival of transplants was approximately 50%, recording that the larger colonies were more likely to survive (Fig. 6, Table S5). Moreover, all the transplants presented negative growth or shrinkage, with the percentage of injuries increasing with the size of the colonies (Fig. S5, Table S5).

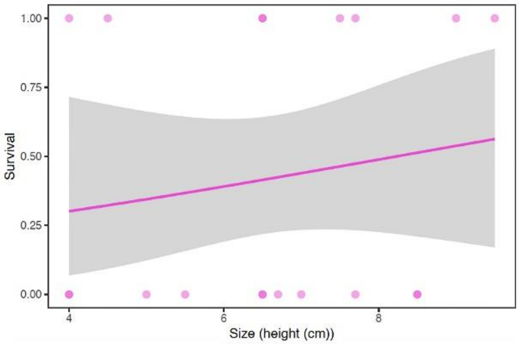

Figure 6. GLM of transplant survival and the initial size of *P. fascialis* colonies transplanted from a ghost fishing line to a boulder bottom between the beginning of the restoration action (October 2017) and after 6 months (July 2018).

3.3 Costs of active restoration actions

The cost of restoring 10 m^2 of *P. fascialis* colonies ranged from €1041 when installing recruitment surfaces to €1089 when performing adult transplantation, resulting in a total cost of €2130 in the case of the application of both techniques at the same time (Table 1). The highest cost of both methodologies was related to personnel salaries and transport expenses, while the materials used in both restoration techniques were the least expensive part (€34 for recruitment enhancement and €85 for adult transplantation) (Table 1). Although these costs are specific to this study site, they can be considered as a baseline reference for other study sites.

Table 1. Estimated costs for different concepts to restore one bryozoan's populations (area of 10 m^2) depending on the restoration technique used. Note that travel costs may vary depending on the location.

Concept	Rate	Cost	Total (€)
Recruitment enhancement			
Installation of artificial surfaces			
Transport			
Boat (gasoil)	5 km	1.3/L	6.5€
Car (gasoil)	300 km	0.40€/km	120€
Material			
Plastic grids	15 plates 5x5 cm	17.50€/1 roll (1x5 m)	17.50€
Flanges	15 units	0.84€/50 units	0.84€
Stainless bar	4 units	2.75€/unit	11€
Thread	1 roll	5.75€/unit	5.75€
Scissors	1 unit	1.95€/unit	1.95€
Workers			
Salary	3 persons x 1 day	281.76€/person	845.28€
Air diving cylinder	1 dive x 2 persons	11.70€/dive	23.4€
Annual diving insurance	2 persons x 1 day	4.31 € day/person	8.61€
			~1040€
Adult colony transplantation			
Restoration action			
Transport			
Boat (gasoil)	5 km	1.3/km	6.5€
Car (gasoil)	300 km	0.40€/km	120€
Material			
Epoxy putty	1 unit of 2 components	70€/kg	70€
Plastic screws	30 units	2.89€/10 units	8.67€
Nylon thread	500 cm (20 cm x 30 transplants)	4.81€/30 m	4.81€
Scissors	1 unit	1.95€/unit	1.95€
Workers			
Salary	3 persons x 1 day	281.76€/person	845.28€
Air diving cylinder	2 dives x 2 persons	11.70€/dive	23.4€
Annual diving insurance	2 persons x 1 day	4.31 € day/person	8.61€
			~1089€
Total			**~2130€**

4. Discussion

This study represents the first attempt to develop restoration measures for Mediterranean bryozoan species, with a focus on two techniques previously used effectively for other benthic marine species, such as corals, macroalgae and seagrasses. Although both techniques showed promising results, the recruitment enhancement of bryozoans seems to be the most effective technique given the high recruitment observed and considering that it is a non-invasive methodology. In contrast, the transplantation of adults should only be undertaken in some particular cases, such as when bryozoans can be obtained from lost fishing nets or are found detached at the bottom from different causes to avoid impacts on natural populations.

Recruitment plays a vital role in the persistence, resilience, and recovery of coastal benthic ecosystems, as observed in several coral species (Richmond, 1997; Hughes and Tanner, 2000). Given this importance, artificial surfaces have been used to provide available substrates to increase the settlement and recruitment of some species (Edwards and Clark, 1999). In this study, plastic grids represented the best artificial substrate to enhance the recruitment of *P. fascialis*. Given the typical globular shape and vertical growth of colonies (Cocito et al., 1998b), plastic grids may enhance their structural growth forms, as previously observed in other studies of corals, in which coral larvae preferred to settle in complex interstices of substrates rather than on flat surfaces (Carleton and Sammarco, 1987). The present study showed high rates of recruitment during the first months due to the newly available surfaces provided by the installation of artificial substrates, and after this period, the number of the colonies decreased due to an increase in competition from other organisms, as observed in benthic organisms (Greene and Schoener, 1982). Previous studies found that the availability of new substrates after disturbances enhanced the recruitment of *P. fascialis*, recording 23 recruits/m^2 six months after a severe storm, with the number of recruits decreasing when the substrate was increasingly covered (Cocito, et al., 1998a). Similarly, the present study found a total of 48 recruits on the 15 installed plastic grids 4 months after their installation, with their number decreasing in subsequent surveys, highlighting the occurrence of competition among colonies for the available space (Cocito, et al., 1998a).

In many benthic species, recruitment is characterized by irregular annual variation and stochastic peaks (Gotelli, 1988; Garrabou and Harmelin, 2002). According to Cocito et al., (1998a), seasonality patterns in *P. fascialis* recruitment could be explained by high ovicell abundance during spring months, resulting in a high concentration of larvae, which is in accordance with the high number of recruits being recorded in July 2018. However, high levels of recruits were not recorded in July 2017, suggesting that there were other factors enhancing the recruitment patterns of *P. fascialis,* such as the current regime, sedimentation rates or larval settlement preferences (Caines and Gagnon, 2012; Perkol-Finkel and Benayahu, 2007), that need to be considered in future works as well as in the study of the occurrence of recruitment peaks at large temporal scales.

The high growth rates observed agree with previous studies that estimated a mean growth rate of 9.8 cm/year for *P. fascialis* (Cocito et al., 2006). The highest growth values were observed during the cold months of the year (October-March), while in the warmer season, growth rates decreased, as observed in previous studies (Cocito et al., 1998b). Accordingly, necrosis was highest during the warmer months, illustrating the vulnerability of the studied species to high temperatures (Pagès-Escolà et al., 2018), with high necrotic proportions occurring in the largest colonies (~70% of the total cover after summer 2018). These results contrast with previous studies that found lower levels of necrosis in *P. fascialis* populations (never exceeding 26% of the total cover at 11 m depth and 8% at 22 m depth; Cocito and Sgorbini, 2014) and any seasonality pattern in partial mortality throughout the year (Cocito et al., 1998a; Cocito et al., 2006). Such differences could be related to the different environments in which the studies were carried out. Moreover, the seasonality of the growth and necrosis patterns of the studied species may be driven by other factors not recorded in the present study, such as higher rates of algal epibiosis, which affects *P. fascialis* during the summer months (Stebbing, 1971b; Cocito et al., 1998b). In bryozoans, epibiosis may reduce the total cover and growth, increasing the partial mortality (Stebbing, 1971b; Cocito et al., 1998b), highlighting the need to account for this factor in the measurement of partial mortality rates in future works. In addition to seasonal thermal variation and epibiosis, other factors not considered in this study may affect growth rates and partial mortality patterns in sessile suspension feeders, such as the quantity and quality of suspended food particles and the concentration of CO_2 and bicarbonate, which especially affect carbonate bryozoans (McKinney and Jackson, 1991; Lombardi et al., 2011c). Nevertheless, higher levels of recruitment and higher growth rates were observed than those exhibited by other benthic species, such as corals or gorgonians (Garrabou and Harmelin, 2002; Linares et al., 2007; Teixidó et al., 2011), suggesting that *P. fascialis* is characterized by faster population dynamics, as previous studies have noted (Cocito and Sgorbini, 2014), and may recover and adapt more rapidly to environmental changes in comparison to other species that presented slow dynamics (McKinney and Lockwood, 1999).

Previous studies have highlighted that bathymetric distribution or habitat type could also influence the abundance of *P. fascialis* populations (Sala et al., 1996; Garrabou et al., 1998; Cocito and Sgorbini, 2014). Related to this, Medes Islands Reserve coralligenous walls are characterized by the presence of the gorgonian *Paramuricea clavata,* which provides additional free substrate for epibiotic colonization by suspension feeders such as bryozoans (Sala et al., 1996; Ballesteros, 2006). In this community, the density of *P. fascialis* colonies is high because of the exposed epibiotic positions on the gorgonian branches, enhancing prey capture (Sala et al., 1996; Lombardi et al., 2008b). However, at sites frequented by divers, physical impacts appear to displace these species from their natural habitat to more cryptic and less environmentally suitable locations (Sala et al., 1996), explaining why no *P. fascialis* recruits were found on the plastic grids located on coralligenous walls. Despite previous studies that recorded fewer *P. fascialis* colonies on boulder bottoms in Medes Islands Reserve (Sala et al., 1996; Garrabou et al., 1998), in the present study, plastic grids were installed in an area of the marine reserve seldom visited by divers, providing new available and suitable substrates for *P. fascialis,* thus enhancing its recruitment. The results highlight the importance of considering diving frequency when selecting locations for restoration actions.

Due to the fragility of the calcified *P. fascialis* structure (Sala et al., 1996), the best technique for transplanting adult colonies consists of the manipulation of the colonies *ex situ* (on the boat) because it involves the more careful and precise attachment of the base of the colonies to the plastic screws than *in situ* (underwater) techniques. Specifically, nylon thread is the best material for the attachment of the transplants to plastic screws due to its fine and light structure, suggesting that it did not disrupt the two-dimensional growth of the colony. Previous studies on coral restoration showed high variability in transplant survival rates (0-90%), with a median survival of restored colonies of approximately 65% after one to two years of restoration actions (Bayraktarov et al., 2016; Montero-Serra et al., 2018). This study showed relatively high survival rates (~50%), which are similar to the ones observed following other successful transplantation actions for Mediterranean benthic species, such as gorgonians *Paramuricea clavata* and *Eunicella singularis,* which had survival rates of between 30 and 50% at least one year after transplantation (Montero-Serra et al., 2018).

Nonetheless, the present work indicates some shortcomings of transplantations, such as the loss of colonies and high partial mortality rates, as well as reduced growth rates of transplants, which have also been observed in coral transplants on tropical reefs (Edwards and Clark, 1999). However, transplant mortality not only occurs through a failure of the attachment technique, but can also be related to a lack of suitable environmental conditions (Linares et al., 2008). Accordingly, the survival and shrinkage of adult transplants recorded in summer 2018 may have been affected by the positive thermal anomaly observed during this period that affected natural populations of *P. fascialis* (Pagès-Escolà et al., 2018). Likewise, recruits on the artificial substrates also showed an increase in necrosis during summer 2018. As noted above, other factors, such as algal epibiosis, may influence the partial mortality and growth rates of bryozoans. It is therefore important to take into account the potential risk of future warming events and algal epibiosis when implementing restoration measures, suggesting that bryozoan restoration measures should begin during the early cold months to enhance successful results for restoration purposes.

Despite the high economic costs of restoring marine habitats (Bayrakaratov et al., 2016), in this study, restoration actions were applied using *low-cost* and *low-tech* approaches, encouraging the implementation of these techniques by non-scientists and managers of marine protected areas at large scales. Previous works have demonstrated the impacts of diving on populations of sessile marine species, such as bryozoans and corals, in small marine protected areas with high levels of diving activity, such as our study site (Sala et al., 1996; Coma et al., 2004). In combination with the establishment of marine protected areas and other conservation efforts, such as the reduction in the number of divers in vulnerable habitats and locations, active restoration actions such as those proposed in this study could help to restore and protect the damaged populations in these small marine protected areas and increase public awareness about the threats for these species (Linares et al., 2008).

Bryozoan bioconstructions are widely distributed across temperate environments, where seasonality and variability in environmental parameters can facilitate their success (Wood et al., 2012). However, several local and global stressors are causing a reduction in their structural complexity, with the consequent loss of biodiversity and the ecological services provided by habitat-forming species (Gray, 1997; Moberg and Folke, 1999; Cadotte et al., 2011). Bioconstructions are generated by the aggregation and accumulation of the calcareous skeleton of marine organisms, resulting in physical structures that can grow at various depths and can be variable in shape and dimension (Laborel, 1987; Cocito, 2004). Large, erect bryozoans are considered frame builders characterized by presenting well-skeletonized structures that provide most of the volume and rigidity to the framework (Cocito, 2004; Lombardi et al., 2014). In the Mediterranean Sea, *P. fascialis* is the largest erect bryozoan and can create colonies up to 1 m in diameter, and it is considered a frame builder and habitat-forming species due to its biogenic constructions (Cocito, 2004; Wood et al., 2012; Lombardi et al., 2014). The habitat generated by *P. fascialis* enhances the associated marine biodiversity, providing new secondary substrates for colonization by other organisms, such as small bryozoans, and offering refuge and protection from predation and competition for other organisms, such as crustaceans, bivalves and fishes (Ferdeghini and Cocito, 1999; Cocito, 2004; Wood et al., 2012). Moreover, *P. fascialis* is considered one of the major contributors to the carbonate budget due to its complex structures, which increase the carbon standing stocks (Cocito and Ferdeghini, 2001), and like other benthic filter-feeding species, it maintains phytoplankton levels through active filtering and decreases the sedimentation of particulate material, controlling the eutrophication of the environment (Laubier, 1966; Office et al., 1982). Beyond its ecological benefits, this species is threatened by erosion caused by divers (Sala et al., 1996; Garrabou et al., 1998), warming (Cocito and Sgorbini, 2014; Pagès-Escolà et al., 2018), severe storms (Cocito and Sgorbini, 2001), pollution (Harmelin and Capo, 2002) and siltation (Cocito, et al., 1998b). In this context, the reduction in habitat complexity provided by *P. fascialis* may decrease the associated biodiversity, carbonate stocks, and water quality (Laubier, 1966; Miller et al., 2002; Airoldi, 2003). In conclusion, it is vital to conserve and apply active restoration actions to preserve this Mediterranean bryozoan and its related ecological services.

Although the present study has some limitations, such as the lack of replicates and control sites and the short temporal scale, which must be taken into account in the interpretation of the results, it represents the first attempt to restore impacted bryozoan populations at the local scale, providing effective and low-cost techniques as well as novel insights into the ecological restoration of understudied but common marine invertebrates. Nevertheless, it is crucial to explore in future works the establishment of a formal restoration plan, including quantitative baseline surveys, reference sites, systemic monitoring and the mitigation of local stressors (McDonald et al., 2016).

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GENERAL DISCUSSION

In recent decades, marine ecosystems have been highly affected by multiple and interacting human threats, compromising the future of marine populations. In this context, understanding the ecology and biology of marine species at different spatial scales is vital for their proper management and conservation. Bryozoans are a wide and common group of benthic invertebrates that are usually ignored in ecological studies and are considered a minor phylum. In spite of the poor understanding of its biology and ecology, the largest structural bryozoans can act as a habitat-forming species, increasing the structure and diversity of marine benthic ecosystems. Until this moment, the lack of bryozoan studies may be related to the complexity and diversity of life cycles and growth forms that they present and their wide distribution and lack of economic value. Enlarging their ecological knowledge is vital for properly conserving and managing natural populations in the context of the increasing local and global stressors. In this regard, this thesis contributed to the knowledge of bryozoans, unravelling the species discoveries and describing the global diversity patterns of this taxonomic group and, at the local scale, exploring the population dynamics, thermal preferences and conservation measures of the Mediterranean bryozoans.

1. The importance of performing ecological studies at different scales

This PhD thesis highlights for the first time the importance of integrating different approaches and methodologies to understand the effects of human stressors on the ecology and conservation of bryozoans. The general workflow of this thesis can be differentiated into three blocks: data collection, data analyses, and the identification and proposal of management and conservation actions (Fig. 1). Regarding the data collection, we conducted two different types of studies depending on the data sources. The first type was based on the search for resource information through open databases that provided global and local taxonomy information, diversity metrics and environmental data. In the second case, we obtained data that was collected through the study of natural populations by applying population monitoring actions and experimental studies in laboratories. The next step was data analyses, which allowed us to identify the global and local diversity patterns of bryozoans through resource-based studies and to obtain information about the life history traits and the vulnerability of species to different human stressors through monitoring and experimental studies. Finally, the information provided by this thesis aims to contribute to the management and conservation of bryozoans. At a global scale, our results allow us to identify where efforts are required to protect the most rich and vulnerable regions under different increasing human impact scenarios. At the local scale, our thesis highlights the need to implement continuous formal monitoring plans of the natural populations to evaluate the impact of human stressors on marine ecosystems, to select optimal ecological species and to develop passive or active conservation measures when needed. All parts are discussed below.

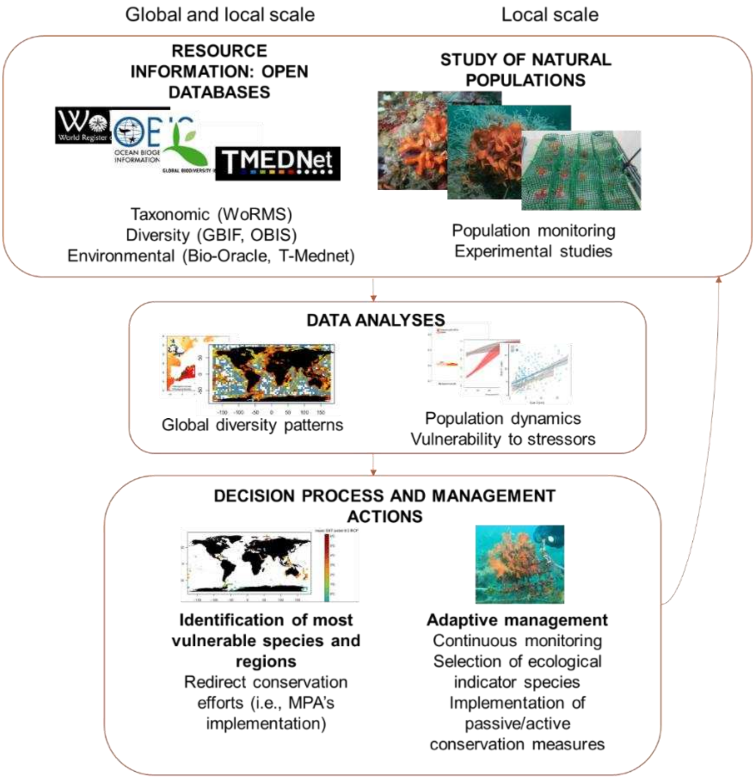


Figure 1. Workflow developed in the present thesis, based on three general parts: data collection, data analyses and decision process and management actions.

2. Combining open-access databases with the study of natural populations

2.1 Open-access databases: a powerful resource for ecological studies with some flaws

In recent decades, open-access databases have gained a major role in ecological studies, offering the opportunity to easily obtain global and local information about the biological and ecological parameters of species. In addition, they are composed of information provided by different studies and institutions, which promotes and facilitates collaborations (Soberón and Peterson, 2004; Costello et al., 2013a,b). The use of different open databases is an approach used in the majority of the chapters of the present thesis; these resources provide valuable information to unravel the ecological patterns of bryozoans and other marine groups.

However, open databases have some limitations derived from the inaccuracy of the data, which are sometimes, biased and of poor quality on information networks (Hortal et al., 2007). As we evinced in Chapter 2, one of the reasons may be the limited and unequal sampling effort across the globe and over time, which creates spatial and temporal biases (Soberón and Peterson, 2004; Hortal et al., 2007; Santos et al., 2010). Another limitation resides in the fact that open databases integrate data from a heterogeneous range of inventories, such as museums, private collections, and literature, all of which present different methodologies and analyses of the diversity data (Newbold, 2010; Santos et al., 2010). Moreover, some records in the databases do not include coordinates or are not correct georeferenced, which prevents them from being included in the biogeographical analyses (Soberón and Peterson, 2004; Newbold, 2010). Another concern behind open-access databases is the incorrect taxonomic identifications of species that may result in the inaccuracy of data. For instance, in Chapter 3, we found *P. fascialis* records for the North Atlantic region in the GBIF and OBIS open databases. However, recent studies have highlighted the taxonomic disagreement between the different species of the genus *Pentapora*. As a result, *P. foliacea,* which is distributed in North Atlantic regions, may often incorrectly be identified as *P. fascialis*, which is distributed across the Mediterranean (Lombardi et al., 2010). This fact suggests that all the occurrences registered in GBIF and OBIS that were identified as *P. fascialis* in the North Atlantic regions were incorrectly named, highlighting the need for integrated use of the open databases with taxonomic and ecological knowledge. Related to this, taxonomy is constantly changing and evolving, with many species names changing and being updates, resulting in the fact that the different names in open databases may be given to the same species at different times (Soberón and Peterson, 2004; Newbold, 2010). Moreover, the proper identification of specimens may be related to the level of taxonomic knowledge or expertise, which may also represent a source of temporal and spatial biases, with some groups more correctly identified than others (Soberón et al., 2000; Soberón and Peterson, 2004; Newbold, 2010; Troia and McManamay, 2016). Furthermore, environmental databases may also present some shortcomings, such as data spatial gaps, limited spatial and temporal resolutions or differences between data sources (Hortal et al., 2007).

Apart from all these limitations, global open databases constitute a valuable resource that provides information for ecological, conservation and biogeographical studies (Table 1). Specifically, in this thesis, we used different sources to obtain biodiversity and environmental data, trying to take into account in each case the limitations noted above. The first information source used was the taxonomic open database WoRMS (World Register of Marine Species), which has contributed to improving the knowledge of the naming and classification of species. It represents a useful tool because it accounts for some limitations in taxonomy, such as the presence of synonyms, wrong or not accepted species names in databases (Costello et al., 2013a). In Chapter 1, we used this database to download the extant and fossil bryozoan data, allowing us to explore the discovery patterns since the beginning of species descriptions. Moreover, in this chapter, we actualized the list of fossil bryozoans with the assistance of a taxonomic editor (Phil Bock) who carefully revised the database, improving the knowledge that we had about past biodiversity. Moreover, other taxonomic editor (Dennis Gordon) help us to identify possible error sources in extant bryozoan data.

Other information sources used were GBIF (Global Biodiversity Information Facility) and OBIS (Ocean Biogeographic Information System), which are open databases where museums, institutions, and studies can publish their databases about species occurrences and distributions (Costello et al., 2013a,b). These global networks of biodiversity data have helped to increase the numbers of biodiversity conservation studies in recent years. Although most the diversity studies have only focused on and analysed one of these databases to explore diversity patterns (Miloslavich et al., 2010; Tittensor et al., 2010), in Chapter 2, we combined both data sources to increase the data reliability. Moreover, to solve some of the limitations of these databases, in these analyses, we checked all species names through WoRMS to avoid incorrect identification and look for species names updates. In addition, we deleted all the occurrences without spatial coordinates. Finally, other open environmental databases were used in the present thesis, such as BioOracle or T-Mednet, to obtain the global and local environmental data, which are shown in Chapters 2 and 3, respectively.

2.2 Studying natural populations: the need to combine monitoring programmes with experimental approaches

Monitoring programmes represent an important data source for understanding the dynamics and functioning of natural ecosystems. They are also very useful to managers for deciding whether conservation and management efforts are needed (Lovett et al., 2007; Lindenmayer and Likens, 2009). For instance, the population dynamics and the vulnerability of *P. fascialis* to local human stressors were unravelled in Chapter 4 based on the marine biodiversity monitoring programme of the Montgrí, the Medes Islands and the Baix Ter Natural Park (Catalonia, Spain). Moreover, monitoring programmes allow the identification of extreme or unusual events in the environmental or atmospheric conditions, such as heatwaves or storms, and their consequences for natural ecosystems (Garrabou et al., 2009; Teixidó et al., 2013), as we investigated in Chapters 3 and 4. Besides their benefits, the monitoring of natural populations have been usually identified to present some limitations, such as the high cost of supporting long-term programmes, the need to implement an optimal design from the beginning to the end of the study , and the complexity of selecting ecological indicators that represent the whole community (Lindenmayer and Likens, 2009). To address these shortcomings, previous works have identified some key factors for implementing effective monitoring programmes based on the adaptive management actions that should determine and compile clear scientific objectives and include the review, feedback, and adaptation of the monitoring design during its implementation (Lovett et al., 2007). Accordingly, in Chapter 4, we monitored *P. fascialis* populations through a 4-year programme, examining annually the design and increasing the spatial effort (number of locations) in the first years of monitoring, which has been crucial for the evaluation of the impact of diving on this species.

On the other hand, to identify the functioning, drivers, and consequences of natural processes, it is vital to integrate observations obtained by monitoring programmes with experimental data (Hewitt et al., 2007; Sagarin and Pauchard, 2010). Accordingly, the thermal tolerances of many benthic species were tested in aquaria experiments to unravel the vulnerability of species to climate change (e.g., Torrents et al., 2008; Linares et al., 2013; Kersting et al., 2015; Crisci et al., 2017; Savva et al., 2018). In Chapter 3, we experimentally studied the thermotolerances of two bryozoan species in aquaria, which allowed us to understand the differences in population trends between these two species that were recorded in the field. However, working in controlled conditions presents some limitations, such as the high cost of performing an optimal experimental design and the need to have a good understanding of the target species to maintain them in the aquaria. In this regard, though previous studies have performed aquaria experiments with *Myriapora truncata*, before this thesis, there was a poor understating about the maintenance of *P. fascialis* individuals under controlled conditions. To uncover the optimal conditions for the maintenance of this species, before the design experiment, we carried out a set of trials using different materials to attach the colonies to the aquaria, and different sources of food supplementation were tested based in different methodologies used to maintain other bryozoans, corals, and gorgonians (Linares et al., 2013; De la Nuez-Hernández, 2014; Kersting et al., 2015). After the successful trials, we discovered that the best technique for maintaining *P. fascialis* colonies in aquaria was to support the individuals with plastic grids, which was contrary to the conditions for maintaining *M. truncata* individuals, which were attached to a plastic base with epoxy glue. Similarly, we also studied the optimal temporal resolution of the experiment that would allow us to detect changes in the necrosis rates. At a minimum, this workflow highlights the need to integrate information from local observations and literature followed by a testing period of the different techniques to implement a correct experimental design.

Besides the limitations of the monitoring programmes and experimental approaches, they offered several challenges and opportunities to study and understand the natural processes, as we showed in this thesis. Similarly, the open-data access databases represented potential information sources to use in local and global studies (Table 1). Although this methodology was only applied for bryozoans, we recommend and encourage the application of similar approaches for other benthic species in future studies.

Table 1. Benefits, limitations, and recommendations of the data sources used in the present thesis

Data source	Benefits	Limitations
Open access data-sources	Easy collection of global and local information	Data biased due to differences in sampling effort
	Promote and facilitate the collaboration between the institutions	Difficulty of integrating the data providing of heterogeneous inventories sources
	Allow testing macroecological hypothesis	Limited spatial and temporal resolution (in environmental databases)
	Valuable information at the species level of their occurrence and diversity patterns.	Incorrect identification of species. No inclusion of changes or updates in species names. Poor data completeness: some data do not include coordinates or are incorrectly georeferenced
Monitoring programmes	Understanding the population dynamics of species	High cost of implementation of an optimal design
	Identification of extreme and unusual events	Difficulty of selecting the optimal ecological indicators
Experimental designs	Understanding of the functioning, drivers, and consequences of natural processes	High cost of implementation to carry an optimal design
	Testing physiological processes (such as thermal tolerance preferences of species)	Lack of knowledge of the target species to maintain them at controlled conditions.

3. Understanding global diversity patterns is vital in a fast-changing world

3.1 More effort is needed to improve marine diversity inventories

In Chapter 1, we evidenced that the current biodiversity on Earth represents only a small proportion of that in the fossil record, observing a large number of bryozoan species which became extinct in the past. The trends in the discovery patterns of extant and bryozoan species showed an increase in the exploration of the oceans since the 1750s, when the formal description and naming of species began (Linnaeus, 1758). Beyond the continuous increase of discoveries during the last century, our study reflected a major difficulty in the description of new species in recent decades, highlighting the need to enforce the descriptions of new species to complete biodiversity inventories before species will become extinct, given the increasing human threats to the marine environment (Mora et al., 2007; Costello et al., 2013a).

In this sense, more efforts are required to increase and improve the use of open-access databases and to coordinate specimen collections, descriptions, and curations among different institutions encouraging more global collaborations and financial support for increasing species descriptions and taxonomy efficiency (Costello et al., 2013a,b). During the first period of species discovery, the highest efforts on species description have been concentrated in North America and Europe, suggesting higher funding for marine research provided by developed countries at temperate latitudes (Costello et al., 2013a). This aligns with the highest sampling effort that we recorded in Chapter 2, showing a peak of occurrences in the North Atlantic Ocean. In contrast, despite the increase in the number of papers describing new species around the world during the recent decades, the proportion of authors in North America and Europa decreased in recent years. This is opposite to the pattern in Asian and Latin American countries, which suggests an increase in the efforts of species descriptions by some developing countries in recent and future years (Costello et al., 2013a). Related to this, in Chapter 2, we showed that more efforts are needed to quantify Earth's biodiversity in some regions, such as at low latitudes or in the tropics, which are mainly conducted by developing countries. For this reason, it is vital to explore whether the drop in species records for some groups in the tropics occurred naturally or if it was due to sampling bias, such as suggested by recent studies (Menegotto and Rangel, 2018). Furthermore, the variations in sampling efforts among regions could reflect differences in the accessibility to different habitats, such as the difficulty of sampling deep-sea areas (Mora et al., 2007), highlighting the need to increase efforts in these remote and understudied habitats.

Finally, in Chapter 2 we highlighted the need to account for the differences in the sampling effort in the quantitative models using a sampling frequency index, which obtained better and more accurate fittings of benthic diversity patterns. To date, previous studies have used rarefied species richness to model diversity as a response to different environmental variables (Morato et al., 2010; Chaudhary et al., 2017). However, this method implies the removal of some parts of the data. For this reason, to increase the accuracy of future studies, we recommend applying similar approaches in quantitative modelling and projections of species diversity.

3.2 Bryozoan latitudinal patterns diverge from the most traditional understanding

Quantifying diversity patterns is crucial to understanding ecological processes and properly managing natural populations. In Chapter 2, we demonstrated that the most traditionally accepted latitudinal pattern that posits an increase in species richness in the tropics was not valid for bryozoans and other benthic groups, such as bivalves or sponges, which has also been observed on other marine groups such as turtles and marine mammals (Clarke and Crame, 1997; Stephens and Wiens, 2003; Chaudhary et al., 2016; Edgar et al., 2017). This highlights the need to reformulate the ecological theory to understand latitudinal diversity patterns in marine species and consider other factors such as the competition between the species, their habitat suitability, and the climatic history patterns and geographic isolation events, such as the case of Antarctica (Clarke and Crame, 1992; Dayton et al., 1994; Bowen et al., 2013; Chaudhary et al., 2017; Rabosky et al., 2018).

As other studies have noted before (Barnes and Griffiths, 2008; Griffiths et al., 2009), we found that the highest bryozoan richness was located in the Southern Ocean, suggesting that the group has a preference for temperate and cold habitats, which is in accordance with the recorded decrease in bryozoan species richness along the SST range gradient. Another possibility could be that the high diversity in the Southern ocean may be related to differences in the sampling biases between the regions, with high intensities of sampling carried out in the Southern Ocean, which may influence the high diversity metrics of bryozoans and other groups, such as the brachiopods registered in this region (Walsh, 1996; Gordon, 1999; Clarke and Johnston, 2003). However, the bryozoans are one of the best-sampled taxa around the world and are considered to be well represented in the most poorly sampled shelfs in the world (Barnes and Griffiths, 2008), suggesting that other factors should determine the recorded patterns. In this way, the asymmetry found in the latitudinal pattern between two hemispheres could also be related to the differences in the climatic and geographic conditions. To understand better these patterns, future studies should account for biological interactions, demographic processes or endemism rates, which could be related to the latitudinal pattern and should be explored in future works.

The identification of the hotspot areas is vital to quantify the vulnerability of marine ecosystems to climate change scenarios (Spalding et al., 2007). Specifically, our analyses showed that some regions, such as the Arctic Sea, will be more impacted by warming at the end of this century, highlighting the need to protect and conserve their populations. In contrast, the Southern Ocean will be less impacted, suggesting that the high bryozoan diversity in this area will be less affected by climate change than other benthic groups, such as corals, sponges and ascidians, which have high diversity rates in the tropical and northern regions, where a large increase in SST is expected at the end of this century. Moreover, the fact that the Antarctic hotspots will be less affected by ocean warming than other areas could be a possible reason that explains the highest bryozoan diversity recorded in this area, suggesting that since over evolutionary time, such as the interglacial periods, this area has suffered less thermal stress than others. This pattern has been similarly observed in other terrestrial studies, such as in the Amazon forest, where the highest diversity has been recorded in areas that have been least affected by historical climatic variability (Malhi et al., 2008), or in the Mediterranean regions, where the high number of endemic species may be related to the fact that this region was a glacial refugia for terrestrial species during the Pleistocene (Hewitt, 1996).

4. Evaluating the responses of marine populations to human stressors

4.1 Life history traits may determine the responses and recovery of species

This PhD thesis highlights the importance of unravelling the life history strategies to identify the response of species to increasing human perturbations. In chapter 4, we showed that the Mediterranean *Pentapora fascialis* exhibited fast growth and high recruitment rates, suggesting a high capacity for recovery under anthropogenic pressures (Fig. 2). Accordingly, previous studies have shown that longevity is positively correlated with survival and negatively correlated with growth rates (Salguero-Gómez et al., 2016). Only a few studies have previously explored the longevity patterns in bryozoan species and have found limited longevity between 10-22 years, which contrasts with the lifespans of other benthic long-lived groups such as octocorals or sponges, which can live between 10-1000 years and 1-10,000 years, respectively (Montero-Serra et al., 2018).

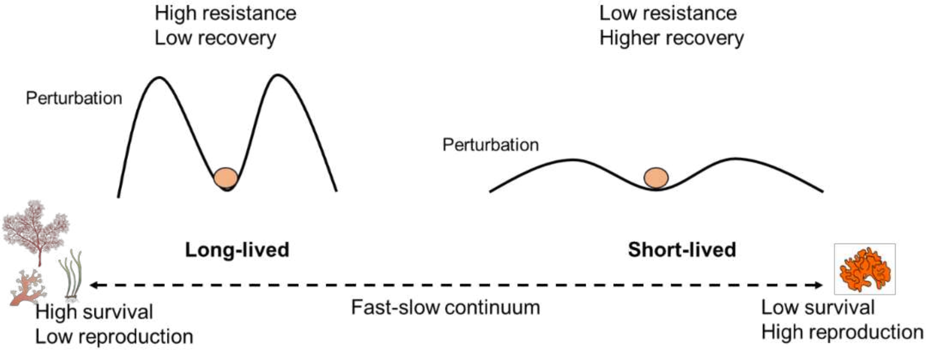


Figure 2. Diagram of the effects of perturbations on life history traits between long-lived and short-lived species along fast-slow continuum.

Although short-lived species are characterized by low resistance to external perturbations, they present higher resilience (understood as the capacity to face recurrent disturbances by resisting or recovering; Côté and Darling, 2010; Bernhardt and Leslie, 2013) due to their higher growth rates, suggesting that *P. fascialis* will not be as affected by human perturbations as other benthic species that have slow population dynamics, such as corals, gorgonians and some seaweeds (Linares et al., 2007; Montero-Serra et al., 2015) (Fig. 2). However, besides its fast population dynamics, we showed evidence of its vulnerability to human physical impacts, such as those caused by scuba diving. The bryozoan populations in areas frequented by divers in the Medes Island Marine Reserve have remained at very low densities since the 1990s, suggesting that the resilience of this species may be lower if the threats are recurrent, which does not allow for population recovery. In addition, the human-induced perturbations in bryozoan populations may reduce their abundance, decrease their survival rates and cause fragmentation of their habitat at large temporal scales, resulting in the loss of the ecological services provided by this habitat-forming species. At a minimum, the loss of the species associated with the bryozoan bioconstructions may represent a decrease in the functional and response diversities of these communities, decreasing their capacities for buffering the effects of environmental changes and making them more vulnerable to anthropic perturbations (Mori et al., 2013).

4.2 Impacts of diving on bryozoan populations: *P. fascialis* as an ecological indicator of diving

Previous studies have highlighted that ecological indicators of the impacts of diving should be large and abundant erect species with rigid skeletons, which are sensitive to the erosion caused by divers and should represent engineering species that contribute to and increase the structure and biodiversity of the benthic communities. Moreover, these species should allow ethical and non-extractive monitoring based on visual or photographic censuses because most of the studies take places inside MPAs, and the repeatability has to be ensured (Table 2; Linares et al., 2010b). Finally, the species should be easily identifiable and have a definite form or clear morphological and growth patterns so that the individuals are more easily locates and measures underwater; these are uncommon parameters for the majority of bryozoan species, making them less suitable as ecological indicators of diving (Table 2; Linares et al., 2010b).

Although it can be difficult to identify bryozoans at the species level, this obstacle can be solved by selecting the easily identifiable species, such as *P. fascialis* or *M. truncata*; or if this is not possible, the surveys can be conducted through exhaustive photographic analyses and with the help of a trained taxonomist, both of which were performed in Chapters 3, 4 and 5 (in this PhD thesis, the taxonomist M. Zabala helped us to solve some related issues). In relation to the location and measurement of the individuals, we adapted and modified previous methodologies to monitor *P. fascialis* populations (Sala et al., 1996; Garrabou et al., 1998) by installing permanent transects on the bottom that are usually used to monitor other benthic long-lived species such as gorgonians (Linares et al., 2010b). Specifically, the monitoring was basically performed *in situ* and was complemented with photographic analyses, which helped us to identify individual colonies. Future studies on the impacts of diving on bryozoan species should explore and consider these limitations and apply similar methodologies to properly use them as ecological indicators (Table 2).

Table 2. Identification of the adequacy of the major benthic groups in the Mediterranean Sea as ecological indicators of the impacts of diving. *Considering the installation of the permanent transects, photographic and in situ monitoring actions, and an optimal taxonomical knowledge (Adapted from Linares et al., 2010b).

Criteria	**Statistical**		**Ethic**		**Ecological**		
Descriptors	Abundance	Repeatability (definite form)	Large size	Easy taxonomy	Engineering species	Rigid skeletons	Sensible erosion
Bryozoans	✓	✓*	✓	✓*	✓	✓	✓
Gorgonians	✓	✓	✓	✓	✓	✓	✓
Calcareous algae	✓		✓		✓	✓	✓
Molluscs		✓	✓	✓		✓	
Scleractinian corals			✓	✓		✓	✓
Fleshy algae	✓		✓				
Hydrozoans	✓						
Ascidians			✓				
Polychaetes	✓						

Until now, *P. fascialis* and *M. truncata* have been identified as optimal ecological indicators of diving, without analysing the suitability in the context of their population dynamics or recovery capacity (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández et al., 2014). Although in Chapter 4 the impacted bryozoan populations on Medes Island Reserve showed low abundances, reference sites presented higher abundances and larger sizes than the sites frequently visited by divers, suggesting that *P. fascialis* was an optimal indicator of the diving impacts, as previous studies suggested (Sala et al., 1996; Garrabou et al., 1998). As we commented above, the population dynamics of *P. fascialis* were faster than those of other benthic species and show a rapid response to perturbations as well as to the removal of stressors, allowing us to study the effects of human threats on marine communities.

4.3 Revealing the winners and losers among the species facing climate change in the Mediterranean Sea

Studying species-specific thermal tolerances is vital to reveal the winners and losers under climate change and to forecast the future composition and functionality of benthic communities (Gómez-Gras et al., 2019). To date, most studies have focused on tropical benthic species or on temperate charismatic groups, such as corals, gorgonians or seagrasses (i.e., Torrents et al., 2008; Linares et al., 2013; Naumann et al., 2013; Kersting et al., 2015; Savva et al., 2018). In this context, in Chapter 3, we explored for the first time the thermal tolerances of bryozoans and showed evidence of divergent responses to warming between two co-occurring Mediterranean species. Despite the fast growth and recovery capacity that was identified for *Pentapora fascialis* in chapter 4, we found that it was characterized by low thermal tolerance. In contrast, we showed a divergent response to warming between this species and the other common Mediterranean bryozoan *Myriapora truncata*, which presented a higher resistance to warming.

The winners and losers of climate change will be determined not only by their thermal tolerances but also by their life history strategies (Madin et al., 2016; Hughes et al., 2018). As noted above, previous studies have shown that the populations with faster growth and higher reproduction will recover more quickly after disturbances than others with slower population dynamics (McKinney and Lockwood, 1999). Besides we showed the low tolerance to warming of *P. fascialis*, the results of Chapter 4 suggest that its faster population dynamics will enhance the recovery of its populations. However, if the heatwaves events are recurrent, they will not allow the recovery of *P. fascialis* populations, and some local extinctions could occur. Furthermore, the loss of these habitat-forming species may drive a reduction of the structural complexity and functionality of benthic ecosystems (Ponti et al., 2014).

Although we observed a low vulnerability to warming in this species, previous studies have shown the impacts of local perturbations, such as diving and storms, on *M. truncata* (De la Nuez-Hernández, 2014), highlighting the need to explore its population dynamics to forecast its vulnerability to human threats. Previous studies have suggested that this species was characterized by slower growth rates than *P. fascialis* due to its morphology and its similarity to other benthic slow-growing species, such as *Corallium rubrum* (Zabala, 1986; Lombardi et al., 2013). In this regard, the preliminary results of a five-year monitoring trial of one *M. truncata* population in Medes Islands between 2008-2012 showed a high annual survival (between 60-80%), slow growth rate (approximately 1.93 mm/year) and low recruitment rate (between 4-17 recruits/year) (Fig. 3) (unpublished author's work).

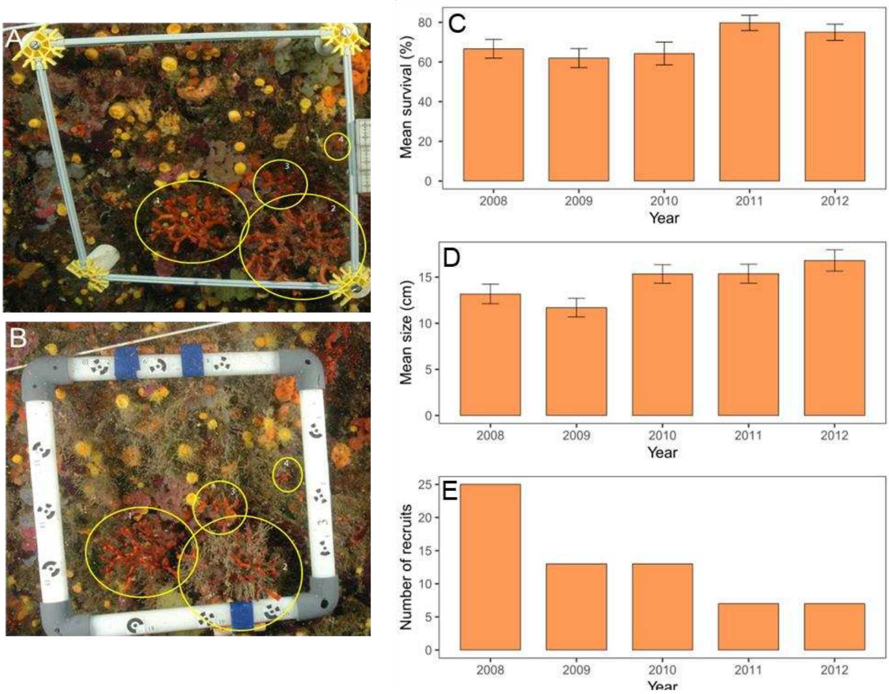


Figure 3. Preliminary results of a 5-year monitoring of M. truncata in Medes Island Reserve. A, B) Example of the photographic monitoring method, identifying individually the colonies between successive years, C) annual mean survival, D) annual mean size, and E) total number of recruits recorded each year.

Previous works have quantified similar values for other slow-growing species, such as *C. rubrum,* which was shown to have an annual survival rate between 65-100% and a mean growth rate of 1.78 mm/year (Garrabou and Harmelin, 2002), or *P. clavata,* which had a mean annual survival rate between 63-97% and a mean growth rate between 2.7-3 cm/year (Mistri and Ceccherelli, 1994; Linares et al., 2010b). Our preliminary results suggested that this species is characterized by slow population dynamics with a low capacity for recovery after impacts, highlighting that the cumulative effects of local and global threats on natural populations may compromise their future viability. In addition, these findings were supported by the fact that in Chapter 5, despite we installed recruitment surfaces on *M. truncata* habitat, we did not register any recruit of this species, which may be related to the low suitability of recruitment surfaces but also to the fact that this species is characterized by low recruitment rates, as other slow-growing species. Accordingly, it is vital to design a formal monitoring plan for this species to reveal its population dynamics and its responses to the increasing and multiple threats.

5. Conservation measures

5.1 Adaptive management plans are required to monitor and conserve bryozoan populations

Marine protected areas usually contribute to an increase in the frequency of divers, which can represent a source of local stress for marine communities, as evidenced in Chapter 4. In locations where there is an overabundance of divers, effective adaptive management and conservation actions are required to protect ecological and cultural values (Dimmock and Musa, 2015). In Chapter 4, the monitoring of *P. fascialis* populations in the Medes Islands showed that this species was highly impacted by diving and revealed the need to decrease the diving quotas in these areas to allow the recovery of these populations. Moreover, we recommend establishing a formal and continuous adaptive management plan for *P. fascialis* to study their future population trends and to properly estimate the optimal number of divers inside the marine reserve without negatives impacts on the bryozoan populations. The recovery of the bryozoan populations should take place in a relatively short period of time due to its rapid population dynamics. In this sense, the full protections declared for the Medallot in 2015 created an ideal experiment to assess the recovery capacity of bryozoan populations; it would also be recommended to reduce the number of divers in other locations to study the potential effects on bryozoan populations.

In addition to the local anthropogenic pressures, climate change threatens marine ecosystems. The IPCC predicts an increase of 2-3 and 4.8ºC (depending on the RCP emissions scenario) in global mean sea surface temperature by the end of this century (IPCC, 2015), compromising the viability of marine populations. In addition to the increase of mean sea surface temperature, in recent years, the recurrent heatwaves have impacted benthic communities, affecting several species of gorgonians and bryozoans (Garrabou et al., 2009; Cocito and Sgorbini, 2014), as we found in Chapter 3. The erosive effects of the divers and the effects of climate change can act synergistically on *P. fascialis* populations, highlighting the need to implement active restoration actions for this species.

5.2 Conservation in a globally changing environment: active measures are needed when only protection does not ensure the viability of the populations

Chapters 3 and 4 showed the vulnerability of *P. fascialis* to anthropogenic stressors, which emphasizes the need for a restoration plan for this species in the Mediterranean Sea. The term "restoration" implies the recovery of an ecosystem that has been degraded, damaged or destroyed from their initial state (SER, 2004). The earliest studies of the Mediterranean bryozoan populations were carried in Medes Islands during the 1990s when populations were already being impacted by divers, without showing any evidence of the "pristine" status of these populations. In Chapter 4, *P. fascialis* colonies in non-frequented locations were much more numerous than those in the frequented ones, suggesting that without the pressure of diving, bryozoan populations may be more abundant on Medes Islands Marine Reserve and reach similar abundance as those registered in the non-frequented areas. For that reason, in this thesis, we used the term "restoration" as the recovery of the bryozoan populations from a threatened status such as that registered in Chapters 3 and 4, which was characterized by a low abundance of bryozoans to a non-impacted situation, where the bryozoan densities were higher and created good-sized populations.

Conservation efforts have traditionally focused on the creation of MPAs. However, in recent decades, the escalating threats to natural systems have highlighted the need to conduct restoration actions, which has resulted in an exponential increase in the number of related works since the 1990s-2000s (Young et al., 2005; Holl and Aide, 2011; Possingham et al., 2015) (Table 1 Appendix). In the Mediterranean Sea, previous studies on active marine restoration actions have focused on popular and emblematic species such as the corals, gorgonians and macroalgae (Fig. 4).

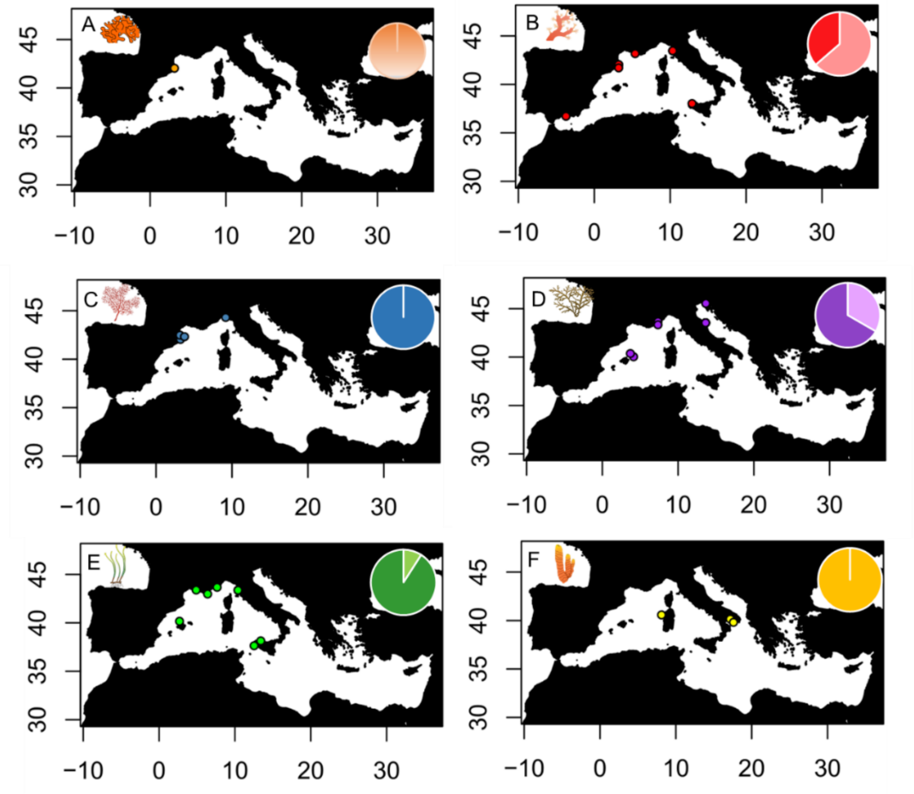


Figure 4. The study location of the restoration actions performed in the Mediterranean Sea on benthic species: A) bryozoans, B) corals, C) gorgonians, D) macroalgae, E) seagrass, and F) sponges. In each case, the proportion of the types of restoration actions was represented: the dark colour represents transplantation actions, and the light colour represents recruitment enhancement actions. Note that for gorgonians and sponges, all studies were focused on transplantation actions. The present thesis represents the only approach where we accounted for restoration actions for bryozoans, and was the only study until now that explored the combination of both techniques. Data was obtained through Google Scholar and Web of Knowledge.

The first studies of the restoration actions for benthic species in the Mediterranean Sea were carried out between the 1970-1980s, and investigated transplantation of gorgonians (Weinberg, 1979) or seagrasses (Cooper, 1979). Since then, most studies on benthic species have explored only one type of restoration technique, such as testing recruitment enhancement or transplantation techniques, but not both in the same study (Fig. 4,). Specifically, recruitment enhancement has been more commonly tested in corals. Conversely, the restoration of gorgonians, macroalgae, seagrasses, and sponges was mostly based on transplantation actions. In Chapter 5, we developed and tested, for the first time, both restoration techniques for bryozoans (recruitment enhancement and transplantation actions). Although we focused our study on *P. fascialis*, we encouraged the testing of similar restoration methodologies for other bryozoan species, such as *Myriapora truncata*.

Beyond the need for these actions, restoration plans present some limitations, such as the high economic cost to apply them, which often results in limited spatial and temporal resolution in most of the studies and hinders the extrapolation of the effects to larger scales (Bayraktarov et al., 2016). However, we highlighted the viability of implementing an affordable and economical plan for bryozoans and encourage managers to apply the method to MPAs. Moreover, the high recruitment recorded for *P. fascialis* in Chapter 4 suggests that it may represent a source of new transplants for the damaged areas, which opens a new window of opportunity for future restoration actions.

5.3 Establishing future management and conservation measures for bryozoans

This thesis reflected the importance of integrating different types of approaches to set up conservation measures for bryozoan populations at global and local scales. As a result of the present thesis, we recommend performing different actions that could not be specific to bryozoan conservation but can also be applied to other benthic species. Specifically, we recommend:

- To quantify the current diversity in order to complete the inventories. Knowing the total number of species is needed to provide a reference point for past, current and future losses of diversity. Moreover, the future projections on species descriptions will help us to identify the needed efforts to complete the species inventories.
- To unravel the diversity patterns and their main drivers. There is a need to challenge the most accepted latitudinal pattern for some marine groups by accounting for the differences in sampling effort frequency between

regions in environmental modelling.

- To identify hotspot areas and projects the impact of global warming to identify priority areas for conservation efforts.

At the local scale, we make the following recommendations:

- To monitor natural populations to estimate the life history traits of marine species and to detect long-term shifts driven by anthropogenic stressors. Moreover, these data series could be useful to unravel the capacity for recovery of marine populations and to project their future viability. The monitoring of *P. fascialis* will help us to detect the recovery of its populations and to identify when it can be used again as an optimal indicator of anthropogenic threats.
- To detect and remove controllable impacts, such as an excessive number of divers. In this PhD thesis, we showed that an overabundance of divers impacted the bryozoan populations, reducing their number and compromising their related ecological services. For this reason, in highly frequented areas, it is vital to reduce the pressure of diving to ensure the recovery of populations.
- To apply active management actions. In addition to the reduction in diver numbers, it is vital to carry out active restoration plans to enhance and speed up the recovery of bryozoan populations.

6. Future perspectives

The knowledge provided in the present thesis represents a basis for developing further studies on the ecology and conservation of bryozoans. Many unresolved questions have emerged during the development of this thesis, which should be considered in future studies as follows:

- The study of diversity and distributional patterns of fossil bryozoans. Due to the importance of the fossil bryozoans recorded in Chapter 1, it is vital to unravel their past diversity to elucidate how the current patterns have changed from those in the past and to compare the previous environmental drivers of species richness with the extant ones. Moreover, it is important to quantify past extinctions and their drivers.
- Modelling distributional patterns of Mediterranean bryozoans. To estimate the future vulnerability of the Mediterranean bryozoan population, we need to understand the fundamental niches of species.

Moreover, in these models, we should incorporate demographic parameters, such as growth, survival and recruitment values by performing niche-based models. Finally, future studies should project the distributions of these species at the end of this century to predict local extinctions of the bryozoan populations, which will help us identify the most vulnerable populations and properly redirect the management efforts. Although we tried to implement these models in this thesis, the lack of knowledge about the reproduction of the species makes it difficult to accurately develop these models.

- To study the population dynamics of other abundant Mediterranean bryozoan species, such as *Myriapora truncata* and *Reteporella grimaldii.* Bryozoans are characterized by a wide variety of growth forms and life strategies, highlighting the need to study other species to unravel their responses to local and global threats. Although these two species were included in the quantification of the demographic analyses of the Mediterranean bryozoan populations at the beginning of the present thesis, the incorporation of different research approaches resulted in a lack of time to learn the new skills and methods and did not allow us to advance in these analyses.
- To investigate asexual reproduction in bryozoans. Fragmentation processes are an important part of the bryozoan population dynamics. For this reason, it is crucial to understand the magnitude of asexual reproduction in *P. fascialis* population dynamics, particularly by performing genetic studies to identify whether colonies derive from sexual or asexual reproduction. However, these genetic analyses are usually based on the study of microsatellites (Féral, 2002; Held and Leese, 2007), and in bryozoans, the microsatellite analyses are poorly developed. In this sense, it is imperative to develop microsatellite markers or other genetic techniques for bryozoans to also understand the genetic connectivity among populations.
- To evaluate the role of *Pentapora fascialis* as a focus of biodiversity. Despite previous studies that have identified *P. fascialis* as a habitat-forming species, there is a need to explore the direct effects of this species on the associated flora and fauna.
- To study the effects of ocean acidification in *P. fascialis.* Previous studies have demonstrated the impact of acidification on other bryozoan species, such as *Myriapora truncata,* suggesting that *P. fascialis* could also be

affected by acidification, making them more vulnerable to climate change.

- To evaluate the active management measures on a long-term scale. Although we assessed the adequacy of the restoration actions on Medes Island bryozoan populations in the short term, these actions should be monitored in the long term to evaluate the efficiency of these active restoration actions inside an adaptive management plan.

Conclusions

Chapter I

- There are nearly three times more bryozoan species described in the fossil record than there are extant species.
- There has been an increase in the taxonomic efforts during the past century, which have been characterized by an increase in the number of taxonomists, reflecting an increasing interest in ocean discovery.
- The number of species described per author has been declining since the 1930s, suggesting that at the beginning of bryozoan discovery, it was easier to describe new species.
- Future projections have shown an increase in the discovery of species; it is predicted that approximately 10% and 20% more fossil and extant species, respectively, will be described at the end of this century.

Chapter II

- The latitudinal diversity pattern recorded for bryozoans showed a higher diversity in high latitudes, which contrasts with the most accepted latitudinal pattern that shows an increase in species in the tropics.
- Bryozoans showed higher diversity in the Southern Ocean being the largest diversity area. Differences in sampling effort were detected between regions, with higher effort in the temperate North Atlantic.
- The depth, nitrate, and SST were identified as the best predictors for bryozoans and sessile marine diversity.
- Larger increases in the mean SST are predicted in the northern hotspot areas under the different RCP scenarios, suggesting a high spatial heterogeneity of potential warming impacts. On the other hand, the Southern Ocean will be the less impacted.

Chapter III

- We found differences in survival between *P. fascialis* and *M. truncata* in the field after a thermal anomaly, which showed a clear impact on the populations of *P. fascialis* independently of the protection level and habitat type.
- The colonies of both species showed higher growth rates in the control than in both thermal stress treatments, but there were only significant differences for *P. fascialis* in the thermal stress treatment. Signs of skeletal damage in the temperature treatments were clearly observed in *P. fascialis.*

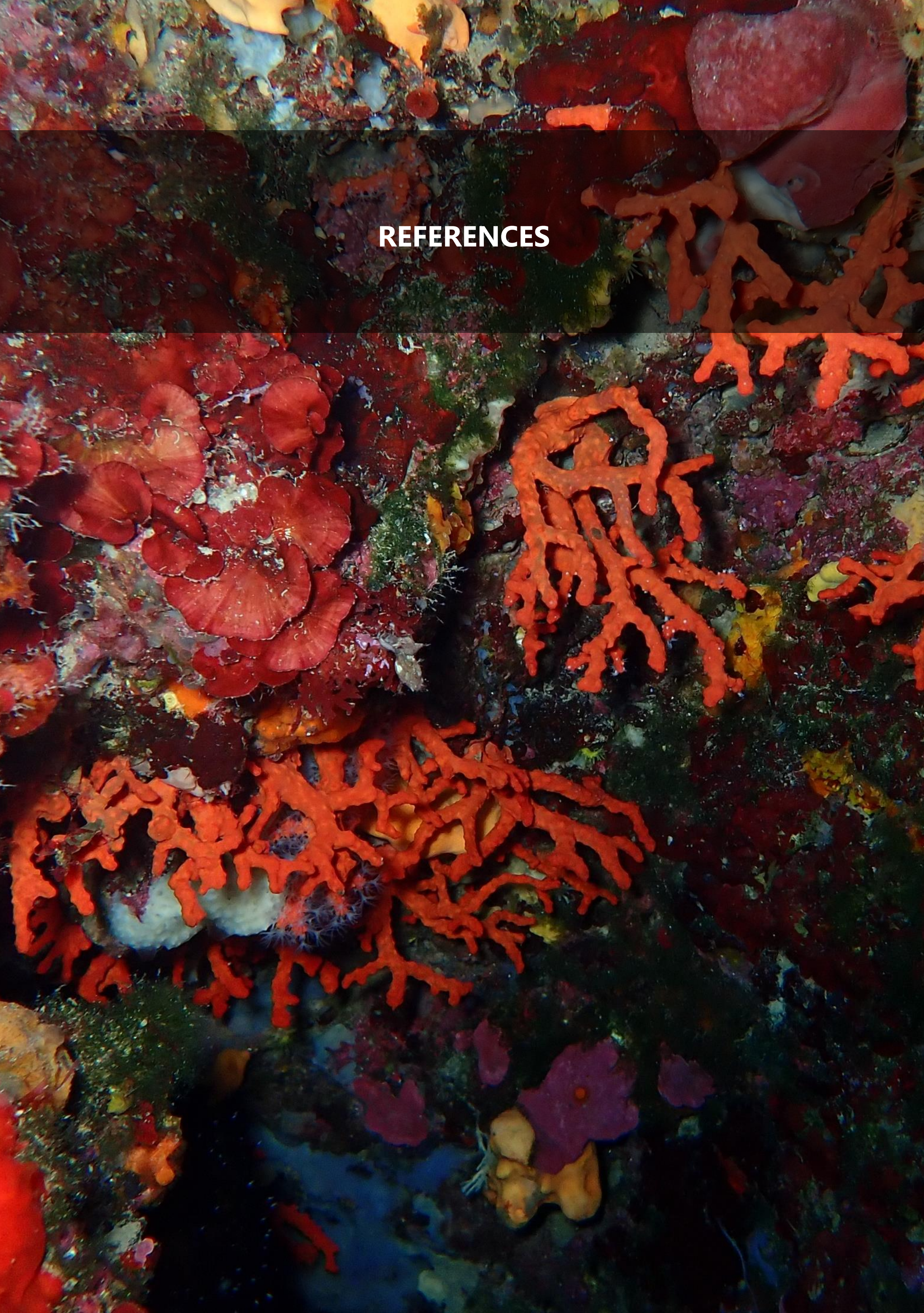
- The distribution patterns of both species reflected their environmental tolerances. *M. truncata* was distributed across shallower and warmer waters, while *P. fascialis* was able to inhabit deeper waters.

Chapter IV

- Diving impacts on the density, recruitment, survival, and size of *P. fascialis* colonies.
- The bryozoan population densities on non-frequented locations has increased since the 1990s. However, the densities on frequented locations remained very low, suggesting that the high levels of diving have not allowed the development of large and abundant populations.
- Bryozoan recruitment events are stochastic and show inter-annual variation characterized by bi-annual peaks, suggesting that our species model displayed faster population dynamics than those of other benthic species, such as corals or gorgonians.
- Higher growth and lower necrosis rates were found during the colder months.
- Although MPAs have been recognized as useful tools for the management and conservation of marine populations, the effects of high visit frequency by divers on the bryozoan populations highlights the need to reduce the number of divers and to implement active restoration measures.

Chapter V

- The installation of artificial substrates for bryozoans seems to be the most effective restoration technique, given that it is a non-invasive methodology that results in observable high recruitment. The transplantation of adults should only be considered in particular cases, such as the detection of lost fishing nets impacting the bryozoan colonies.
- Plastic grids represent the best artificial substrate for facilitating the recruitment of new bryozoan colonies.
- The best methodology for transplanting adult colonies is to fix the colonies to the substrate with a nylon thread attached to the colony *ex situ* (on the boat).
- The methodology developed in this thesis represents a reliable, low cost and short-term restoration action; we encourage MPA managers to apply it to promote the recovery of damaged bryozoan populations.



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SUPPLEMENTARY MATERIAL

Supplementary material Chapter I

Table S1. The top 40 marine bryozoan families with the number of total described accepted living species, their number of genera and the year of the description of the first and most recent species until 2014.

Table S2. For all bryozoan families with freshwater species, their number of accepted living species and the earliest and most recent years of description per family until 2017. *Some of these freshwater species are also brackish.

Table S3. For the top 40 bryozoan families with fossil species (some but not all wholly extinct), the number of described species and the year of the description of the first and most recent species until 2017.

Table S4. The 30 most prolific authors of accepted living marine species to 2014. The number of species described, the earliest and latest year of these descriptions, and species described per year until 2014.

Table S5. The 17 most prolific authors of accepted living freshwater species. All the other authors described just one species. The number of species described, earliest and latest years of description, and species described per year, until 2017.

Table S6. The 30 most prolific authors of accepted fossil species. The number of species described, earliest and latest years of description, and species described per year until 2017.

Figure S1. (A, B, C) The number of first authors and (D, E, F) the number of species'/authors for each decade from the 1750s to 2017 for freshwater (B, E) and fossil species (C, F), and from the 1750s and 2014 for marine species (A, D). The trend lines are two-year moving average.

Figure S2. Generalized linear models of species described vs publication lifetime for (A) marine, (B) freshwater and (C) fossil species. We adjusted the models to a Poisson distribution.

Table S1. The top 40 marine bryozoan families with the number of total described accepted living species, their number of genera and the year of the description of the first and most recent species until 2014.

Rank	Family	No. of species	No. of genera	Year of first description	Year of latest description
1	Smittinidae	339	19	1766	2010
2	Phidoloporidae	325	20	1826	2011
3	Calloporidae	277	34	1767	2011
4	Celleporidae	257	19	1766	2009
5	Bugulidae	240	22	1758	2007
6	Candidae	208	26	1758	2014
7	Microporellidae	182	11	1766	2009
8	Bitectiporidae	139	14	1766	2009
9	Cribrilinidae	137	20	1780	2013
10	Lepraliellidae	119	8	1816	2006
11	Tubuliporidae	117	11	1766	2009
12	Romancheinidae	110	23	1828	2007
13	Cellariidae	104	15	1758	2005
14	Conescharellinidae	97	7	1851	2004
15	Flustridae	96	17	1758	1999
16	Crisiidae	94	7	1758	2009
17	Schizoporellidae	92	4	1766	2009
18	Lichenoporidae	82	9	1758	2010
19	Bryocryptellidae	75	11	1786	2005
20	Beaniidae	70	4	1840	2007
21	Alcyonidiidae	68	5	1813	2006
22	Microporidae	68	15	1796	2009
23	Chaperiidae	66	10	1854	2009
24	Petraliellidae	66	8	1826	2007
25	Adeonidae	62	9	1812	2007
26	Plagioeciidae	59	12	1816	2010
27	Escharinidae	58	9	1803	2008
28	Electridae	54	11	1767	2011
29	Lanceoporidae	54	4	1851	2006
30	Horneridae	53	4	1758	1996
31	Arachnopusiidae	47	6	1854	2007
32	Exochellidae	47	3	1806	2007
33	Adeonellidae	45	1	1816	2005
34	Lacernidae	45	13	1826	2014
35	Steginoporellidae	44	4	1854	2006
36	Oncousoeciidae	43	9	1826	2010
37	Vesiculariidae	43	6	1758	1992
38	Umbonulidae	41	8	1780	2005
39	Cupuladriidae	39	5	1823	2008
40	Hippoporidridae	38	7	1854	2007

Table S2. For all bryozoan families with freshwater species, their number of accepted living species and the earliest and most recent years of description per family until 2017. *Some of these freshwater species are also brackish.

Rank	Family	No. of species	No. of genera	Year of first description	Year of latest description
1	Plumatellidae	66	7	1758	2017
2	Lophopodidae	9	3	1768	1959
3	Victorellidae*	8	4	1870	1996
4	Hislopiidae	7	1	1858	2011
5	Fredericellidae	7	2	1779	2017
6	Pectinatellidae	3	2	1851	1907
7	Paludicellidae	2	1	1831	1916
8	Arachnidiidae	1	1	1903	1903
9	Cristatellidae	1	1	1798	1798
10	Natanellidae	1	1	2017	2017
11	Pottsiellidae	1	1	1884	1884
12	Stephanellidae	1	1	1908	1908
13	Tapajosellidae	1	1	2017	2017

Table S3. For the top 40 bryozoan families with fossil species (some but not all wholly extinct), the number of described species and the year of the description of the first and most recent species until 2017.

Rank	**Family**	**No. of species**	**Year of first description**	**Year of latest description**
1	Fenestellidae	1545	1820	2016
2	Fistuliporidae	1310	1766	2016
3	Cribrilinidae	713	1826	2017
4	Onychocellidae	580	1826	2017
5	Calloporidae	499	1821	2017
6	Polyporidae	463	1839	2017
7	Stenoporidae	441	1836	2016
8	Membraniporidae	434	1828	2016
9	Atactotoechidae	367	1801	2012
10	Acanthocladiidae	338	1839	2017
11	Rhabdomesidae	310	1820	2015
12	Monticuliporidae	287	1836	2017
13	Semicosciniidae	284	1832	2015
14	Dyscritellidae	242	1826	2012
15	Plagioeciidae	224	1868	2016
16	Amplexoporidae	224	1821	2017
17	Hexagonellidae	206	1850	2015
18	Leioclemidae	206	1846	2015
19	Trematoporidae	188	1858	2012
20	Oncousoeciidae	182	1831	2015
21	Rhomboporidae	181	1821	2014
22	Romancheinidae	172	1836	2015
23	Cystodictyonidae	169	1838	2017
24	Rhinidictyidae	168	1836	2015
25	Heterotrypidae	160	1839	2015
26	Cerioporidae	158	1850	2015
27	Celleporidae	151	1821	2006
28	Arthrostylidae	149	1814	2017
29	Tubuliporidae	148	1831	2015
30	Eridotrypellidae	144	1821	2017
31	Lichenoporidae	143	1833	2016
32	Smittinidae	135	1823	2008
33	Ceramoporidae	133	1838	2007
34	Halloporidae	131	1839	2009
35	Microporidae	123	1850	2015
36	Entalophoridae	118	1803	2015
37	Lepraliellidae	116	1821	2010
38	Adeonidae	116	1826	2016
39	Streblotrypidae	115	1814	2015
40	Eleidae	113	1862	2016

Table S4. The 30 most prolific authors of accepted living marine species to 2014. The number of species described, the earliest and latest year of these descriptions, and species described per year until 2014.

Rank	First author	No. of species	Year of first description	Year of latest description	Publication lifetime	Species/year
1	Canu	366	1917	1934	18	26
2	Hayward	348	1974	2011	37	10
3	Gordon	317	1982	2014	32	9
4	Busk	322	1851	1886	36	9
5	Hincks	217	1851	1895	45	5
6	Harmer	209	1891	1957	67	3
7	d'Hondt	185	1970	2006	37	5
8	MacGillivray	185	1842	1895	54	3
9	Osburn	160	1912	1953	41	4
10	Kluge	159	1906	1962	57	3
11	Waters	149	1878	1927	50	3
12	Soule	128	1950	2004	55	2
13	Jullien	126	1880	1903	24	5
14	Liu	117	1982	2001	20	6
15	Tilbrook	115	1998	2006	9	13
16	Moyano	108	1965	2011	46	2
17	d'Orbigny	83	1839	1854	16	5
18	O'Donoghue	81	1923	1957	35	2
19	Smitt	77	1865	1875	11	7
20	Silén	72	1938	1976	39	2
21	Levinsen	70	1909	1917	8	9
22	Calvet	69	1896	1931	36	2
23	Harmelin	63	1969	2009	41	2
24	Borg	61	1924	1944	21	3
25	Marcus	59	1921	1955	35	2
26	Norman	55	1864	1909	46	1
27	Hastings	52	1930	1963	34	2
28	Winston	46	1984	2013	30	2
29	Gontar	43	1979	2011	33	1
30	Okada	42	1918	1938	21	2

Table S5. The 17 most prolific authors of accepted living freshwater species. All the other authors described just one species. The number of species described, earliest and latest years of description, and species described per year, until 2017.

Rank	First author	No. of species	Year of first description	Year of latest description	Publication lifetime	Species/ year
1	Wood	21	1988	2017	30	0.7
2	Wiebach	10	1964	1976	13	0.8
3	Annandale	9	1909	1919	11	0.8
4	Kraepelin	6	1887	1914	28	0.2
5	Hirose	4	2011	2011	1	4
6	Abrikosov	3	1925	1925	1	3
7	Oka	3	1907	1908	2	1.5
8	Rao	3	1961	1985	25	0.1
9	Rousselet	3	1904	1907	4	0.8
10	Taticchi	3	2010	2011	2	1.5
11	Allman	2	1844	1844	1	2
12	Braem	2	1911	1951	41	< 0.1
13	Jullien	2	1880	1885	6	0.3
14	Lacourt	2	1947	1959	13	0.2
15	Pallas	2	1768	1768	1	2
16	Rogick	2	1942	1945	4	0.5
17	Toriumi	2	1941	1952	12	0.2

Table S6. The 30 most prolific authors of accepted fossil species. The number of species described, earliest and latest years of description, and species described per year until 2017.

Rank	First author	No. of species	Year of first description	Year of latest description	Publication lifetime	Species/year
1	Canu	1541	1897	1935	39	40
2	Ulrich	673	1878	1936	59	11
3	D'Orbigny	645	1842	1855	15	43
4	Hall	610	1847	1895	49	12
5	Voigt	430	1923	1999	84	5
6	Yang	402	1950	1988	39	10
7	Morozova	363	1955	2006	52	7
8	Brydone	357	1906	1936	31	12
9	Nekhoroshev	341	1926	1977	52	7
10	Bassler	307	1903	1952	51	6
11	Reuss	298	1846	1875	30	10
12	Schulga	291	1931	1983	53	5
13	Trizna	270	1939	1961	23	12
14	Gorjunova	250	1964	2015	52	5
15	Ernst	242	1998	2017	20	12
16	Astrova	213	1940	1972	38	6
17	Liu	209	1976	1991	26	8
18	Lang	198	1906	1925	20	10
19	Von Hagenow	182	1839	1851	13	14
20	Sakagami	181	1960	2000	41	4
21	Maplestone	166	1898	1913	34	5
22	MacGillivray	165	1869	1895	27	6
23	Nikiforova	157	1927	1953	27	6
24	Taylor	156	1980	2016	37	4
25	Crockford	153	1941	1962	22	7
26	Guha	145	1989	2007	19	8
27	Busk	139	1854	1886	35	4
28	Modzalevskaya	127	1953	1982	30	4
29	Pushkin	120	1973	2005	33	4
30	Lu	114	1958	1999	42	3

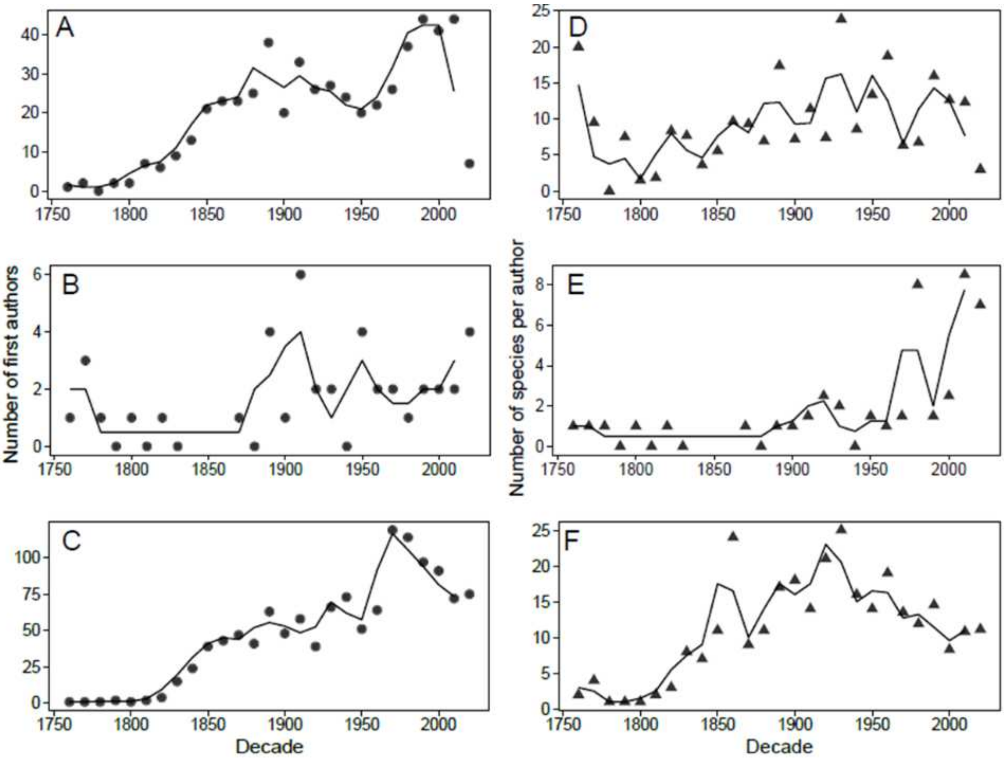

Figure S1. (A, B, C) The number of first authors and (D, E, F) the number of species'/authors for each decade from the 1750s to 2017 for freshwater (B, E) and fossil species (C, F), and from the 1750s and 2014 for marine species (A, D). The trend lines are two-year moving average.

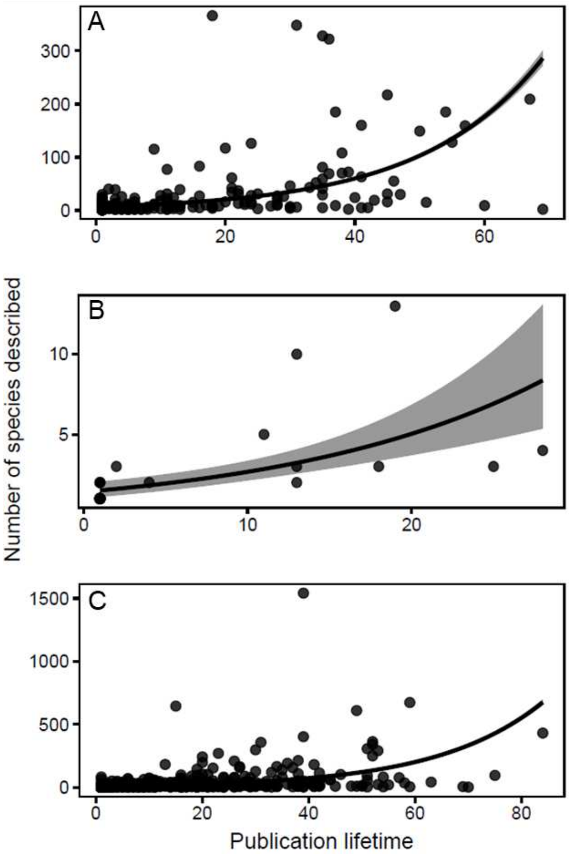

Figure S2. Generalized linear models of species described vs publication lifetime for (A) marine, (B) freshwater and (C) fossil species. We adjusted the models to a Poisson distribution.

Supplementary material Chapter II

Table S1. Sample size occurrence data for studied groups obtained from OBIS and GBIF.

Table S2. Environmental downloaded predictors.

Table S3. Coefficient of Spearman's correlation between studied environmental variables

Table S4. Sampling effort frequency for each Spalding's biogeographical and IHO region.

Table S5. Generalized Linear Models (GLM) between rarefied species richness (ES50) and latitude for marine sessile groups.

Table S6. Generalized Linear Models (GLM) coefficients for bryozoans (n=740) and marine sessile species (n=1731), modelling response variable (rarefied species richness (ES50)) as function of each selected environmental variable).

Table S7. Generalized Linear Models (GLM) coefficients for bryozoans (n=740) and marine sessile species (1731), modelling response variable (non-rarefied species richness) as function of each selected environmental variable, including the interaction of sampling effort index.

Table S8. Generalized Linear Models (GLM) between the predicted increase in mean SST and latitude for bryozoans and marine sessile species, adding the effect of the RCP emission scenario (4.5 and 8.5).

Figure S1. Predicted mean increase (mean±SE) of SST mean in hotspot areas under different RCP emission scenarios (light color: 2.5; dark color: 8.5) for marine sessile species (blue) and bryozoans (orange).

Table S1. Sample size occurrence data for studied groups obtained from OBIS and GBIF.

Studied group	**OBIS data**	**GBIF data**	**Total cleaned**
Bryozoa	**177,409**	**333,518**	**146,149**
Anthozoa	235,904	1,179,354	719,130
Ascideacea	131,998	154,652	106,671
Bivalvia	1,104,577	766,608	704,406
Macroalgae	741,441	926,085	529,583
Porifera	426,341	511,169	310,478
Polychaeta	1,235,764	392,680	481,355
Cirripeda	105,235	107,161	56,212
Seagrasses	23,043	323,426	14,317
Marine sessile species	**4,181,712**	**4,694,656**	**3,068,301**

Table S2. Environmental downloaded predictors.

Variable	**Spatial Resolution**	**Source**
Mean SST (ºC)	0.083º	BioOracle2
Min. SST (ºC)	0.083º	BioOracle2
Max. SST (ºC)	0.083º	BioOracle2
Range SST (ºC)	0.083º	BioOracle2
Maximum Depth (m)	0.083º	BioOracle2
Mean Depth (m)	0.083º	BioOracle2
Mean chlorophyll (¾mol/mŸ)	0.083º	BioOracle2
Max. chlorophyll (¾mol/mŸ)	0.083º	BioOracle2
Mean nitrate (mol.m-3)	0.083º	BioOracle2
Mean phosphate (mol.m-3)	0.083º	BioOracle2

Table S3. Coefficient of Spearman's correlation between studied environmental variables

	Min. SST	**Min. SST**	**Min. SST**	**Min. SST**	**Mean depht**	**Max. depth**	**Mean chlorophyll**	**Max. chlorophyll**	**Mean nitrate**	**Mean phosphate**
Min. SST	1.00	0.96	-0.09	0.99	-0.30	-0.29	-0.19	-0.20	-0.62	-0.63
Max. SST	0.96	1.00	0.21	0.98	-0.25	-0.23	-0.10	-0.11	-0.70	-0.69
Range SST	-0.09	0.21	1.00	0.04	0.16	0.16	0.28	0.31	-0.31	-0.24
Mean SST	0.99	0.98	0.04	1.00	-0.28	-0.27	-0.16	-0.17	-0.66	-0.66
Mean depth	-0.30	-0.25	0.16	-0.28	1.00	1.00	0.33	0.36	-0.02	0.02
Max. depth	-0.29	-0.23	0.16	-0.27	1.00	1.00	0.33	0.35	-0.03	0.01
Mean chlorophyll	-0.19	-0.10	0.28	-0.16	0.33	0.33	1.00	0.95	0.00	0.04
Max. chlorophyll	-0.20	-0.11	0.31	-0.17	0.36	0.35	0.95	1.00	0.00	0.04
Mean nitrate	-0.62	-0.70	-0.31	-0.66	-0.02	-0.03	0.00	0.00	1.00	0.93
Mean phosphate	-0.63	-0.69	-0.24	-0.66	0.02	0.01	0.04	0.04	0.93	1.00

Table S4. Sampling effort frequency for each Spalding's biogeographical and IHO region.

		Sampling effort (0-1) for marine sessile species	Sampling effort (0-1) for bryozoans
Artic Sea		**0.0020**	**0.0033**
	Arctic Ocean	0.0002	0.0005
	Baffin Bay	0.0003	0.0001
	Barentsz Sea	0.002	0.003
	Beaufort Sea	0.002	0.0024
	Bering Sea	0.018	0.0216
	Chukchi Sea	0.004	0.0049
	Davis Strait	0.002	0.0031
	East Siberian Sea	<0.0001	<0.0001
	Greenland Sea	0.0013	0.0012
	Hudson Bay	0.0002	0.0002
	Hudson Strait	0.0005	0.0005
	Kara Sea	0.0005	0.0005
	Labrador Sea	0.0051	0.0146
	Laptev Sea	0.0003	0.0003
	The Northwestern Passages	0.0001	<0.0001
	White Sea	0.002	0.0002
Central Indo-Pacific		**0.0192**	**0.0264**
	Arafura Sea	0.0214	0.0214
	Banda Sea	0.0138	0.0138
	Celebes Sea	0.0200	0.0200
	Ceram Sea	0.0122	0.0122
	Coral Sea	0.0536	0.0616
	Flores Sea	0.0261	0.0261

	Makassar Strait	0.0056	0.0056
	Molukka Sea	0.0172	0.0172
	Philippine Sea	0.0062	0.0130
	Solomon Sea	0.0050	0.0027
	South China Sea	0.0025	0.0046
	Sulu Sea	0.0070	0.0033
	Timor Sea	0.0203	0.0002
Southern ocean		**0.0016**	**0.0035**
	Southern Ocean	0.0016	0.0035
Temperate Australasia		**0.0116**	**0.0129**
	Great Australian Bight	0.01346	0.02030
	Tasman Sea	0.01090	0.01272
Temperate Northern Atlantic		**0.02530**	**0.0455**
	Adriatic Sea	0.00644	0.00644
	Baltic Sea	0.10202	0.10202
	Bay of Biscay	0.07913	0.07913
	Black Sea	0.01104	0.01349
	Celtic Sea	0.19133	0.19133
	Gulf of St. Lawrence	0.02478	0.024783
	Ionian Sea	0.00543	0.00543
	Mediterranean Sea - Eastern Basin	0.00300	0.02155
	Mediterranean Sea - Western Basin	0.03496	0.09107
	North Atlantic Ocean	0.01471	0.35242
	North Sea	0.35242	0.02367
	Norwegian Sea	0.04804	0.23889
Temperate Northern Pacific		**0.0070**	**0.0231**
	Eastern China Sea	0.00796	0.01653
	Gulf of Alaska	0.00756	0.007562
	Japan Sea	0.00123	0.00137
	North Pacific Ocean	0.00690	0.025
	Sea of Okhotsk	0.00012	<0.0001
	The Coastal Waters of Southeast Alaska and British Columbia	0.10978	0.064
	Yellow Sea	0.01170	0.01170
Temperate South America		**0.0019**	**0.0058**
	South Atlantic Ocean	0.00147	0.0237
	South Pacific Ocean	0.00225	0.0024
Tropical Atlantic		**0.0358**	**0.0394**
	Caribbean Sea	0.03593	0.04216
	Gulf of Guinea	0.00133	0.00133
	Gulf of Mexico	0.04940	0.04940
Western Indo-Pacific		**0.0023**	**0.0066**
	Andaman or Burma Sea	0.0072	0.01274
	Arabian Sea	0.0025	0.00548
	Bay of Bengal	0.0047	0.00834
	Gulf of Aden	0.0018	0.00187
	Indian Ocean	0.0017	0.00563
	Laccadive Sea	0.0126	0.01268
	Mozambique Channel	0.0146	0.01985
	Persian Gulf	0.0027	0.00271
	Red Sea	0.0039	0.00395

Table S5. Generalized Linear Models (GLM) between rarefied species richness (ES50) and latitude for marine sessile groups.

Studied group	**Coefficient**	**Estimate**	**Std. error**	**p-value**	**AIC**
Total marine sessile species	Intercept	3.13	0.02	<0.001	14370
	Latitude	0.001	0.001	0.239	
Bryozoa	Intercept	2.8	0.03	<0.001	5633.8
	Latitude	-0.004	0.001	<0.001	
Anthozoa	Intercept	2.77	0.03	<0.001	10065
	Latitude	-0.001	0.001	0.09	
Ascideacea	Intercept	2.51	0.03	<0.001	5010.2
	Latitude	-0.003	0.001	0.6	
Bivalvia	Intercept	2.85	0.03	<0.001	10245
	Latitude	0.0001	0.001	0.4	
Cirripedia	Intercept	1.70	0.03	<0.001	6010.7
	Latitude	-0.001	0.001	0.48	
Macroalgae	Intercept	2.98	0.04	<0.001	5713.6
	Latitude	0.003	0.001	<0.01	
Polychaeta	Intercept	2.65	0.03	<0.001	7236.4
	Latitude	0.002	0.001	<0.01	
Seagrasses	Intercept	1.31	0.06	<0.001	1028.3
	Latitude	-0.01	0.002	<0.001	
Porifera	Intercept	2.64	0.03	<0.001	8667.4
	Latitude	-0.004	0.001	<0.001	

Table S6. Generalized Linear Models (GLM) coefficients for bryozoans (n=740) and marine sessile species (n=1731), modelling response variable (rarefied species richness (ES50)) as function of each selected environmental variable).

		Bryozoans			**Marine sessile species**		
Model	**Coefficients**	**Estimate**	**Std. error**	**p-value**	**Estimate**	**Std. error**	**p-value**
Richness ~ Maximum depth	Intercept	3.04	0.07	<0.001	3.59	0.05	<0.001
	Maximum depth	0.001	<0.001	<0.001	0.001	<0.001	<0.001
Richness ~ mean SST	Intercept	2.77	0.07	<0.001	2.989	0.04	<0.001
	Mean SST	-0.003	0.004	0.331	0.007	0.002	0.002
Richness ~ range SST	Intercept	2.78	0.08	<0.001	3.01	0.04	<0.001
	Range SST	-0.01	0.01	0.338	0.02	0.008	0.03
Richness ~ Nitrate	Intercept	2.6	0.06	<0.001	3.18	0.03	<0.001
	Nitrate	0.01	0.007	0.008	-0.01	0.004	<0.001
	Intercept	2.68	0.05	<0.001	3.04	0.02	<0.001

Richness ~ Max. chlorophyll	Max. Chlor.	0.02	0.015	0.138	0.06	0.01	<0.001
Richness ~ Nitrate + range SST	Intercept	2.57	0.11	<0.001	3.12	0.058	<0.001
	Nitrate	0.02	0.007	2.656	-0.013	0.004	0.002
	Range SST	0.005	0.014	0.394	0.011	0.008	0.21
Richness ~ Nitrate + mean SST	Intercept	2.42	0.12	<0.001	3.12	0.084	<0.001
	Nitrate	0.029	0.009	<0.01	-0.01	0.006	0.053
	Mean SST	0.008	0.005	0.09	0.002	0.003	0.51
Richness ~ Nitrate + Max. chlor.	Intercept	2.58	0.06	<0.001	3.12	0.035	<0.001
	Nitrate	0.018	0.007	0.009	-0.01	0.004	<0.001
	Max. chlor.	0.018	0.015	0.21	0.066	0.011	<0.001
Richness ~ Maximum depth + Max. chlor.	Intercept	3.091	0.083	<0.001	3.598	0.057	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Max. chlor.	-0.017	-0.015	0.275	<0.001	0.011	<0.001
Richness ~ Maximum depth + mean SST	Intercept	3.029	0.08	<0.001	3.429	0.054	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Mean SST	0.002	0.004	0.677	0.015	0.002	<0.001
Richness ~ Maximum depth + range SST	Intercept	3.211	0.1	<0.001	3.56	0.066	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Range SST	-0.028	0.013	0.03	0.006	0.008	0.428
Richness ~ Maximum depth + Nitrate	Intercept	2.936	0.079	<0.001	3.68	0.058	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Nitrate	0.017	0.007	0.012	-0.015	0.004	<0.001
Richness ~ Maximum depth + range SST + Nitrate	Intercept	3.037	0.12	<0.001	3.69	0.073	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Range SST	-0.014	0.014	0.29	-0.001	0.008	0.84
	Nitrate	0.014	0.007	0.04	-0.16	0.004	<0.001
Richness ~ Maximum depth + Mean SST + Nitrate	Intercept	2.53	0.12	<0.001	3.31	0.08	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Mean SST	0.023	0.005	<0.001	0.02	0.003	<0.001
	Nitrate	0.044	0.009	<0.001	0.011	0.006	0.08

Table S7. Generalized Linear Models (GLM) coefficients for bryozoans (n=740) and marine sessile species (1731), modelling response variable (non-rarefied species richness) as function of each selected environmental variable, including the interaction of sampling effort index.

		Bryozoa			**Marine sessile species**		
Formula	**Coefficients**	**Estimates**	**Std. error**	**p-value**	**Estimates**	**Std. error**	**p-value**
Richness ~ Maximum depth * SE	Intercept	3.66	0.094	<0.001	5.47	0.07	<0.001
	Maximum depth	<0.001	<0.001	<0.001	0.004	<0.001	<0.001
	SE	5.439	1.01	<0.001	12.3	0.98	<0.001
	Maximum depth * SE	-0.02	0.003	<0.001	-0.05	0.001	<0.001
Richness ~ mean SST * SE	Intercept	3.50	0.09	<0.001	4.04	0.06	<0.001
	Mean SST	-0.02	0.01	<0.001	0.01	0.003	<0.001
	SE	8.55	2.60	0.001	41.39	2.73	<0.001
	Mean SST * SE	0.60	0.18	0.001	1.48	0.19	<0.001
Richness ~ range SST * SE	Intercept	3.37	0.11	<0.001	3.82	0.08	<0.001
	Range SST	-0.06	0.02	<0.001	0.08	0.01	<0.001
	SE	32.9	3.06	<0.001	132.94	3.19	<0.001
	Range SST*SE	-1.6	0.36	<0.001	-8.4	0.37	<0.001
Richness ~ Nitrate* SE	Intercept	2.59	0.78	<0.001	4.64	0.05	<0.001
	Nitrate	0.05	0.01	<0.001	-0.32	0.03	<0.001
	SE	19.89	1.90	<0.001	59.43	1.67	<0.001
	Nitrate* SE	0.09	0.34	0.775	6.11	1.05	<0.001
Richness ~ Max. Chlorophyll * SE	Intercept	3.04	0.06	<0.001	4.08	0.04	<0.001
	Max. Chlorophyll	0.08	0.02	<0.001	0.18	0.02	<0.001
	SE	20.97	1.36	<0.001	87.87	1.41	<0.001
	Max. chlorophyll* SE	-1.62	0.26	<0.001	-5.83	0.26	<0.001
Richness ~ Nitrate + range SST * SE	Intercept	2.46	0.13	<0.001	4.23	0.08	<0.001
	Nitrate	0.06	0.009	<0.001	-0.27	0.03	<0.001
	Range SST	0.02	0.02	0.243	0.05	0.01	<0.001
	SE	42.05	3.12	<0.001	118.42	3.21	<0.001
	Nitrate*SE	-0.51	0.35	0.147	2.82	1.05	<0.01
	Range SST*SE	-2.36	0.37	<0.001	-7.49	0.38	<0.001
Richness ~ Nitrate + mean SST	Intercept	2.51	0.15	<0.001	5.02	0.13	<0.001
	Nitrate	0.06	0.012	<0.001	-0.41	0.05	<0.001
	Mean SST	0.006	0.006	0.31	-0.02	0.005	<0.001
	SE	-9.02	4.49	0.04	-6.91	5.59	0.216
	Nitrate*SE	2.17	0.41	<0.001	21.29	1.58	<0.001
	Mean SST*SE	1.35	0.22	<0.001	3.49	0.29	<0.001
Richness ~ Nitrate + Max. chlorophyll *SE	Intercept	2.59	0.08	<0.001	5.40	0.10	<0.001
	Nitrate	0.05	0.009	<0.001	-0.05	0.01	0.01
	Max. chlorophyll	0.07	0.02	<0.001	0.09	0.02	<0.001
	SE	23.63	1.92	<0.001	6.84	0.82	<0.001
	Nitrate *SE	0.38	0.36	0.28	0.77	0.14	<0.001
	Max. chlorophyll *SE	-1.81	0.26	<0.001	-1.49	0.33	<0.001
Richness ~ Max. depth + Max. chlorophyll *SE	Intercept	3.640	0.11	0.001	5.44	0.086	<0.001
	Max. depth	0.002	<0.001	<0.001	<0.001	<0.001	<0.001
	Max. chlorophyll	0.08	0.025	0.721	0.017	0.018	0.367

	SE	6.95	1.52	<0.001	1.178	1.471	<0.001
	Max. depth *SE	-0.014	0.001	<0.001	-0.052	0.252	<0.001
	Max. chlorophyll *SE	-0.33	0.264	0.205	-0.029	0.001	0.908
Richness ~ Maximum depth + mean SST *SE	Intercept	3.859	0.105	<0.001	5.085	0.079	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Mean SST	-0.021	0.005	<0.001	0.032	0.003	<0.001
	SE	1.254	2.598	0.629	6.36	2.44	<0.001
	Maximum depth*SE	-0.015	0.001	<0.001	-0.047	0.001	<0.001
	Mean SST*SE	0.34	0.199	0.081	0.022	0.185	0.22
Richness ~ Maximum depth + range SST *SE	Intercept	4.04	0.13	<0.001	5.29	0.098	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Range SST	-0.092	0.017	<0.001	0.023	0.012	0.05
	SE	12.13	3.043	<0.001	0.31	2.96	<0.001
	Maximum depth*SE	-0.015	0.001	<0.001	-0.051	0.001	<0.001
	Range SST*SE	-0.46	0.35	0.186	-2.48	0.34	<0.001
Richness ~ Maximum depth + Nitrate *SE	Intercept	3.127	0.11	<0.001	5.80	0.081	<0.001
	Maximum depth	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Nitrate	0.061	0.008	<0.001	-0.28	0.029	<0.001
	SE	8.71	2.01	<0.001	8.64	1.74	<0.001
	Maximum depth*SE	0.016	0.001	<0.001	-0.04	0.001	<0.001
	Nitrate*SE	0.225	0.34	0.508	2.28	1.004	0.023
Richness ~ Maximum depth + range SST + Nitrate *SE	Intercept	3.16	0.15	<0.001	5.71	0.104	<0.001
	Nitrate	<0.001	<0.001	<0.001	-0.28	0.029	<0.001
	Maximum detph	-0.016	0.018	0.36	<0.001	<0.001	<0.001
	Range SST	0.057	0.009	<0.001	0.007	0.012	0.52
	Sampling effort	19.25	3.17	<0.001	26.12	3.058	<0.001
	Nitrate*SE	-0.015	0.001	<0.001	2.94	1.015	<0.01
	Maximum depth*SE	-1.09	0.35	<0.01	-0.046	0.001	<0.001
	Range SST*SE	-0.19	0.35	0.57	-2.21	0.34	<0.001
Richness ~ Maximum depth + mean SST + Nitrate *SE	Intercept	2.59	0.151	<0.001	5.40	0.011	<0.001
	Nitrate	<0.001	<0.001	<0.001	-0.13	0.046	<0.01
	Maximum detph	0.028	0.007	<0.001	<0.001	<0.001	<0.001
	Mean SST	0.093	0.012	<0.001	0.018	0.005	<0.001
	Sampling effort	-0.84	4.31	0.845	-0.19	0.48	<0.001
	Nitrate*SE	-0.016	0.001	<0.001	9.61	1.3993	<0.001
	Maximum depth*SE	0.41	0.25	0.07	-0.047	0.001	<0.001
	Mean SST *SE	0.48	0.39	0.261	1.35	0.258	<0.001

Table S8. Generalized Linear Models (GLM) between the predicted increase in mean SST and latitude for bryozoans and marine sessile species, adding the effect of the RCP emission scenario (4.5 and 8.5).

Studied group	**Formula**	**Coefficient**	**Estimate**	**Std. error**	**p-value**	**AIC**
Marine sessile species	SST increase ~ latitude*RCP scenario	Intercept	-0.61	0.22	<0.001	231.51
		Latitude	-0.001	0.01	0.71	
		RCP scenario	0.42	0.03	<0.001	
		Latitude*RCP scenario	0.003	0.001	<0.001	
Bryozoans	SST increase ~ latitude* RCP scenario	Intercept	-0.72	0.10	<0.001	464.54
		Latitude	-0.003	0.002	0.293	
		RCP scenario	0.40	0.015	<0.001	
		Latitude*RCP scenario	0.002	0.001	<0.001	

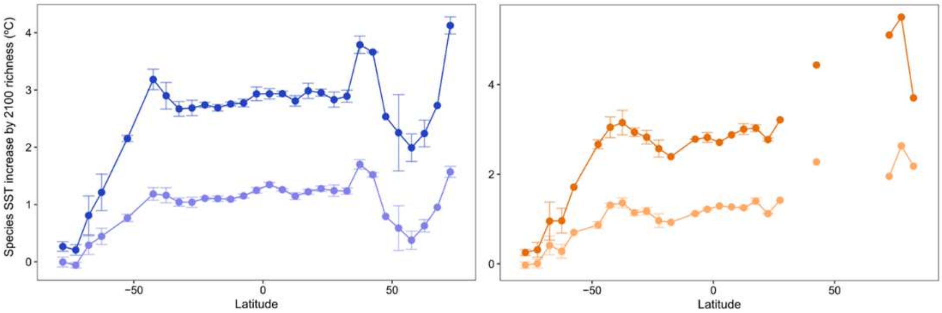

Figure S1. Predicted mean increase (mean±SE) of SST mean in hotspot areas under different RCP emission scenarios (light color: 2.5; dark color: 8.5) for marine sessile species (blue) and bryozoans (orange).

Supplementary material Chapter III

Table S1. Statistical results of Generalized Mixed Models (GLMs) of mass mortality event in the field indicating each model in each case with the response variable (S = survival) and the interaction between Species and the studied variables

Table S2. Statistical results of Generalized Mixed Models (GLMs) of mass mortality event in the field both species indicating in each case the response variable (Survival) and the studied variables.

Table S3. Statistical results of Linear Models (LMs) in two experiments between the studied variables and the interaction of treatments and species.

Table S4. Statistical results of Linear Models (LMs) in Thermal stress experiment (25ºC) between the studied variables and the two treatments.

Table S5. Statistical results of Linear Models (LMs) in the increasing temperature experiment between the studied variables and the two treatments.

Table S6. SEM variables (mean ± SE) of colonies between species and treatment in thermal stress experiment and increasing temperature experiment.

Table S7. Summary of non-lethal effects on oxygen consumption and mineralogical variables between species in thermal stress experiment (25ºC).

Figure S1. Demographic analyses of monitored populations during the mass mortality event.

Figure S2. Photographic analyses of thermal stress experiment at 25ºC (A) and increasing temperature experiment.

Figure S3. Study area and location of monitored localities within the Medes Islands Marine Reserve (points).

Table S1. Statistical results of Generalized Mixed Models (GLMs) of mass mortality event in the field indicating each model in each case with the response variable (S = survival) and the interaction between Species and the studied variables

Models	**Variables**	**Coefficients**				**AICc**
		Estimate	Std. Error	*z value*	*p*	
Survival ~ Species*Season	Intercept	-1.2566	0.10785	-11.681	**<0.001**	2042.059
	Species	0.2885	0.1495	1.930	0.0535	
	Season	0.09032	0.1503	0.601	0.5479	
	Species*Season	-0.7869	0.222	3.539	**<0.001**	
Survival ~ Species*Habitat	Intercept	-1.2066	0.0755	-15.984	**<0.001**	2032.883
	Species	0.0708	0.1118	0.634	0.526	
	Habitat	-0.4028	0.7782	-0.518	0.605	
	Species*Habitat	-1.2023	0.8635	-1.392	0.164	
Survival ~ Species* Protection	Intercept	-1.0746	0.0825	-13.023	**<0.001**	2030.34
	Species	0.00102	0.1228	0.008	0.9933	
	Protection	-0.7018	0.2055	-3.415	**<0.001**	
	Species*Protection	-0.07299	0.2819	-0.259	0.7956	
Survival ~ Species*Colony Area	Intercept	-1.8278	0.10519	-17.376	**<0.001**	1496.911
	Species	-0.0317	0.15564	-0.204	0.838	
	Colony Area	0.2607	0.02610	9.988	**<0.001**	
	Season*Colony Area	-0.2367	0.02630	-9.001	**<0.001**	

Table S2. Statistical results of Generalized Mixed Models (GLMs) of mass mortality event in the field both species indicating in each case the response variable (Survival) and the studied variables.

Models	**Variables**	***Myriapora truncata***					***Pentapora fascialis***				
		Coefficients				**AICc**	**Coefficients**				**AICc**
		Estimate	Std. Error	*z value*	*p*		Estimate	Std. Error	Estimate	Std. Error	
Survival ~ Season	Intercept	-1.2566	0.1076	-11.681	**<0.001**	1083.248	-0.9681	0.1038	-9.324	**<0.001**	958.8
	Season	0.0903	0.1503	0.601	0.548		-0.6966	0.1639	-4.251	**<0.001**	
Survival ~ Habitat	Intercept	-1.2066	0.0755	-15.984	**<0.001**	1083.317	-1.1357	0.0825	-13.762	**<0.001**	949.57
	Habitat	-0.4028	0.7783	-0.518	0.605		-1.6051	0.374	-4.292	**<0.001**	
Survival ~ Protection	Intercept	-1.0746	0.0825	-13.023	**<0.001**	1070.655	-1.0736	0.0910	-11.797	**<0.001**	959.69
	Protection	-0.7018	0.2055	-3.415	**<0.001**		-0.7748	0.1929	-4.016	**<0.001**	
Survival ~ Colony Area	Intercept	-1.8278	0.1052	-17.376	**<0.001**	815.997	-1.8595	0.11471	-16.212	**<0.001**	681.51
	Colony Area	0.2607	0.0261	9.988	**<0.001**		0.02404	0.00316	7.608	**<0.001**	
Survival ~ Season*Habitat	Intercept	-1.2411	0.1077	-11.517	**<0.001**	1083.965	-0.7501	0.1072	-6.994	**<0.001**	915.45
	Season	0.0684	0.1510	0.453	0.615		-0.8684	0.1722	-5.043	**<0.001**	
	Habitat	-13.3249	360.3785	-0.037	0.971		-16.8160	486.9721	-0.035	0.972	
	Season*Habitat	13.8045	360.3795	0.038	0.969		16.4535	486.9723	0.034	0.973	
Survival ~ Season*Protection	Intercept	-1.1795	0.1199	-9.840	**<0.001**	1071.403	-0.7503	0.1201	-6.245	**<0.001**	944.76
	Season	0.2046	0.1654	1.237	0.2161		-0.7083	0.1870	-3.787	**<0.001**	
	Protection	-0.3681	0.2739	-1.344	0.1790		-0.7874	0.2413	-3.184	**<0.01**	
	Season*Protection	-0.7072	0.4181	-1.691	0.0908		-0.0053	0.4008	-0.013	0.9895	
Survival ~ Season*Colony Area	Intercept	-1.863	0.1445	-12.896	**<0.001**	819.286	-2.0800	0.1673	-12.434	**<0.001**	641.69
	Season	0.0765	0.2108	0.363	0.716		0.2132	0.2409	0.885	0.376	
	Colony Area	0.2681	0.0386	6.935	**<0.001**		0.0639	0.0086	7.442	**<0.001**	
	Season*Colony Area	-0.0147	0.0524	-0.281	0.779		-0.0495	0.0092	-5.396	**<0.001**	

Table S3. Statistical results of Linear Models (LMs) in two experiments between the studied variables and the interaction of treatments and species.

Models	Variables	Thermal experiment (25°C)					Increasing temperature experiment (25>30°C)				
		Coefficients					Coefficients				
		Estimate	Std. Error	t value	*p*	Adjusted R-squared	Estimate	Std. Error	t value	*p*	Adjusted R-squared
Mean necrosis ~Treatment * Sp * Day	Intercept	-0.93167	1.5334	-0.608	0.5492	0.9547	-7.2063	4.9068	-1.469	0.1506	0.8998
	Treatment	0.93167	2.1684	0.430	0.6713		7.2063	6.9393	1.038	0.3059	
	Sp	-4.3421	2.1684	-2.002	0.0567		-4.2691	6.9393	-0.615	0.5422	
	Day	0.0981	0.0626	1.568	0.1299		0.4576	0.1162	3.938	**<0.001**	
	Treatment * Sp	3.8121	3.0667	1.243	0.2258		1.3072	9.8136	0.133	0.8947	
	Treatment * Day	-0.0981	0.0885	-1.109	0.2785		-0.4576	0.1643	-2.785	**<0.01**	
	Sp * Day	1.1169	0.0885	12.617	**<0.001**		1.2354	0.1643	7.518	**<0.001**	
	Treatment * Sp * Day	-1.0631	0.1252	-8.492	**<0.001**		-1.0216	0.2324	-4.396	**<0.001**	
Mean growth ~ Treatment * Sp	Intercept	-0.42915	0.2141	-2.004	**0.0473**	0.01288	0.0265	0.0967	0.274	0.7846	0.169
	Treatment	-0.01407	0.3027	-0.046	0.9630		-0.0076	0.1297	-0.059	0.9531	
	Sp	0.23303	0.3027	0.770	0.4431		0.5164	0.1368	3.775	**<0.001**	
	Treatment*sp	-0.34465	0.4281	-0.805	0.4225		-0.5735	0.1835	-3.125	**<0.01**	
O_2 consumption ~ Treatment * Sp	Intercept	31.8533	13.4068	2.376	**0.0448**		-	-	-	-	-
	Treatment	-92.33	0.6155	-1.500	0.1720		-	-	-	-	
	Sp	-4.7724	18.9601	-2.525	0.8076		-	-	-	-	
	Treatment * Sp	0.2448	0.8704	0.281	0.7857		-	-	-	-	
Density ovicells ~ Treatment * Sp	Intercept	0.0074	0.0114	0.645	0.5194	0.03511	0.0901	0.0273	3.299	**<0.01**	0.008
	Treatment	-0.0074	0.0164	-0.451	0.6525		0.0118	0.0409	0.290	0.7719	
	Sp	-0.0074	0.0165	-0.450	0.6531		-0.0149	0.0378	-0.396	0.6925	
	Treatment*Sp	0.0716	0.0231	3.094	**<0.01**		0.0570	0.0564	1.012	0.3122	
Damaged zooids ~Treatment * Sp	Intercept	5.533^{-16}	0.0096	0	1	0.03186	0.0491	0.0227	2.160	**0.0313**	0.0167
	Treatment	-1.019^{-15}	0.0138	0	1		0.0630	0.0341	1.848	0.0652	
	Sp	-4.67^{-16}	0.0138	0	1		-0.0266	0.0315	-0.844	0.3989	
	Treatment * Sp	0.05	0.0194	2.567	**0.0105**		0.0224	0.047	0.478	0.6326	
Area of primary orifice ~ Treatment * Sp	Intercept	0.0361	0.0024	14.748	**<0.001**	0.0941	0.0358	0.0016	21.961	**<0.001**	0.094
	Treatment	-0.0021	0.0035	-0.618	0.5370		0.0041	0.0024	1.674	0.0949	
	Sp	-0.0143	0.0035	-4.076	**<0.001**		-0.0112	0.0022	-4.971	**<0.001**	
	Treatment * Sp	0.0114	0.0049	2.310	**0.0213**		-0.0002	0.0034	-0.075	0.9403	
$MgCO_3$ ~Treatment * Sp	Intercept	8.3305	0.3284	25.366	**<0.001**	0.166	-	-	-	-	-
	Treatment	-26.45	0.4644	-0.569	0.575		-	-	-	-	
	Sp	0.5855	0.4644	1.261	0.222		-	-	-	-	
	Treatment * Sp	0.511	0.6568	0.839	0.411		-	-	-	-	
Calcite 1~Treatment * Sp	Intercept	73.242	3.2	22.885	**<0.001**	0.4199	-	-	-	-	-
	Treatment	-1.759	4.526	-0.389	0.7016		-	-	-	-	
	Sp	-17.894	4.526	-3.953	**<0.001**		-	-	-	-	
	Treatment * Sp	10.105	6.401	1.579	0.13		-	-	-	-	
Calcite 2~Treatment * Sp	Intercept	26.062	5.020	5.192	**<0.001**	0.4129	-	-	-	-	-
	Treatment	1.363	7.099	0.192	0.850		-	-	-	-	
	Sp	-10.917	7.099	-1.538	0.140		-	-	-	-	
	Treatment * Sp	-16.509	10.040	-1.644	0.116		-	-	-	-	
Aragonite ~Treatment * Sp	Intercept	0.6956	3.2421	0.215	0.832	0.8079	-	-	-	-	-
	Treatment	0.3962	4.5850	0.086	0.932		-	-	-	-	
	Sp	28.8102	4.5850	6.284	**<0.001**		-	-	-	-	
	Treatment * Sp	6.4036	6.4841	0.988	0.335		-	-	-	-	

Table S4. Statistical results of Linear Models (LMs) in Thermal stress experiment (25ºC) between the studied variables and the two treatments.

Models	**Variables**	***Myriapora truncata***					***Pentapora fascialis***				
		Coefficients					**Coefficients**				
		Estimate	Std. Error	t value	*p*	Adjusted R-squared	Estimate	Std. Error	t value	*p*	Adjusted R-squared
Necrosis ~Treatment*Day	Intercept	-0.93167	0.5417	-1.720	0.111	0.5856	-5.2738	2.0997	-2.512	0.0273	0.952
	Treatment	0.93167	0.7660	1.216	0.247		4.7437	2.9694	1.598	0.1361	
	Day	0.09816	0.0221	4.439	**<0.001**		1.2151	0.0857	14.176	**<0.001**	
	Treatment*Day	-0.09816	0.0312	-3.139	**<0.01**		-1.1613	0.1212	-9.580	**<0.001**	
Mean growth ~ Treatment	Intercept	-0.42915	0.1754	-2.466	0.0175	**0.01719**	-1.1961	0.2468	-0.795	0.430	0.01789
	Treatment	-0.01407	0.2481	-0.057	0.9550		-0.3587	0.3490	-1.028	0.308	
O_2 consumption ~ Treatment	Intercept	31.8533	9.5672	3.329	**0.0291**	0.4061	27.0810	16.363	1.654	0.173	-0.0383
	Treatment	-0.9233	0.4392	-2.102	0.1034		-0.6786	0.7515	-0.903	0.418	
Density ovicells ~ Treatment	Intercept	0.0074	0.0053	1.398	0.163	0.0036	-6.104^{-17}	0.0157	0	1	0.0281
	Treatment	-0.0074	0.0076	-0.977	0.329		0.0642	0.0217	2.954	**<0.01**	
Density avicularia ~ Treatment	Intercept	-	-	-	-	-	0.02344	0.0189	1.237	0.2170	0.012
	Treatment	-	-	-	-		0.04399	0.0262	1.831	0.0682	
Damaged zooids ~Treatment	Intercept	-	-	-	-	-	-1.628^{-16}	0.0139	0	1	0.0208
	Treatment	-	-	-	-		0.05	0.0193	2.586	**0.0102**	
Damaged zooids ~Treatment* Colony zone	Intercept	-	-	-	-	-	2.768^{-16}	0.0096	0	1	0.0195
	Treatment	-	-	-	-		0.0428	0.0135	3.163	**<0.01**	
	Colony zone	-	-	-	-		-3.614^{17}	0.0139	0	1	
	Treatment* Colony zone	-	-	-	-		-0.0351	0.0196	-1.790	0.0739	
Area of primary orifice ~ Treatment	Intercept	0.0636	0.0023	15.190	**<0.001**	0.00154	0.0218	0.0025	8.436	**<0.001**	0.0208
	Treatment	-0.00216	0.0034	-0.636	0.525		0.0092	0.0035	2.584	**0.0103**	
Area of primary orifice ~ Treatment * Colony zone	Intercept	0.0292	0.0032	9.116	**<0.001**	0.0273	0.0206	0.0036	5.715	**<0.001**	0.0142
	Treatment	0.0055	0.0046	1.183	0.2384		0.0105	0.0049	2.130	**0.0341**	
	Colony zone	0.0147	0.0047	3.140	**<0.01**		0.0024	0.0052	0.462	0.6443	
	Treatment* Colony zone	-0.0164	0.0067	-2.437	**0.0155**		-0.0026	0.002	-0.368	0.7132	
$MgCO_3$ ~Treatment	Intercept	8.3305	0.2215	37.613	**<0.001**	-0.0268	8.916	0.4082	21.840	**<0.001**	-0.0735
	Treatment	-0.2645	0.3132	-0.844	0.418		0.2866	0.5773	0.496	0.63	
Calcite 1~Treatment	Intercept	73.242	1.419	51.627	**<0.001**	-0.0214	55.348	4.298	12.878	**<0.001**	0.0745
	Treatment	-1.759	2.006	-0.877	0.401		8.346	6.078	1.373	0.2	
Calcite 2~Treatment	Intercept	26.062	1.516	17.190	**<0.001**	-0.0573	15.146	6.935	2.184	0.0539	0.1118
	Treatment	1.363	2.144	0.636	0.539		-15.146	9.808	-1.544	0.1536	
Aragonite ~Treatment	Intercept	0.6956	0.3610	1.927	0.0829	-0.0375	29.506	4.571	6.455	**<0.001**	0.0095
	Treatment	0.3962	0.5106	0.776	0.4558		6.8	6.464	1.052	0.318	

Table S5. Statistical results of Linear Models (LMs) in the increasing temperature experiment between the studied variables and the two treatments.

Models	Variables	*Myriapora truncata*					*Pentapora fascialis*				
		Coefficients					**Coefficients**				
		Estimate	Std. Error	t value	*p*	Adjusted R-squared	Estimate	Std. Error	t value	*p*	Adjusted R-squared
Necrosis (%) ~Treatment*Day	Intercept	-7.2063	5.2819	-1.364	**0.1893**	0.4858	-11.4754	4.5006	-2.550	0.0201	0.9473
	Treatment	7.2063	7.4697	0.965	**0.3475**		8.5135	6.3648	1.338	0.1977	
	Day	0.4576	0.1251	3.659	**<0.01**		1.6929	0.1066	15.886	**<0.001**	
	Treatment*Day	-0.4576	0.1769	-2.587	**0.0186**		-1.4792	0.1507	-9.815	**<0.001**	
Mean growth ~ Treatment	Intercept	0.0265	0.0034	7.793	**<0.001**	0.033	0.5430	0.1368	3.970	**<0.001**	0.1456
	Treatment	-0.007	0.0045	-1.676	0.0997		-0.5812	0.1835	-3.167	**<0.01**	
Density ovicells ~ Treatment	Intercept	0.0901	0.0267	3.374	**<0.001**	-0.004	0.0751	0.0267	2.816	**<0.01**	0.008
	Treatment	0.0118	0.0400	0.297	0.767		0.0678	0.0396	1.745	0.0827	
Density avicularia ~ Treatment	Intercept	-	-	-	-	-	0.0451	0.0225	1.997	**0.0470**	0.0103
	Treatment	-	-	-	-		0.0630	0.0335	1.880	0.0612	
Damaged zooids ~Treatment	Intercept	0.0491	0.0241	2.039	**0.0426**	0.009	0.0225	0.0205	1.096	0.2742	0.027
	Treatment	0.0630	0.0361	1.745	0.0824		0.0855	0.0305	2.804	**<0.01**	
Damaged zooids ~Treatment* Colony zone	Intercept	0.0645	0.0334	1.928	0.0552	0.031	0.0422	0.0278	1.517	0.1305	0.049
	Treatment	0.111	0.0498	2.247	**0.0256**		0.0103	0.0417	0.249	0.8038	
	Colony zone	-0.0311	0.0477	-0.653	0.5142		-0.0422	0.0408	-1.036	0.3013	
	Treatment* Colony zone	-0.1027	0.0715	-1.436	0.1524		0.1562	0.0604	2.587	**0.0103**	
Area of primary orifice ~ Treatment	Intercept	0.0358	0.0019	18.801	**<0.001**	0.0047	0.0246	0.0012	19.207	**<0.001**	0.0125
	Treatment	0.0041	0.0028	1.433	0.153		0.0038	0.0019	2.022	**0.0443**	
Area of primary orifice ~ Treatment * Colony zone	Intercept	0.0329	0.0026	12.639	**<0.001**	0.056	0.0253	0.0017	14.402	**<0.001**	0.007
	Treatment	0.0003	0.0038	0.080	0.937		0.0039	0.0026	1.482	0.140	
	Colony zone	0.0059	0.0037	1.610	0.1009		-0.0015	0.0026	-0.597	0.551	
	Treatment* Colony zone	0.0080	0.0055	1.445	0.150		-0.00006	0.0038	-0.018	0.983	

Table S6. SEM variables (mean ± SE) of colonies between species and treatment in thermal stress experiment and increasing temperature experiment.

Treatment	Sp	Colony zone	Density zooids	Mean area primary orifice	Density damaged zooids	Density ovicells	Mean ovicells size (area)	Density avicularia	Mean avicularia size
Control	*M. truncata*	Proximal part	4±0.54	0.029±0.002	0	0	0	-	-
		Distal part	3.5±0.22	0.044±0.005	0	0.05±0.05	0.063	-	-
T (25°C)		Proximal part	3.56±0.21	0.035±0.005	0	0	0	-	-
		Distal part	3.61±0.26	0.034±0.002	0	0	0	-	-
Control	*P. fascialis*	Proximal part	3.67±0.23	0.021±0.001	0	0	0	0.05±0.05	0.028
		Distal part	3.44±0.11	0.024±0.002	0	0	0	0.11±0.07	0.09±0.07
T (25°C)		Proximal part	1.22±0.36	0.028±0.006	0.33±0.14	0.22±0.22	0.031±0.001	0.44±0.26	0.04±0.004
		Distal part	3.56±0.36	0.031±0.005	0.06±0.02	0.27±0.27	0.033±0.003	0.11±0.11	0.03±0.001
Control	*M. truncata*	Proximal part	3.44±0.21	0.033±0.001	0	0.39±0.16	0.054±0.001	-	-
		Distal part	3.33±0.12	0.039±0.003	0	0.22±0.17	0.038±0.016	-	-
T (30°C)		Proximal part	2.83±0.29	0.033±0.001	0.5±0.21	0.11±0.11	0.07±0.016	-	-
		Distal part	2.61±0.13	0.047±0.004	0.11±0.07	0.44±0.17	0.074±0.009	-	-
Control	*P. fascialis*	Proximal part	3.94±0.056	0.025±0.001	0	0.5±0.32	0.03±0.001	0.33±0.21	0.03±0.003
		Distal part	3.44±0.19	0.024±0.001	0	0.05±0.05	0.023	0	0
T (30°C)		Proximal part	3.16±0.26	0.029±0.004	0	0.17±0.17	0.027±0.001	0.5±0.22	0.04±0.004
		Distal part	3±0.15	0.027±0.001	0.5±0.27	0.72±0.37	0.035±0.004	0.17±0.22	0.03±0.01

Supplementary Table S7. Summary of non-lethal effects on oxygen consumption and mineralogical variables between species in thermal stress experiment (25ºC).

Variable	**Treatment**	*Myriapora truncata*	*Pentapora fascialis*
		Mean ± SE	**Mean ± SE**
O_2 consumption (μmol/g*day)	Control	15.24±2.42	14.87±1.59
	T (25°C)	8.77±1.90	10.12±5.01
wt% $MgCO_3$	Control	8.16±0.14	9.20±0.17
	T (25°C)	8.39±0.27	9.39±0.18
wt% Calcite 1	Control	71.48±0.94	63.69±1.8
	T (25°C)	73.24±1.77	55.35±5.81
wt% Calcite 2	Control	27.43±0.21	0
	T (25°C)	26.06±1.94	15.15±24.02
wt% Aragonite	Control	1.09±0.38	36.31±1.80
	T (25°C)	0.69±0.35	38.44±3.59

Supplementary material

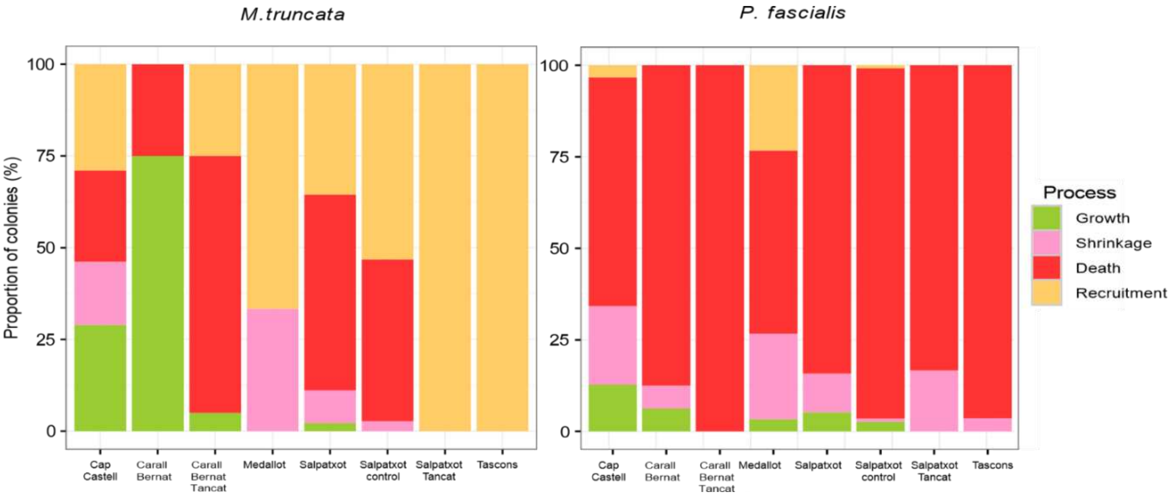

Figure S1. Demographic analyses of monitored populations during the mass mortality event

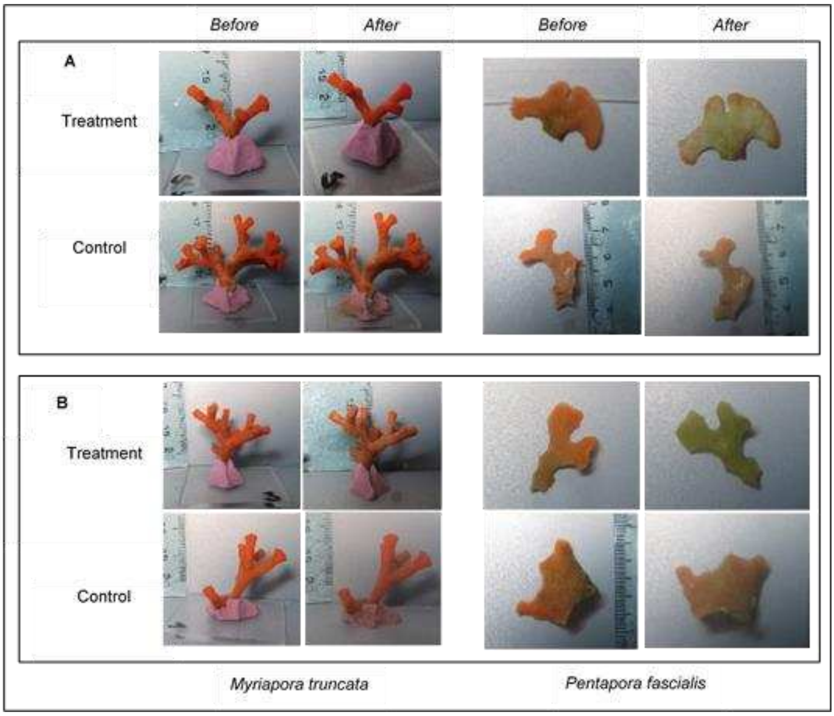

Figure S2. Photographic analyses of thermal stress experiment at 25ºC (A) and increasing temperature experiment (B).

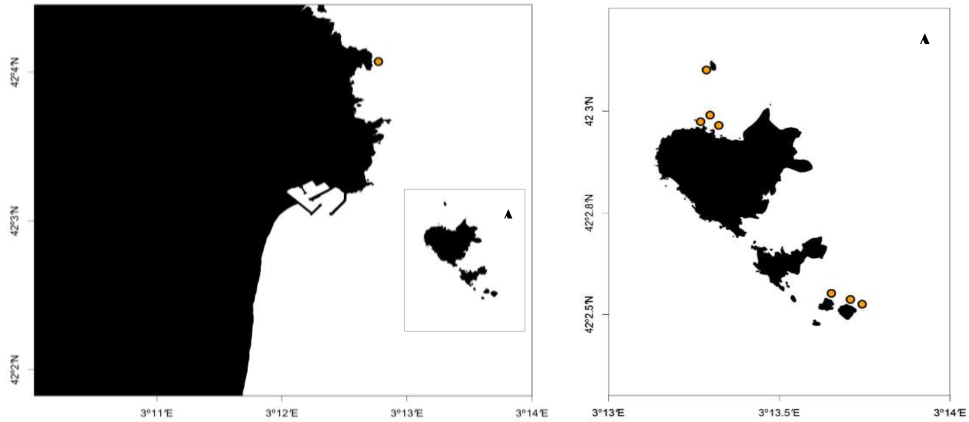

Figure S3. Study area and location of monitored localities within the Medes Islands Marine Reserve (points).

Supplementary material Chapter IV

Table S1. Previous studies using *Pentapora fascialis* as an indicator benthic species of perturbations on the Mediterranean Sea.

Table S2. Depth and number of divers on the monitored locations during the study period.

Table S3. KS Test of size distribution between each population and each monitoring period.

Table S4. Generalized linear models (GLM) between response variables (survival, necrosis, and size *t1*) and the initial size of the colonies accounting for the frequentation levels (frequented VS non-frequented). In each case, we fitted the model accordingly with the distribution of the response variables (Negative binomial for necrosis; Poisson for size; Binomial for survival).

Figure S1. Monitoring design showing a part of a permanent transect with the location of the 0.5 m^2 squares (A). Details of the monitoring actions (B, C).

Table S1. Previous studies using *Pentapora fascialis* as an indicator benthic species of perturbations on the Mediterranean Sea.

Perturbation	**Location**	**Depth**	**Variables studied**	**Ref.**
Diving	Giglio Island (Italy)	16-36	Relative frequency of colonies, colony width	Casoli et al., 2017
Diving	Capo Gallo - Isola delle Femmine MPA	-	Trait vulnerabiltiy index (based on coverage, height, growth rate among others)	Di Franco et al., 2009
Storm	Tino Island (Italy)	11-22m	Colony cover, mortality	Cocito et al., 1998
Diving	Medes Islands (Spain)	14-18m	**Density** (4-1 colony/m^2 on boulders; 7-2 colonies/m^2 on walls), diameter, height, degree of exposure	Garrabou et al., 1998
Diving	Medes Islands (Spain)	14-30m	**Density (**mean density of 3.3 + 2.5 colonies m^2), diameter, height (mean 4.6cm), degree of exposure	Sala et al 1996

Table S2. Depth and number of divers on the monitored locations during the study period.

Locality	**Depth**	**Number of Divers 2016**	**Number of Divers 2017**	**Number of Divers 2018**
Cap Castell	20	0	0	0
Freu	21	0	0	0
Medallot	17	0	0	0
Cova del Dofí	20	2644	1634	2806
Cova de la Vaca	22	5452	5379	5101
Pota del Llop	22	2089	2265	2150
Salpatxot	19	4239	3709	4403
Tascó Gros	21	3322	2953	3244

Table S3. KS Test of size distribution between each population and each monitoring period.

Population1	***Population2***	***D***	***P-value***
Cap Castell_2017_Octubre	Cap Castell_2018_Juliol	0.24	0.09
Cap Castell_2017_Octubre	Cap Castell_2018_Octubre	0.44	<0.001
Cap Castell_2017_Octubre	Cova de la Vaca_2016_Juliol	0.15	0.96
Cap Castell_2017_Octubre	Cova de la Vaca_2016_Octubre	0.44	0.66
Cap Castell_2017_Octubre	Cova de la Vaca_2018_Juliol	0.20	0.97
Cap Castell_2017_Octubre	Cova del Dofí_2016_Juliol	0.27	0.53
Cap Castell_2017_Octubre	Cova del Dofí_2016_Octubre	0.16	0.98
Cap Castell_2017_Octubre	Cova del Dofí_2017_Octubre	0.66	0.39
Cap Castell_2017_Octubre	Freu_2017_Octubre	0.36	0.01
Cap Castell_2017_Octubre	Freu_2018_Juliol	0.50	<0.001
Cap Castell_2017_Octubre	Freu_2018_Octubre	0.56	<0.001
Cap Castell_2017_Octubre	Medallot_2015_Octubre	0.34	0.09
Cap Castell_2017_Octubre	Medallot_2016_Juliol	0.24	0.69
Cap Castell_2017_Octubre	Medallot_2016_Octubre	0.44	0.12
Cap Castell_2017_Octubre	Medallot_2017_Juliol	0.37	0.58
Cap Castell_2017_Octubre	Medallot_2017_Octubre	0.52	0.12
Cap Castell_2017_Octubre	Medallot_2018_Juliol	0.22	0.25
Cap Castell_2017_Octubre	Medallot_2018_Octubre	0.53	<0.001
Cap Castell_2017_Octubre	Pota del Llop_2016_Juliol	0.38	0.04
Cap Castell_2017_Octubre	Pota del Llop_2016_Octubre	0.25	0.91
Cap Castell_2017_Octubre	Pota del Llop_2017_Octubre	0.57	0.91
Cap Castell_2017_Octubre	Pota del Llop_2018_Juliol	0.31	0.61
Cap Castell_2017_Octubre	Pota del Llop_2018_Octubre	0.18	1.00
Cap Castell_2017_Octubre	Salpatxot_2016_Juliol	0.34	0.19
Cap Castell_2017_Octubre	Salpatxot_2017_Octubre	0.64	0.11
Cap Castell_2017_Octubre	Salpatxot_2018_Octubre	0.37	0.84
Cap Castell_2017_Octubre	Tascó Gros_2015_Octubre	0.32	0.10
Cap Castell_2017_Octubre	Tascó Gros_2016_Juliol	0.21	0.31
Cap Castell_2017_Octubre	Tascó Gros_2016_Octubre	0.27	0.42
Cap Castell_2017_Octubre	Tascó Gros_2017_Juliol	0.14	0.91
Cap Castell_2017_Octubre	Tascó Gros_2017_Octubre	0.66	0.05
Cap Castell_2017_Octubre	Tascó Gros_2018_Juliol	0.30	0.13
Cap Castell_2017_Octubre	Tascó Gros_2018_Octubre	0.35	0.35
Cap Castell_2018_Juliol	Cap Castell_2017_Octubre	0.24	0.09

Cap Castell_2018_Juliol	Cap Castell_2018_Octubre	0.26	<0.001
Cap Castell_2018_Juliol	Cova de la Vaca_2016_Juliol	0.25	0.29
Cap Castell_2018_Juliol	Cova de la Vaca_2016_Octubre	0.51	0.43
Cap Castell_2018_Juliol	Cova de la Vaca_2018_Juliol	0.30	0.61
Cap Castell_2018_Juliol	Cova del Dofí_2016_Juliol	0.32	0.21
Cap Castell_2018_Juliol	Cova del Dofí_2016_Octubre	0.21	0.76
Cap Castell_2018_Juliol	Cova del Dofí_2017_Octubre	0.75	0.22
Cap Castell_2018_Juliol	Freu_2017_Octubre	0.14	0.47
Cap Castell_2018_Juliol	Freu_2018_Juliol	0.29	<0.001
Cap Castell_2018_Juliol	Freu_2018_Octubre	0.34	<0.001
Cap Castell_2018_Juliol	Medallot_2015_Octubre	0.30	0.07
Cap Castell_2018_Juliol	Medallot_2016_Juliol	0.13	0.99
Cap Castell_2018_Juliol	Medallot_2016_Octubre	0.23	0.77
Cap Castell_2018_Juliol	Medallot_2017_Juliol	0.32	0.69
Cap Castell_2018_Juliol	Medallot_2017_Octubre	0.28	0.75
Cap Castell_2018_Juliol	Medallot_2018_Juliol	0.07	0.99
Cap Castell_2018_Juliol	Medallot_2018_Octubre	0.39	<0.001
Cap Castell_2018_Juliol	Pota del Llop_2016_Juliol	0.14	0.86
Cap Castell_2018_Juliol	Pota del Llop_2016_Octubre	0.32	0.58
Cap Castell_2018_Juliol	Pota del Llop_2017_Octubre	0.49	0.97
Cap Castell_2018_Juliol	Pota del Llop_2018_Juliol	0.49	0.09
Cap Castell_2018_Juliol	Pota del Llop_2018_Octubre	0.42	0.51
Cap Castell_2018_Juliol	Salpatxot_2016_Juliol	0.44	0.01
Cap Castell_2018_Juliol	Salpatxot_2017_Octubre	0.45	0.41
Cap Castell_2018_Juliol	Salpatxot_2018_Octubre	0.33	0.90
Cap Castell_2018_Juliol	Tascó Gros_2015_Octubre	0.17	0.56
Cap Castell_2018_Juliol	Tascó Gros_2016_Juliol	0.15	0.33
Cap Castell_2018_Juliol	Tascó Gros_2016_Octubre	0.16	0.88
Cap Castell_2018_Juliol	Tascó Gros_2017_Juliol	0.29	0.05
Cap Castell_2018_Juliol	Tascó Gros_2017_Octubre	0.42	0.38
Cap Castell_2018_Juliol	Tascó Gros_2018_Juliol	0.09	0.99
Cap Castell_2018_Juliol	Tascó Gros_2018_Octubre	0.17	0.97
Cap Castell_2018_Octubre	Cap Castell_2017_Octubre	0.44	<0.001
Cap Castell_2018_Octubre	Cap Castell_2018_Juliol	0.26	<0.001
Cap Castell_2018_Octubre	Cova de la Vaca_2016_Juliol	0.43	0.01
Cap Castell_2018_Octubre	Cova de la Vaca_2016_Octubre	0.59	0.28
Cap Castell_2018_Octubre	Cova de la Vaca_2018_Juliol	0.47	0.12

Cap Castell_2018_Octubre	Cova del Dofí_2016_Juliol	0.42	0.05
Cap Castell_2018_Octubre	Cova del Dofí_2016_Octubre	0.38	0.12
Cap Castell_2018_Octubre	Cova del Dofí_2017_Octubre	0.88	0.10
Cap Castell_2018_Octubre	Freu_2017_Octubre	0.15	0.52
Cap Castell_2018_Octubre	Freu_2018_Juliol	0.16	0.17
Cap Castell_2018_Octubre	Freu_2018_Octubre	0.18	0.22
Cap Castell_2018_Octubre	Medallot_2015_Octubre	0.29	0.10
Cap Castell_2018_Octubre	Medallot_2016_Juliol	0.37	0.11
Cap Castell_2018_Octubre	Medallot_2016_Octubre	0.25	0.69
Cap Castell_2018_Octubre	Medallot_2017_Juliol	0.55	0.11
Cap Castell_2018_Octubre	Medallot_2017_Octubre	0.25	0.87
Cap Castell_2018_Octubre	Medallot_2018_Juliol	0.25	0.05
Cap Castell_2018_Octubre	Medallot_2018_Octubre	0.23	0.25
Cap Castell_2018_Octubre	Pota del Llop_2016_Juliol	0.25	0.22
Cap Castell_2018_Octubre	Pota del Llop_2016_Octubre	0.55	0.07
Cap Castell_2018_Octubre	Pota del Llop_2017_Octubre	0.69	0.74
Cap Castell_2018_Octubre	Pota del Llop_2018_Juliol	0.69	<0.001
Cap Castell_2018_Octubre	Pota del Llop_2018_Octubre	0.59	0.15
Cap Castell_2018_Octubre	Salpatxot_2016_Juliol	0.62	<0.001
Cap Castell_2018_Octubre	Salpatxot_2017_Octubre	0.24	0.98
Cap Castell_2018_Octubre	Salpatxot_2018_Octubre	0.55	0.34
Cap Castell_2018_Octubre	Tascó Gros_2015_Octubre	0.26	0.16
Cap Castell_2018_Octubre	Tascó Gros_2016_Juliol	0.32	<0.001
Cap Castell_2018_Octubre	Tascó Gros_2016_Octubre	0.25	0.38
Cap Castell_2018_Octubre	Tascó Gros_2017_Juliol	0.50	<0.001
Cap Castell_2018_Octubre	Tascó Gros_2017_Octubre	0.35	0.60
Cap Castell_2018_Octubre	Tascó Gros_2018_Juliol	0.33	0.02
Cap Castell_2018_Octubre	Tascó Gros_2018_Octubre	0.36	0.24
Cova de la Vaca_2016_Juliol	Cap Castell_2017_Octubre	0.15	0.96
Cova de la Vaca_2016_Juliol	Cap Castell_2018_Juliol	0.25	0.29
Cova de la Vaca_2016_Juliol	Cap Castell_2018_Octubre	0.43	0.01
Cova de la Vaca_2016_Juliol	Cova de la Vaca_2016_Octubre	0.31	0.96
Cova de la Vaca_2016_Juliol	Cova de la Vaca_2018_Juliol	0.21	0.98
Cova de la Vaca_2016_Juliol	Cova del Dofí_2016_Juliol	0.19	0.96
Cova de la Vaca_2016_Juliol	Cova del Dofí_2016_Octubre	0.16	1.00
Cova de la Vaca_2016_Juliol	Cova del Dofí_2017_Octubre	0.53	0.70
Cova de la Vaca_2016_Juliol	Freu_2017_Octubre	0.31	0.17

Cova de la Vaca_2016_Juliol	Freu_2018_Juliol	0.40	0.02
Cova de la Vaca_2016_Juliol	Freu_2018_Octubre	0.43	0.02
Cova de la Vaca_2016_Juliol	Medallot_2015_Octubre	0.27	0.47
Cova de la Vaca_2016_Juliol	Medallot_2016_Juliol	0.25	0.75
Cova de la Vaca_2016_Juliol	Medallot_2016_Octubre	0.37	0.41
Cova de la Vaca_2016_Juliol	Medallot_2017_Juliol	0.39	0.61
Cova de la Vaca_2016_Juliol	Medallot_2017_Octubre	0.37	0.57
Cova de la Vaca_2016_Juliol	Medallot_2018_Juliol	0.27	0.33
Cova de la Vaca_2016_Juliol	Medallot_2018_Octubre	0.51	0.01
Cova de la Vaca_2016_Juliol	Pota del Llop_2016_Juliol	0.30	0.35
Cova de la Vaca_2016_Juliol	Pota del Llop_2016_Octubre	0.24	0.97
Cova de la Vaca_2016_Juliol	Pota del Llop_2017_Octubre	0.65	0.82
Cova de la Vaca_2016_Juliol	Pota del Llop_2018_Juliol	0.35	0.57
Cova de la Vaca_2016_Juliol	Pota del Llop_2018_Octubre	0.29	0.94
Cova de la Vaca_2016_Juliol	Salpatxot_2016_Juliol	0.24	0.79
Cova de la Vaca_2016_Juliol	Salpatxot_2017_Octubre	0.65	0.13
Cova de la Vaca_2016_Juliol	Salpatxot_2018_Octubre	0.47	0.62
Cova de la Vaca_2016_Juliol	Tascó Gros_2015_Octubre	0.32	0.25
Cova de la Vaca_2016_Juliol	Tascó Gros_2016_Juliol	0.21	0.59
Cova de la Vaca_2016_Juliol	Tascó Gros_2016_Octubre	0.35	0.28
Cova de la Vaca_2016_Juliol	Tascó Gros_2017_Juliol	0.24	0.60
Cova de la Vaca_2016_Juliol	Tascó Gros_2017_Octubre	0.59	0.14
Cova de la Vaca_2016_Juliol	Tascó Gros_2018_Juliol	0.31	0.25
Cova de la Vaca_2016_Juliol	Tascó Gros_2018_Octubre	0.37	0.41
Cova de la Vaca_2016_Octubre	Cap Castell_2017_Octubre	0.44	0.66
Cova de la Vaca_2016_Octubre	Cap Castell_2018_Juliol	0.51	0.43
Cova de la Vaca_2016_Octubre	Cap Castell_2018_Octubre	0.59	0.28
Cova de la Vaca_2016_Octubre	Cova de la Vaca_2016_Juliol	0.31	0.96
Cova de la Vaca_2016_Octubre	Cova de la Vaca_2018_Juliol	0.52	0.61
Cova de la Vaca_2016_Octubre	Cova del Dofí_2016_Juliol	0.33	0.95
Cova de la Vaca_2016_Octubre	Cova del Dofí_2016_Octubre	0.39	0.86
Cova de la Vaca_2016_Octubre	Cova del Dofí_2017_Octubre	0.50	0.93
Cova de la Vaca_2016_Octubre	Freu_2017_Octubre	0.57	0.32
Cova de la Vaca_2016_Octubre	Freu_2018_Juliol	0.63	0.20
Cova de la Vaca_2016_Octubre	Freu_2018_Octubre	0.64	0.19
Cova de la Vaca_2016_Octubre	Medallot_2015_Octubre	0.35	0.91
Cova de la Vaca_2016_Octubre	Medallot_2016_Juliol	0.50	0.59

Cova de la Vaca_2016_Octubre	Medallot_2016_Octubre	0.67	0.27
Cova de la Vaca_2016_Octubre	Medallot_2017_Juliol	0.47	0.81
Cova de la Vaca_2016_Octubre	Medallot_2017_Octubre	0.50	0.70
Cova de la Vaca_2016_Octubre	Medallot_2018_Juliol	0.52	0.42
Cova de la Vaca_2016_Octubre	Medallot_2018_Octubre	0.63	0.24
Cova de la Vaca_2016_Octubre	Pota del Llop_2016_Juliol	0.54	0.43
Cova de la Vaca_2016_Octubre	Pota del Llop_2016_Octubre	0.33	0.98
Cova de la Vaca_2016_Octubre	Pota del Llop_2017_Octubre	0.67	0.89
Cova de la Vaca_2016_Octubre	Pota del Llop_2018_Juliol	0.43	0.84
Cova de la Vaca_2016_Octubre	Pota del Llop_2018_Octubre	0.42	0.93
Cova de la Vaca_2016_Octubre	Salpatxot_2016_Juliol	0.29	0.99
Cova de la Vaca_2016_Octubre	Salpatxot_2017_Octubre	0.75	0.29
Cova de la Vaca_2016_Octubre	Salpatxot_2018_Octubre	0.67	0.52
Cova de la Vaca_2016_Octubre	Tascó Gros_2015_Octubre	0.47	0.58
Cova de la Vaca_2016_Octubre	Tascó Gros_2016_Juliol	0.45	0.60
Cova de la Vaca_2016_Octubre	Tascó Gros_2016_Octubre	0.54	0.45
Cova de la Vaca_2016_Octubre	Tascó Gros_2017_Juliol	0.45	0.64
Cova de la Vaca_2016_Octubre	Tascó Gros_2017_Octubre	0.67	0.38
Cova de la Vaca_2016_Octubre	Tascó Gros_2018_Juliol	0.49	0.52
Cova de la Vaca_2016_Octubre	Tascó Gros_2018_Octubre	0.44	0.77
Cova de la Vaca_2018_Juliol	Cap Castell_2017_Octubre	0.20	0.97
Cova de la Vaca_2018_Juliol	Cap Castell_2018_Juliol	0.30	0.61
Cova de la Vaca_2018_Juliol	Cap Castell_2018_Octubre	0.47	0.12
Cova de la Vaca_2018_Juliol	Cova de la Vaca_2016_Juliol	0.21	0.98
Cova de la Vaca_2018_Juliol	Cova de la Vaca_2016_Octubre	0.52	0.61
Cova de la Vaca_2018_Juliol	Cova del Dofí_2016_Juliol	0.36	0.63
Cova de la Vaca_2018_Juliol	Cova del Dofí_2016_Octubre	0.18	1.00
Cova de la Vaca_2018_Juliol	Cova del Dofí_2017_Octubre	0.71	0.41
Cova de la Vaca_2018_Juliol	Freu_2017_Octubre	0.37	0.36
Cova de la Vaca_2018_Juliol	Freu_2018_Juliol	0.43	0.17
Cova de la Vaca_2018_Juliol	Freu_2018_Octubre	0.47	0.13
Cova de la Vaca_2018_Juliol	Medallot_2015_Octubre	0.28	0.80
Cova de la Vaca_2018_Juliol	Medallot_2016_Juliol	0.21	0.99
Cova de la Vaca_2018_Juliol	Medallot_2016_Octubre	0.38	0.62
Cova de la Vaca_2018_Juliol	Medallot_2017_Juliol	0.31	0.94
Cova de la Vaca_2018_Juliol	Medallot_2017_Octubre	0.38	0.74
Cova de la Vaca_2018_Juliol	Medallot_2018_Juliol	0.24	0.86

Cova de la Vaca_2018_Juliol	Medallot_2018_Octubre	0.41	0.32
Cova de la Vaca_2018_Juliol	Pota del Llop_2016_Juliol	0.37	0.47
Cova de la Vaca_2018_Juliol	Pota del Llop_2016_Octubre	0.33	0.87
Cova de la Vaca_2018_Juliol	Pota del Llop_2017_Octubre	0.71	0.75
Cova de la Vaca_2018_Juliol	Pota del Llop_2018_Juliol	0.29	0.94
Cova de la Vaca_2018_Juliol	Pota del Llop_2018_Octubre	0.32	0.96
Cova de la Vaca_2018_Juliol	Salpatxot_2016_Juliol	0.43	0.36
Cova de la Vaca_2018_Juliol	Salpatxot_2017_Octubre	0.71	0.15
Cova de la Vaca_2018_Juliol	Salpatxot_2018_Octubre	0.29	1.00
Cova de la Vaca_2018_Juliol	Tascó Gros_2015_Octubre	0.27	0.82
Cova de la Vaca_2018_Juliol	Tascó Gros_2016_Juliol	0.21	0.94
Cova de la Vaca_2018_Juliol	Tascó Gros_2016_Octubre	0.34	0.63
Cova de la Vaca_2018_Juliol	Tascó Gros_2017_Juliol	0.29	0.75
Cova de la Vaca_2018_Juliol	Tascó Gros_2017_Octubre	0.51	0.42
Cova de la Vaca_2018_Juliol	Tascó Gros_2018_Juliol	0.23	0.92
Cova de la Vaca_2018_Juliol	Tascó Gros_2018_Octubre	0.38	0.62
Cova del Dofí_2016_Juliol	Cap Castell_2017_Octubre	0.27	0.53
Cova del Dofí_2016_Juliol	Cap Castell_2018_Juliol	0.32	0.21
Cova del Dofí_2016_Juliol	Cap Castell_2018_Octubre	0.42	0.05
Cova del Dofí_2016_Juliol	Cova de la Vaca_2016_Juliol	0.19	0.96
Cova del Dofí_2016_Juliol	Cova de la Vaca_2016_Octubre	0.33	0.95
Cova del Dofí_2016_Juliol	Cova de la Vaca_2018_Juliol	0.36	0.63
Cova del Dofí_2016_Juliol	Cova del Dofí_2016_Octubre	0.23	0.93
Cova del Dofí_2016_Juliol	Cova del Dofí_2017_Octubre	0.50	0.78
Cova del Dofí_2016_Juliol	Freu_2017_Octubre	0.40	0.09
Cova del Dofí_2016_Juliol	Freu_2018_Juliol	0.46	0.02
Cova del Dofí_2016_Juliol	Freu_2018_Octubre	0.39	0.10
Cova del Dofí_2016_Juliol	Medallot_2015_Octubre	0.23	0.79
Cova del Dofí_2016_Juliol	Medallot_2016_Juliol	0.33	0.52
Cova del Dofí_2016_Juliol	Medallot_2016_Octubre	0.50	0.15
Cova del Dofí_2016_Juliol	Medallot_2017_Juliol	0.38	0.68
Cova del Dofí_2016_Juliol	Medallot_2017_Octubre	0.33	0.77
Cova del Dofí_2016_Juliol	Medallot_2018_Juliol	0.34	0.22
Cova del Dofí_2016_Juliol	Medallot_2018_Octubre	0.51	0.03
Cova del Dofí_2016_Juliol	Pota del Llop_2016_Juliol	0.33	0.37
Cova del Dofí_2016_Juliol	Pota del Llop_2016_Octubre	0.33	0.77
Cova del Dofí_2016_Juliol	Pota del Llop_2017_Octubre	0.58	0.91

Cova del Dofí_2016_Juliol	Pota del Llop_2018_Juliol	0.33	0.71
Cova del Dofí_2016_Juliol	Pota del Llop_2018_Octubre	0.33	0.89
Cova del Dofí_2016_Juliol	Salpatxot_2016_Juliol	0.26	0.77
Cova del Dofí_2016_Juliol	Salpatxot_2017_Octubre	0.58	0.26
Cova del Dofí_2016_Juliol	Salpatxot_2018_Octubre	0.50	0.59
Cova del Dofí_2016_Juliol	Tascó Gros_2015_Octubre	0.31	0.42
Cova del Dofí_2016_Juliol	Tascó Gros_2016_Juliol	0.23	0.66
Cova del Dofí_2016_Juliol	Tascó Gros_2016_Octubre	0.38	0.29
Cova del Dofí_2016_Juliol	Tascó Gros_2017_Juliol	0.33	0.31
Cova del Dofí_2016_Juliol	Tascó Gros_2017_Octubre	0.58	0.18
Cova del Dofí_2016_Juliol	Tascó Gros_2018_Juliol	0.33	0.32
Cova del Dofí_2016_Juliol	Tascó Gros_2018_Octubre	0.28	0.82
Cova del Dofí_2016_Octubre	Cap Castell_2017_Octubre	0.16	0.98
Cova del Dofí_2016_Octubre	Cap Castell_2018_Juliol	0.21	0.76
Cova del Dofí_2016_Octubre	Cap Castell_2018_Octubre	0.38	0.12
Cova del Dofí_2016_Octubre	Cova de la Vaca_2016_Juliol	0.16	1.00
Cova del Dofí_2016_Octubre	Cova de la Vaca_2016_Octubre	0.39	0.86
Cova del Dofí_2016_Octubre	Cova de la Vaca_2018_Juliol	0.18	1.00
Cova del Dofí_2016_Octubre	Cova del Dofí_2016_Juliol	0.23	0.93
Cova del Dofí_2016_Octubre	Cova del Dofí_2017_Octubre	0.64	0.50
Cova del Dofí_2016_Octubre	Freu_2017_Octubre	0.25	0.65
Cova del Dofí_2016_Octubre	Freu_2018_Juliol	0.37	0.12
Cova del Dofí_2016_Octubre	Freu_2018_Octubre	0.43	0.06
Cova del Dofí_2016_Octubre	Medallot_2015_Octubre	0.26	0.71
Cova del Dofí_2016_Octubre	Medallot_2016_Juliol	0.21	0.96
Cova del Dofí_2016_Octubre	Medallot_2016_Octubre	0.32	0.68
Cova del Dofí_2016_Octubre	Medallot_2017_Juliol	0.35	0.81
Cova del Dofí_2016_Octubre	Medallot_2017_Octubre	0.39	0.58
Cova del Dofí_2016_Octubre	Medallot_2018_Juliol	0.16	0.98
Cova del Dofí_2016_Octubre	Medallot_2018_Octubre	0.47	0.07
Cova del Dofí_2016_Octubre	Pota del Llop_2016_Juliol	0.25	0.75
Cova del Dofí_2016_Octubre	Pota del Llop_2016_Octubre	0.27	0.93
Cova del Dofí_2016_Octubre	Pota del Llop_2017_Octubre	0.55	0.95
Cova del Dofí_2016_Octubre	Pota del Llop_2018_Juliol	0.45	0.34
Cova del Dofí_2016_Octubre	Pota del Llop_2018_Octubre	0.27	0.98
Cova del Dofí_2016_Octubre	Salpatxot_2016_Juliol	0.31	0.59
Cova del Dofí_2016_Octubre	Salpatxot_2017_Octubre	0.55	0.35

Cova del Dofí_2016_Octubre	Salpatxot_2018_Octubre	0.36	0.91
Cova del Dofí_2016_Octubre	Tascó Gros_2015_Octubre	0.28	0.60
Cova del Dofí_2016_Octubre	Tascó Gros_2016_Juliol	0.17	0.95
Cova del Dofí_2016_Octubre	Tascó Gros_2016_Octubre	0.24	0.85
Cova del Dofí_2016_Octubre	Tascó Gros_2017_Juliol	0.27	0.60
Cova del Dofí_2016_Octubre	Tascó Gros_2017_Octubre	0.55	0.26
Cova del Dofí_2016_Octubre	Tascó Gros_2018_Juliol	0.27	0.61
Cova del Dofí_2016_Octubre	Tascó Gros_2018_Octubre	0.32	0.68
Cova del Dofí_2017_Octubre	Cap Castell_2017_Octubre	0.66	0.39
Cova del Dofí_2017_Octubre	Cap Castell_2018_Juliol	0.75	0.22
Cova del Dofí_2017_Octubre	Cap Castell_2018_Octubre	0.88	0.10
Cova del Dofí_2017_Octubre	Cova de la Vaca_2016_Juliol	0.53	0.70
Cova del Dofí_2017_Octubre	Cova de la Vaca_2016_Octubre	0.50	0.93
Cova del Dofí_2017_Octubre	Cova de la Vaca_2018_Juliol	0.71	0.41
Cova del Dofí_2017_Octubre	Cova del Dofí_2016_Juliol	0.50	0.78
Cova del Dofí_2017_Octubre	Cova del Dofí_2016_Octubre	0.64	0.50
Cova del Dofí_2017_Octubre	Freu_2017_Octubre	0.84	0.13
Cova del Dofí_2017_Octubre	Freu_2018_Juliol	0.88	0.10
Cova del Dofí_2017_Octubre	Freu_2018_Octubre	0.85	0.12
Cova del Dofí_2017_Octubre	Medallot_2015_Octubre	0.61	0.50
Cova del Dofí_2017_Octubre	Medallot_2016_Juliol	0.75	0.29
Cova del Dofí_2017_Octubre	Medallot_2016_Octubre	0.78	0.28
Cova del Dofí_2017_Octubre	Medallot_2017_Juliol	0.80	0.32
Cova del Dofí_2017_Octubre	Medallot_2017_Octubre	0.67	0.43
Cova del Dofí_2017_Octubre	Medallot_2018_Juliol	0.80	0.18
Cova del Dofí_2017_Octubre	Medallot_2018_Octubre	0.92	0.08
Cova del Dofí_2017_Octubre	Pota del Llop_2016_Juliol	0.83	0.16
Cova del Dofí_2017_Octubre	Pota del Llop_2016_Octubre	0.50	0.85
Cova del Dofí_2017_Octubre	Pota del Llop_2017_Octubre	1.00	0.67
Cova del Dofí_2017_Octubre	Pota del Llop_2018_Juliol	0.57	0.69
Cova del Dofí_2017_Octubre	Pota del Llop_2018_Octubre	0.75	0.44
Cova del Dofí_2017_Octubre	Salpatxot_2016_Juliol	0.43	0.90
Cova del Dofí_2017_Octubre	Salpatxot_2017_Octubre	1.00	0.13
Cova del Dofí_2017_Octubre	Salpatxot_2018_Octubre	1.00	0.18
Cova del Dofí_2017_Octubre	Tascó Gros_2015_Octubre	0.81	0.18
Cova del Dofí_2017_Octubre	Tascó Gros_2016_Juliol	0.71	0.28
Cova del Dofí_2017_Octubre	Tascó Gros_2016_Octubre	0.88	0.13

Cova del Dofí_2017_Octubre	Tascó Gros_2017_Juliol	0.61	0.50
Cova del Dofí_2017_Octubre	Tascó Gros_2017_Octubre	1.00	0.11
Cova del Dofí_2017_Octubre	Tascó Gros_2018_Juliol	0.72	0.28
Cova del Dofí_2017_Octubre	Tascó Gros_2018_Octubre	0.78	0.28
Freu_2017_Octubre	Cap Castell_2017_Octubre	0.36	0.01
Freu_2017_Octubre	Cap Castell_2018_Juliol	0.14	0.47
Freu_2017_Octubre	Cap Castell_2018_Octubre	0.15	0.52
Freu_2017_Octubre	Cova de la Vaca_2016_Juliol	0.31	0.17
Freu_2017_Octubre	Cova de la Vaca_2016_Octubre	0.57	0.32
Freu_2017_Octubre	Cova de la Vaca_2018_Juliol	0.37	0.36
Freu_2017_Octubre	Cova del Dofí_2016_Juliol	0.40	0.09
Freu_2017_Octubre	Cova del Dofí_2016_Octubre	0.25	0.65
Freu_2017_Octubre	Cova del Dofí_2017_Octubre	0.84	0.13
Freu_2017_Octubre	Freu_2018_Juliol	0.15	0.38
Freu_2017_Octubre	Freu_2018_Octubre	0.22	0.14
Freu_2017_Octubre	Medallot_2015_Octubre	0.35	0.04
Freu_2017_Octubre	Medallot_2016_Juliol	0.25	0.56
Freu_2017_Octubre	Medallot_2016_Octubre	0.22	0.85
Freu_2017_Octubre	Medallot_2017_Juliol	0.42	0.40
Freu_2017_Octubre	Medallot_2017_Octubre	0.23	0.93
Freu_2017_Octubre	Medallot_2018_Juliol	0.14	0.75
Freu_2017_Octubre	Medallot_2018_Octubre	0.26	0.21
Freu_2017_Octubre	Pota del Llop_2016_Juliol	0.13	0.95
Freu_2017_Octubre	Pota del Llop_2016_Octubre	0.42	0.30
Freu_2017_Octubre	Pota del Llop_2017_Octubre	0.56	0.92
Freu_2017_Octubre	Pota del Llop_2018_Juliol	0.56	0.04
Freu_2017_Octubre	Pota del Llop_2018_Octubre	0.50	0.31
Freu_2017_Octubre	Salpatxot_2016_Juliol	0.49	0.01
Freu_2017_Octubre	Salpatxot_2017_Octubre	0.34	0.79
Freu_2017_Octubre	Salpatxot_2018_Octubre	0.42	0.70
Freu_2017_Octubre	Tascó Gros_2015_Octubre	0.16	0.77
Freu_2017_Octubre	Tascó Gros_2016_Juliol	0.22	0.17
Freu_2017_Octubre	Tascó Gros_2016_Octubre	0.13	0.99
Freu_2017_Octubre	Tascó Gros_2017_Juliol	0.40	0.01
Freu_2017_Octubre	Tascó Gros_2017_Octubre	0.30	0.81
Freu_2017_Octubre	Tascó Gros_2018_Juliol	0.23	0.30
Freu_2017_Octubre	Tascó Gros_2018_Octubre	0.29	0.55

Freu_2018_Juliol	Cap Castell_2017_Octubre	0.50	<0.001
Freu_2018_Juliol	Cap Castell_2018_Juliol	0.29	<0.001
Freu_2018_Juliol	Cap Castell_2018_Octubre	0.16	0.17
Freu_2018_Juliol	Cova de la Vaca_2016_Juliol	0.40	0.02
Freu_2018_Juliol	Cova de la Vaca_2016_Octubre	0.63	0.20
Freu_2018_Juliol	Cova de la Vaca_2018_Juliol	0.43	0.17
Freu_2018_Juliol	Cova del Dofí_2016_Juliol	0.46	0.02
Freu_2018_Juliol	Cova del Dofí_2016_Octubre	0.37	0.12
Freu_2018_Juliol	Cova del Dofí_2017_Octubre	0.88	0.10
Freu_2018_Juliol	Freu_2017_Octubre	0.15	0.38
Freu_2018_Juliol	Freu_2018_Octubre	0.11	0.74
Freu_2018_Juliol	Medallot_2015_Octubre	0.33	0.03
Freu_2018_Juliol	Medallot_2016_Juliol	0.41	0.05
Freu_2018_Juliol	Medallot_2016_Octubre	0.33	0.33
Freu_2018_Juliol	Medallot_2017_Juliol	0.57	0.09
Freu_2018_Juliol	Medallot_2017_Octubre	0.29	0.71
Freu_2018_Juliol	Medallot_2018_Juliol	0.28	0.01
Freu_2018_Juliol	Medallot_2018_Octubre	0.14	0.80
Freu_2018_Juliol	Pota del Llop_2016_Juliol	0.27	0.12
Freu_2018_Juliol	Pota del Llop_2016_Octubre	0.57	0.05
Freu_2018_Juliol	Pota del Llop_2017_Octubre	0.69	0.74
Freu_2018_Juliol	Pota del Llop_2018_Juliol	0.69	<0.001
Freu_2018_Juliol	Pota del Llop_2018_Octubre	0.65	0.08
Freu_2018_Juliol	Salpatxot_2016_Juliol	0.58	<0.001
Freu_2018_Juliol	Salpatxot_2017_Octubre	0.31	0.84
Freu_2018_Juliol	Salpatxot_2018_Octubre	0.57	0.29
Freu_2018_Juliol	Tascó Gros_2015_Octubre	0.22	0.23
Freu_2018_Juliol	Tascó Gros_2016_Juliol	0.33	<0.001
Freu_2018_Juliol	Tascó Gros_2016_Octubre	0.27	0.25
Freu_2018_Juliol	Tascó Gros_2017_Juliol	0.55	<0.001
Freu_2018_Juliol	Tascó Gros_2017_Octubre	0.37	0.52
Freu_2018_Juliol	Tascó Gros_2018_Juliol	0.38	<0.001
Freu_2018_Juliol	Tascó Gros_2018_Octubre	0.44	0.08
Freu_2018_Octubre	Cap Castell_2017_Octubre	0.56	<0.001
Freu_2018_Octubre	Cap Castell_2018_Juliol	0.34	<0.001
Freu_2018_Octubre	Cap Castell_2018_Octubre	0.18	0.22
Freu_2018_Octubre	Cova de la Vaca_2016_Juliol	0.43	0.02

Freu_2018_Octubre	Cova de la Vaca_2016_Octubre	0.64	0.19
Freu_2018_Octubre	Cova de la Vaca_2018_Juliol	0.47	0.13
Freu_2018_Octubre	Cova del Dofí_2016_Juliol	0.39	0.10
Freu_2018_Octubre	Cova del Dofí_2016_Octubre	0.43	0.06
Freu_2018_Octubre	Cova del Dofí_2017_Octubre	0.85	0.12
Freu_2018_Octubre	Freu_2017_Octubre	0.22	0.14
Freu_2018_Octubre	Freu_2018_Juliol	0.11	0.74
Freu_2018_Octubre	Medallot_2015_Octubre	0.38	0.02
Freu_2018_Octubre	Medallot_2016_Juliol	0.47	0.02
Freu_2018_Octubre	Medallot_2016_Octubre	0.35	0.29
Freu_2018_Octubre	Medallot_2017_Juliol	0.64	0.05
Freu_2018_Octubre	Medallot_2017_Octubre	0.23	0.94
Freu_2018_Octubre	Medallot_2018_Juliol	0.34	<0.001
Freu_2018_Octubre	Medallot_2018_Octubre	0.21	0.42
Freu_2018_Octubre	Pota del Llop_2016_Juliol	0.33	0.05
Freu_2018_Octubre	Pota del Llop_2016_Octubre	0.64	0.02
Freu_2018_Octubre	Pota del Llop_2017_Octubre	0.72	0.69
Freu_2018_Octubre	Pota del Llop_2018_Juliol	0.72	<0.001
Freu_2018_Octubre	Pota del Llop_2018_Octubre	0.70	0.05
Freu_2018_Octubre	Salpatxot_2016_Juliol	0.63	<0.001
Freu_2018_Octubre	Salpatxot_2017_Octubre	0.34	0.77
Freu_2018_Octubre	Salpatxot_2018_Octubre	0.64	0.19
Freu_2018_Octubre	Tascó Gros_2015_Octubre	0.26	0.17
Freu_2018_Octubre	Tascó Gros_2016_Juliol	0.38	<0.001
Freu_2018_Octubre	Tascó Gros_2016_Octubre	0.33	0.13
Freu_2018_Octubre	Tascó Gros_2017_Juliol	0.60	<0.001
Freu_2018_Octubre	Tascó Gros_2017_Octubre	0.44	0.33
Freu_2018_Octubre	Tascó Gros_2018_Juliol	0.43	<0.001
Freu_2018_Octubre	Tascó Gros_2018_Octubre	0.48	0.05
Medallot_2015_Octubre	Cap Castell_2017_Octubre	0.34	0.09
Medallot_2015_Octubre	Cap Castell_2018_Juliol	0.30	0.07
Medallot_2015_Octubre	Cap Castell_2018_Octubre	0.29	0.10
Medallot_2015_Octubre	Cova de la Vaca_2016_Juliol	0.27	0.47
Medallot_2015_Octubre	Cova de la Vaca_2016_Octubre	0.35	0.91
Medallot_2015_Octubre	Cova de la Vaca_2018_Juliol	0.28	0.80
Medallot_2015_Octubre	Cova del Dofí_2016_Juliol	0.23	0.79
Medallot_2015_Octubre	Cova del Dofí_2016_Octubre	0.26	0.71

Medallot_2015_Octubre	Cova del Dofí_2017_Octubre	0.61	0.50
Medallot_2015_Octubre	Freu_2017_Octubre	0.35	0.04
Medallot_2015_Octubre	Freu_2018_Juliol	0.33	0.03
Medallot_2015_Octubre	Freu_2018_Octubre	0.38	0.02
Medallot_2015_Octubre	Medallot_2016_Juliol	0.23	0.81
Medallot_2015_Octubre	Medallot_2016_Octubre	0.35	0.41
Medallot_2015_Octubre	Medallot_2017_Juliol	0.37	0.64
Medallot_2015_Octubre	Medallot_2017_Octubre	0.26	0.90
Medallot_2015_Octubre	Medallot_2018_Juliol	0.23	0.40
Medallot_2015_Octubre	Medallot_2018_Octubre	0.36	0.09
Medallot_2015_Octubre	Pota del Llop_2016_Juliol	0.35	0.12
Medallot_2015_Octubre	Pota del Llop_2016_Octubre	0.31	0.74
Medallot_2015_Octubre	Pota del Llop_2017_Octubre	0.57	0.92
Medallot_2015_Octubre	Pota del Llop_2018_Juliol	0.57	0.06
Medallot_2015_Octubre	Pota del Llop_2018_Octubre	0.48	0.42
Medallot_2015_Octubre	Salpatxot_2016_Juliol	0.42	0.09
Medallot_2015_Octubre	Salpatxot_2017_Octubre	0.49	0.39
Medallot_2015_Octubre	Salpatxot_2018_Octubre	0.39	0.81
Medallot_2015_Octubre	Tascó Gros_2015_Octubre	0.20	0.72
Medallot_2015_Octubre	Tascó Gros_2016_Juliol	0.19	0.60
Medallot_2015_Octubre	Tascó Gros_2016_Octubre	0.27	0.52
Medallot_2015_Octubre	Tascó Gros_2017_Juliol	0.34	0.12
Medallot_2015_Octubre	Tascó Gros_2017_Octubre	0.43	0.42
Medallot_2015_Octubre	Tascó Gros_2018_Juliol	0.28	0.27
Medallot_2015_Octubre	Tascó Gros_2018_Octubre	0.26	0.79
Medallot_2016_Juliol	Cap Castell_2017_Octubre	0.24	0.69
Medallot_2016_Juliol	Cap Castell_2018_Juliol	0.13	0.99
Medallot_2016_Juliol	Cap Castell_2018_Octubre	0.37	0.11
Medallot_2016_Juliol	Cova de la Vaca_2016_Juliol	0.25	0.75
Medallot_2016_Juliol	Cova de la Vaca_2016_Octubre	0.50	0.59
Medallot_2016_Juliol	Cova de la Vaca_2018_Juliol	0.21	0.99
Medallot_2016_Juliol	Cova del Dofí_2016_Juliol	0.33	0.52
Medallot_2016_Juliol	Cova del Dofí_2016_Octubre	0.21	0.96
Medallot_2016_Juliol	Cova del Dofí_2017_Octubre	0.75	0.29
Medallot_2016_Juliol	Freu_2017_Octubre	0.25	0.56
Medallot_2016_Juliol	Freu_2018_Juliol	0.41	0.05
Medallot_2016_Juliol	Freu_2018_Octubre	0.47	0.02

Medallot_2016_Juliol	Medallot_2015_Octubre	0.23	0.81
Medallot_2016_Juliol	Medallot_2016_Octubre	0.31	0.72
Medallot_2016_Juliol	Medallot_2017_Juliol	0.25	0.98
Medallot_2016_Juliol	Medallot_2017_Octubre	0.42	0.49
Medallot_2016_Juliol	Medallot_2018_Juliol	0.14	0.99
Medallot_2016_Juliol	Medallot_2018_Octubre	0.45	0.07
Medallot_2016_Juliol	Pota del Llop_2016_Juliol	0.27	0.61
Medallot_2016_Juliol	Pota del Llop_2016_Octubre	0.25	0.96
Medallot_2016_Juliol	Pota del Llop_2017_Octubre	0.50	0.98
Medallot_2016_Juliol	Pota del Llop_2018_Juliol	0.42	0.43
Medallot_2016_Juliol	Pota del Llop_2018_Octubre	0.42	0.67
Medallot_2016_Juliol	Salpatxot_2016_Juliol	0.40	0.24
Medallot_2016_Juliol	Salpatxot_2017_Octubre	0.58	0.26
Medallot_2016_Juliol	Salpatxot_2018_Octubre	0.33	0.95
Medallot_2016_Juliol	Tascó Gros_2015_Octubre	0.27	0.59
Medallot_2016_Juliol	Tascó Gros_2016_Juliol	0.13	1.00
Medallot_2016_Juliol	Tascó Gros_2016_Octubre	0.25	0.78
Medallot_2016_Juliol	Tascó Gros_2017_Juliol	0.21	0.84
Medallot_2016_Juliol	Tascó Gros_2017_Octubre	0.55	0.24
Medallot_2016_Juliol	Tascó Gros_2018_Juliol	0.11	1.00
Medallot_2016_Juliol	Tascó Gros_2018_Octubre	0.17	1.00
Medallot_2016_Octubre	Cap Castell_2017_Octubre	0.44	0.12
Medallot_2016_Octubre	Cap Castell_2018_Juliol	0.23	0.77
Medallot_2016_Octubre	Cap Castell_2018_Octubre	0.25	0.69
Medallot_2016_Octubre	Cova de la Vaca_2016_Juliol	0.37	0.41
Medallot_2016_Octubre	Cova de la Vaca_2016_Octubre	0.67	0.27
Medallot_2016_Octubre	Cova de la Vaca_2018_Juliol	0.38	0.62
Medallot_2016_Octubre	Cova del Dofí_2016_Juliol	0.50	0.15
Medallot_2016_Octubre	Cova del Dofí_2016_Octubre	0.32	0.68
Medallot_2016_Octubre	Cova del Dofí_2017_Octubre	0.78	0.28
Medallot_2016_Octubre	Freu_2017_Octubre	0.22	0.85
Medallot_2016_Octubre	Freu_2018_Juliol	0.33	0.33
Medallot_2016_Octubre	Freu_2018_Octubre	0.35	0.29
Medallot_2016_Octubre	Medallot_2015_Octubre	0.35	0.41
Medallot_2016_Octubre	Medallot_2016_Juliol	0.31	0.72
Medallot_2016_Octubre	Medallot_2017_Juliol	0.56	0.27
Medallot_2016_Octubre	Medallot_2017_Octubre	0.33	0.82

Medallot_2016_Octubre	Medallot_2018_Juliol	0.25	0.73
Medallot_2016_Octubre	Medallot_2018_Octubre	0.39	0.25
Medallot_2016_Octubre	Pota del Llop_2016_Juliol	0.25	0.81
Medallot_2016_Octubre	Pota del Llop_2016_Octubre	0.56	0.22
Medallot_2016_Octubre	Pota del Llop_2017_Octubre	0.56	0.94
Medallot_2016_Octubre	Pota del Llop_2018_Juliol	0.56	0.18
Medallot_2016_Octubre	Pota del Llop_2018_Octubre	0.56	0.36
Medallot_2016_Octubre	Salpatxot_2016_Juliol	0.57	0.06
Medallot_2016_Octubre	Salpatxot_2017_Octubre	0.33	0.92
Medallot_2016_Octubre	Salpatxot_2018_Octubre	0.56	0.49
Medallot_2016_Octubre	Tascó Gros_2015_Octubre	0.27	0.72
Medallot_2016_Octubre	Tascó Gros_2016_Juliol	0.29	0.55
Medallot_2016_Octubre	Tascó Gros_2016_Octubre	0.25	0.86
Medallot_2016_Octubre	Tascó Gros_2017_Juliol	0.48	0.08
Medallot_2016_Octubre	Tascó Gros_2017_Octubre	0.36	0.81
Medallot_2016_Octubre	Tascó Gros_2018_Juliol	0.31	0.51
Medallot_2016_Octubre	Tascó Gros_2018_Octubre	0.33	0.70
Medallot_2017_Juliol	Cap Castell_2017_Octubre	0.37	0.58
Medallot_2017_Juliol	Cap Castell_2018_Juliol	0.32	0.69
Medallot_2017_Juliol	Cap Castell_2018_Octubre	0.55	0.11
Medallot_2017_Juliol	Cova de la Vaca_2016_Juliol	0.39	0.61
Medallot_2017_Juliol	Cova de la Vaca_2016_Octubre	0.47	0.81
Medallot_2017_Juliol	Cova de la Vaca_2018_Juliol	0.31	0.94
Medallot_2017_Juliol	Cova del Dofí_2016_Juliol	0.38	0.68
Medallot_2017_Juliol	Cova del Dofí_2016_Octubre	0.35	0.81
Medallot_2017_Juliol	Cova del Dofí_2017_Octubre	0.80	0.32
Medallot_2017_Juliol	Freu_2017_Octubre	0.42	0.40
Medallot_2017_Juliol	Freu_2018_Juliol	0.57	0.09
Medallot_2017_Juliol	Freu_2018_Octubre	0.64	0.05
Medallot_2017_Juliol	Medallot_2015_Octubre	0.37	0.64
Medallot_2017_Juliol	Medallot_2016_Juliol	0.25	0.98
Medallot_2017_Juliol	Medallot_2016_Octubre	0.56	0.27
Medallot_2017_Juliol	Medallot_2017_Octubre	0.50	0.50
Medallot_2017_Juliol	Medallot_2018_Juliol	0.31	0.79
Medallot_2017_Juliol	Medallot_2018_Octubre	0.62	0.08
Medallot_2017_Juliol	Pota del Llop_2016_Juliol	0.37	0.64
Medallot_2017_Juliol	Pota del Llop_2016_Octubre	0.30	0.97

Medallot_2017_Juliol	Pota del Llop_2017_Octubre	0.40	1.00
Medallot_2017_Juliol	Pota del Llop_2018_Juliol	0.46	0.58
Medallot_2017_Juliol	Pota del Llop_2018_Octubre	0.55	0.51
Medallot_2017_Juliol	Salpatxot_2016_Juliol	0.59	0.16
Medallot_2017_Juliol	Salpatxot_2017_Octubre	0.75	0.16
Medallot_2017_Juliol	Salpatxot_2018_Octubre	0.47	0.81
Medallot_2017_Juliol	Tascó Gros_2015_Octubre	0.42	0.44
Medallot_2017_Juliol	Tascó Gros_2016_Juliol	0.32	0.73
Medallot_2017_Juliol	Tascó Gros_2016_Octubre	0.38	0.66
Medallot_2017_Juliol	Tascó Gros_2017_Juliol	0.41	0.48
Medallot_2017_Juliol	Tascó Gros_2017_Octubre	0.60	0.33
Medallot_2017_Juliol	Tascó Gros_2018_Juliol	0.28	0.88
Medallot_2017_Juliol	Tascó Gros_2018_Octubre	0.24	0.99
Medallot_2017_Octubre	Cap Castell_2017_Octubre	0.52	0.12
Medallot_2017_Octubre	Cap Castell_2018_Juliol	0.28	0.75
Medallot_2017_Octubre	Cap Castell_2018_Octubre	0.25	0.87
Medallot_2017_Octubre	Cova de la Vaca_2016_Juliol	0.37	0.57
Medallot_2017_Octubre	Cova de la Vaca_2016_Octubre	0.50	0.70
Medallot_2017_Octubre	Cova de la Vaca_2018_Juliol	0.38	0.74
Medallot_2017_Octubre	Cova del Dofí_2016_Juliol	0.33	0.77
Medallot_2017_Octubre	Cova del Dofí_2016_Octubre	0.39	0.58
Medallot_2017_Octubre	Cova del Dofí_2017_Octubre	0.67	0.43
Medallot_2017_Octubre	Freu_2017_Octubre	0.23	0.93
Medallot_2017_Octubre	Freu_2018_Juliol	0.29	0.71
Medallot_2017_Octubre	Freu_2018_Octubre	0.23	0.94
Medallot_2017_Octubre	Medallot_2015_Octubre	0.26	0.90
Medallot_2017_Octubre	Medallot_2016_Juliol	0.42	0.49
Medallot_2017_Octubre	Medallot_2016_Octubre	0.33	0.82
Medallot_2017_Octubre	Medallot_2017_Juliol	0.50	0.50
Medallot_2017_Octubre	Medallot_2018_Juliol	0.30	0.72
Medallot_2017_Octubre	Medallot_2018_Octubre	0.29	0.79
Medallot_2017_Octubre	Pota del Llop_2016_Juliol	0.20	0.99
Medallot_2017_Octubre	Pota del Llop_2016_Octubre	0.50	0.44
Medallot_2017_Octubre	Pota del Llop_2017_Octubre	0.67	0.86
Medallot_2017_Octubre	Pota del Llop_2018_Juliol	0.67	0.11
Medallot_2017_Octubre	Pota del Llop_2018_Octubre	0.67	0.24
Medallot_2017_Octubre	Salpatxot_2016_Juliol	0.60	0.10

Medallot_2017_Octubre	Salpatxot_2017_Octubre	0.33	0.95
Medallot_2017_Octubre	Salpatxot_2018_Octubre	0.50	0.70
Medallot_2017_Octubre	Tascó Gros_2015_Octubre	0.21	0.99
Medallot_2017_Octubre	Tascó Gros_2016_Juliol	0.35	0.54
Medallot_2017_Octubre	Tascó Gros_2016_Octubre	0.29	0.85
Medallot_2017_Octubre	Tascó Gros_2017_Juliol	0.52	0.13
Medallot_2017_Octubre	Tascó Gros_2017_Octubre	0.33	0.92
Medallot_2017_Octubre	Tascó Gros_2018_Juliol	0.33	0.66
Medallot_2017_Octubre	Tascó Gros_2018_Octubre	0.44	0.48
Medallot_2018_Juliol	Cap Castell_2017_Octubre	0.22	0.25
Medallot_2018_Juliol	Cap Castell_2018_Juliol	0.07	0.99
Medallot_2018_Juliol	Cap Castell_2018_Octubre	0.25	0.05
Medallot_2018_Juliol	Cova de la Vaca_2016_Juliol	0.27	0.33
Medallot_2018_Juliol	Cova de la Vaca_2016_Octubre	0.52	0.42
Medallot_2018_Juliol	Cova de la Vaca_2018_Juliol	0.24	0.86
Medallot_2018_Juliol	Cova del Dofí_2016_Juliol	0.34	0.22
Medallot_2018_Juliol	Cova del Dofí_2016_Octubre	0.16	0.98
Medallot_2018_Juliol	Cova del Dofí_2017_Octubre	0.80	0.18
Medallot_2018_Juliol	Freu_2017_Octubre	0.14	0.75
Medallot_2018_Juliol	Freu_2018_Juliol	0.28	0.01
Medallot_2018_Juliol	Freu_2018_Octubre	0.34	<0.001
Medallot_2018_Juliol	Medallot_2015_Octubre	0.23	0.40
Medallot_2018_Juliol	Medallot_2016_Juliol	0.14	0.99
Medallot_2018_Juliol	Medallot_2016_Octubre	0.25	0.73
Medallot_2018_Juliol	Medallot_2017_Juliol	0.31	0.79
Medallot_2018_Juliol	Medallot_2017_Octubre	0.30	0.72
Medallot_2018_Juliol	Medallot_2018_Octubre	0.39	0.01
Medallot_2018_Juliol	Pota del Llop_2016_Juliol	0.15	0.85
Medallot_2018_Juliol	Pota del Llop_2016_Octubre	0.31	0.70
Medallot_2018_Juliol	Pota del Llop_2017_Octubre	0.47	0.98
Medallot_2018_Juliol	Pota del Llop_2018_Juliol	0.45	0.17
Medallot_2018_Juliol	Pota del Llop_2018_Octubre	0.37	0.70
Medallot_2018_Juliol	Salpatxot_2016_Juliol	0.41	0.05
Medallot_2018_Juliol	Salpatxot_2017_Octubre	0.47	0.39
Medallot_2018_Juliol	Salpatxot_2018_Octubre	0.31	0.95
Medallot_2018_Juliol	Tascó Gros_2015_Octubre	0.13	0.95
Medallot_2018_Juliol	Tascó Gros_2016_Juliol	0.15	0.59

Medallot_2018_Juliol	Tascó Gros_2016_Octubre	0.13	0.99
Medallot_2018_Juliol	Tascó Gros_2017_Juliol	0.29	0.11
Medallot_2018_Juliol	Tascó Gros_2017_Octubre	0.43	0.36
Medallot_2018_Juliol	Tascó Gros_2018_Juliol	0.11	0.97
Medallot_2018_Juliol	Tascó Gros_2018_Octubre	0.17	0.97
Medallot_2018_Octubre	Cap Castell_2017_Octubre	0.53	<0.001
Medallot_2018_Octubre	Cap Castell_2018_Juliol	0.39	<0.001
Medallot_2018_Octubre	Cap Castell_2018_Octubre	0.23	0.25
Medallot_2018_Octubre	Cova de la Vaca_2016_Juliol	0.51	0.01
Medallot_2018_Octubre	Cova de la Vaca_2016_Octubre	0.63	0.24
Medallot_2018_Octubre	Cova de la Vaca_2018_Juliol	0.41	0.32
Medallot_2018_Octubre	Cova del Dofí_2016_Juliol	0.51	0.03
Medallot_2018_Octubre	Cova del Dofí_2016_Octubre	0.47	0.07
Medallot_2018_Octubre	Cova del Dofí_2017_Octubre	0.92	0.08
Medallot_2018_Octubre	Freu_2017_Octubre	0.26	0.21
Medallot_2018_Octubre	Freu_2018_Juliol	0.14	0.80
Medallot_2018_Octubre	Freu_2018_Octubre	0.21	0.42
Medallot_2018_Octubre	Medallot_2015_Octubre	0.36	0.09
Medallot_2018_Octubre	Medallot_2016_Juliol	0.45	0.07
Medallot_2018_Octubre	Medallot_2016_Octubre	0.39	0.25
Medallot_2018_Octubre	Medallot_2017_Juliol	0.62	0.08
Medallot_2018_Octubre	Medallot_2017_Octubre	0.29	0.79
Medallot_2018_Octubre	Medallot_2018_Juliol	0.39	0.01
Medallot_2018_Octubre	Pota del Llop_2016_Juliol	0.35	0.09
Medallot_2018_Octubre	Pota del Llop_2016_Octubre	0.62	0.05
Medallot_2018_Octubre	Pota del Llop_2017_Octubre	0.65	0.80
Medallot_2018_Octubre	Pota del Llop_2018_Juliol	0.65	0.02
Medallot_2018_Octubre	Pota del Llop_2018_Octubre	0.67	0.09
Medallot_2018_Octubre	Salpatxot_2016_Juliol	0.71	<0.001
Medallot_2018_Octubre	Salpatxot_2017_Octubre	0.38	0.68
Medallot_2018_Octubre	Salpatxot_2018_Octubre	0.62	0.26
Medallot_2018_Octubre	Tascó Gros_2015_Octubre	0.27	0.30
Medallot_2018_Octubre	Tascó Gros_2016_Juliol	0.44	<0.001
Medallot_2018_Octubre	Tascó Gros_2016_Octubre	0.30	0.32
Medallot_2018_Octubre	Tascó Gros_2017_Juliol	0.62	<0.001
Medallot_2018_Octubre	Tascó Gros_2017_Octubre	0.42	0.46
Medallot_2018_Octubre	Tascó Gros_2018_Juliol	0.44	0.01

Medallot_2018_Octubre	Tascó Gros_2018_Octubre	0.50	0.07
Pota del Llop_2016_Juliol	Cap Castell_2017_Octubre	0.38	0.04
Pota del Llop_2016_Juliol	Cap Castell_2018_Juliol	0.14	0.86
Pota del Llop_2016_Juliol	Cap Castell_2018_Octubre	0.25	0.22
Pota del Llop_2016_Juliol	Cova de la Vaca_2016_Juliol	0.30	0.35
Pota del Llop_2016_Juliol	Cova de la Vaca_2016_Octubre	0.54	0.43
Pota del Llop_2016_Juliol	Cova de la Vaca_2018_Juliol	0.37	0.47
Pota del Llop_2016_Juliol	Cova del Dofí_2016_Juliol	0.33	0.37
Pota del Llop_2016_Juliol	Cova del Dofí_2016_Octubre	0.25	0.75
Pota del Llop_2016_Juliol	Cova del Dofí_2017_Octubre	0.83	0.16
Pota del Llop_2016_Juliol	Freu_2017_Octubre	0.13	0.95
Pota del Llop_2016_Juliol	Freu_2018_Juliol	0.27	0.12
Pota del Llop_2016_Juliol	Freu_2018_Octubre	0.33	0.05
Pota del Llop_2016_Juliol	Medallot_2015_Octubre	0.35	0.12
Pota del Llop_2016_Juliol	Medallot_2016_Juliol	0.27	0.61
Pota del Llop_2016_Juliol	Medallot_2016_Octubre	0.25	0.81
Pota del Llop_2016_Juliol	Medallot_2017_Juliol	0.37	0.64
Pota del Llop_2016_Juliol	Medallot_2017_Octubre	0.20	0.99
Pota del Llop_2016_Juliol	Medallot_2018_Juliol	0.15	0.85
Pota del Llop_2016_Juliol	Medallot_2018_Octubre	0.35	0.09
Pota del Llop_2016_Juliol	Pota del Llop_2016_Octubre	0.36	0.59
Pota del Llop_2016_Juliol	Pota del Llop_2017_Octubre	0.57	0.92
Pota del Llop_2016_Juliol	Pota del Llop_2018_Juliol	0.57	0.06
Pota del Llop_2016_Juliol	Pota del Llop_2018_Octubre	0.52	0.31
Pota del Llop_2016_Juliol	Salpatxot_2016_Juliol	0.48	0.04
Pota del Llop_2016_Juliol	Salpatxot_2017_Octubre	0.45	0.51
Pota del Llop_2016_Juliol	Salpatxot_2018_Octubre	0.36	0.88
Pota del Llop_2016_Juliol	Tascó Gros_2015_Octubre	0.15	0.93
Pota del Llop_2016_Juliol	Tascó Gros_2016_Juliol	0.20	0.52
Pota del Llop_2016_Juliol	Tascó Gros_2016_Octubre	0.15	0.99
Pota del Llop_2016_Juliol	Tascó Gros_2017_Juliol	0.38	0.05
Pota del Llop_2016_Juliol	Tascó Gros_2017_Octubre	0.30	0.84
Pota del Llop_2016_Juliol	Tascó Gros_2018_Juliol	0.18	0.82
Pota del Llop_2016_Juliol	Tascó Gros_2018_Octubre	0.30	0.61
Pota del Llop_2016_Octubre	Cap Castell_2017_Octubre	0.25	0.91
Pota del Llop_2016_Octubre	Cap Castell_2018_Juliol	0.32	0.58
Pota del Llop_2016_Octubre	Cap Castell_2018_Octubre	0.55	0.07

Pota del Llop_2016_Octubre	Cova de la Vaca_2016_Juliol	0.24	0.97
Pota del Llop_2016_Octubre	Cova de la Vaca_2016_Octubre	0.33	0.98
Pota del Llop_2016_Octubre	Cova de la Vaca_2018_Juliol	0.33	0.87
Pota del Llop_2016_Octubre	Cova del Dofí_2016_Juliol	0.33	0.77
Pota del Llop_2016_Octubre	Cova del Dofí_2016_Octubre	0.27	0.93
Pota del Llop_2016_Octubre	Cova del Dofí_2017_Octubre	0.50	0.85
Pota del Llop_2016_Octubre	Freu_2017_Octubre	0.42	0.30
Pota del Llop_2016_Octubre	Freu_2018_Juliol	0.57	0.05
Pota del Llop_2016_Octubre	Freu_2018_Octubre	0.64	0.02
Pota del Llop_2016_Octubre	Medallot_2015_Octubre	0.31	0.74
Pota del Llop_2016_Octubre	Medallot_2016_Juliol	0.25	0.96
Pota del Llop_2016_Octubre	Medallot_2016_Octubre	0.56	0.22
Pota del Llop_2016_Octubre	Medallot_2017_Juliol	0.30	0.97
Pota del Llop_2016_Octubre	Medallot_2017_Octubre	0.50	0.44
Pota del Llop_2016_Octubre	Medallot_2018_Juliol	0.31	0.70
Pota del Llop_2016_Octubre	Medallot_2018_Octubre	0.62	0.05
Pota del Llop_2016_Octubre	Pota del Llop_2016_Juliol	0.36	0.59
Pota del Llop_2016_Octubre	Pota del Llop_2017_Octubre	0.50	0.98
Pota del Llop_2016_Octubre	Pota del Llop_2018_Juliol	0.50	0.39
Pota del Llop_2016_Octubre	Pota del Llop_2018_Octubre	0.33	0.95
Pota del Llop_2016_Octubre	Salpatxot_2016_Juliol	0.36	0.66
Pota del Llop_2016_Octubre	Salpatxot_2017_Octubre	0.75	0.13
Pota del Llop_2016_Octubre	Salpatxot_2018_Octubre	0.50	0.70
Pota del Llop_2016_Octubre	Tascó Gros_2015_Octubre	0.42	0.35
Pota del Llop_2016_Octubre	Tascó Gros_2016_Juliol	0.32	0.63
Pota del Llop_2016_Octubre	Tascó Gros_2016_Octubre	0.38	0.57
Pota del Llop_2016_Octubre	Tascó Gros_2017_Juliol	0.23	0.96
Pota del Llop_2016_Octubre	Tascó Gros_2017_Octubre	0.63	0.22
Pota del Llop_2016_Octubre	Tascó Gros_2018_Juliol	0.30	0.77
Pota del Llop_2016_Octubre	Tascó Gros_2018_Octubre	0.28	0.94
Pota del Llop_2017_Octubre	Cap Castell_2017_Octubre	0.57	0.91
Pota del Llop_2017_Octubre	Cap Castell_2018_Juliol	0.49	0.97
Pota del Llop_2017_Octubre	Cap Castell_2018_Octubre	0.69	0.74
Pota del Llop_2017_Octubre	Cova de la Vaca_2016_Juliol	0.65	0.82
Pota del Llop_2017_Octubre	Cova de la Vaca_2016_Octubre	0.67	0.89
Pota del Llop_2017_Octubre	Cova de la Vaca_2018_Juliol	0.71	0.75
Pota del Llop_2017_Octubre	Cova del Dofí_2016_Juliol	0.58	0.91

Pota del Llop_2017_Octubre	Cova del Dofí_2016_Octubre	0.55	0.95
Pota del Llop_2017_Octubre	Cova del Dofí_2017_Octubre	1.00	0.67
Pota del Llop_2017_Octubre	Freu_2017_Octubre	0.56	0.92
Pota del Llop_2017_Octubre	Freu_2018_Juliol	0.69	0.74
Pota del Llop_2017_Octubre	Freu_2018_Octubre	0.72	0.69
Pota del Llop_2017_Octubre	Medallot_2015_Octubre	0.57	0.92
Pota del Llop_2017_Octubre	Medallot_2016_Juliol	0.50	0.98
Pota del Llop_2017_Octubre	Medallot_2016_Octubre	0.56	0.94
Pota del Llop_2017_Octubre	Medallot_2017_Juliol	0.40	1.00
Pota del Llop_2017_Octubre	Medallot_2017_Octubre	0.67	0.86
Pota del Llop_2017_Octubre	Medallot_2018_Juliol	0.47	0.98
Pota del Llop_2017_Octubre	Medallot_2018_Octubre	0.65	0.80
Pota del Llop_2017_Octubre	Pota del Llop_2016_Juliol	0.57	0.92
Pota del Llop_2017_Octubre	Pota del Llop_2016_Octubre	0.50	0.98
Pota del Llop_2017_Octubre	Pota del Llop_2018_Juliol	0.86	0.54
Pota del Llop_2017_Octubre	Pota del Llop_2018_Octubre	0.75	0.76
Pota del Llop_2017_Octubre	Salpatxot_2016_Juliol	0.79	0.61
Pota del Llop_2017_Octubre	Salpatxot_2017_Octubre	0.75	0.76
Pota del Llop_2017_Octubre	Salpatxot_2018_Octubre	0.67	0.89
Pota del Llop_2017_Octubre	Tascó Gros_2015_Octubre	0.50	0.97
Pota del Llop_2017_Octubre	Tascó Gros_2016_Juliol	0.52	0.95
Pota del Llop_2017_Octubre	Tascó Gros_2016_Octubre	0.50	0.97
Pota del Llop_2017_Octubre	Tascó Gros_2017_Juliol	0.71	0.71
Pota del Llop_2017_Octubre	Tascó Gros_2017_Octubre	0.80	0.66
Pota del Llop_2017_Octubre	Tascó Gros_2018_Juliol	0.48	0.98
Pota del Llop_2017_Octubre	Tascó Gros_2018_Octubre	0.44	0.99
Pota del Llop_2018_Juliol	Cap Castell_2017_Octubre	0.31	0.61
Pota del Llop_2018_Juliol	Cap Castell_2018_Juliol	0.49	0.09
Pota del Llop_2018_Juliol	Cap Castell_2018_Octubre	0.69	<0.001
Pota del Llop_2018_Juliol	Cova de la Vaca_2016_Juliol	0.35	0.57
Pota del Llop_2018_Juliol	Cova de la Vaca_2016_Octubre	0.43	0.84
Pota del Llop_2018_Juliol	Cova de la Vaca_2018_Juliol	0.29	0.94
Pota del Llop_2018_Juliol	Cova del Dofí_2016_Juliol	0.33	0.71
Pota del Llop_2018_Juliol	Cova del Dofí_2016_Octubre	0.45	0.34
Pota del Llop_2018_Juliol	Cova del Dofí_2017_Octubre	0.57	0.69
Pota del Llop_2018_Juliol	Freu_2017_Octubre	0.56	0.04
Pota del Llop_2018_Juliol	Freu_2018_Juliol	0.69	<0.001

Pota del Llop_2018_Juliol	Freu_2018_Octubre	0.72	<0.001
Pota del Llop_2018_Juliol	Medallot_2015_Octubre	0.57	0.06
Pota del Llop_2018_Juliol	Medallot_2016_Juliol	0.42	0.43
Pota del Llop_2018_Juliol	Medallot_2016_Octubre	0.56	0.18
Pota del Llop_2018_Juliol	Medallot_2017_Juliol	0.46	0.58
Pota del Llop_2018_Juliol	Medallot_2017_Octubre	0.67	0.11
Pota del Llop_2018_Juliol	Medallot_2018_Juliol	0.45	0.17
Pota del Llop_2018_Juliol	Medallot_2018_Octubre	0.65	0.02
Pota del Llop_2018_Juliol	Pota del Llop_2016_Juliol	0.57	0.06
Pota del Llop_2018_Juliol	Pota del Llop_2016_Octubre	0.50	0.39
Pota del Llop_2018_Juliol	Pota del Llop_2017_Octubre	0.86	0.54
Pota del Llop_2018_Juliol	Pota del Llop_2018_Octubre	0.43	0.74
Pota del Llop_2018_Juliol	Salpatxot_2016_Juliol	0.21	0.98
Pota del Llop_2018_Juliol	Salpatxot_2017_Octubre	0.86	0.05
Pota del Llop_2018_Juliol	Salpatxot_2018_Octubre	0.43	0.84
Pota del Llop_2018_Juliol	Tascó Gros_2015_Octubre	0.46	0.19
Pota del Llop_2018_Juliol	Tascó Gros_2016_Juliol	0.43	0.20
Pota del Llop_2018_Juliol	Tascó Gros_2016_Octubre	0.50	0.18
Pota del Llop_2018_Juliol	Tascó Gros_2017_Juliol	0.29	0.75
Pota del Llop_2018_Juliol	Tascó Gros_2017_Octubre	0.80	0.05
Pota del Llop_2018_Juliol	Tascó Gros_2018_Juliol	0.48	0.14
Pota del Llop_2018_Juliol	Tascó Gros_2018_Octubre	0.52	0.23
Pota del Llop_2018_Octubre	Cap Castell_2017_Octubre	0.18	1.00
Pota del Llop_2018_Octubre	Cap Castell_2018_Juliol	0.42	0.51
Pota del Llop_2018_Octubre	Cap Castell_2018_Octubre	0.59	0.15
Pota del Llop_2018_Octubre	Cova de la Vaca_2016_Juliol	0.29	0.94
Pota del Llop_2018_Octubre	Cova de la Vaca_2016_Octubre	0.42	0.93
Pota del Llop_2018_Octubre	Cova de la Vaca_2018_Juliol	0.32	0.96
Pota del Llop_2018_Octubre	Cova del Dofí_2016_Juliol	0.33	0.89
Pota del Llop_2018_Octubre	Cova del Dofí_2016_Octubre	0.27	0.98
Pota del Llop_2018_Octubre	Cova del Dofí_2017_Octubre	0.75	0.44
Pota del Llop_2018_Octubre	Freu_2017_Octubre	0.50	0.31
Pota del Llop_2018_Octubre	Freu_2018_Juliol	0.65	0.08
Pota del Llop_2018_Octubre	Freu_2018_Octubre	0.70	0.05
Pota del Llop_2018_Octubre	Medallot_2015_Octubre	0.48	0.42
Pota del Llop_2018_Octubre	Medallot_2016_Juliol	0.42	0.67
Pota del Llop_2018_Octubre	Medallot_2016_Octubre	0.56	0.36

Pota del Llop_2018_Octubre	Medallot_2017_Juliol	0.55	0.51
Pota del Llop_2018_Octubre	Medallot_2017_Octubre	0.67	0.24
Pota del Llop_2018_Octubre	Medallot_2018_Juliol	0.37	0.70
Pota del Llop_2018_Octubre	Medallot_2018_Octubre	0.67	0.09
Pota del Llop_2018_Octubre	Pota del Llop_2016_Juliol	0.52	0.31
Pota del Llop_2018_Octubre	Pota del Llop_2016_Octubre	0.33	0.95
Pota del Llop_2018_Octubre	Pota del Llop_2017_Octubre	0.75	0.76
Pota del Llop_2018_Octubre	Pota del Llop_2018_Juliol	0.43	0.74
Pota del Llop_2018_Octubre	Salpatxot_2016_Juliol	0.32	0.90
Pota del Llop_2018_Octubre	Salpatxot_2017_Octubre	0.75	0.21
Pota del Llop_2018_Octubre	Salpatxot_2018_Octubre	0.33	0.99
Pota del Llop_2018_Octubre	Tascó Gros_2015_Octubre	0.48	0.40
Pota del Llop_2018_Octubre	Tascó Gros_2016_Juliol	0.38	0.67
Pota del Llop_2018_Octubre	Tascó Gros_2016_Octubre	0.44	0.57
Pota del Llop_2018_Octubre	Tascó Gros_2017_Juliol	0.21	1.00
Pota del Llop_2018_Octubre	Tascó Gros_2017_Octubre	0.80	0.12
Pota del Llop_2018_Octubre	Tascó Gros_2018_Juliol	0.47	0.41
Pota del Llop_2018_Octubre	Tascó Gros_2018_Octubre	0.53	0.42
Salpatxot_2016_Juliol	Cap Castell_2017_Octubre	0.34	0.19
Salpatxot_2016_Juliol	Cap Castell_2018_Juliol	0.44	0.01
Salpatxot_2016_Juliol	Cap Castell_2018_Octubre	0.62	<0.001
Salpatxot_2016_Juliol	Cova de la Vaca_2016_Juliol	0.24	0.79
Salpatxot_2016_Juliol	Cova de la Vaca_2016_Octubre	0.29	0.99
Salpatxot_2016_Juliol	Cova de la Vaca_2018_Juliol	0.43	0.36
Salpatxot_2016_Juliol	Cova del Dofí_2016_Juliol	0.26	0.77
Salpatxot_2016_Juliol	Cova del Dofí_2016_Octubre	0.31	0.59
Salpatxot_2016_Juliol	Cova del Dofí_2017_Octubre	0.43	0.90
Salpatxot_2016_Juliol	Freu_2017_Octubre	0.49	0.01
Salpatxot_2016_Juliol	Freu_2018_Juliol	0.58	<0.001
Salpatxot_2016_Juliol	Freu_2018_Octubre	0.63	<0.001
Salpatxot_2016_Juliol	Medallot_2015_Octubre	0.42	0.09
Salpatxot_2016_Juliol	Medallot_2016_Juliol	0.40	0.24
Salpatxot_2016_Juliol	Medallot_2016_Octubre	0.57	0.06
Salpatxot_2016_Juliol	Medallot_2017_Juliol	0.59	0.16
Salpatxot_2016_Juliol	Medallot_2017_Octubre	0.60	0.10
Salpatxot_2016_Juliol	Medallot_2018_Juliol	0.41	0.05
Salpatxot_2016_Juliol	Medallot_2018_Octubre	0.71	<0.001

Salpatxot_2016_Juliol	Pota del Llop_2016_Juliol	0.48	0.04
Salpatxot_2016_Juliol	Pota del Llop_2016_Octubre	0.36	0.66
Salpatxot_2016_Juliol	Pota del Llop_2017_Octubre	0.79	0.61
Salpatxot_2016_Juliol	Pota del Llop_2018_Juliol	0.21	0.98
Salpatxot_2016_Juliol	Pota del Llop_2018_Octubre	0.32	0.90
Salpatxot_2016_Juliol	Salpatxot_2017_Octubre	0.79	0.04
Salpatxot_2016_Juliol	Salpatxot_2018_Octubre	0.57	0.40
Salpatxot_2016_Juliol	Tascó Gros_2015_Octubre	0.45	0.05
Salpatxot_2016_Juliol	Tascó Gros_2016_Juliol	0.36	0.11
Salpatxot_2016_Juliol	Tascó Gros_2016_Octubre	0.45	0.10
Salpatxot_2016_Juliol	Tascó Gros_2017_Juliol	0.36	0.18
Salpatxot_2016_Juliol	Tascó Gros_2017_Octubre	0.79	0.02
Salpatxot_2016_Juliol	Tascó Gros_2018_Juliol	0.48	0.03
Salpatxot_2016_Juliol	Tascó Gros_2018_Octubre	0.49	0.14
Salpatxot_2017_Octubre	Cap Castell_2017_Octubre	0.64	0.11
Salpatxot_2017_Octubre	Cap Castell_2018_Juliol	0.45	0.41
Salpatxot_2017_Octubre	Cap Castell_2018_Octubre	0.24	0.98
Salpatxot_2017_Octubre	Cova de la Vaca_2016_Juliol	0.65	0.13
Salpatxot_2017_Octubre	Cova de la Vaca_2016_Octubre	0.75	0.29
Salpatxot_2017_Octubre	Cova de la Vaca_2018_Juliol	0.71	0.15
Salpatxot_2017_Octubre	Cova del Dofí_2016_Juliol	0.58	0.26
Salpatxot_2017_Octubre	Cova del Dofí_2016_Octubre	0.55	0.35
Salpatxot_2017_Octubre	Cova del Dofí_2017_Octubre	1.00	0.13
Salpatxot_2017_Octubre	Freu_2017_Octubre	0.34	0.79
Salpatxot_2017_Octubre	Freu_2018_Juliol	0.31	0.84
Salpatxot_2017_Octubre	Freu_2018_Octubre	0.34	0.77
Salpatxot_2017_Octubre	Medallot_2015_Octubre	0.49	0.39
Salpatxot_2017_Octubre	Medallot_2016_Juliol	0.58	0.26
Salpatxot_2017_Octubre	Medallot_2016_Octubre	0.33	0.92
Salpatxot_2017_Octubre	Medallot_2017_Juliol	0.75	0.16
Salpatxot_2017_Octubre	Medallot_2017_Octubre	0.33	0.95
Salpatxot_2017_Octubre	Medallot_2018_Juliol	0.47	0.39
Salpatxot_2017_Octubre	Medallot_2018_Octubre	0.38	0.68
Salpatxot_2017_Octubre	Pota del Llop_2016_Juliol	0.45	0.51
Salpatxot_2017_Octubre	Pota del Llop_2016_Octubre	0.75	0.13
Salpatxot_2017_Octubre	Pota del Llop_2017_Octubre	0.75	0.76
Salpatxot_2017_Octubre	Pota del Llop_2018_Juliol	0.86	0.05

Salpatxot_2017_Octubre	Pota del Llop_2018_Octubre	0.75	0.21
Salpatxot_2017_Octubre	Salpatxot_2016_Juliol	0.79	0.04
Salpatxot_2017_Octubre	Salpatxot_2018_Octubre	0.75	0.29
Salpatxot_2017_Octubre	Tascó Gros_2015_Octubre	0.50	0.35
Salpatxot_2017_Octubre	Tascó Gros_2016_Juliol	0.52	0.27
Salpatxot_2017_Octubre	Tascó Gros_2016_Octubre	0.38	0.76
Salpatxot_2017_Octubre	Tascó Gros_2017_Juliol	0.71	0.06
Salpatxot_2017_Octubre	Tascó Gros_2017_Octubre	0.55	0.51
Salpatxot_2017_Octubre	Tascó Gros_2018_Juliol	0.54	0.25
Salpatxot_2017_Octubre	Tascó Gros_2018_Octubre	0.53	0.42
Salpatxot_2018_Octubre	Cap Castell_2017_Octubre	0.37	0.84
Salpatxot_2018_Octubre	Cap Castell_2018_Juliol	0.33	0.90
Salpatxot_2018_Octubre	Cap Castell_2018_Octubre	0.55	0.34
Salpatxot_2018_Octubre	Cova de la Vaca_2016_Juliol	0.47	0.62
Salpatxot_2018_Octubre	Cova de la Vaca_2016_Octubre	0.67	0.52
Salpatxot_2018_Octubre	Cova de la Vaca_2018_Juliol	0.29	1.00
Salpatxot_2018_Octubre	Cova del Dofí_2016_Juliol	0.50	0.59
Salpatxot_2018_Octubre	Cova del Dofí_2016_Octubre	0.36	0.91
Salpatxot_2018_Octubre	Cova del Dofí_2017_Octubre	1.00	0.18
Salpatxot_2018_Octubre	Freu_2017_Octubre	0.42	0.70
Salpatxot_2018_Octubre	Freu_2018_Juliol	0.57	0.29
Salpatxot_2018_Octubre	Freu_2018_Octubre	0.64	0.19
Salpatxot_2018_Octubre	Medallot_2015_Octubre	0.39	0.81
Salpatxot_2018_Octubre	Medallot_2016_Juliol	0.33	0.95
Salpatxot_2018_Octubre	Medallot_2016_Octubre	0.56	0.49
Salpatxot_2018_Octubre	Medallot_2017_Juliol	0.47	0.81
Salpatxot_2018_Octubre	Medallot_2017_Octubre	0.50	0.70
Salpatxot_2018_Octubre	Medallot_2018_Juliol	0.31	0.95
Salpatxot_2018_Octubre	Medallot_2018_Octubre	0.62	0.26
Salpatxot_2018_Octubre	Pota del Llop_2016_Juliol	0.36	0.88
Salpatxot_2018_Octubre	Pota del Llop_2016_Octubre	0.50	0.70
Salpatxot_2018_Octubre	Pota del Llop_2017_Octubre	0.67	0.89
Salpatxot_2018_Octubre	Pota del Llop_2018_Juliol	0.43	0.84
Salpatxot_2018_Octubre	Pota del Llop_2018_Octubre	0.33	0.99
Salpatxot_2018_Octubre	Salpatxot_2016_Juliol	0.57	0.40
Salpatxot_2018_Octubre	Salpatxot_2017_Octubre	0.75	0.29
Salpatxot_2018_Octubre	Tascó Gros_2015_Octubre	0.42	0.72

Salpatxot_2018_Octubre	Tascó Gros_2016_Juliol	0.38	0.82
Salpatxot_2018_Octubre	Tascó Gros_2016_Octubre	0.38	0.87
Salpatxot_2018_Octubre	Tascó Gros_2017_Juliol	0.43	0.70
Salpatxot_2018_Octubre	Tascó Gros_2017_Octubre	0.67	0.38
Salpatxot_2018_Octubre	Tascó Gros_2018_Juliol	0.39	0.80
Salpatxot_2018_Octubre	Tascó Gros_2018_Octubre	0.44	0.77
Tascó Gros_2015_Octubre	Cap Castell_2017_Octubre	0.32	0.10
Tascó Gros_2015_Octubre	Cap Castell_2018_Juliol	0.17	0.56
Tascó Gros_2015_Octubre	Cap Castell_2018_Octubre	0.26	0.16
Tascó Gros_2015_Octubre	Cova de la Vaca_2016_Juliol	0.32	0.25
Tascó Gros_2015_Octubre	Cova de la Vaca_2016_Octubre	0.47	0.58
Tascó Gros_2015_Octubre	Cova de la Vaca_2018_Juliol	0.27	0.82
Tascó Gros_2015_Octubre	Cova del Dofí_2016_Juliol	0.31	0.42
Tascó Gros_2015_Octubre	Cova del Dofí_2016_Octubre	0.28	0.60
Tascó Gros_2015_Octubre	Cova del Dofí_2017_Octubre	0.81	0.18
Tascó Gros_2015_Octubre	Freu_2017_Octubre	0.16	0.77
Tascó Gros_2015_Octubre	Freu_2018_Juliol	0.22	0.23
Tascó Gros_2015_Octubre	Freu_2018_Octubre	0.26	0.17
Tascó Gros_2015_Octubre	Medallot_2015_Octubre	0.20	0.72
Tascó Gros_2015_Octubre	Medallot_2016_Juliol	0.27	0.59
Tascó Gros_2015_Octubre	Medallot_2016_Octubre	0.27	0.72
Tascó Gros_2015_Octubre	Medallot_2017_Juliol	0.42	0.44
Tascó Gros_2015_Octubre	Medallot_2017_Octubre	0.21	0.99
Tascó Gros_2015_Octubre	Medallot_2018_Juliol	0.13	0.95
Tascó Gros_2015_Octubre	Medallot_2018_Octubre	0.27	0.30
Tascó Gros_2015_Octubre	Pota del Llop_2016_Juliol	0.15	0.93
Tascó Gros_2015_Octubre	Pota del Llop_2016_Octubre	0.42	0.35
Tascó Gros_2015_Octubre	Pota del Llop_2017_Octubre	0.50	0.97
Tascó Gros_2015_Octubre	Pota del Llop_2018_Juliol	0.46	0.19
Tascó Gros_2015_Octubre	Pota del Llop_2018_Octubre	0.48	0.40
Tascó Gros_2015_Octubre	Salpatxot_2016_Juliol	0.45	0.05
Tascó Gros_2015_Octubre	Salpatxot_2017_Octubre	0.50	0.35
Tascó Gros_2015_Octubre	Salpatxot_2018_Octubre	0.42	0.72
Tascó Gros_2015_Octubre	Tascó Gros_2016_Juliol	0.18	0.63
Tascó Gros_2015_Octubre	Tascó Gros_2016_Octubre	0.13	1.00
Tascó Gros_2015_Octubre	Tascó Gros_2017_Juliol	0.38	0.04
Tascó Gros_2015_Octubre	Tascó Gros_2017_Octubre	0.35	0.70

Tascó Gros_2015_Octubre	Tascó Gros_2018_Juliol	0.21	0.57
Tascó Gros_2015_Octubre	Tascó Gros_2018_Octubre	0.27	0.70
Tascó Gros_2016_Juliol	Cap Castell_2017_Octubre	0.21	0.31
Tascó Gros_2016_Juliol	Cap Castell_2018_Juliol	0.15	0.33
Tascó Gros_2016_Juliol	Cap Castell_2018_Octubre	0.32	<0.001
Tascó Gros_2016_Juliol	Cova de la Vaca_2016_Juliol	0.21	0.59
Tascó Gros_2016_Juliol	Cova de la Vaca_2016_Octubre	0.45	0.60
Tascó Gros_2016_Juliol	Cova de la Vaca_2018_Juliol	0.21	0.94
Tascó Gros_2016_Juliol	Cova del Dofí_2016_Juliol	0.23	0.66
Tascó Gros_2016_Juliol	Cova del Dofí_2016_Octubre	0.17	0.95
Tascó Gros_2016_Juliol	Cova del Dofí_2017_Octubre	0.71	0.28
Tascó Gros_2016_Juliol	Freu_2017_Octubre	0.22	0.17
Tascó Gros_2016_Juliol	Freu_2018_Juliol	0.33	<0.001
Tascó Gros_2016_Juliol	Freu_2018_Octubre	0.38	<0.001
Tascó Gros_2016_Juliol	Medallot_2015_Octubre	0.19	0.60
Tascó Gros_2016_Juliol	Medallot_2016_Juliol	0.13	1.00
Tascó Gros_2016_Juliol	Medallot_2016_Octubre	0.29	0.55
Tascó Gros_2016_Juliol	Medallot_2017_Juliol	0.32	0.73
Tascó Gros_2016_Juliol	Medallot_2017_Octubre	0.35	0.54
Tascó Gros_2016_Juliol	Medallot_2018_Juliol	0.15	0.59
Tascó Gros_2016_Juliol	Medallot_2018_Octubre	0.44	<0.001
Tascó Gros_2016_Juliol	Pota del Llop_2016_Juliol	0.20	0.52
Tascó Gros_2016_Juliol	Pota del Llop_2016_Octubre	0.32	0.63
Tascó Gros_2016_Juliol	Pota del Llop_2017_Octubre	0.52	0.95
Tascó Gros_2016_Juliol	Pota del Llop_2018_Juliol	0.43	0.20
Tascó Gros_2016_Juliol	Pota del Llop_2018_Octubre	0.38	0.67
Tascó Gros_2016_Juliol	Salpatxot_2016_Juliol	0.36	0.11
Tascó Gros_2016_Juliol	Salpatxot_2017_Octubre	0.52	0.27
Tascó Gros_2016_Juliol	Salpatxot_2018_Octubre	0.38	0.82
Tascó Gros_2016_Juliol	Tascó Gros_2015_Octubre	0.18	0.63
Tascó Gros_2016_Juliol	Tascó Gros_2016_Octubre	0.25	0.42
Tascó Gros_2016_Juliol	Tascó Gros_2017_Juliol	0.25	0.19
Tascó Gros_2016_Juliol	Tascó Gros_2017_Octubre	0.48	0.24
Tascó Gros_2016_Juliol	Tascó Gros_2018_Juliol	0.17	0.63
Tascó Gros_2016_Juliol	Tascó Gros_2018_Octubre	0.18	0.95
Tascó Gros_2016_Octubre	Cap Castell_2017_Octubre	0.27	0.42
Tascó Gros_2016_Octubre	Cap Castell_2018_Juliol	0.16	0.88

Tascó Gros_2016_Octubre	Cap Castell_2018_Octubre	0.25	0.38
Tascó Gros_2016_Octubre	Cova de la Vaca_2016_Juliol	0.35	0.28
Tascó Gros_2016_Octubre	Cova de la Vaca_2016_Octubre	0.54	0.45
Tascó Gros_2016_Octubre	Cova de la Vaca_2018_Juliol	0.34	0.63
Tascó Gros_2016_Octubre	Cova del Dofí_2016_Juliol	0.38	0.29
Tascó Gros_2016_Octubre	Cova del Dofí_2016_Octubre	0.24	0.85
Tascó Gros_2016_Octubre	Cova del Dofí_2017_Octubre	0.88	0.13
Tascó Gros_2016_Octubre	Freu_2017_Octubre	0.13	0.99
Tascó Gros_2016_Octubre	Freu_2018_Juliol	0.27	0.25
Tascó Gros_2016_Octubre	Freu_2018_Octubre	0.33	0.13
Tascó Gros_2016_Octubre	Medallot_2015_Octubre	0.27	0.52
Tascó Gros_2016_Octubre	Medallot_2016_Juliol	0.25	0.78
Tascó Gros_2016_Octubre	Medallot_2016_Octubre	0.25	0.86
Tascó Gros_2016_Octubre	Medallot_2017_Juliol	0.38	0.66
Tascó Gros_2016_Octubre	Medallot_2017_Octubre	0.29	0.85
Tascó Gros_2016_Octubre	Medallot_2018_Juliol	0.13	0.99
Tascó Gros_2016_Octubre	Medallot_2018_Octubre	0.30	0.32
Tascó Gros_2016_Octubre	Pota del Llop_2016_Juliol	0.15	0.99
Tascó Gros_2016_Octubre	Pota del Llop_2016_Octubre	0.38	0.57
Tascó Gros_2016_Octubre	Pota del Llop_2017_Octubre	0.50	0.97
Tascó Gros_2016_Octubre	Pota del Llop_2018_Juliol	0.50	0.18
Tascó Gros_2016_Octubre	Pota del Llop_2018_Octubre	0.44	0.57
Tascó Gros_2016_Octubre	Salpatxot_2016_Juliol	0.45	0.10
Tascó Gros_2016_Octubre	Salpatxot_2017_Octubre	0.38	0.76
Tascó Gros_2016_Octubre	Salpatxot_2018_Octubre	0.38	0.87
Tascó Gros_2016_Octubre	Tascó Gros_2015_Octubre	0.13	1.00
Tascó Gros_2016_Octubre	Tascó Gros_2016_Juliol	0.25	0.42
Tascó Gros_2016_Octubre	Tascó Gros_2017_Juliol	0.34	0.19
Tascó Gros_2016_Octubre	Tascó Gros_2017_Octubre	0.43	0.50
Tascó Gros_2016_Octubre	Tascó Gros_2018_Juliol	0.18	0.89
Tascó Gros_2016_Octubre	Tascó Gros_2018_Octubre	0.20	0.97
Tascó Gros_2017_Juliol	Cap Castell_2017_Octubre	0.14	0.91
Tascó Gros_2017_Juliol	Cap Castell_2018_Juliol	0.29	0.05
Tascó Gros_2017_Juliol	Cap Castell_2018_Octubre	0.50	<0.001
Tascó Gros_2017_Juliol	Cova de la Vaca_2016_Juliol	0.24	0.60
Tascó Gros_2017_Juliol	Cova de la Vaca_2016_Octubre	0.45	0.64
Tascó Gros_2017_Juliol	Cova de la Vaca_2018_Juliol	0.29	0.75

Tascó Gros_2017_Juliol	Cova del Dofí_2016_Juliol	0.33	0.31
Tascó Gros_2017_Juliol	Cova del Dofí_2016_Octubre	0.27	0.60
Tascó Gros_2017_Juliol	Cova del Dofí_2017_Octubre	0.61	0.50
Tascó Gros_2017_Juliol	Freu_2017_Octubre	0.40	0.01
Tascó Gros_2017_Juliol	Freu_2018_Juliol	0.55	<0.001
Tascó Gros_2017_Juliol	Freu_2018_Octubre	0.60	<0.001
Tascó Gros_2017_Juliol	Medallot_2015_Octubre	0.34	0.12
Tascó Gros_2017_Juliol	Medallot_2016_Juliol	0.21	0.84
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Tascó Gros_2017_Juliol	Medallot_2018_Octubre	0.62	<0.001
Tascó Gros_2017_Juliol	Pota del Llop_2016_Juliol	0.38	0.05
Tascó Gros_2017_Juliol	Pota del Llop_2016_Octubre	0.23	0.96
Tascó Gros_2017_Juliol	Pota del Llop_2017_Octubre	0.71	0.71
Tascó Gros_2017_Juliol	Pota del Llop_2018_Juliol	0.29	0.75
Tascó Gros_2017_Juliol	Pota del Llop_2018_Octubre	0.21	1.00
Tascó Gros_2017_Juliol	Salpatxot_2016_Juliol	0.36	0.18
Tascó Gros_2017_Juliol	Salpatxot_2017_Octubre	0.71	0.06
Tascó Gros_2017_Juliol	Salpatxot_2018_Octubre	0.43	0.70
Tascó Gros_2017_Juliol	Tascó Gros_2015_Octubre	0.38	0.04
Tascó Gros_2017_Juliol	Tascó Gros_2016_Juliol	0.25	0.19
Tascó Gros_2017_Juliol	Tascó Gros_2016_Octubre	0.34	0.19
Tascó Gros_2017_Juliol	Tascó Gros_2017_Octubre	0.66	0.05
Tascó Gros_2017_Juliol	Tascó Gros_2018_Juliol	0.30	0.16
Tascó Gros_2017_Juliol	Tascó Gros_2018_Octubre	0.38	0.28
Tascó Gros_2017_Octubre	Cap Castell_2017_Octubre	0.66	0.05
Tascó Gros_2017_Octubre	Cap Castell_2018_Juliol	0.42	0.38
Tascó Gros_2017_Octubre	Cap Castell_2018_Octubre	0.35	0.60
Tascó Gros_2017_Octubre	Cova de la Vaca_2016_Juliol	0.59	0.14
Tascó Gros_2017_Octubre	Cova de la Vaca_2016_Octubre	0.67	0.38
Tascó Gros_2017_Octubre	Cova de la Vaca_2018_Juliol	0.51	0.42
Tascó Gros_2017_Octubre	Cova del Dofí_2016_Juliol	0.58	0.18
Tascó Gros_2017_Octubre	Cova del Dofí_2016_Octubre	0.55	0.26
Tascó Gros_2017_Octubre	Cova del Dofí_2017_Octubre	1.00	0.11
Tascó Gros_2017_Octubre	Freu_2017_Octubre	0.30	0.81

Tascó Gros_2017_Octubre	Freu_2018_Juliol	0.37	0.52
Tascó Gros_2017_Octubre	Freu_2018_Octubre	0.44	0.33
Tascó Gros_2017_Octubre	Medallot_2015_Octubre	0.43	0.42
Tascó Gros_2017_Octubre	Medallot_2016_Juliol	0.55	0.24
Tascó Gros_2017_Octubre	Medallot_2016_Octubre	0.36	0.81
Tascó Gros_2017_Octubre	Medallot_2017_Juliol	0.60	0.33
Tascó Gros_2017_Octubre	Medallot_2017_Octubre	0.33	0.92
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Tascó Gros_2017_Octubre	Medallot_2018_Octubre	0.42	0.46
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Tascó Gros_2017_Octubre	Pota del Llop_2016_Octubre	0.63	0.22
Tascó Gros_2017_Octubre	Pota del Llop_2017_Octubre	0.80	0.66
Tascó Gros_2017_Octubre	Pota del Llop_2018_Juliol	0.80	0.05
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Tascó Gros_2017_Octubre	Salpatxot_2016_Juliol	0.79	0.02
Tascó Gros_2017_Octubre	Salpatxot_2017_Octubre	0.55	0.51
Tascó Gros_2017_Octubre	Salpatxot_2018_Octubre	0.67	0.38
Tascó Gros_2017_Octubre	Tascó Gros_2015_Octubre	0.35	0.70
Tascó Gros_2017_Octubre	Tascó Gros_2016_Juliol	0.48	0.24
Tascó Gros_2017_Octubre	Tascó Gros_2016_Octubre	0.43	0.50
Tascó Gros_2017_Octubre	Tascó Gros_2017_Juliol	0.66	0.05
Tascó Gros_2017_Octubre	Tascó Gros_2018_Juliol	0.46	0.34
Tascó Gros_2017_Octubre	Tascó Gros_2018_Octubre	0.58	0.23
Tascó Gros_2018_Juliol	Cap Castell_2017_Octubre	0.30	0.13
Tascó Gros_2018_Juliol	Cap Castell_2018_Juliol	0.09	0.99
Tascó Gros_2018_Juliol	Cap Castell_2018_Octubre	0.33	0.02
Tascó Gros_2018_Juliol	Cova de la Vaca_2016_Juliol	0.31	0.25
Tascó Gros_2018_Juliol	Cova de la Vaca_2016_Octubre	0.49	0.52
Tascó Gros_2018_Juliol	Cova de la Vaca_2018_Juliol	0.23	0.92
Tascó Gros_2018_Juliol	Cova del Dofí_2016_Juliol	0.33	0.32
Tascó Gros_2018_Juliol	Cova del Dofí_2016_Octubre	0.27	0.61
Tascó Gros_2018_Juliol	Cova del Dofí_2017_Octubre	0.72	0.28
Tascó Gros_2018_Juliol	Freu_2017_Octubre	0.23	0.30
Tascó Gros_2018_Juliol	Freu_2018_Juliol	0.38	<0.001
Tascó Gros_2018_Juliol	Freu_2018_Octubre	0.43	<0.001
Tascó Gros_2018_Juliol	Medallot_2015_Octubre	0.28	0.27
Tascó Gros_2018_Juliol	Medallot_2016_Juliol	0.11	1.00

Tascó Gros_2018_Juliol	Medallot_2016_Octubre	0.31	0.51
Tascó Gros_2018_Juliol	Medallot_2017_Juliol	0.28	0.88
Tascó Gros_2018_Juliol	Medallot_2017_Octubre	0.33	0.66
Tascó Gros_2018_Juliol	Medallot_2018_Juliol	0.11	0.97
Tascó Gros_2018_Juliol	Medallot_2018_Octubre	0.44	0.01
Tascó Gros_2018_Juliol	Pota del Llop_2016_Juliol	0.18	0.82
Tascó Gros_2018_Juliol	Pota del Llop_2016_Octubre	0.30	0.77
Tascó Gros_2018_Juliol	Pota del Llop_2017_Octubre	0.48	0.98
Tascó Gros_2018_Juliol	Pota del Llop_2018_Juliol	0.48	0.14
Tascó Gros_2018_Juliol	Pota del Llop_2018_Octubre	0.47	0.41
Tascó Gros_2018_Juliol	Salpatxot_2016_Juliol	0.48	0.03
Tascó Gros_2018_Juliol	Salpatxot_2017_Octubre	0.54	0.25
Tascó Gros_2018_Juliol	Salpatxot_2018_Octubre	0.39	0.80
Tascó Gros_2018_Juliol	Tascó Gros_2015_Octubre	0.21	0.57
Tascó Gros_2018_Juliol	Tascó Gros_2016_Juliol	0.17	0.63
Tascó Gros_2018_Juliol	Tascó Gros_2016_Octubre	0.18	0.89
Tascó Gros_2018_Juliol	Tascó Gros_2017_Juliol	0.30	0.16
Tascó Gros_2018_Juliol	Tascó Gros_2017_Octubre	0.46	0.34
Tascó Gros_2018_Juliol	Tascó Gros_2018_Octubre	0.15	1.00
Tascó Gros_2018_Octubre	Cap Castell_2017_Octubre	0.35	0.35
Tascó Gros_2018_Octubre	Cap Castell_2018_Juliol	0.17	0.97
Tascó Gros_2018_Octubre	Cap Castell_2018_Octubre	0.36	0.24
Tascó Gros_2018_Octubre	Cova de la Vaca_2016_Juliol	0.37	0.41
Tascó Gros_2018_Octubre	Cova de la Vaca_2016_Octubre	0.44	0.77
Tascó Gros_2018_Octubre	Cova de la Vaca_2018_Juliol	0.38	0.62
Tascó Gros_2018_Octubre	Cova del Dofí_2016_Juliol	0.28	0.82
Tascó Gros_2018_Octubre	Cova del Dofí_2016_Octubre	0.32	0.68
Tascó Gros_2018_Octubre	Cova del Dofí_2017_Octubre	0.78	0.28
Tascó Gros_2018_Octubre	Freu_2017_Octubre	0.29	0.55
Tascó Gros_2018_Octubre	Freu_2018_Juliol	0.44	0.08
Tascó Gros_2018_Octubre	Freu_2018_Octubre	0.48	0.05
Tascó Gros_2018_Octubre	Medallot_2015_Octubre	0.26	0.79
Tascó Gros_2018_Octubre	Medallot_2016_Juliol	0.17	1.00
Tascó Gros_2018_Octubre	Medallot_2016_Octubre	0.33	0.70
Tascó Gros_2018_Octubre	Medallot_2017_Juliol	0.24	0.99
Tascó Gros_2018_Octubre	Medallot_2017_Octubre	0.44	0.48
Tascó Gros_2018_Octubre	Medallot_2018_Juliol	0.17	0.97

Tascó Gros_2018_Octubre	Medallot_2018_Octubre	0.50	0.07
Tascó Gros_2018_Octubre	Pota del Llop_2016_Juliol	0.30	0.61
Tascó Gros_2018_Octubre	Pota del Llop_2016_Octubre	0.28	0.94
Tascó Gros_2018_Octubre	Pota del Llop_2017_Octubre	0.44	0.99
Tascó Gros_2018_Octubre	Pota del Llop_2018_Juliol	0.52	0.23
Tascó Gros_2018_Octubre	Pota del Llop_2018_Octubre	0.53	0.42
Tascó Gros_2018_Octubre	Salpatxot_2016_Juliol	0.49	0.14
Tascó Gros_2018_Octubre	Salpatxot_2017_Octubre	0.53	0.42
Tascó Gros_2018_Octubre	Salpatxot_2018_Octubre	0.44	0.77
Tascó Gros_2018_Octubre	Tascó Gros_2015_Octubre	0.27	0.70
Tascó Gros_2018_Octubre	Tascó Gros_2016_Juliol	0.18	0.95
Tascó Gros_2018_Octubre	Tascó Gros_2016_Octubre	0.20	0.97
Tascó Gros_2018_Octubre	Tascó Gros_2017_Juliol	0.38	0.28
Tascó Gros_2018_Octubre	Tascó Gros_2017_Octubre	0.58	0.23
Tascó Gros_2018_Octubre	Tascó Gros_2018_Juliol	0.15	1.00

Table S4. Generalized linear models (GLM) between response variables (survival, necrosis, and size *t1*) and the initial size of the colonies accounting for the frequentation levels (frequented VS non-frequented). In each case, we fitted the model accordingly with the distribution of the response variables (Negative binomial for necrosis; Poisson for size; Binomial for survival).

MODEL	Coefficients	Estimate	Std. error	Z value	p
Survival ~ size t0* protection	Intercept	-0.19	0.11	-1.77	0.08
	Size	0.04	0.02	2.28	**0.02**
	Protection	0.27	0.06	4.14	**<0.001**
	Size*Protection	-0.01	0.01	-0.98	0.32
Necrosis ~ size t0* protection	Intercept	1.16	6.38	0.183	0.855
	Size	-0.35	1.24	-0.286	0.775
	Protection	5.65	3.69	1.53	0.126
	Size* Protection	0.24	0.68	0.36	0.719
Size t1 ~ size t0 * protection	Intercept	0.50	0.25	1.99	0.04
	Size	0.12	0.03	3.59	**<0.001**
	Protection	0.53	0.13	4.01	**<0.001**
	Size* Protection	-0.03	0.01	-1.72	0.08

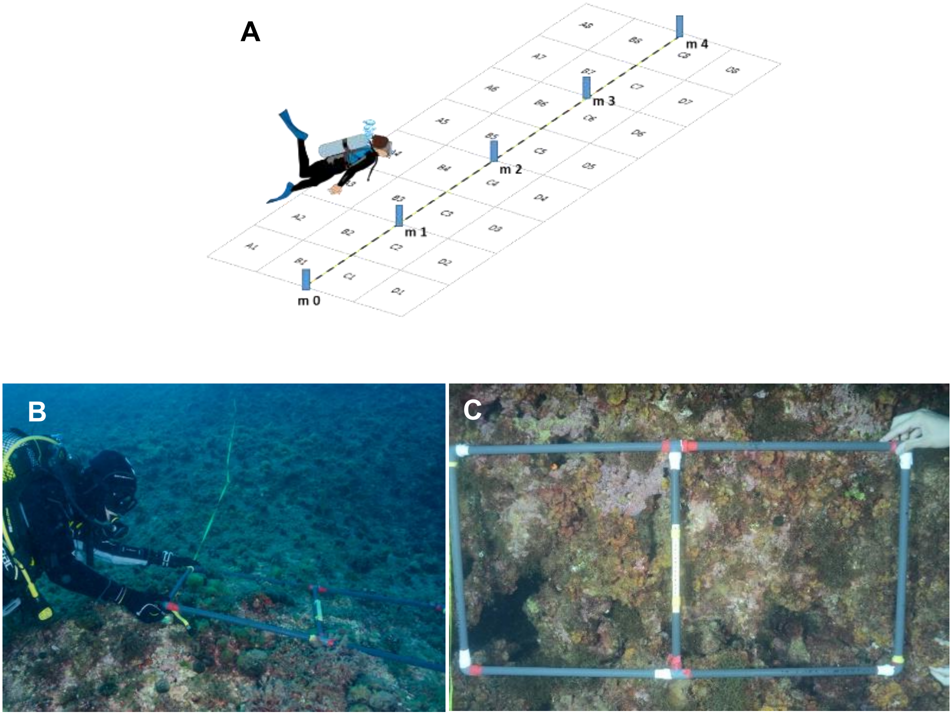

Figure S1. Monitoring design showing a part of a permanent transect with the location of the 0.5 m^2 squares (A). Details of the monitoring actions (B, C).

Supplementary material Chapter V

Table S1. Generalized linear models (GLM's) for recruitment enhancement experiment for *P. fascialis* between different responses variable and the predictor variable (monitoring action: time). The distribution of the response variable was fitted as binomial family for survival and recruitment, Gaussian for size (area), growth, shrinkage and density, and gamma for necrosis.

Table S2. Generalized linear models (GLM's) for recruitment enhancement experiment for *P. fascialis* between the response variable (growth, shrinkage, and necrosis respectively) and the predictor variable (size). The distribution of the response variable was fitted as gaussian family for growth and shrinkage, and gamma for necrosis.

Table S3. Generalized linear models (GLM's) for recruitment enhancement experiment for *Pentapora fascialis* between response variable (survival) and the initial value of predictor variables (size, time, recruitment, necrosis, growth and shrinkage). The distribution of the response variable was fitted as binomial family.

Table S4. Generalized linear models (GLM's) for transplants methodology experiment for *P. fascialis* between the response variable (survival) and the predictor variable (methodology). The distribution of response variable was fitted as binomial family.

Table S5. Generalized linear models (GLM's) for transplants of *P. fascialis* between the response variable (survival and growth respectively) and the initial values of predictor variable (size (height)). The distribution of the response variable was fitted as binomial family for survival and Gaussian for growth.

Figure S1. Types of recruitment surfaces for the enhancement of the recruitment of P. fascialis: A) 5x5 cm plain-surface natural rock/stone plates attached to the directly to the substrate using two-component epoxy putty; B) Structural 10x10 cm plastic grids each one subjected by a zip tie to a stainless bar fixed to the substrate and identified by a color code.

Figure S2. Partial mortality patterns of *P. fascialis* colonies. A) Colony without showing any signs of necrosis; B) Colony showing first signs of necrosis expressed as the loss of colony coloration; C) Detail of necrosed tissue.

Figure S3. Pilot action to find the best methodology for adult transplantation *P.fascialis* colonies. A) Restoration area; B) Manipulation of the colonies *in situ* ; C) Transport of adult colonies from the sea bottom to the boat to tying ex situ the colonies to the plastic screws; D) Methodology to manually tying the colonies to the plastic screws on the boat; E) Colonies attached do the plastic screws on the boat; F) Colony attached directly to the bottom using two-component epoxy putty; G) Colony attached to the bottom using a flange and plastic screw; and H) Colony attached to the bottom using a nylon thread and plastic screw.

Figure S4. A) Mean shrinkage (mm^2/month) between monitoring actions (time). B) GLM of mean shrinkage (mm^2/month) *vs* the initial size of the colonies.

Figure S5. Shrinkage (cm) *vs* initial size between the restoration action (October 2017) and after 8 months (July 2018).

Table S1. Generalized linear models (GLM's) for recruitment enhancement experiment for *P. fascialis* between different responses variable and the predictor variable (monitoring action: time). The distribution of the response variable was fitted as binomial family for survival and recruitment, Gaussian for size (area), growth, shrinkage and density, and gamma for necrosis.

MODEL	Coefficients	Estimate	Std. error	Z value	pr	AIC
Density ~ time	Intercept	5.88	0.55	10.62	**<0.001**	26.64
	Time	-0.39	0.142	-2.79	**0.006**	
Survival~ time	Intercept	2.99	0.428	6.996	**<0.001**	323.74
	Time	-0.578	0.12	-4.815	**<0.001**	
Size (area) ~ time	Intercept	3.11	0.14	21.59	**<0.001**	3983.6
	Time	0.74	0.04	16.58	**<0.001**	
Growth ~ time	Intercept	2.89	0.26	10.823	**<0.001**	3429.9
	Time	0.71	0.08	8.528	**<0.001**	
Shrinkage ~ time	Intercept	-12.72	42.48	-0.299	0.765	773.63
	Time	-21.21	11.84	-1.792	0.077	
Necrosis~ time	Intercept	-0.39	0.06	-6.21	**<0.001**	10323
	Time	0.85	0.015	53.013	**<0.001**	
Recruitment~ time	Intercept	3.08	0.44	6.99	**<0.001**	267.41
	Time	-1.48	0.17	-8.56	**<0.001**	

Table S2. Generalized linear models (GLM's) for recruitment enhancement experiment for *P. fascialis* between the response variable (growth, shrinkage, and necrosis respectively) and the predictor variable (size). The distribution of the response variable was fitted as gaussian family for growth and shrinkage, and gamma for necrosis.

MODEL	Coefficients	Estimate	Std. error	Z value	pr	AIC
Growth ~ size (area)	Intercept	-64.24	5.52	-11.62	**<0.001**	3764.7
	Size (area)	0.95	0.004	228.57	**<0.001**	
Shrinkage ~ size (area)	Intercept	-51.96	13.729	-3.785	**<0.001**	765.27
	Size (area)	-0.281	0.081	-3.505	**<0.001**	
Necrosis ~ size (area)	Intercept	14.39	1.687	8.531	**<0.001**	3017
	Size (area)	-0.001	0.001	-0.808	0.42	

Table S3. Generalized linear models (GLM's) for recruitment enhancement experiment for *Pentapora fascialis* between response variable (survival) and the initial value of predictor variables (size, time, recruitment, necrosis, growth and shrinkage). The distribution of the response variable was fitted as binomial family.

MODEL	Coefficients	Estimate	Std. error	Z value	pr	AIC
Survival ~ size (area)	Intercept	0.934	0.177	5.273	**<0.001**	362.01
	Size (area)	0.001	0.001	1.863	0.062	
	Time	-0.53	0.115	-4.628	**<0.001**	
Survival ~ size (area) * time	Intercept	3.49	0.661	5.286	**<0.001**	318.21
	Area	0.002	0.004	0.454	0.650	
	Time	-0.94	0.195	-4.860	**<0.001**	
	Size (area) * time	0.001	0.001	0.503	0.615	
Survival ~ recruitment	Intercept	0.84	0.14	5.84	**<0.001**	345.7
	Recruitment	1.52	0.37	4.04	**<0.001**	
Survival~ necrosis	Intercept	1.58	0.15	10.05	**<0.001**	341.83
	Necrosis	-0.02	0.01	-5.26	**<0.001**	
Survival ~ growth	Intercept	0.618	0.179	3.448	**<0.001**	325.82
	Growth	0.008	0.002	3.329	**<0.001**	
Survival ~ shrinkage	Intercept	0.22	0.37	0.595	0.552	90.537
	Shrinkage	-0.003	0.003	-0.981	0.326	

Table S4. Generalized linear models (GLM's) for transplants methodology experiment for *P. fascialis* between the response variable (survival) and the predictor variable (methodology). The distribution of response variable was fitted as binomial family.

MODEL	Coefficients	Estimate	Std. error	T value	pr	AIC
Survival ~ Methodology	Intercept	0.37	0.26	1.44	0.246	3.71
	Methodology	0.08	0.07	1.12	**0.034**	

Table S5. Generalized linear models (GLM's) for transplants of *P. fascialis* between the response variable (survival and growth respectively) and the initial values of predictor variable (size (height)). The distribution of the response variable was fitted as binomial family for survival and Gaussian for growth.

MODEL	Coefficients	Estimate	Std. error	Z value	pr	AIC
Survival ~ Size (height)	Intercept	-1.65	1.96	-0.83	0.406	29.367
	Size	0.19	0.286	0.695	0.487	
Growth ~Size (height)	Intercept	4.583	2.643	1.734	0.158	23.401
	Size	-1-168	0.373	-3.131	0.035	

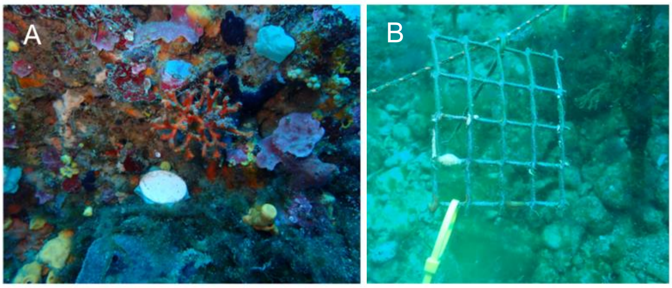

Figure S1. Types of recruitment surfaces for the enhancement of the recruitment of P. fascialis: A) 5x5 cm plain-surface natural rock/stone plates attached to the directly to the substrate using two-component epoxy putty; B) Structural 10x10 cm plastic grids each one subjected by a zip tie to a stainless bar fixed to the substrate and identified by a color code.

Figure S2. Partial mortality patterns of *P. fascialis* colonies. A) Colony without showing any signs of necrosis; B) Colony showing first signs of necrosis expressed as the loss of colony coloration; C) Detail of necrosed tissue.

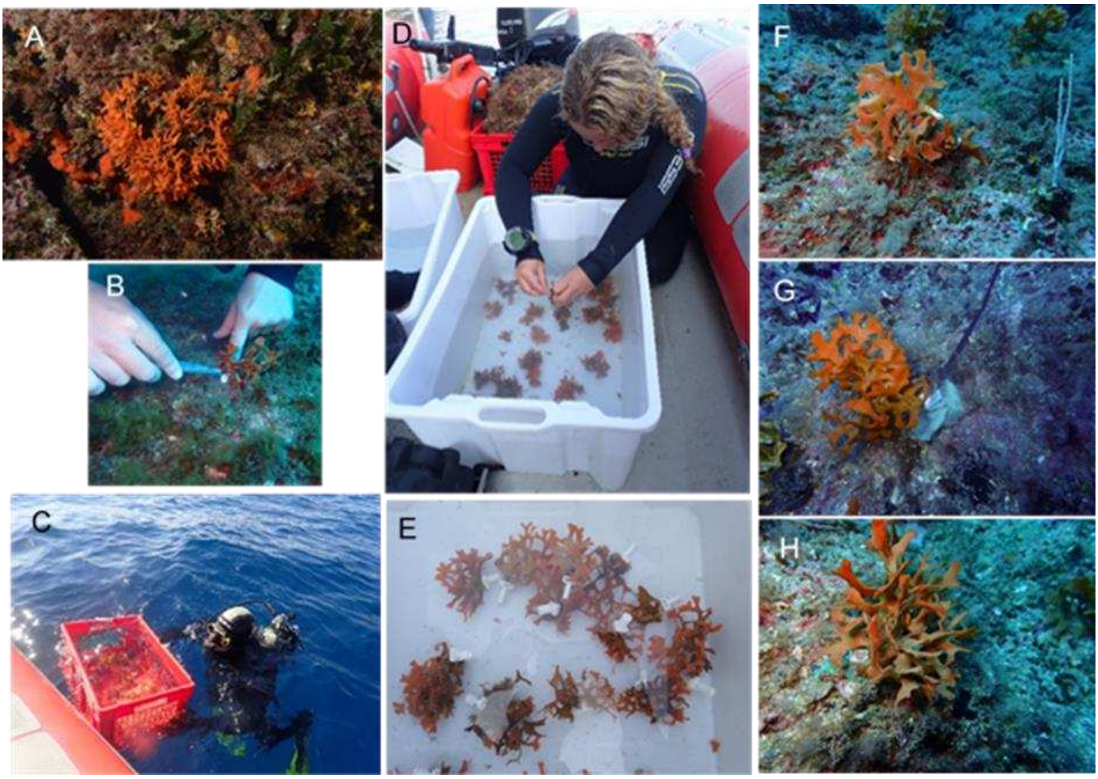

Figure S3. Pilot action to find the best methodology for adult transplantation *P.fascialis* colonies. A) Restoration area; B) Manipulation of the colonies *in situ*; C) Transport of adult colonies from the sea bottom to the boat to tying ex situ the colonies to the plastic screws; D) Methodology to manually tying the colonies to the plastic screws on the boat; E) Colonies attached do the plastic screws on the boat; F) Colony attached directly to the bottom using two-component epoxy putty; G) Colony attached to the bottom using a flange and plastic screw; and H) Colony attached to the bottom using a nylon thread and plastic screw.

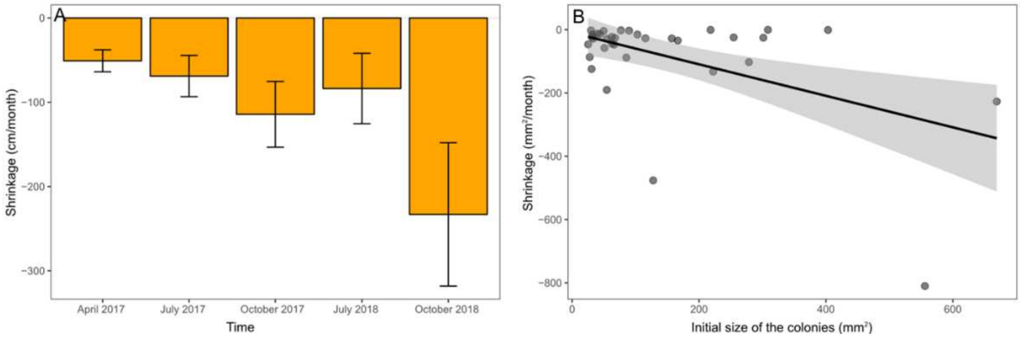

Figure S4. A) Mean shrinkage (mm^2/month) between monitoring actions (time). B) GLM of mean shrinkage (mm^2/month) *vs* the initial size of the colonies.

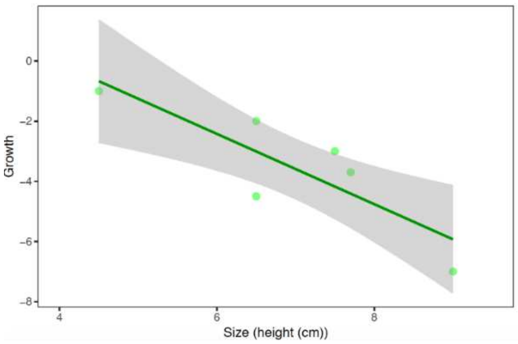

Figure S5. Shrinkage (cm) *vs* initial size between the restoration action (October 2017) and after 8 months (July 2018).

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Divergent responses to warming of two common co-occurring Mediterranean bryozoans

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Climate change threatens the structure and function of marine ecosystems, highlighting the importance of understanding the response of species to changing environmental conditions. However, thermal tolerance determining the vulnerability to warming of many abundant marine species is still poorly understood. In this study, we quantified in the field the effects of a temperature anomaly recorded in the Mediterranean Sea during the summer of 2015 on populations of two common sympatric bryozoans, *Myriapora truncata* and *Pentapora fascialis*. Then, we experimentally assessed their thermal tolerances in aquaria as well as different sublethal responses to warming. Differences between species were found in survival patterns in natural populations, *P. fascialis* showing significantly lower survival rates than *M. truncata*. The thermotolerance experiments supported field observations: *P. fascialis* started to show signs of necrosis when the temperature was raised to 25–26 °C and completely died between 28–29 °C, coinciding with the temperature when we observed first signs of necrosis in *M. truncata*. The results from this study reflect different responses to warming between these two co-occurring species, highlighting the importance of combining multiple approaches to assess the vulnerability of benthic species in a changing climate world.

Marine ecosystems are highly affected by climate change, with impacts predicted to increase in the coming years[1–3]. Specifically, climatic projections of global sea surface temperature predict 0.3–4.8 °C increase by the end of the 21st century, depending on the CO_2 emissions scenario[4]. In addition to the expected steady increase in temperature, in recent years there has been an increase in the frequency of heat waves, causing mass mortality events in marine ecosystems and affecting a wide variety of species such as gorgonians, sponges, algae and fishes in temperate and tropical seas[2,5–7]. Increases in recurrence of these mortalities can lead to population declines and widespread shifts in species distributions, which are currently occurring in all ecosystems as a consequence of environmental changes[8,9].

The fundamental niche of marine species is determined by their thermal tolerances, where their functional traits raise the optimal values, and an increase of temperature can affect negatively their physiological and demographic processes[10–12]. Due to climate change, in recent years there has been an increment of species that are frequently exposed to conditions over their thermotolerance limits, as the case of coral bleaching events[13,14] or mass mortalities of Mediterranean populations of gorgonians[5,6]. As a result, species with low tolerance to warming are at the greatest risk of local extinction because of their limited thermoregulatory ability[15,16]. Related to this, the mortality of non-thermotolerant habitat-forming or key species can have serious consequences on the entire community, reducing species richness and structural complexity of prominent habitats such as kelp forests or coral reefs[1,17].

The Mediterranean Sea is a biodiversity hotspot, highly threatened by climate change[18,19]. To understand the response of Mediterranean marine species to global warming, several studies have performed thermotolerance experiments in multiple co-occurring Mediterranean benthic species, such as anthozoans, revealing highly divergent levels of sensitivity[20–22]. In some cases, these divergences occur at population level, as in shallow populations of the red coral *Corallium rubrum* (Linnaeus, 1758), where some populations can be more tolerant to an increase

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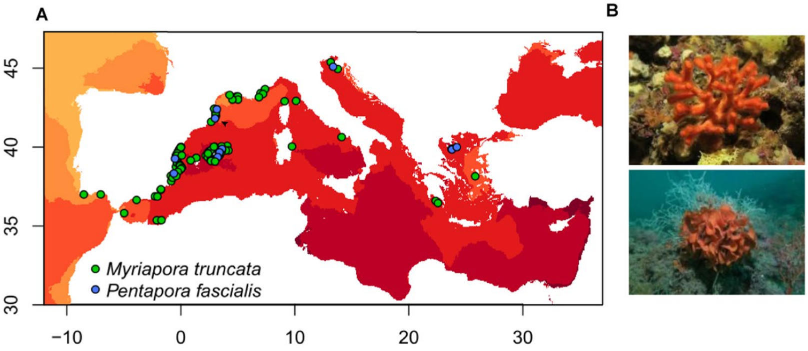

Figure 1. (**A**) The Mediterranean Sea and the study area (arrow) with maximum temperatures of the warmest month (August) represented by a color gradient and the distribution of studied species (occurrence data downloaded from OBIS and GBIF) represented by green and blue dots. (**B**) Model species: *Myriapora truncata* (top) and *Pentapora fascialis* (bottom).

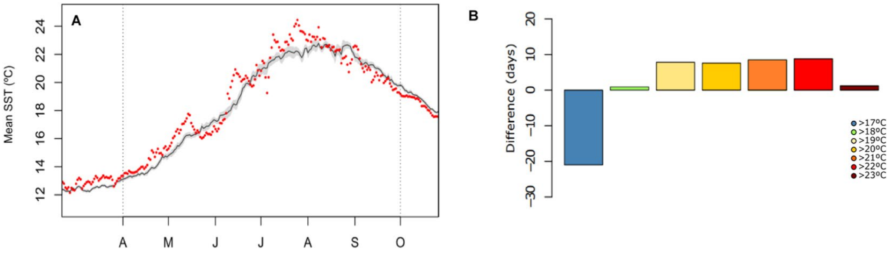

Figure 2. (**A**) Mean annual sea temperature recorded in 2015 (red dots) and the mean temperature recorded from 2005 to 2014 (gray line). (**B**) Difference in the number of days with high temperatures recorded in 2015 and those recorded from the mean of the previous years (2005–2014).

of temperature[23]. However, while most of the thermotolerance preference studies have focused on charismatic taxa, such as gorgonians or corals, there is a lack of knowledge about other abundant benthic organisms.

In this study, we focused on bryozoans, abundant colonial filter-feeding invertebrates that inhabit many types of benthic ecosystems, being absent or rare on muddy seabeds. In the Mediterranean Sea, bryozoans are prominent organisms on hard rocky benthic ecosystems, where their colonies can significantly increase the habitat complexity and provide shelter and microhabitats for other organisms[18,24,25]. Because of the fragility of some erect species to physical disturbances, some bryozoans are known as excellent ecological indicators for different stressors, such as storms or physical stress from recreational diving[26–28]. In this study, we selected two model co-occurring species of common and abundant Mediterranean bryozoans, *Myriapora truncata* (Pallas, 1766) and *Pentapora fascialis* (Pallas, 1766), with different distribution patterns at local and regional scales. Despite these two erect calcified species inhabiting similar hard rocky habitats across the Mediterranean, *M. truncata* populations are found from 1 m depth in marine caves to 60 m in coralligenous bottoms, reaching 130 m in Tunisian area. In contrast, populations of *P. fascialis* are found between 15–100 m depth in rocky bottoms[29] (Fig. 1). Despite previous field and experimental studies that have studied the effects of warming on Mediterranean bryozoans, most studies have focused on mineralogical, physiological and structural parameters[30,31]. To date, there is a lack of knowledge about the effects of temperature anomalies on demographic parameters of bryozoan populations and our study represents the first attempt to combine results from field and laboratory. Specifically, we combined field data of two erect heavily calcified species during a temperature anomaly in the Mediterranean in the summer of 2015, and the experimental study of the lethal and sublethal effects of thermal stress on both species in aquaria under controlled conditions.

Results

Field study.

Thermal regime in study area. Our results revealed a thermal anomaly in Medes islands during the summer of 2015 when the sea water temperature was higher than the average of the previous years (2005–2014) (19.32 ± 0.22 °C versus 18.99 ± 0.24 °C). Despite this difference was not significant, the maximum temperature reached during summer 2015 was higher than the previous years (24.5 °C versus 22.7 °C), with significantly more days of high temperatures (>22 °C) ($p < 0.001$) (Fig. 2).

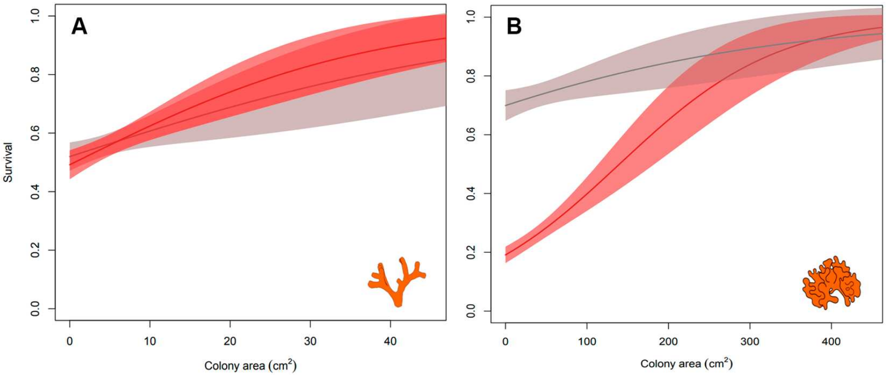

Figure 3. Survival of colonies of *Myriapora truncata* (**A**) and *Pentapora fascialis* (**B**) during winter 2014 (grey) and summer 2015 (red).

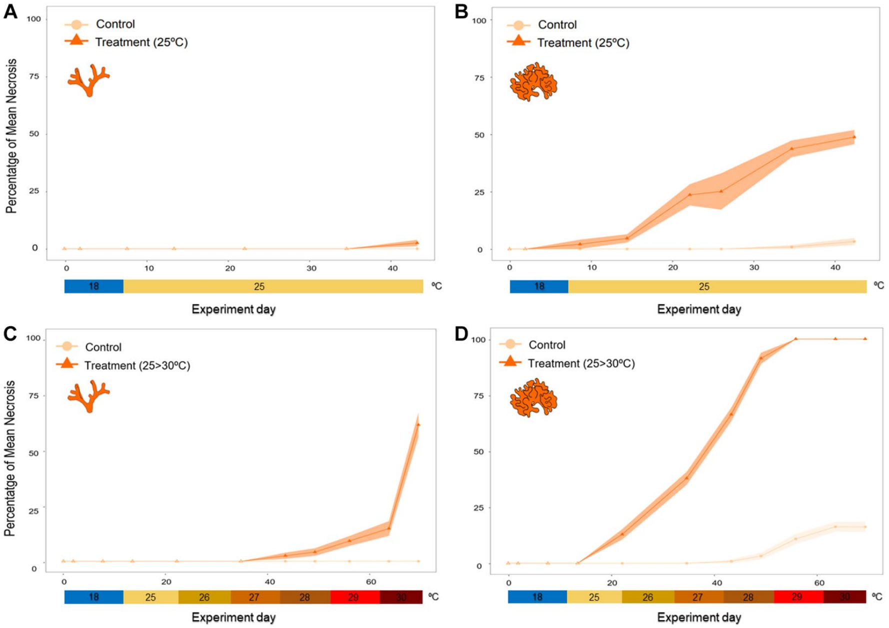

Figure 4. Partial mortality of both species (*Myriapora truncata* (**A,C**); *Pentapora fascialis* (**B, D**)) during thermal stress at 25 °C treatment (**A,B**) and increasing temperature treatment (from 25 °C to 30 °C treatment) (**C,D**).

Thermal anomaly effects in natural populations. We found differences in the survival between the two species in the field after the summer of 2015 (Supplementary Table S1). All colonies of *Myriapora truncata* showed a similar high survival in both studied periods (winter 2014: October 2014 – April 2015; summer 2015: April 2015 – October 2015). In contrast, survival of *Pentapora fascialis* colonies significantly decreased in summer 2015 at all localities ($p < 0.001$), independently of the protection level and habitat type (Fig. 3, Supplementary Table S2). In this period, most *P. fascialis* colonies died or were affected by necrosis (Supplementary Fig. S1). Survival rates were positively related to colony size ($p < 0.001$, Fig. 3, Supplementary Table S2).

Thermal stress under laboratory conditions.

Patterns of necrosis. There were significant differences between the response of species to thermal stress at 25 °C ($p < 0.001$) (Figs 4 and 5, Supplementary Tables S3 and Fig. S2), while in control treatments no sign of mortality was detected for either species. Specifically, colonies of

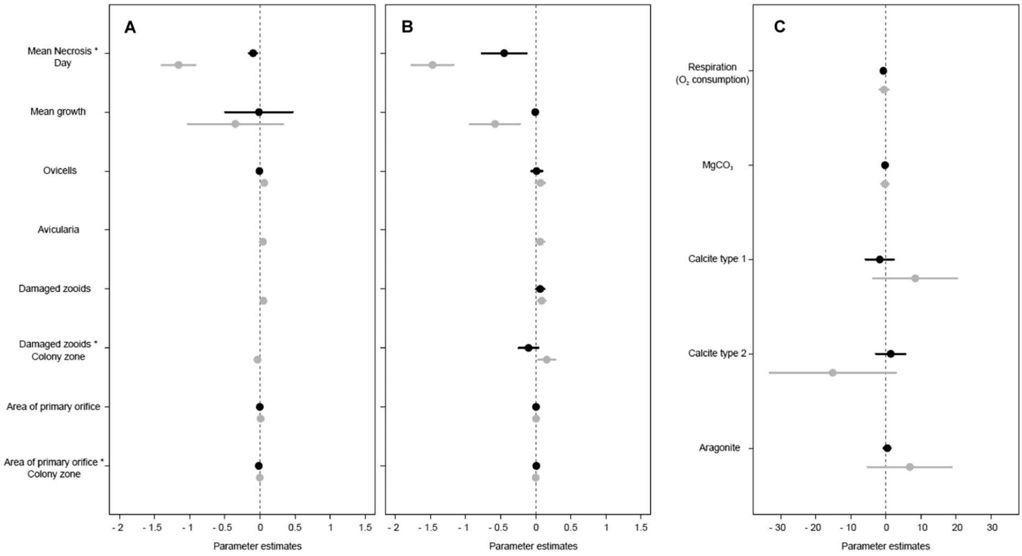

Figure 5. Summary of LM's parameter coefficients and 95% confidence intervals of studied species (in black, *Myriapora truncata*: in grey, *Pentapora fascialis*) for variables responses between treatments in thermal stress at 25 °C (**A**), increasing temperature experiment (**B**) (see Tables S4, S5) and non-lethal effects variables on thermal stress at 25 °C (**C**).

M. truncata did not show any signals of necrosis until the end of the experiment (44 days), when the colonies started to show small percentages of partial mortality (seen as a loss of coloration, see methodology). In contrast, colonies of *P. fascialis* started to exhibit necrosis around day 15. At the end of the experiment, all colonies showed around 50% partial mortality (Figs 4 and 5, Supplementary Table S4).

In the increasing temperature treatment, there were also differences between the responses of the two species to temperature ($p < 0.001$) (Figs 4 and 5, Supplementary Table S3 and Fig. S2). Colonies of *M. truncata* started to show necrosis only after 45–50 days when the temperature was 28 °C, and necrosis increased rapidly to 70% when the temperature was raised to 30 °C. In contrast, signs of partial mortality in *P. fascialis* colonies were observed after 15–20 days at 25–26 °C, about 20 days earlier and with 2 °C cooler temperature treatment than *M. truncata*. After this period, necrosis increased gradually with temperature, showing a 100% of mortality of all colonies when the temperature reached 28 °C after 45 days from the beginning of the experiment (Figs 4 and 5, Supplementary Table S5).

Growth rates. Colonies of both species showed higher growth rates in control than in both stress treatments, the differences being larger in *P. fascialis* rather than in *M. truncata*, but only significant for *P. fascialis* in the increasing temperature treatment ($p < 0.01$) (Figs 5 and 6, Supplementary Table S5).

Respiration rates. A decrease in oxygen consumption was found in all colonies of both species exposed to temperature treatments. However, this was not significant in both species or between them (Fig. 5, Supplementary Tables S4 and S7).

Structural and mineralogical analyses. Signs of skeletal damage in the temperature treatments were clearly observed in *P. fascialis* but were less evident in *M. truncata*. In the first treatment (25 °C), while colonies of *M. truncata* showed no signs of damaged zooids, colonies of *P. fascialis* showed some damaged zooids ($p = 0.010$) (Figs 5 and 7, Supplementary Tables S3 and S4). Moreover, the mean area of the primary orifice in *P. fascialis* was higher in colonies under thermal stress treatment ($p = 0.010$) (Supplementary Table S6).

In the increasing temperature treatment, despite colonies of *M. truncata* showed some damaged zooids, there were no significant differences between treatments. In contrast, *P. fascialis* also showed damaged zooids in colonies under the increasing temperature treatment, zooids at the distal growth tips of the colonies being most affected ($p = 0.010$) (Fig. 5, Supplementary Table S5). Moreover, as in thermal stress experiment, colonies of this species showed higher values for the mean area of the primary orifice ($p = 0.044$) (Supplementary Table S6). The other structural variables showed no trends between treatments and experiments (Supplementary Tables S3 and S4).

Mineralogical analyses did not show clear differences between treatments; however, we observed higher values of Mg in both species and of aragonite in *P. fascialis* when the colonies were exposed to high temperatures (Fig. 5, Supplementary Tables S4 and S7).

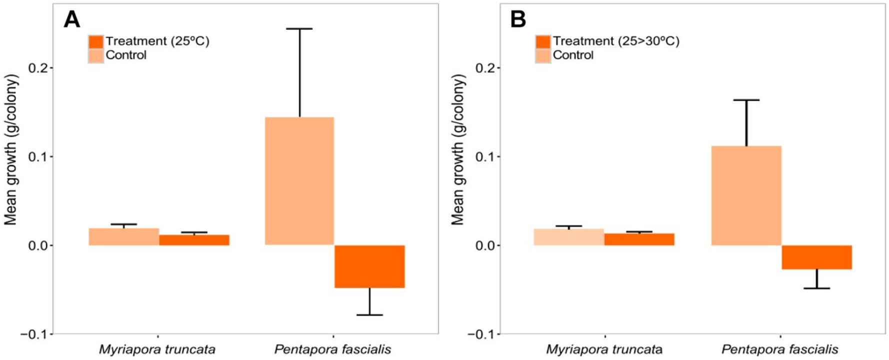

Figure 6. Mean growth (g/colony) between the beginning and the final in thermal stress (25 °C) experiment (**A**) and increasing temperature experiment (**B**) in both species.

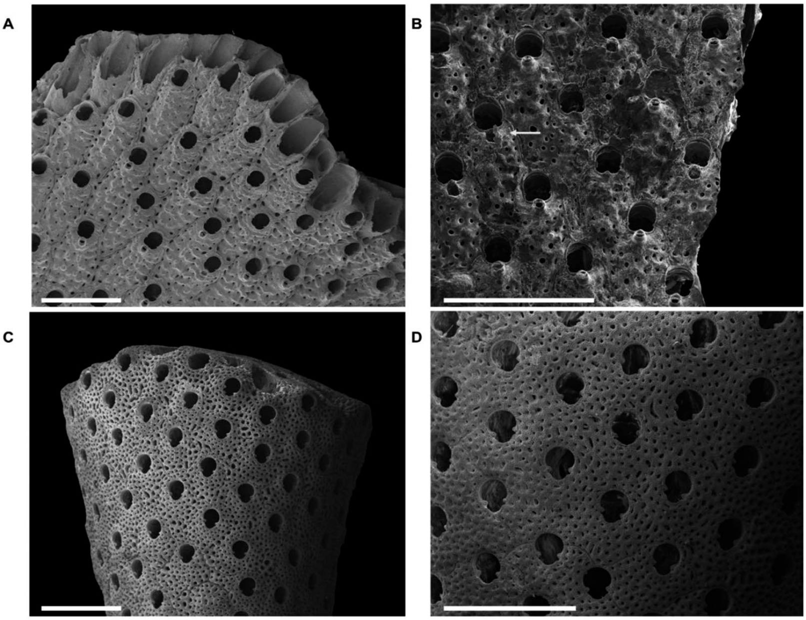

Figure 7. SEM images of *Pentapora fascialis* (**A**,**B**) and *Myriapora truncata* (**C**,**D**). (**A**,**C**) Growing colony edges under control treatment. (**B**) Group of autozooids with some suboral avicularia (arrowed) broken of *P. fascialis* under thermal stress treatment. (**D**) Portion of healthy colony of *M. truncata* under thermal stress treatment. *Scale bar* 1 mm.

Discussion

Assessing the thermal vulnerability of under-studied but abundant groups of organisms which are important members of many benthic communities such as bryozoans is vital to better understand how the distribution and structure of benthic communities will change under a warming ocean. Our results provide novel insights into the contrasting thermal vulnerability of two abundant and sympatric bryozoan species, highlighting the importance of studying species-specific responses.

Survival patterns in the field revealed a clearly contrasting vulnerability of each species to a thermal anomaly that occurred during summer 2015, showing a clear impact on populations of *Pentapora fascialis* (mainly affecting small-sized colonies), and negligible effects on *Myriapora truncata*. This result agrees with data from previous mass mortality events in the Mediterranean, which revealed *P. fascialis* to be among the affected species together with gorgonians, corals or sponges[5,6,32]. However, these previous studies did not detect differences between these two co-occurring bryozoan species. In agreement with field observations, aquarium experiments revealed differences in the vulnerability to thermal stress between the studied species, where *M. truncata* displayed a higher resistance to a wide range of thermal stress conditions. The maximum registered temperatures in our study area are 23–24 °C and an increment of 1–2 °C is predicted for the end of this century[4], suggesting that the ongoing warming trend may be critical for populations of *P. fascialis* in the future. Our findings also showed the importance of linking observational and experimental studies to understand the effects of climate change and its consequences for marine species inhabiting in similar habitats.

Beyond the lethal effects of thermal stress, our study also demonstrates other non-lethal effects of warming in *P. fascialis*, and in *M. truncata* to a less extent. On one hand, our results showed a decrease of growth caused by warming, which has been described in other studies focused on bryozoans[30,33,34]. On the other hand, in both species we registered a decreasing trend of respiration rates in colonies submitted to thermal stress, which suggest sublethal effects on their metabolic activity under thermal stress, in spite of the absence of necrosis in *M. truncata*. Moreover, structural analyses confirmed the negative effects of temperature on *P. fascialis*. In particular, analyses on Scanning Electron Microscope (SEM) showed a major proportion of damaged zooids in colonies exposed to temperature treatments in this species. Similarly, mean area of primary orifices was higher in temperature treatments, which may indicate that this orifice was broken and was registered as damaged zooids. These results suggest a dissolution or removing of the skeleton around the orifice increasing its area. Previous studies showed that temperature has effects on zooid size, skeletal growth, biomineral deposition and carbonate production on many species of bryozoans[35,36]. However, some of them showed that only a positive interaction between temperature and pH caused the corrosion of the *M. truncata* skeleton[31,37] highlighting the need to improve our understanding of the mechanisms behind the physiological responses of *P. fascialis* to thermal stress. On the other way, although the differences were not significant, we observed higher values of Mg in both species and of aragonite in *P. fascialis* respectively when the colonies were exposed to high temperatures. These findings agree with previous studies in other groups and other bryozoan species[38,39]. However, our results should be taken cautiously given the reduced sample size and the short-term exposures to these conditions.

Life history traits may also influence the response of species under climate change scenario[40]. Despite a general lack of information about the life history traits and population dynamics of bryozoans, there is evidence that *P. fascialis* grows faster than *M. truncata*[29,41]. The high vulnerability showed by *P. fascialis* is in accordance with the idea that species with faster dynamics are more vulnerable to environmental changes[42]. Future studies should explore the relationship between life-history traits and vulnerability in bryozoans and other temperate invertebrates.

The distributional patterns of species reflect their realized niche and environmental tolerances[43]. Both bryozoan species inhabit similar habitats across the Mediterranean, from shallow hard-rocky bottoms to coralligenous assemblages, however it is known that populations of *M. truncata* can be shallower than *P. fascialis*[29]. In this way, we hypothesize that in the areas where the temperature is warmer, *P. fascialis* may habit deeper where the temperature is not so high, contrary to populations of *M. truncata*. Accordingly, many studies showed that the coexistence of similar species involves divergences in some ecological aspect, as temperature tolerance, to adapt to different parts of the environmental gradient[44,45] which agrees with our results. Nevertheless, it is crucial to explore the relationship between distribution patterns and environmental variables to accurately model their ecological niches. However, it is important to take into account the limitations of working with open databases. In our study, we found that due to the actual disagreement about whether *P. fascialis* and *P. foliacea* are separate species, all registers in north-Atlantic bryozoan *P. foliacea* were recorded as. *P. fascialis*[46]. This highlights the importance to complement the use of open databases such as OBIS or GBIF with the taxonomic and ecological knowledge of the target species to avoid errors in the interpretation of distributional patterns.

To sum up, to understand the future of ectotherms under climate change it is necessary a better understanding of how species diverge in climatic niches to forecast the response of species to warmer conditions and which are in risk of local extinction[15]. Future studies should integrate a better knowledge of ecological niches, demographic processes and physiological responses to predict the future of vulnerable populations in a changing world.

Methods

Study species and study area. Populations of both species were monitored in 7 locations at 18–25 m depth in the Montgrí, Medes Islands and Baix Ter Natural Park in the North-Western Mediterranean (Fig. 1, Supplementary Fig. S3). We monitored all the locations every 6-months through one year (October 2014, April 2015 and October 2015) to describe bryozoan population dynamics between the summer and winter periods. Selected locations were classified by protection level (unfrequented *versus* highly frequented by recreational SCUBA divers) and by type of habitat (hard rock bottoms or coralligenous walls). In each location, we installed a permanent transect of 10 m^2 where colonies of *P. fascialis* and *M. truncata* were individually identified, and their heights, diameters, and degrees of exposure were measured *in situ* by SCUBA diving following similar procedures[26]. Moreover, we photographed all the colonies to obtain other parameters such as colony area through image analyses (Photoshop CC2017). Through demographic analyses, we obtained parameters such as survival and recruitment between the studied periods (winter 2014: October 2014 – April 2015; summer 2015: April 2015 – October 2015). In modular marine species, the age of individual colonies is hard to assess and life-history traits as survival or growth are often modeled as a function of colony size[47]. Thus, we fitted a set of regression models of survival and colony size data to explore the potential effects of multiple factors (season, habitat type, etc.).

On the other hand, local thermal regimes during the monitoring period were quantified by high-resolution hourly temperature recordings at 20 m depth obtained from the T-MedNet platform (http://www.t-mednet.org/).

Experimental thermal stress study. *Sample collection and experimental design.* To explore differential responses to thermal stress between the two bryozoan species, we studied them under experimentally controlled conditions. One fragment of 3–5 cm height from 90 healthy colonies of each species were sampled at the same depth (approximately 20 m) in Medes Islands during October 2016 and transported in aerated seawater to the Experimental Aquarium Facilities of the Institute of Marine Sciences in Barcelona (in less than 24 hours). All the colonies were set in aquaria tanks (approximately 48 l volume), continuously supplied with seawater (salinity 38 ppm) and a current of flow rate around 60 l h^{-1} generated by a submersible pump and were subjected to an acclimation period of 7 days at 18 °C[21,48]. The colonies were fed three times per week with 3 ml of a liquid mixture of particles between 10 to 450 μm in size (Benthos Nutrition Marine Active Supplement, Maim, Vic, Spain) in each aquarium.

We designed 3 different treatments, one control, and 2 different temperature treatments; each utilized of three tanks (replicates) containing 10 colonies from each species. In the control treatment, seawater temperature was maintained by a continuous flow-through of new water at 18 °C. In the temperature treatments, the seawater was heated with submersible resistance heaters regulated by temperature controllers (Aqua Medic T controllers). The first temperature treatment simulated a relatively large period of high temperatures subjecting the colonies to 25 °C for a period of 44 days. This temperature has been recorded in several mass mortality events and identified as a critical threshold for several Mediterranean invertebrate species[22,48,49]. In contrast, the second temperature treatment was subjected to a sequential increase of temperature from 25 °C to 30 °C, to investigate thermotolerance features of both species and detect the maximum critical temperature. Specifically, the temperature was increased firstly to 25 °C and, from there it was increased 1 °C every 5–7 days until reaching 30 °C when the experiment finished after 72 days. This methodology was previously used in several studies and demonstrated to be effective to study thermotolerance ranks in benthic species[20,21].

Variables studied. We carried out photographic monitoring of all the colonies at regular intervals of 3–6 days and we quantified the proportion of necrosis (dead tissue) expressed as % of the total area through image analysis (Photoshop CC2017). Necrosis was expressed as the proportion of the areas presenting a loss of colony coloration derived from the partial or total lost of living tissue covering the skeleton[6,41,50], following previous studies on corals or gorgonians[20,21,51]. Necrosis rates were estimated in 10% intervals, and we considered a colony to be affected by partial mortality when it showed recent necrosis over 10% of tissue[21]. On the other hand, to obtain the mean growth of the colonies, all of them were weighted at the beginning and at the end of the experiment using the buoyant weight technique[52].

We also tested whether thermal stress may drive physiological non-lethal effects by comparing respiration rates between the temperature treatment at 25 °C and the control. To achieve this, 6 healthy specimens for each treatment and species were incubated for 12 hours in individual chambers (130 ml in volume) that were completely filled with 50 μm pre-filtered seawater (without any air space) and hermetically closed, according to the standardized protocol[53]. Moreover, 6 chambers, filled with pre-filtered sea water without any bryozoan, were used as controls. Chambers were maintained at a constant temperature in a water bath (18 and 25 °C, respectively), and a Teflon-coated magnetic stirrer ensured water movement inside each incubation chamber. Oxygen concentration in each chamber was recorded at the beginning and end of the incubation, using an optode sensor (YSI ProODO Optical Dissolved Oxygen meter, precision 0.2 mg L^{-1}). Variation in the oxygen concentration measured from the control chambers was subtracted from those measured in the bryozoan chambers, and oxygen consumptions were derived from the dissolved oxygen over the incubation and were normalized by colony weight.

To perform skeletal structure and mineralogical analysis, at the end of the experiment we collected from all treatments different fragments from two colony areas (proximal and distal zones) from each specimen in both species. The samples were stored and prepared to be observed with a Scanning Electron Microscope (SEM). Specifically, we selected 3 replicates of 1×1 mm^2 per colony and zone, and we registered structural variables such as the density of zooids, ovicells, avicularia, damaged or broken zooids, and the mean area of the primary orifice[29,37]. Moreover, to evaluate the non-lethal effects in the skeletal content, we quantified calcite and Mg content of the calcite (type 1: low-magnesium calcite; type 2: high-magnesium calcite)[54] and aragonite on colonies subjected to thermal stress experiment (25 °C) at the end of the experiment. We performed mineralogical analyses cutting 3 replicates (2×2 mm^2) from the growing edge following previously described methodologies[55]. The pieces with 10 grains of pure halite (NaCl) as an internal standard were powdered using a quartz pestle and mortar. The samples were sandwiched between films of polyester of 3.6 microns of thickness. X-ray powder diffraction (XRD) was performed on PANalytical X'Pert PRO MPD powder diffractometer (240 mm goniometer radius) equipped with a PIXcel detector and operating with a Cu Kα ($\lambda = 1.5418$ Å) radiation source generated at a voltage of 45 kV and a current of 40 mA at the Scientific and Technological Centers of the UB (CCiT-UB). An angular range of 4 to 65° 2θ was measured with a step size of 0.026° and a 200 s counting time per step. Soller and incident slits were set to 0.04 rad and 0.7 mm, respectively. To determine the proportions of aragonite and calcite, peak intensities were fitted to standard patterns generated from 100% aragonite and 100% calcite. The wt% $MgCO_3$ in calcite was calculated by measuring the position of the d104 peak, assuming a linear interpolation between $CaCO_3$ and $MgCO_3$[56] and recalibrated for the specific machine used. A linear trend of d104 versus mol% $MgCO_3$ can be observed in the range between 0 and 17 mol% $MgCO_3$[57]. All data of this study fall into this range.

Statistical analysis. To reveal differences between maximum temperatures between our study period and the previous years we used Linear Models (LM). Moreover, to analyze the results of field study we used General mixed models (GLM) fitting binomial distributions of the errors to test the relation between the survival and census period (time), locality, protection level, habitat type, and colony-size (colony area). On the other hand, we used LM's to test for differences between aquaria treatments and species in several parameters that indicate lethal and sub-lethal physiological effects: percentage of necrosis, growth rate, respiration rates, skeletal structure (as density of zooids, ovicells, avicularia, damaged or broken zooids, and the medium area of primary orifice) and mineralogy (Mg content, calcite and aragonite). All statistical analysis and graphics were produced using R version 3.1.2[58] (R Core Developer Team 2014).

Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Author Contributions

B.H. and C.L. designed the field study, J.G. and C.L. designed the experiments, B.H., C.L., I.M.S. and M.P.E. participate in field surveys, B.F., D.G.G., A.G., I.M.S. and M.P.E. conducted the experiments, M.P.E. analyzed the results and wrote the first draft. All authors revised the manuscript.

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Original Articles

Unravelling the population dynamics of the Mediterranean bryozoan *Pentapora fascialis* to assess its role as an indicator of recreational diving for adaptive management of marine protected areas

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ABSTRACT

Marine Protected Areas (MPAs) have been recognized as effective management and conservation tools to protect marine coastal ecosystems. However, due to an increasing interest in marine ecosystems, recreational activities such as scuba diving are rapidly growing in these areas, highlighting the need to implement adaptive management strategies based on continuous monitoring and evaluation of protected areas. To date, several studies have quantified the impact of diving using benthic species as indicators, such as bryozoans, but usually ignoring their population dynamics. Here, we studied the population dynamics of the abundant and common bryozoan *Pentapora fascialis* on a Mediterranean MPA with high levels of diving activity. Specifically, we monitored eight different localities with two different levels of diving frequentation (non-frequented *versus* frequented) from October 2015 to October 2018, accounting for the demographic parameters before and after the summer. Our results showed the impact of diving on the density, recruitment, survival, and size of colonies, reaching higher values on non-frequented localities. In addition, we detected two peaks of recruitment during July 2016 and July 2018, suggesting that bryozoan recruitment events are stochastic, with a high inter-annual variation. Contrastingly, regardless of the diver frequentation level, we found higher growth rates during the colder months and higher necrosis rates after the summer in all the studied localities. Besides the aforementioned differences, the densities observed in this study were much higher compared to previous studies performed in the same area during the 1990s. Taken together, these results suggested rapid population dynamics of *P. fascialis*, with fast growth rates and a high capacity to recover from perturbations. Despite the quantified effects of diving on our studied species, their abundance in frequented sites remained very low over the whole study period, compromising the use of *P. fascialis* as an optimal indicator of diving impact for adaptive management of temperate benthic populations. Overall, our results highlight the importance of continuous monitoring programs to unravel the population dynamics of indicator species to effectively manage marine populations and evaluate the impact of human activities on marine protected areas.

1. Introduction

Over the last decades, marine coastal ecosystems have been increasingly impacted by multiple and interacting anthropogenic stressors, such as habitat destruction or climate change, resulting in a biodiversity loss and an alteration of the ecosystem functioning (Halpern et al., 2008; Cardinale et al., 2012). The creation of Marine Protected Areas (MPAs) has been recognized as an effective management and conservation action to protect and restore marine ecosystems (Milazzo et al., 2002; Harley et al., 2006). However, the establishment of new MPAs worldwide has contributed to an exponential increment of tourism attracted by the high biodiversity and ecological services that they provide (Davis and Tisdell, 1995; Badalamenti et al., 2000). In this context, effective management of MPAs requires linking social-ecological considerations through adaptive management strategies, based on continuous monitoring and evaluation, to assess the protection goals in

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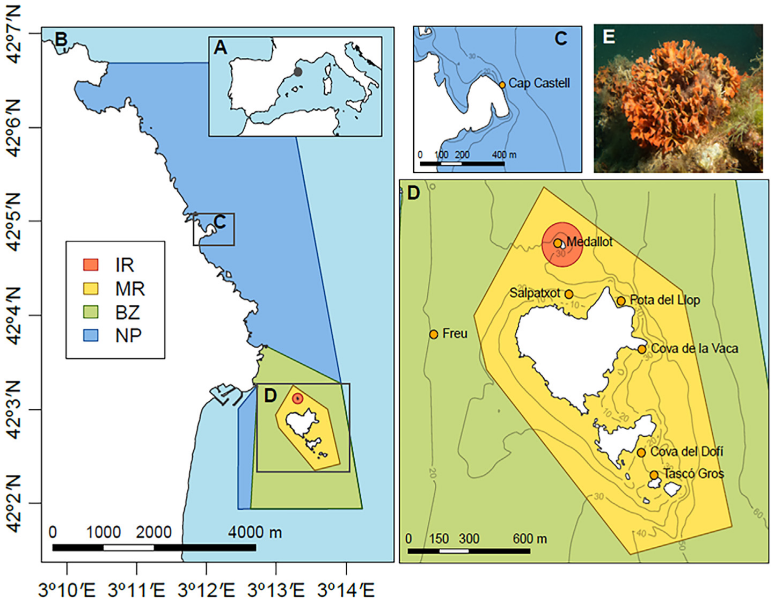

Fig. 1. Map of the study site and image of the species monitored. General location of the study area in the NW Mediterranean (A). Location of The Montgrí, The Medes Islands and The Baix Ter Natural Park (B). Detail of the Cap Castell location (C) and the Medes Islands (D). Colors represent different levels of protection: Integral Reserve (IR), Marine Reserve (MR), Buffer Zone (BZ) and Natural Park (NP). Image of the monitored species, the bryozoan *Pentapora fascialis* (E).

the context of increasing anthropic perturbations (Agardy et al., 2011; Ban et al., 2012).

MPAs can provide economic benefits through fishing and tourism activities such as diving or snorkeling, among others (Sala et al., 2013). Specifically, economic benefits of tourism in marine protected areas contribute significantly to their local economy, ranging from US$2 million per year for some Caribbean Islands (Fernandes and Van't Hof, 1995) to ~US$5 billion gained in 2006–2007 in the Great Barrier Reef, Australia (McCook et al., 2010). In these areas, diving has become popular worldwide and nowadays it represents one of the major touristic activities in MPAs (Rouphael and Inglis, 2001; Hawkins et al., 2005; Parsons and Thur, 2008; Di Franco et al., 2009). At local scale, previous studies have documented the high interest of divers to visit MPAs, such as the case of the small but popular Medes Islands marine reserve located in the NW Mediterranean Sea (Spain), where around 67,000 divers were annually registered, which generate direct benefits of €235,000 coming only from diving fees (Sala et al., 2013). The total benefit of the protection of this area is estimated around €10 million annually, considering all the economic benefits derived from the tourism sector (i.e., hotels, restaurants) and the creation of working places that grew in association with diving activity (Merino et al., 2009; Capella, 2010).

Despite the conservation and economic benefits of MPAs, the over-frequentation of divers in these areas can have negative consequences for marine benthic communities (contrasting with their ecological values). Some studies have demonstrated that scuba divers may affect marine organisms in several ways, both intentionally and unintentionally, increasing the degradation of marine ecosystems (Davis and Tisdell, 1995; Hawkins et al., 1999; Milazzo et al., 2002; Uyarra and Côté, 2007). Specifically, they may impact directly to benthic organisms, breaking or damaging them, resulting in a partial or total loss of colonies (Garrabou et al., 1998) and negative population growth rates (Linares and Doak, 2010), or indirectly, increasing sediment resuspension or creating air bubbles that might remain trapped on marine caves (Lloret et al., 2006; Luna-Pérez et al., 2010). Accordingly, these impacts may result in high partial mortality rates, decreasing the cover of benthic invertebrates such as hard corals, gorgonians, or sponges (Milazzo et al., 2002; Zakai and Chadwick-Furman, 2002; Luna-Pérez et al., 2010).

To unravel the impact of diving on benthic organisms, some works have studied diver behavior directly (Zakai and Chadwick-Furman, 2002; Di Franco et al., 2009; Luna et al., 2009), but the majority of works have focused on the study of indicator species (Garrabou et al., 1998; Linares et al., 2010; De la Nuez-Hernández et al., 2014). Adequate indicator species should have some key characteristics, such as a high abundance and a wide distribution to ensure sampling repeatability. In this regard, gorgonians and hard corals are considered optimal indicators of human perturbations (Linares et al., 2010). Up to now, most of the previous studies have focused on tropical seas (Hawkins et al., 1999; Barker and Roberts, 2004; Dearden et al., 2010), with few examples in other areas, such as the Mediterranean Sea (Sala et al., 1996; Coma et al., 2004; De la Nuez-Hernández et al., 2014). In this area, bryozoans, among other organisms, have been widely used as indicators of diving impact due to their high abundance and fragility (Ballesteros, 2006). Despite the fact that previous works have registered the impact of diving on these organisms (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández et al., 2014), there is a lack of knowledge about their population dynamics, compromising the use of these organisms as optimal indicators of physical impacts.

The main goal of this study was to unravel the effect of diving on the common Mediterranean bryozoan *Pentapora fascialis* (Pallas, 1766), analyzing its population dynamics through an *in situ* monitoring. The study was carried between 2015 and 2018, monitoring eight different locations within a Mediterranean MPA characterized by different levels of diving frequentation. On each location, we installed one fixed transect which was monitored annually before and after the summer, identifying individually all the colonies and registering the density, size, and partial mortality of the colonies. Moreover, we analyzed demographic parameters between monitoring periods, such as survival, recruitment, and growth, to unravel differences between frequented and non-frequented locations. Our study represents the first attempt to study the population dynamics of the bryozoan *P. fascialis,* with important direct applications for the adaptive management of benthic communities in MPAs.

2. Materials and methods

2.1. Study area

Our study was performed in the Montgrí, the Medes Islands and the Baix Ter Natural Park (Catalonia, Spain) in the Northwestern Mediterranean Sea (Fig. 1A). In this protected area, the Medes Islands Marine Reserve represents one of the protected areas most frequented by divers in the Mediterranean Sea (Sala et al., 2013). This MPA is characterized by different levels of protection: a Marine Reserve (MR), where diving is allowed but regulated by buoys with a maximum number of divers per year, anchoring is forbidden, and navigation is regulated; a Buffer Zone (BZ), where diving, artisanal fishing, and angling are allowed; and a Natural Park (NP), which comprises the remaining coast of Montgrí, where diving, anchoring, artisanal fishing, and spearfishing are allowed without restrictions (Fig. 1) (Hereu and Quintana, 2012; Sala et al., 2013). Recently, in 2015, one of the study locations (Medallot) inside the Marine Reserve (MR) was declared as an Integral Reserve (IR), and all the activities inside this area were forbidden except scientific diving (Hereu et al., 2017).

2.2. Monitored species

Pentapora fascialis is a common bryozoan in the Mediterranean benthic communities, distributed from 15 to 100 m depth on hard rocky bottoms (Zabala, 1986) (Fig. 1E). Adult erect colonies reach up to 30 cm in diameter and 20 cm in height, with a high mean growth of 9.8 ± 4 cm/year (Zabala, 1986; Cocito et al., 2006). Due to its physical structure, it is considered a habitat-forming species that increases the associated biodiversity (Cocito, 2004). Previous studies concluded that this species is a good indicator of the impact of diving and other physical perturbations, such as storms, due to the fragility of its skeleton and its lack of commercial value (Sala et al., 1996; Garrabou et al., 1998) (Supplementary Table S1). However, there is a lack of basic knowledge about its population dynamics, and only a few previous studies explored demographic aspects, such as mean annual growth (Cocito et al., 2006).

2.3. Sampling sites and data collection

This study was carried out at eight different locations of the MPA where we identified populations of *P. fascialis* at similar depth range (between 17 and 22 m depth) (Fig. 1). Localities were selected according to its protection level, recreational diving activity and the presence of *P. fascialis* populations. Study locations were classified by the diving frequentation level (unfrequented *versus* frequented by divers), classifying the locations inside the Marine Reserve as Frequented (Cova del Dofí, Cova de la Vaca, Pota del Llop, Salpatxot and Tascó Gros) and the locations outside the Marine Reserve or in the Integral Reserve as Non-Frequented (Cap Castell, Freu and Medallot) (Fig. 1). Despite outside the Marine Reserve diving is allowed and can be performed by anchoring, it is basically performed from buoys which identify the suitable sites to dive and facilitates their access to the divers. For this reason, the two studied locations outside the Marine Reserve (Cap Castell and Freu) were placed in remote areas without diving buoys, which ensures that they were not frequented by divers, and if diving occurs, it was very rare as demonstrated by the fact that during all the study no divers have been observed in these locations. Specifically, no divers were registered in the non-frequented locations in the period 2016–2018; in contrast, between 1,600 and 5,500 divers were registered annually at frequented locations. Detailed information on the divers registered per year during the whole study period at each locality is available (Supplementary Table S2).

In each location, we installed a permanent transect of 6 m length and 2 m width marked with plastic screws attached to the substrate with epoxy glue (Supplementary Fig. S1). The size of the transects was selected in order to have a representative number of bryozoans. We installed the permanent transects in six of our eight study locations between October 2015 (Medallot and Tascó Gros) and July 2016 (Cova de la Vaca, Cova del Dofí, Pota del Llop, and Salpatxot), and in the two other localities were installed in October 2017 (Freu and Cap Castell). To monitor each transect, we used plastic quadrats of 0.5 × 0.5 m (0.25 m^2), being four quadrats in one line of each transect, and hence, 48 quadrats in each total transect (12 m^2). All quadrats were surveyed during all the monitoring. In each of these quadrats, we identified and registered individually all the colonies to follow them during the whole study period, measuring their maximum height (with a plastic ruler) and visually estimating the percentage of affected surface (necrosis). This parameter was expressed as the proportion of the area presenting a loss of colony coloration derived from the partial or total loss of living tissue covering the skeleton, following previous methodologies (Sala et al., 1996; Pagès-Escolà et al., 2018).

To quantify the impact of diving, we monitored all the locations before (July) and after the summer (October), following previous studies (De la Nuez-Hernández et al., 2014). For each location and survey period, we estimated the following demographic parameters: (i) survival, as the ratio between the number of remaining colonies and the total colonies at the beginning of each period, considering as dead the colonies with 100% of necrosis; (ii) recruitment, as the number of new colonies that appeared after each monitoring; (iii) and growth, as the difference of size (height) between surveys. Finally, we analyzed the number of total colonies, recruits and adults (estimated as the colonies that were not identified as recruits) on each quadrat and we extrapolated to the number of colonies/m^2 on each studied location (Sala et al., 1996).

2.4. Data analysis

In order to evaluate the diving impact on *P. fascialis* populations, we performed a set of Generalized Linear Mixed Models (GLMMs) (Bolker et al., 2009). The total, adult and recruit densities of *P. fascialis*, height, necrosis, survival, and growth were fitted as the dependent variables. The explanatory variables year, month (before/after the summer), and diving frequentation (frequented/non-frequented) were included as fixed factors, and the sampled location, nested to the frequentation level, was included as a random effect. For each model, the data distribution of the response variable was inspected and fitted to the most likely distribution (binomial, negative binomial, poisson or gaussian). The analyses were conducted using the package “lme4” for R (Bates et al., 2014).

To test the relation between the survival and necrosis with the initial size of the colonies, we performed Generalized Linear Models (GLMs) (McCullagh and Nelder, 1989) considering the level of frequentation to analyze if there were statistical differences between frequented and non-frequented zones. Moreover, to analyze the growth of the colonies, we fitted the same model testing the relation between the initial size *vs* the posterior size of the colonies. As noted above, the data distribution of each response variable was inspected for each model and fitted to the most likely distribution.

According to previous studies, to detect changes in *P. fascialis* populations, population size structure was calculated by pooling colonies in size classes of 1.5 cm (Sala et al., 1996). Differences among locations, years and months were tested using the non-parametric two-sample Kolmogorov-Smirnov (K-S test; Legendre and Legendre, 1998).

All statistical analyses were performed with the software R, version 3.3.3 (R Development Core Team, 2017).

3. Results

3.1. Density

Our results showed higher densities in non-frequented locations

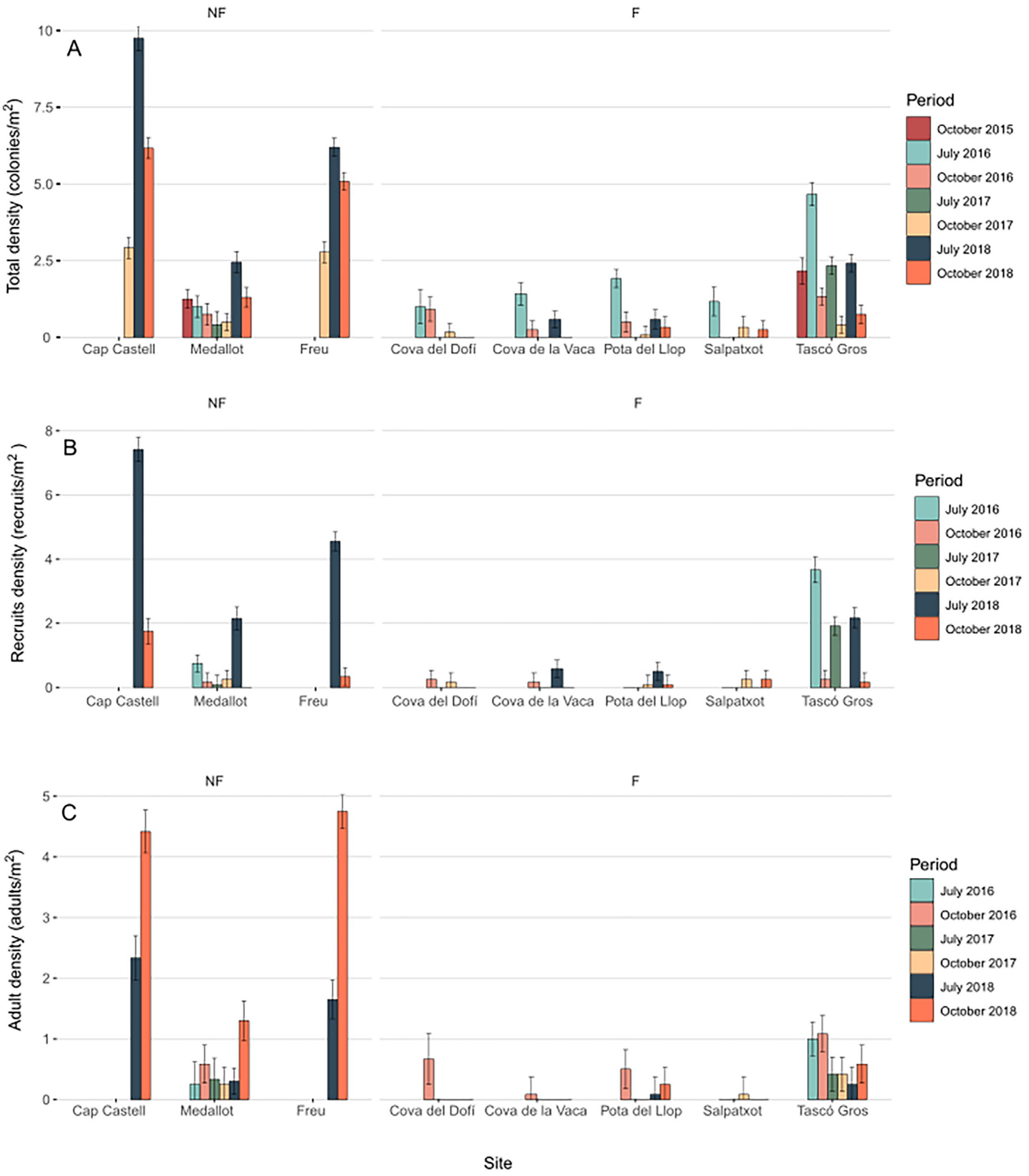

Fig. 2. A) Total density of colonies (mean ± SE), B) recruits density (mean ± SE), and C) adult density (mean ± SE) for each location grouped according to the diving frequentation (NF, non-frequented; F, frequented) and for each monitoring period. Note that the scale of the figures is different. For figures B and C, the first monitoring was not represented since the data from the previous year is required to differentiate between adult colonies and recruits.

compared to the frequented ones, reaching the highest values of 6.2 ± 0.28 colonies/m^2 (mean ± SE) in the location of Freu and 9.75 ± 0.39 colonies/m^2 in the location of Cap Castell, both in July 2018 (Fig. 2A, Table 1). Despite the fact that most of the frequented locations presented lower densities, reaching values from 0 to 1.91 ± 0.29 colonies/m^2, the location of Tascó Gros (2.41 ± 0.29 colonies/m^2) showed similar densities to the non-frequented location of Medallot (2.45 ± 0.34 colonies/m^2) in July 2018 (Fig. 2A). We found statistically significant differences between years, showing higher densities in July 2016 and 2018 (GLMM, z = −4.52, $p < 0.001$; Table 1). Similarly, we found significant differences between months, showing higher values of density in July and a

Table 1
Result of the generalized linear mixed models (GLMM) for each response variable (density colonies, density recruits, size, survival, and necrosis). Protection, year and month were considered as fixed and the locality as the random factor. In each case, we fitted the model accordingly with the distribution of the response variables (Negative binomial for total, recruit and adult densities and necrosis; Poisson for size; Binomial for survival; Gaussian for growth). For each model, we presented the statistics and the marginal and conditional R2 to estimate the importance of the random variable. Significant analyses were indicated in bold (< 0.05).

Response variable	Predictors (Fixed factors)	Estimate	Std. Error	Z value	*p*	Marginal R^2	Conditional R^2
Density total colonies	Intercept	−1.84	0.58	−3.16	< **0.001**	0.26	0.34
	Protection	1.47	0.39	3.69	< **0.001**		
	Year	−0.90	0.19	−4.52	< **0.001**		
	Month	−0.97	0.20	−4.79	< **0.001**		
	Protection*Year	0.54	0.13	4.04	< **0.001**		
	Protection*Month	0.41	0.13	3.02	< **0.01**		
Density Recruits	Intercept	−3.09	0.72	−4.27	< **0.001**	0.34	0.45
	Protection	0.88	0.49	1.8	0.06		
	Year	−0.01	0.27	−0.06	0.95		
	Month	−0.58	0.24	−2.35	**0.01**		
	Protection*Year	0.24	0.19	1.24	0.21		
	Protection*Month	−0.19	0.15	−1.22	0.22		
Density Adults	Intercept	−4.18	1.02	−4.08	< **0.001**	0.30	0.34
	Protection	2.04	0.68	2.98	< **0.01**		
	Year	−1.54	0.38	−3.98	< **0.001**		
	Month	0.49	0.36	1.37	0.16		
	Protection*Year	1.20	0.26	4.55	< **0.001**		
	Protection*Month	−0.10	0.22	−0.49	0.62		
Size (height)	Intercept	0.98	0.21	4.54	< **0.001**	0.092	0.149
	Protection	0.37	0.13	2.74	< **0.01**		
	Year	−0.11	0.12	−0.92	0.35		
	Month	0.07	0.12	0.59	0.55		
	Protection*Year	0.11	0.08	1.42	0.15		
	Protection*Month	0.1	0.08	0.13	0.89		
Growth	Intercept	1.72	0.56	3.07	**0.002**	0.16	0.16
	Protection	0.44	0.32	1.39	0.16		
	Year	0.74	0.59	1.25	0.20		
	Month	−0.47	0.52	−0.91	0.37		
	Protection*Year	−0.4	0.37	−1.08	0.27		
	Protection*Month	−0.61	0.29	−2.04	**0.04**		
Survival	Intercept	−2.72	0.55	−4.91	< **0.001**	0.113	0.133
	Protection	1.37	0.33	4.18	< **0.001**		
	Year	−0.55	0.38	−1.47	0.14		
	Month	−0.04	0.36	−0.12	0.90		
	Protection*Year	0.37	0.22	1.71	0.08		
	Protection*Month	0.05	0.22	0.27	0.78		
Necrosis	Intercept	1.01	3.34	0.30	0.76	0.390	0.828
	Protection	−0.13	2.17	−0.06	0.95		
	Year	2.30	0.89	2.56	**0.01**		
	Month	2.17	0.94	2.29	**0.02**		
	Protection*Year	−1.51	0.51	−2.95	< **0.01**		
	Protection*Month	0.12	0.51	0.24	0.81		

significant decrease in the number of colonies in October (GLMM, $z = -4.79$, $p < 0.001$; Table 1).

Similarly, we found higher levels of recruitment in non-frequented locations, reaching 7.42 ± 0.38 recruits/m^2 in the location of Cap Castell and 4.55 ± 0.29 recruits/m^2 in the location of Freu, both in July 2018 (Fig. 2B). We found lower numbers of recruits on frequented locations during all the monitoring, with the exception of the location of Tascó Gros, where, during July 2016 and 2017, we registered higher numbers of recruits (3.66 ± 0.40 recruits/m^2 and 1.91 ± 0.280 recruits/m^2 respectively) than in non-frequented location of Medallot (0.75 ± 0.26 recruits/m^2 and 0.08 ± 0.28 recruits/m^2 respectively). However, the number of recruits were similar in the two locations in July 2018 (Tascó Gros reaching 2.16 ± 0.32 recruits/m^2 *vs* Medallot reaching 2.15 ± 0.36 recruits/m^2) (Fig. 2B). Accordingly, we also found statistical differences between months, reflected in the higher recruitment peaks of July in non-frequented locations and the frequented location of Tascó Gros (GLMM, $z = -2.35$, $p = 0.01$; Table 1). Despite the high peak of recruitment in 2016 and 2018, we did not find statistically significant differences between years due to the high variability (Table 1).

Like for recruit densities, we observed higher adult densities in non-frequented locations, reaching 4.42 ± 0.35 adults/m^2 and 4.75 ± 0.32 adults/m^2 in the locations of Cap Castell and Freu, respectively, in October 2018 (Fig. 2C). Although we found lower levels of adults in frequented locations, the location of Tascó Gros showed similar levels of adults than the non-frequented location of Medallot during the monitoring period (Fig. 2C). However, in October 2018 the location of Medallot showed higher levels of adults (1.3 ± 0.32 adults/m^2) than the frequented Tascó Gros (0.58 ± 0.31 adults/m^2). We obtained significant differences in the adult densities between years (GLMM, $z = -3.98$, $p < 0.001$; Table 1), but we did not find them between months (Table 1).

3.2. Size structure

Despite the fact that we did not find any pattern on the population size structure between different frequentation levels (Supplementary Table S3), we accounted the higher proportion of larger colonies in non-frequented locations together with the frequented locations of Tascó Gros and Cova del Dofí, reaching large class sizes (10–12 cm height,

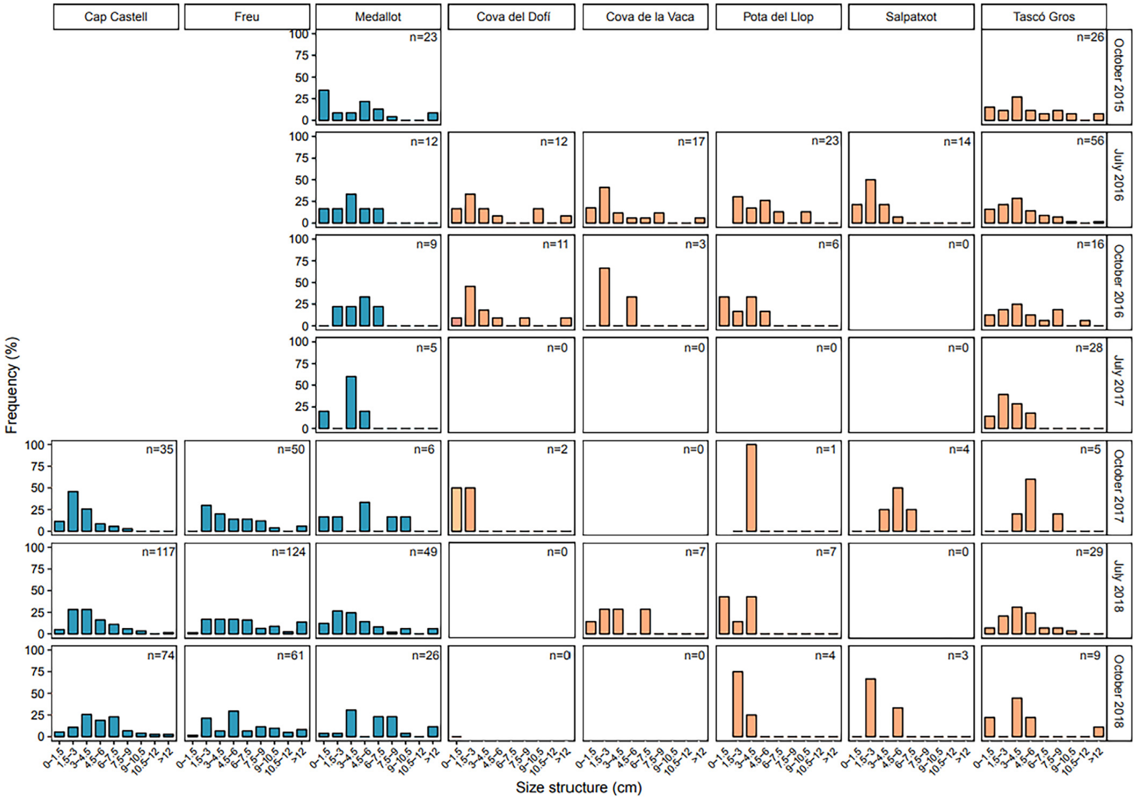

Fig. 3. Temporal evolution of size structure (height, cm) of the colonies at each sampling location. The non-frequented locations are presented in blue and the frequented locations are presented in orange. The number of colonies registered (n) is indicated for each location and sampling.

Fig. 3). In fact, we found significant differences in the mean size between levels of frequentation, being higher in non-frequented sites (Table 1). Moreover, we did not observe any differences in the mean size between years and months regardless of the registered increase of recruitment density in July 2016 and July 2018. Conversely, we registered statistical differences between July and October 2018 in most of the locations, independently of their level of frequentation, highlighting the decrease in the number of colonies during this period (Supplementary Table S3).

3.3. Survival

The highest survival rates were found in non-frequented locations, reaching the highest mean survival values of 1 in the location of Medallot, 0.7 ± 0.06 in the location of Freu, and 0.62 ± 0.08 in the location of Cap Castell in July 2018 (Table 1, Fig. 4A). However, we also found a high survival in the frequented location of Tascó Gros in July 2018 (0.6 ± 0.25). Despite the fact that we did not find any patterns between years and months, locations with a large sample size of colonies (non-frequented: Cap Castell, Freu, Medallot; and frequented: Tascó Gros) showed lower levels of survival after the summer, decreasing between July 2018 and October 2018. The survival of the colonies increased with their initial size (GLM, z = 2.28, $p = 0.02$; Fig. 5A, Supplementary Table S4), without showing differences between levels of frequentation. However, our results suggested that the survival of the small-sized colonies was higher in non-frequented sites (Fig. 5A).

3.4. Necrosis

We did not find statistically significant differences between non-frequented and frequented locations, both showing higher levels of necrosis in October than in July (GLMM, z = 2.29, $p = 0.02$; Table 1, Fig. 4B). Moreover, we observed significant differences in necrosis between years, showing higher levels of mortality in 2017 and 2018 (GLMM, z = 2.56, $p = 0.01$; Table 1, Fig. 4B).

The necrosis did not show any relation with the initial size of the colonies (Fig. 5B, Supplementary Table S4), showing non-significant differences between levels of frequentation (Fig. 5B, Supplementary Table S4).

3.5. Growth

We did not find significant differences in growth rates between levels of frequentation and between years and months; however, we observed higher growth rates in July reaching the highest mean growth values of 5.25 ± 0.35 cm in the location of Freu in July 2018 (Table 1, Fig. 6).

There was a positive relationship between the initial size of the colonies (t0) and the size observed on the next monitoring period (t1) (GLM, z = 3.59, $p < 0.001$; Supplementary Table S4), without differences in the level of frequentation (Fig. 7, Supplementary Table S4).

4. Discussion

This work represents the first attempt to study the population

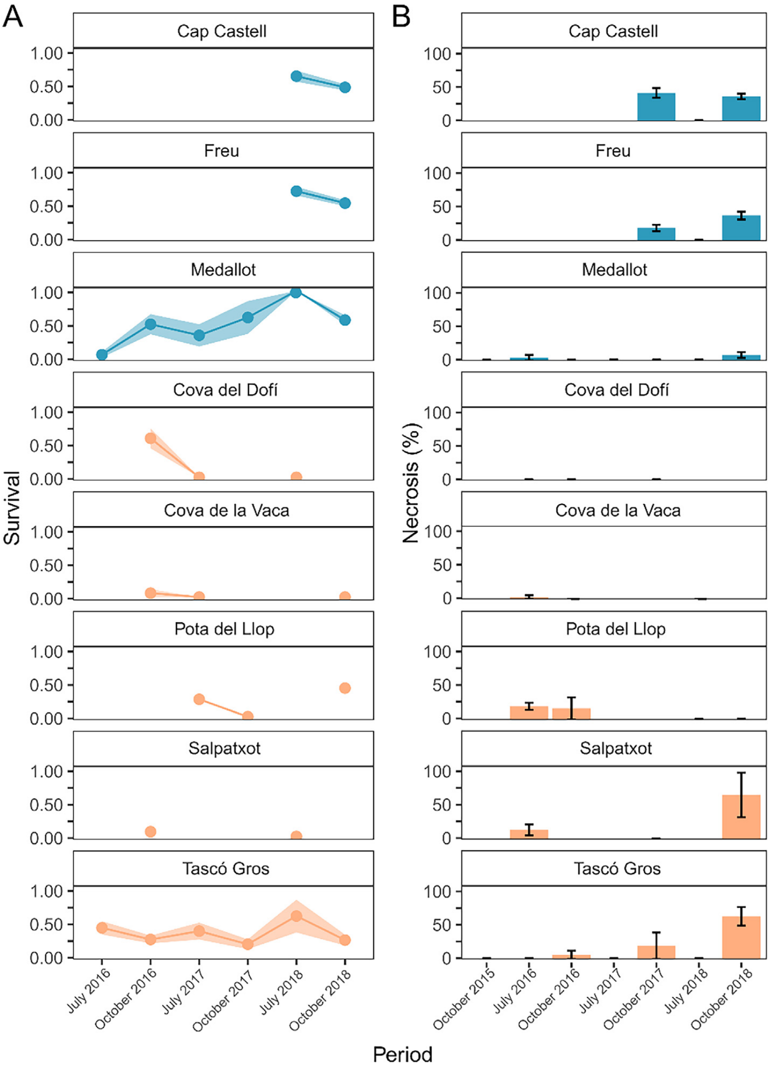

Fig. 4. A) Survival (mean ± SE) and B) Partial mortality (necrosis) considered as proportion of affected surface (mean ± SE) for each study period and at each sampling site in the non-frequented (blue) and frequented (orange) locations.

dynamics of the common Mediterranean bryozoan *P. fascialis* in order to elucidate its suitability as an indicator of recreational diving impact. In accordance to previous studies on the same species (Sala et al., 1996, Garrabou et al., 1998), our results evidence the impact of diving on the abundance and size of the colonies. However, we did not register differences in partial mortality and growth rates between frequented and non-frequented sites.

Like in previous works, our study found a higher abundance of *P. fascialis* in non-frequented locations, highlighting the diving pressure in frequented areas, which presented lower densities of bryozoans (Sala et al., 1996; Garrabou et al., 1998; De la Nuez-Hernández et al., 2014). However, the location of Medallot showed the lowest levels of density among the non-frequented locations, which may be explained by the fact that in this area diving was allowed until 2015, when this location was declared an Integral Reserve and only scientific diving has been allowed since then (Hereu et al., 2017). Although we did not find records of previous abundances of *P. fascialis* before the full protection of this location, its higher density than frequented locations may indicate the recovery of this population against the recent impact of diving and suggest a possible continued increase in its density in the future years.

Density values registered in our study differ from those reported on previous works performed in the same study area. In non-frequented locations, we found a maximum number of colonies of 9.75 colonies/m^2 contrasting with the 3.6 colonies/m^2 registered in the same area during July 1992 (Sala et al., 1996). In frequented locations, we found maximum values of 4.6 colonies/m^2 differing from the 0.6 colonies/m^2, respectively. Since both studies applied similar methodologies, this fact suggests that the abundance of bryozoan populations has increased in non-frequented locations since the 1990s, as well as in some frequented locations such as Tascó Gros, potentially explained by the high recruitment rates registered in this study. However, in the other

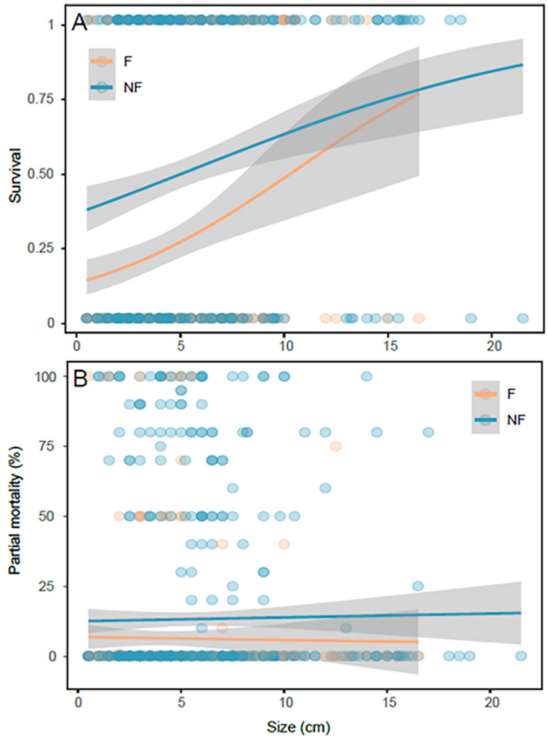

Fig. 5. Relation between the survival (A) and partial mortality (B) with the initial size of the colonies accounting for the level of frequentation, with non-frequented locations (NF) in blue and frequented locations (F) in orange. The lines represent the generalized linear model fitted between the response variable and the predictor. For each model the data distribution of the response variable was fitted to the most likely distribution (binomial distribution for survival, and negative binomial distribution for necrosis).

frequented locations, densities have remained very low since the 1990s, suggesting that the high levels of diving have not allowed the development of abundant and well size-structured populations (Garrabou et al., 1998). Apart from diving impact, it is important to bear in mind other factors such as local differences on habitat, currents or nutrients, which also may affect the abundance and distribution of benthic organisms (Ballesteros, 2006). These factors may explain the high density observed in the frequented location of Tascó Gros, highlighting the need to account for other factors in future studies.

The recruitment of new individuals is a key ecological process for the maintenance, resilience, and recovery of natural populations (Richmond, 1997; Hughes and Tanner, 2000). In the same line as density levels, we found high recruitment rates in non-frequented locations and the frequented location of Tascó Gros, which might be explained by other factors that were not considered in this study. Accordingly, previous studies have demonstrated that the spatial variations of recruitment patterns might be explained by abiotic factors, such as the orientation of the substratum, current regime, or temperature, among others (Hughes et al., 1999; Perkol-Finkel and Benayahu, 2007; Caines and Gagnon, 2012).

Recruitment of most of benthic invertebrates is characterized by irregular annual variations and stochastic peaks (Gotelli, 1988; Caley et al., 1996; Garrabou and Harmelin, 2002). We registered higher levels of recruits in non-frequented locations and Tascó Gros in July compared to October, suggesting that the optimal season for recruitment for *P. fascialis* takes place between winter and spring, when temperatures are lower, accordingly with its thermotolerance preferences (Pagès-Escolà et al., 2018). Our study found higher recruitment rates in 2016 and 2018 than in 2017, suggesting for the first time that recruitment of *P. fascialis* is characterized by biannual pulses. These results suggest that our species model displays faster population dynamics than other benthic species with longer temporal intervals between recruitment peaks, such as corals or gorgonians (Garrabou and Harmelin, 2002; Linares et al., 2007; Montero-Serra et al., 2019).

Despite the occurrence of recruitments peaks, we did not find evidence of the incorporation of small recruits in size-structure analyses. Such lack of changes in size structure suggests that the new colonies registered as recruits were characterized by relatively large sizes, which might be explained by two possibilities. First, the high growth rates of new colonies incorporated to the population during winter, which allows the colonies to reach large sizes by spring, could difficult the detection of small-sized colonies. Another possibility could reside in the fact that a proportion of large recruits could come from asexual reproduction processes such as fragmentation, which might break bryozoan colonies into smaller ones (fragments) that can survive, grow and reproduce (Hawkins and Roberts, 1994; Linacre and Keough, 2003). We suggest that future works should explore in more detail the recruitment process of this species at large spatial and temporal scales, given its importance for population dynamics.

Physical damage caused by direct contact from scuba divers has been well documented in sessile species (Sala et al., 1996; Linares et al., 2010; De la Nuez-Hernández et al., 2014). According to Zakai and Chadwick-Furman (2002), the level of damage to the contacted hard corals by divers may depend on their morphology. Massive structural species are damaged more often, as they tend to suffer breakage and separation of individuals if they are colonial. Our study finds higher values in the mean size of colonies in non-frequented locations. However, we did not find differences in growth rates between frequentation levels, suggesting that the smaller sizes recorded in frequented locations were related to the fragmentation of colonies by divers (Garrabou et al., 1998). Moreover, the survival of colonies incremented with the size of the colonies, being this trend more pronounced in frequented localities, suggesting that the larger colonies tend to resist better the physical impacts such as fragmentation.

In contrast, our study did not show any differences in the partial mortality patterns between frequentation levels, suggesting that other factors might be involved. Previous studies documented extensive mass mortality events affecting Mediterranean benthic macroinvertebrates, such as gorgonians, sponges, and bryozoans, caused by anomalous warming temperatures, highlighting the vulnerability of temperate sessile invertebrates to climate change (Cerrano et al., 2000; Garrabou et al., 2009). Similarly, we observed higher partial mortality (necrosis) and lower survival rates after summers, when temperatures were higher (Nykjaer, 2009). Our results are aligned with the vulnerability of *P. fascialis* to high temperatures (Pagès-Escolà et al., 2018), suggesting future decreases of their Mediterranean populations in a warming scenario, regardless the level of protection.

Nevertheless, our study finds that *P. fascialis* is characterized by higher growth rates during the colder months, as other studies pointed out previously (Cocito et al., 2006). We did not find any related impact of diving on growth rates, unlike other previous studies that observed that the slow growth rates of impacted populations did not allow colonies to recover from year to year (Sala et al., 1996; Cocito et al., 1998; Coma et al., 2004). Despite the vulnerability of our model species to warming and diving (Sala et al., 1996; Garrabou et al., 1998; Pagès-Escolà et al., 2018), the high growth and recruitment rates registered in this study highlight the capacity of bryozoan populations to recover rapidly from anthropic perturbations, which may explain the high densities observed in non-frequented locations. Moreover, our results suggest a possible recovery of bryozoan populations in frequented locations if diving pressure decrease in the future.

During the last decades, the creation of effective MPAs has been

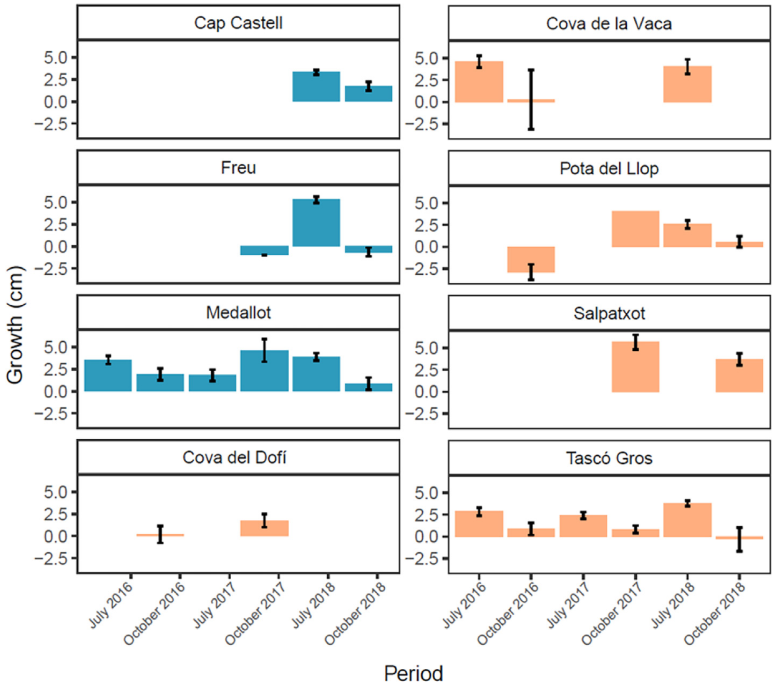

Fig. 6. Mean growth (mean ± SE) (cm) of colonies for each studied period at each non-frequented (blue) and frequented (orange) location.

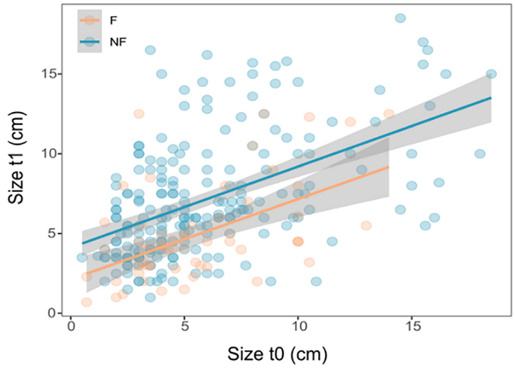

Fig 7. Relation between the posterior size (t1) and the initial size (t0) of the colonies, accounting for the level of frequentation, with non-frequented locations (NF) in blue and frequented locations (F) in orange. The lines represent the generalized linear model fitted between the response variable and the predictor. Data distribution of the response variable was fitted to the most likely distribution (Poisson distribution).

considered a good option to conserve marine ecosystems (Agardy, 1997; Edgar et al., 2014; Costello and Ballantine, 2015). This work demonstrates that diving activities can have a strong impact on benthic communities, contrasting with the conservation and protection goals of MPAs. The sustainability of diving activity depends on the number of divers accessing the sites and the capacity of the ecosystem to recover from perturbations (Harriott et al., 1997). Therefore, to manage recreational scuba diving it is vital to estimate the carrying capacity of benthic communities and establish diving quotas to ensure that natural resources are not destroyed (Salm et al., 2000; Barker and Roberts, 2004). Although previous studies have suggested different tolerable levels of diving, ranging from 500 to 15,000 divers per year (Dixon, 1993; Zakai and Chadwick-Furman, 2002), it is complex to determine a scientifically defendable limit of diving effect due to the different life-history traits of the organisms and the interaction with other perturbations, such as climate change (Linares et al., 2010). Our results showed the difficulty to estimate a non-critical level of divers for marine communities; in fact, one of the most frequented locations (Tascó Gros) showed similar levels of density than the non-frequented location of Medallot. This fact highlights the importance of considering other environmental factors rather than diving pressure, as well as the difficulty of estimating diving quotas to adapt the conservation criteria to our changing era in adaptive management strategies.

5. Conclusions

Continuous monitoring programs, like the presented study, need to be formally established to detect changes in natural populations before the impact of diving becomes critical (Luna et al., 2009). Specifically, our work provides evidence that the populations of *P. fascialis* in Medes Islands Marine Reserve are directly impacted by a high-frequentation of divers. However, most of the frequented populations in this area showed critical abundances compromising the use of our model species as an optimal indicator of the long-term adaptive management. In addition, our results evidenced the fast population dynamics of our model species with a high capacity to recover from anthropic perturbations, such as diving or climate change. Nevertheless, in order to enhance the recovery of impacted populations, it is recommended to reduce the pressure of divers in frequented areas, reevaluate the carrying capacity of these communities, and establish educational programs such as eco-briefings before the dives to increase the environmental awareness (Luna et al., 2009). Our work highlighted the need to implement continuous monitoring actions to properly manage anthropic activities in marine protected areas to preserve and protect marine benthic communities.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105781.

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