Marine protected areas in a changing ocean: Adaptive management can mitigate the synergistic effects of local and climate change impacts

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ARTICLE INFO

ABSTRACT

During the last two decades, several Marine Heatwaves (MHWs) have affected coralligenous assemblages in the Mediterranean Sea, causing catastrophic mass mortalities of several habitat-forming species such as gorgonians, corals, and sponges. Even though Marine Protected Areas (MPAs) are contributing to effectively protect marine ecosystems, the impacts associated to extreme climatic events within MPAs are jeopardizing their protective role. Therefore, minimizing local stressors within MPAs is crucial to minimize interactive effects with global, more difficult to manage, stressors. To address this, we assessed to what extent the regulation of diving frequentation can support more effective protection to climate change, focusing on the case study of the Medes Islands, which has recently suffered the impacts of different global stressors and is one of the most visited MPAs in the Mediterranean Sea. We combined 6 years of demographic data of the red gorgonian *Paramuricea clavata* with population modelling tools, to explore the long-term viability of this species to different managing schemes and mass mortality events scenarios. Overall, our results show that climate-adaptive management of the recreational diving activity under climate change can enhance the long-term viability of this key Mediterranean habitat-forming octocoral, which is otherwise predicted to go locally extinct at shallow depths (<25 m) within the next 20 years. This study provides one of the few attempts to quantify to what extent an adaptive management scheme may help delay climate change impacts in a Marine Protected Area.

1. Introduction

Marine Protected Areas (MPAs) are one of the main management tools to ensure biodiversity conservation and to achieve significant ecological and economic gains in marine ecosystems (Lubchenco and Grorud-Colvert, 2015). However, the accelerated degradation of marine ecosystems fueled by global change drivers is raising major concerns about the MPAs potential to halt the ongoing biodiversity loss (Halpern et al., 2015; Grorud-Colvert et al., 2021). In this context, ocean warming has been related to extreme climatic events, such as marine heatwaves (MHWs) (discrete prolonged anomalously warm water events, Hobday et al., 2016), which are increasing their frequency and severity across

ecosystems (Smale et al., 2019). MHWs have been linked to mass mortality events (MME), which are being increasingly reported and are severely impacting benthic habitat-forming species in tropical and temperate ecosystems worldwide (Wernberg et al., 2011; Hughes et al., 2017; Garrabou et al., 2022). Since most existing MPAs were designed without considering climate change stressors, the effectiveness of MPAs is under debate (Bruno et al., 2018). This ineffectiveness has been most apparent when its effects are so catastrophic that they surpass any enhanced resilience the MPAs may provide (Bates et al., 2019). In view of this concern, climate-adaptive management of MPAs (incorporating climate change in MPA design and management through several pathways) has been proposed as a tool to face climate change at a local scale

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(Roberts et al., 2017; Rilov et al., 2020; O'Regan et al., 2021).

From a management perspective, global stressors can overlap with ongoing local threats. Even in well-established no-take areas, the presence of uncontrolled non-consumptive recreation activities, such as SCUBA diving, has been documented to be detrimental (Pagès-Escolà et al., 2020; Calò et al., 2022). The main impact associated to diver overfrequentation is the direct physical damage caused to reef habitat-forming species, such as corals, gorgonians, sponges and bryozoans (Giglio et al., 2020). Paradoxically, as MPAs tend to attract more visitors than surrounding areas, this local impact can be higher in MPAs than in non-protected zones (Coma et al., 2004; Zupan et al., 2018). Therefore, these local stressors have the potential to exacerbate the effects of global stressors such as MHWs or global warming, hampering the conservation value of MPAs. In designing an adaptive management scheme considering relations among stressors is especially important when their interactions are synergistic, i.e. the combined effect of multiple stressors is greater than their additive effect (Crain et al., 2008). In our case, the interaction between MHWs and diving pressure is particularly relevant in shallow depths, where their impacts are concentrated. Thus, taking management actions to control local recreational activities may enhance the conservation condition of the MPAs in the context of climate change.

The main goal of this study is to explore how local climate-adaptive measures within MPAs can enhance the conservation status of coralligenous assemblages. For this purpose, we study the interactive effect of diving and climate-driven impacts in a small and overfrequented Mediterranean MPA, the Medes Islands. We first performed a demographic monitoring of a key habitat-forming gorgonian (*Paramuricea clavata*) to assess the impact of climate related stressors (mainly MHWs) and recreational diving as well as their interaction. Secondly, we used the field data to predict the long-term viability of this species through size-structured matrix population models. Finally, we explored how different climate and local management scenarios can ensure the conservation of this key habitat-forming species.

2. Methods

2.1. Study system

Our study was performed within the Montgrí, Medes Islands and Baix Ter Natural Park located in the NW Mediterranean Sea. Specifically, it was done in the Medes Islands Marine Reserve (MR), where fishing and anchoring is forbidden, but other activities are regulated, such as navigation or diving, which is allowed but regulated by buoys with a maximum number of divers per year. This MR was created in 1983, encompasses 100.56 ha and currently represents one of the most tourist-frequented no-take areas in the Mediterranean Sea (Sala et al., 2013). Since 1990, this MPA has implemented a long-term monitoring program of marine biodiversity using different species and habitats as indicators.

The red gorgonian *Paramuricea clavata* is one of the indicators selected, due to its important role in the maintenance of biomass, biodiversity and structural complexity in coralligenous assemblages (Ballesteros, 2006), one of the most diverse ecosystems in the Mediterranean Sea, and one of the most vulnerable to MHWs (Garrabou et al., 2019, 2022). The conservation of this species is also of economic interest because its well-developed populations are one of the main attractive features for scuba divers. *Paramuricea clavata* is a long-lived species with slow growth rates, low annual recruitment rates and late reproductive maturity, making it especially vulnerable to perturbations (Linares et al., 2007). In the Medes MR, this species is threatened locally by the involuntary detachment of colonies as a consequence of the high diving activity (Coma et al., 2004; Linares and Doak, 2010; Linares et al., 2010). This impact is especially relevant at our study site, as the red gorgonian colonies are situated in vertical walls of coralligenous nature which might facilitate detachment by substratum failure. Coralligenous reefs are endemic bioherms with different thickness and derive from multilayer calcium carbonate depositions formed by coralline

macroalgae adapted to low light conditions (Ballesteros, 2006; Piazzi et al., 2022), that can be very fragile and unstable. The vertical inclination can further facilitate detachment as colonies exert pressure on the substrate due to their weight, especially the larger ones, which gets worsened when covered by epibionts after thermal-injury and when pushed by repetitive contacts from divers. This species is also regionally affected by temperature-related MME, which locally had low impacts until 2016 (Garrabou et al., 2019). These two stressors are especially detrimental to shallow populations, as the main diving depth range consists of the first 30 m, while seasonal stratification patterns and the resulting thermocline will determine the depths exposed to possible MHWs (Coma et al., 2009), which in Medes Islands tends to pulse between 10 and 25 m (Bensoussan et al., 2010).

During the study period (2016 to 2021), the Medes MR was subjected to a similar number of total dives for the first 4 years (Fig. 1), with around 60,000 dives/yr, dropped by half in 2020 due to the COVID-19 pandemic, and mostly recovered pre-pandemic levels in 2021. To explore the site's exposure to MHWs, we analyzed hourly in-situ temperature measured during the last 20 years in the Medes Islands, obtained from the collaborative T-MEDNet initiative (www.t-mednet.org). We used Hobday's et al. (2016) definition for MHWs: prolonged discrete anomalously warm water events that last at least 5 days and have temperatures above the 90th percentile of the in-situ climatology. Considering the available data, we defined the climatology as the temperature data before the study and explored MHWs for the studied period. Here, we only considered the MHWs detected during the warm period of the year (June to November, JJASON). These analyses show that all monitored years were subjected to MHWs (Fig. 1), with 2018 presenting the highest number of MHW-affected days, while 2017 and 2019 presented the highest maximum intensities. Two other remarkable climate-driven events occurred outside of the expected impacts: i) an anomalous growth of filamentous algae in 2017, potentially linked to increasing temperatures and anomalous calm weather conditions, which caused an outbreak that entangled *P. clavata* branches for several months (Hereu Fina et al., 2017), and ii) Storm Gloria in 2020, one of the largest historical storms over the western Mediterranean basin (Amores et al., 2020).

2.2. Field surveys

To study the demography of *P. clavata* we installed permanent horizontal plots in 6 sites within the MR (see supplementary Fig. A1 for their location). The 6 plots were 3 m long and 1 m wide and fixed at the shallowest distribution range of each studied *P. clavata* patch (15–22 m). Permanent plots were divided into twelve 50 × 50 cm quadrats, to map the colonies within the transect and to identify new colonies (recruits). Each year we identified all the colonies and measured their maximum height in centimeters. In addition, we visually estimated the extent of injury as the percentage of each colony's total surface that showed either a denuded axis (i.e., recent mortality) or overgrowth by other organisms (i.e., past mortality, Linares et al., 2005). We carried out the surveys between September and November, after the diving high season and the summer high temperatures.

2.3. Data analysis

A total of 659 colonies were monitored, obtaining data for the following descriptors: density, as the number of colonies/m²; mean height and size frequency within size-classes; biomass (g/m²), and partial mortality. Biomass was estimated by using a previously adjusted relationship ($B = 0.002H^{2.61}$; relating maximum height (cm) and biomass (g of dry weight); Coma et al., 1998), corrected for the percentage of surface that presented injury (Linares et al., 2008). Partial mortality was estimated in two ways: i) as the percentage of injured colonies, those with 10 % or more injured surface (Linares et al., 2008), and ii) as the mean extent of injury, for which we differentiated recent
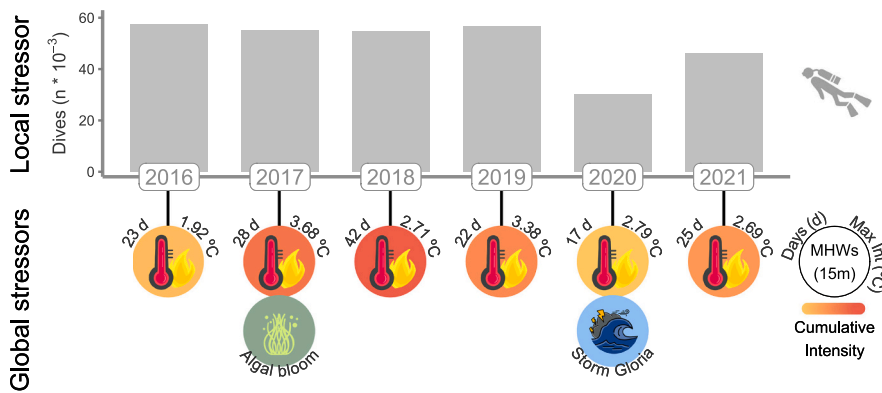
Fig. 1. Schematic summarizing the yearly stressors for *P. clavata* in the Medes MR. The bars show the local stressor (diving activity) as the number of dives recorded within the MR (data provided by the MR management authorities). The colored circles represent the detected global stressors (extreme climate-driven events): filamentous algal bloom in green, storm Gloria in blue and the MHWs at 15 m in orange to red depending on their cumulative intensity. To characterize the MHWs we added the number of days subjected to MHWs and the maximum recorded intensity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

injury (denuded axis) from overall partial mortality. Given that some locations had <100 colonies (with a minimum of 40) and that preliminary analysis showed similar demographic patterns, we performed the analysis by pooling the data for all sites. For the mentioned descriptors, we estimated the means and standard errors from all 72 quadrats (i.e., 6 sites × 12 quadrats per site).

We also estimated total mortality, where we considered two conditions that could cause death to a colony: i) detachment of a colony from its substrate, as the percentage of colonies not found in a given year, but that were alive the previous year (< 100 % injured surface) and ii) overgrowth by partial mortality, as the percentage of colonies that presented a fully injured surface but were alive the previous year. We present the mean annual mortality rates for adult colonies (> 10 cm), to compare them to the rates obtained in this MR 20 years ago (Coma et al., 2004). To explore whether detachment was facilitated by partial mortality, we estimated the detachment rate depending on the injured surface that colonies presented the year prior to their detachment. We used three categories: healthy colonies (< 10 % injured surface), moderately affected colonies (10–50 %) and highly affected colonies (50–99 %).

Linear mixed models (LMMs) were used to assess the impact and possible recovery of the studied colonies throughout the surveyed years, by establishing a model for each variable and comparing each year with the first available value (2016). We defined the models using time (year) as a fixed factor and quadrat nested within site as a random factor. In the context of this study, a significant shift in its mean implied that an impact had occurred, while the opposite meant that the variable remained stable. In the case that one year presented no statistically significant difference but a prior one did, this would suggest a possible recovery of that variable. We assessed the performance of each model using residual diagnostics. Analyses were done using the software R v 4.1.2 (R Core Team, 2021), and the "lme4" (Bates et al., 2021) and "dHARMA" (Hartig, 2022) packages.

2.4. Modelling

We examined the long-term viability of *P. clavata* while considering different management schemes on diving frequentation and different frequencies of climate-driven MME through a size-structured matrix population model (Lefkovitch, 1965). For the model, we implemented 7 size classes based on the life cycle of the species (see supplementary Fig. A2), as defined in previous studies (Linares et al., 2007). We computed the annual matrices by estimating survival, growth, shrinkage, and fecundity rates for each size class (see Appendix A1 for the detailed methodology), and used the R package "popbio" (Stubben and Milligan, 2007) to perform sensitivity and elasticity analyses, to estimate deterministic yearly lambdas (λ), as a measurement of long-term annual growth rates, together with a stochastic lambda (λs), estimated as the average growth rate in a varying environment (Morris and Doak, 2002). We used randomly drawn simulations to project the long-

term viability of *P. clavata* in this location and estimated its quasi-extinction probability using 10 % of the initial colonies present in this study as the extinction threshold. These values were compared with those obtained using matrices estimated for this same locality twenty years ago, before temperature-driven mortality was detected (Linares et al., 2007).

Finally, to underpin the need of MPA management to adapt their conservation strategies to climate change, we estimate λs for many combinations of diving frequentation as local stressor and climate-driven MME as global stressor. For the local stressor, we chose the survival of adult colonies as the vital rate that management strategies should focus on, due to it having the biggest impact on this species' annual growth rates (see supplementary Fig. A3). To visualize the effect of diving, we simulated a percentual reduction or increase in the mortality of adult colonies representing different levels of diving activity. Specifically, the reduction was simulated by lowering the observed mortality in each class down to a 3 %/yr, this being the mortality that we consider natural, including both the mortality caused by overgrowth during this period (≈ 2 %/yr), and the natural detachment recorded in non-scuba impacted sites (≈ 1 %/yr, Coma et al., 2004). Moreover, as there is no clear limit about how much the local impact could worsen, we increased up to double the observed mortality. On the other hand, we simulated the effect of the global impact through the annual probability of a climate-driven MME occurring in the future, from 0 to 100 %. To simulate this effect, we modified the weight in which the climate-affected and non-climate-affected annual transitions get randomly sampled when computing the stochastic growth rate. We classified the transitions within these two categories by using the lambdas estimated in the Medes MR between 2001 and 2004 as a reference (Linares et al., 2007). The simulations covered > 100 possible scenarios for each stressor, resulting in a total of 10,000 computed stochastic lambdas, which we have plotted to analyze and visualize the resulting interaction.

3. Results

3.1. Demographic surveys of red gorgonian populations

During the study period, we recorded a significant drop in the density and biomass of the studied populations (Fig. 2A, B, supplementary Table A1). Both parameters followed a similar pattern, i.e., a large decline up to 2018 followed by a slighter one afterwards, causing a substantial cumulative reduction of the density and biomass of around 40 % for the entire period. Specifically, density declined from 37 ± 3.2 to 23.1 ± 1.6 colonies per m² (mean ± s.e.), while biomass declined from 511.7 ± 48.3 to 296.3 ± 37.1 g per m² (mean ± s.e.,). In addition, the number of observed recruits was very low over the entire period (between 0.44 ± 0.15 and 1.38 ± 0.35 recruits per m², mean ± s.e.), with an annual mean of 0.83 recruits/m².

Comparing the first and last years, mean height showed a small but

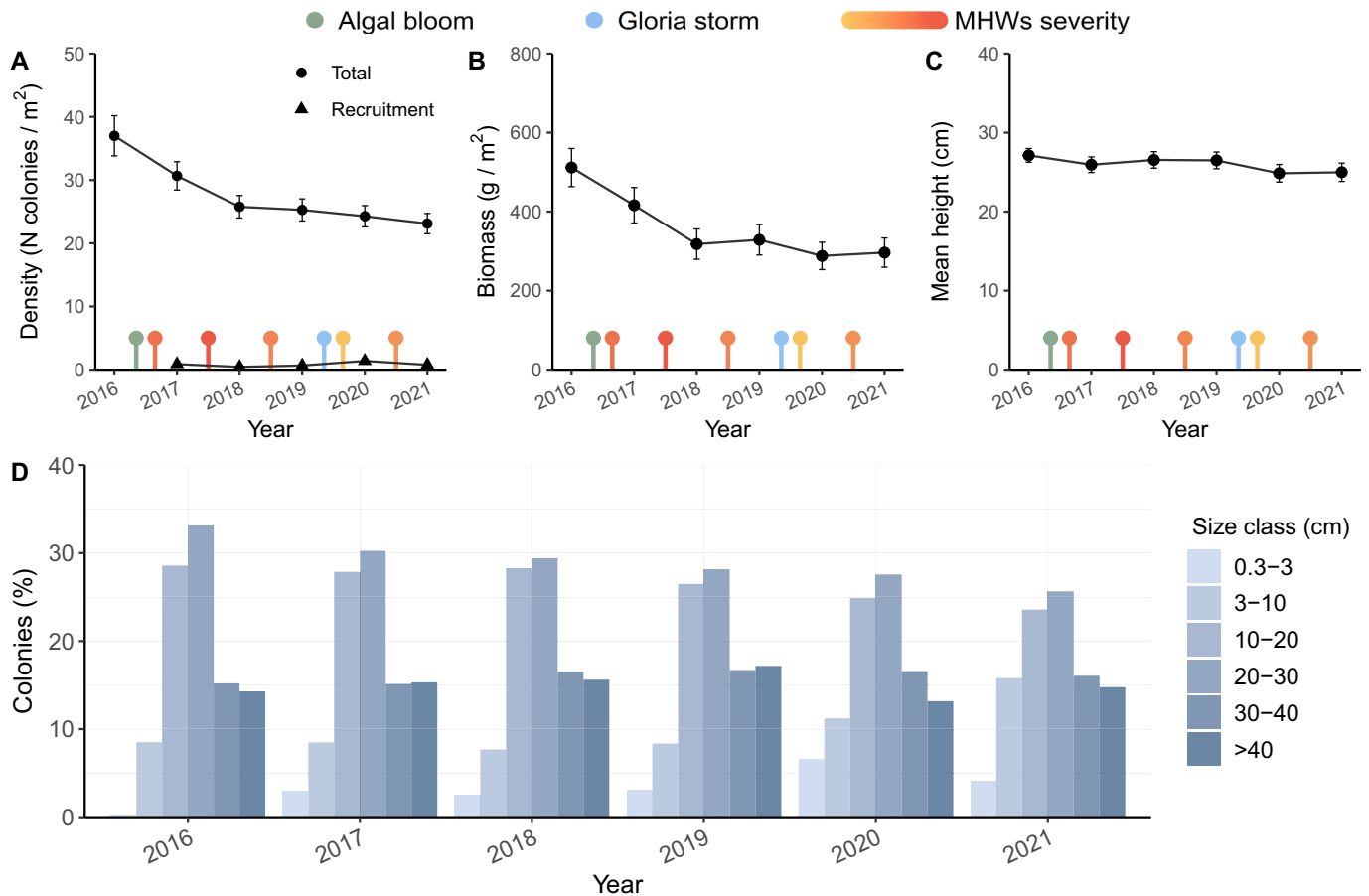**Fig. 2.** A Total density (N colonies per m^2) and recruitment density (N recruits per m^2), B biomass (g per m^2) and C mean height (cm) for the studied *Paramuricea clavata* colonies, with values representing means estimated from all quadrats, while error bars represent standard errors. The colored pins mark which extreme climate events have occurred within each period (filamentous algal bloom in green, storm Gloria in blue and the MHWs in orange to red depending on their cumulative intensity). D Size class frequency (%) for each year, obtained from maximum colony height, using the field-observable classes from the matrix model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant decline to smaller sizes (Fig. 2C), with a total variation of around 2 cm (from 27.1 ± 0.9 to 25.0 ± 1.2 cm, mean ± s.e.; supplementary Table A1). Over the studied period, the size class frequency presented a unimodal distribution (Fig. 2D), but with a slow reduction in the percentage of medium-sized colonies (10–20 cm and 20–30 cm, from an initial 61.7 % to 49.2 %), and increment in the percentage of small colonies (< 10 cm, from an initial 8.8 % to 19.9 %), while larger colonies

(30–40 and > 40 cm) stayed similar, at around 30 % of the population.

The percentage of colonies affected by partial mortality doubled from 2016 to 2018 (Fig. 3A, from 24.9 ± 3.9 % to 54.3 ± 3.8 %, mean ± s.e.) and remained stable afterwards. A similar pattern was observed for the extent of injury (Fig. 3B). All values posterior to 2016 remained significantly different (supplementary Table A1), indicating that the red gorgonian *P. clavata* populations suffered impacts whose effects lasted
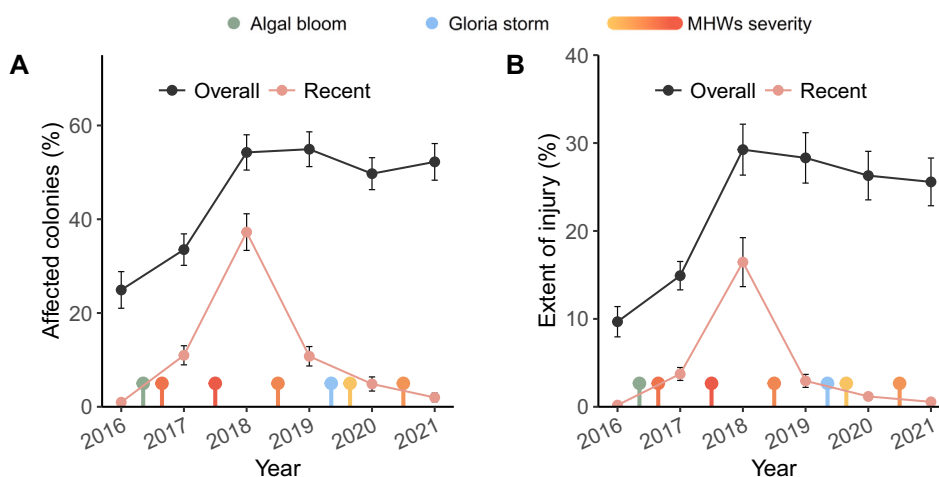

Fig. 3. A Affected colonies (%), considering all of those that presented > 10 % of their surface injured and B extent of injury (%), distinguishing between overall injuries (overgrowth and denuded axis) and recent injuries (denuded axis). Values presented are means estimated from all quadrats, while error bars represent standard errors. The colored pins mark which extreme climate events have occurred within each period (filamentous algal bloom in green, storm Gloria in blue and the MHWs in orange to red depending on their cumulative intensity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for the duration of the study. A clear peak of recent injuries was recorded in 2018 both in the percentage of affected colonies and of the extent of injuries (33.0 ± 3.9 % and 16.5 ± 2.8 %, respectively, mean ± s.e.). In 2017 and 2019, colonies displayed signs of recent necrosis as well, but to a lesser extent than in 2018.

The total mortality rate of adult colonies was 34 % higher during the studied period than the rate recorded 20 years ago (9.75 ± 1.73 %. vs. 7.26 ± 0.86 %, annual mean ± s.e.) (Table 1A, Coma et al., 2004). In fact, the two types of mortality considered here have worsened compared to previous records, with a proportional increase of 115 % for overgrowth and 28 % for detachment. During our study period, colony detachment was the main cause of mortality. Detachment rates increased with the extent of injuries presented the previous year, with rates for highly injured colonies 1.7 times greater than for healthy ones (Table 1B).

3.2. Long-term viability

Annual population growth rates estimated from the matrix population models (see supplementary Fig. A4 for the matrices) show a population decline for all transitions ($\lambda < 1$, Fig. 4), with substantial differences among years (range: 0.840–0.983). Consistently with the pattern described above, a larger decline was recorded in the first two transitions. Both the mean and the stochastic lambda suggested low population growth rates, describing an annual decline of around 10 %, which is higher than the one described twenty years ago (6 % annual decline). Population projections using the stochastic lambda for the 2016–2021 period (0.897), when colonies were subjected to both local and global stressors, show a steep extinction trajectory for shallow gorgonian populations for the next 12 to 20 years in 95 % of the simulations. Median extinction times predicted that the minimum colony abundance threshold would be surpassed in 2037. In contrast, the long-term viability of the studied colonies projected with the growth rates estimated for the 2001–2004 period, prior to onset of global climate-driven stressors, yielded a median extinction time for the year 2057, with the quasi-extinction threshold being crossed in the next 35 to 42 years in 95 % of the simulations.

The estimated stochastic lambdas computed for a range of combinations between the local and global stressors showed that they interact synergistically (Fig. 5). The synergistic effect of these impacts is observable in the curved pattern formed by the lambda isoclines, as an additive relation would create parallel isoclines and a compensatory one would have a curved pattern in the opposite direction. The combination of an increase in both impacts caused a bigger reduction in the stochastic lambda than the one obtained by adding the reduction that each impact causes individually. Within current global stressor conditions, a reduction of around 50 % off the local impact achieved similar stochastic growth rates to the ones recorded during the 2001–2004 period.

4. Discussion

There is an increasing concern that existing MPAs may not be sufficient to protect marine ecosystems from recurrent climate-driven impacts because most were designed without considering the effects caused by climate change (Bruno et al., 2018; Bates et al., 2019). In this context, our study highlights that: i) the synergic interaction between local and global stressors can cause an accelerated decline in relevant habitat-forming species within MPAs; and ii) the adoption of adaptative conservation strategies on local stressors, the diver frequentation in our case, allows us to borrow some time to address climate change. Bearing in mind the increase in the frequency of climate-driven disturbances (Cramer et al., 2018; Garrabou et al., 2021), our results clearly support the reduction of diving impact in Medes MR, through the reduction of diver frequentation and/or the enforcement of low-impact diving behavior, to enhance the long-term viability of the red gorgonian *P. clavata,* therefore, increasing the resilience of highly diverse coralligenous assemblages.

4.1. Synergic effects between local and global stressors worsen the gorgonian population decline

For the past 6 years, a significant decline of *Paramuricea clavata* has been recorded in the Medes MR. The cumulative reduction observed in colony density and biomass is comparable to the one described in previous MMEs of this species (Linares et al., 2005; Gómez-Gras et al., 2021a). Aside from the obvious decline, the recorded shift to shorter colonies should not be underestimated, as it can further reduce the structural complexity that *P. clavata* provides, an essential function within coralligenous assemblages (Ponti et al., 2014; Gómez-Gras et al., 2021b). The fact that the overall injured surface at the start of the study period was similar to the values recorded in the early 2000s reinforces the idea that prior to 2016 this MR remained lowly impacted by MHWs (Coma et al., 2004; Linares et al., 2008). On the other hand, when considering the yearly partial mortality, i.e. the recorded recent injury rates, only 2018 could be considered a temperature-driven MME, as it presents values within the moderate range of other MHW-induced mass mortalities (Cerrano et al., 2000; Garrabou et al., 2009, 2022). Even accounting for the filamentous algae event and the extreme storm that occurred within this period, there is a mismatch between density/biomass loss and partial mortality data. Nevertheless, the 2017 and 2019 recent injury values are still higher than the ones recorded in the same location during the 2003 large-scale MHW (Garrabou et al., 2009). Combined with the in situ MHWs data, these results indicate that temperature conditions have worsened to the point where the red gorgonian is now showing important signs of temperature stress.

The estimation of total mortality rates helps to further clarify why such a steep decline has occurred, since the main reason of colony death

Table 1
A Annual mortality rate (%/y, mean ± s.e.) of *Paramuricea clavata* within the Medes MR, from 1992 to 2000 (*data extracted from Coma et al., 2004) and from 2016 to 2021 (data obtained in this study). The mortality rate has been divided into two causes: a fully injured surface (overgrowth) and the disappearance of the colony (detachment). B Annual detachment rate (%/y for t1, mean ± s.e.) estimated for colonies categorized by the injured surface they presented the previous year (t0). The categories were defined as: healthy colonies (<10 % injured surface), moderately injured colonies (10 to <50 % injured surface) and highly injured colonies (50 % to <100 % injured surface). In addition, the percentage of colonies that comprise each category is indicated within the brackets.

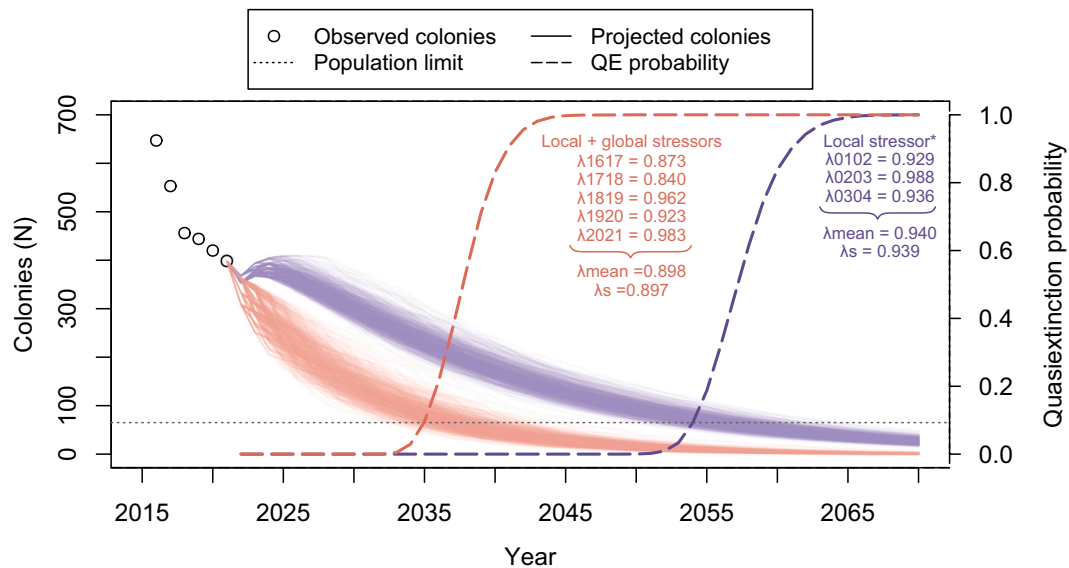| A Period	Mortality rate (%/y)	Mean ± s.e.	B Partial mortality t0	Detachment rate t1
			(Colonies in each category)	(%/y, mean ± s.e.)
1992 – 2000*	Detachment	5.91 ± 0.85	Healthy (59.66%)	6.89 ± 1.66
	Overgrowth	1 ± 0.45	Moderately Injured (27.48%)	7.09 ± 1.52
2016 – 2021	**Detachment**	**7.60 ± 1.85**	Highly Injured (12.85%)	11.7 ± 4.63
	Overgrowth	2.15 ± 0.68		

Fig. 4. Long-term predicted viability of the studied *Paramuricea clavata* colonies, showing the simulated stochastic trajectories in the current scenario, with colonies under local and global stressors, and a scenario where only the local stressor was present, *obtained from the 2001–2004 period (Linares et al., 2007). For each period, the annual deterministic growth rates (λy1y2) from the used matrices have been added, with the years indicating the starting and ending point of each transition, both occurring in Autumn, which means that each transition includes the Summer of the ending year (e.g., 1617 transition includes the effect of the 2017 summer). We also estimated the periods mean lambda (λmean) and stochastic lambda (λ_s). The dashed line represents the quasi-extinction probability, obtained by considering the number of trajectories that surpass the extinction threshold, a 10 % of initial colony abundance, which is represented with a dotted line. The dots represent the colonies observed during this study.
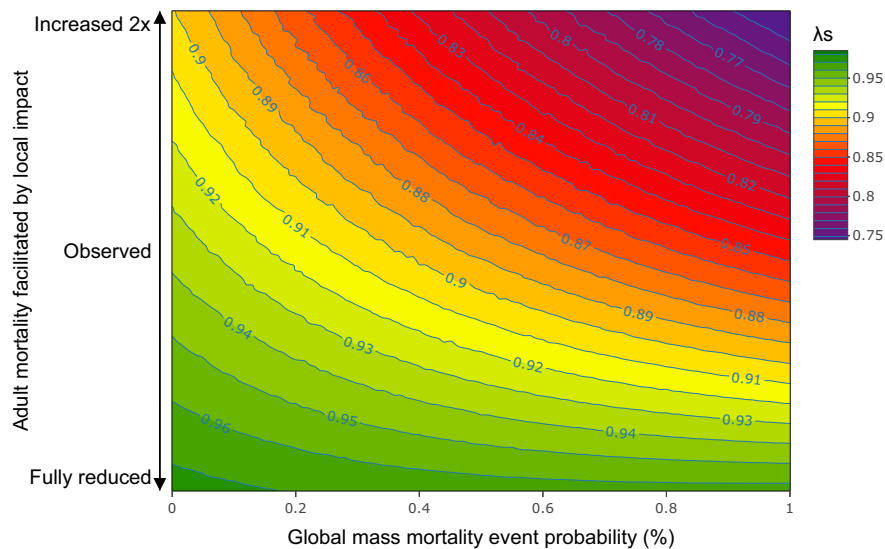

Fig. 5. Stochastic lambda (λ_s) estimated for 10,000 possible combinations between the local and global stressors. The local impact was simulated through a reduction or an increase of the adult mortality, while the global impact was simulated using a higher or lower presence of the climate change induced events that impacted the annual growth rates.

is not a fully injured surface but their detachment. This mortality has been associated to the high diving activity occurring within the Medes MR (Coma et al., 2004) and is supported by multiple studies describing the impact that over-frequentation of divers causes on branching organisms in tropical and temperate reefs (reviewed in Giglio et al., 2020). As a result, the combined effect of the high local diving frequentation with the increase of MHW-driven mortality has caused a bigger decline than expected. This effect may be linked to the increased detachment rates observed for injured colonies and also explains why in the studied period the detachment rate is higher than the one recorded twenty years ago (Coma et al., 2004), even though diving quotas have remained similar. The facilitation of detachment by surface injury could by driven

by the added weight and current drag caused by the epibiotic organisms attached to the injured surface. It is important to note that, while COVID-19 quarantines provided an opportunity of a lesser local impact, no clear benefits could be detected in this "short" time frame. Detachment rates do not follow clear patterns when studied annually (Coma et al., 2004), probably due to substratum failure being the result of the cumulative frequentation over the years, therefore impeding the detection of a benefit for a single year, which could have been further negated by the timing of the Storm Gloria.

No signs of population recovery from the mortality events have been found within the study period in either density, biomass, or partial mortality, although we did observe a slower decline during the later

years. In addition, the low recruitment values observed within the population are far from compensating the colony losses. The recruitment rates obtained in our study were also lower than the ones recorded twenty years ago (0.83 vs 1.9 recruits/m² year, Coma et al., 2001). This decrease is a hint to the negative effect that temperature can cause on the reproductive effort and larval development of *P. clavata* (Kipson et al., 2012).

4.2. Long-term viability and management adaptation

The population growth rates estimated for this period also reflect the observed decline. Temporal variation in the lambda values mainly resulted from the survival of adult colonies at each transition, as pointed out by the sensitivity and elasticity analysis, as well as in previous studies (Linares et al., 2007). Given the difficulty of distinguishing between the impacts caused by local and global stressors, it is extremely valuable to have access to growth rates obtained in the Medes MR before the observation of climate-driven impacts (Linares et al., 2007). When these two periods are compared, both the stochastic growth rates and the long-term population projections show the detrimental effects of combining local and global stressors. The 2001–2004 projections already showed that even without climate-related events, the current diving frequentation alone threatened population viability. But it is in the presence of both stressors that an acceleration of the local extinction trajectories ensues. Even though this projection could seem over-pessimistic, as the study includes several climate change related events in a short time period and implies that such conditions will occur repeatedly every five years, a scenario of increasing frequency of MHWs is expected in the future under the current IPCC scenarios (Smale et al., 2019; Garrabou et al., 2021). Moreover, a recent study on red gorgonian populations that were affected by recurrent marine heatwaves showed a population collapse in only 15 years (Gómez-Gras et al., 2021a), a time-frame similar to the one projected with our data. Such trajectories have also been observed in other coastal ecosystems such as kelp forests and coral reefs (Canadell and Jackson, 2021), which set a precedent of what can be expected after such an initial decline if no measures are taken.

The synergy between local and climate-driven stressors in this MPA will result in a deepening of the upper limit of the studied gorgonian populations where MHWs impacts are stronger (Linares et al., 2005) and diving frequentation is highest. Populations growing at greater depths, which are not directly affected by temperature stress derived from MHWs, are not expected to show such decreasing trajectories. However, the presence of healthy deep populations should not be relied on as a refuge for the recovery of shallow populations, as has been proposed in other ecosystems (Bongaerts et al., 2017), because of the very low genetic connectivity between shallow and deep populations observed for this species (Mokhtar-Jamaï et al., 2011). Understanding and predicting how warming impacts will spread across horizontal and vertical distributions of marine species is a major challenge in conservation (Pecl et al., 2017), especially considering the uncertainty on whether structural marine species will track changing thermal habitats.

In view of the poor future viability predicted for shallow *P. clavata* populations, it is crucial to properly manage the diving activity occurring within the Medes MR. This is clearly showcased when simulating the viability of these colonies under different scenarios of global and local impacts, as the synergistic interaction of these impacts will make it more beneficial to achieve a reduction of adult mortality as temperature conditions worsen. We show that reducing diving-induced detachment to half the currently observed rates would translate into recovering the growth rates obtained prior to the onset of temperature stress events. This could be achieved either through diving quotas or through the enforcement of low-impact diving practices (Giglio et al., 2020).

Modelling efforts such as those presented here provide managers with useful insights to assess different adaptive conservation strategies, as they suggest that local impacts can be tweaked within a climate-responsive management framework based on biological criteria. In the context of the Medes Islands Marine Reserve, having the opportunity to enhance the resilience of *P. clavata* in front of climate change is extremely valuable. Moreover, if the tolerable impact of the local diving activity is not readjusted, it will amplify the catastrophic effects that climate change will certainly cause during the next years. In the scope of the current concern that MPAs may not be enough to enhance the resilience of habitat-forming species in front of climate change (Bates et al., 2019), this study can be taken as an example of how the effects of warming on a key octocoral can be delayed through an adaptive MPA management of local stressors. While the time gained might seem trivial, it could make a difference, as the next years will be critical in deciding the future state of climate change. Although reducing carbon emissions should be management's most pressing agenda on a global scale, including the climate change dimension in an MPAs management plans can enhance, as we show in this study, the persistence of habitat forming species and the biodiversity that they sustain.

CRediT authorship contribution statement

Yanis Zentner: Software, Investigation, Formal analysis, Data Curation, Writing-Original draft preparation, Visualization. **Graciel·la Rovira**: Investigation, Data Curation, Writing - Review & Editing. **Núria Margarit**: Investigation, Visualization. **Júlia Ortega**: Investigation. **David Casals**: Investigation. **Alba Medrano**: Validation, Investigation. **Marta Pagès-Escolà**: Investigation. **Eneko Aspillaga**: Investigation, Writing - Review & Editing. **Pol Capdevila**: Investigation, Writing - Review & Editing. **Laura Figuerola-Ferrando**: Investigation, Writing - Review & Editing. **Joan Lluís Riera**: Validation, Writing - Review & Editing. **Bernat Hereu**: Investigation, Writing - Review & Editing, Funding acquisition. **Joaquim Garrabou**: Writing - Review & Editing, Supervision, Funding acquisition. **Cristina Linares**: Conceptualization, Methodology, Investigation, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110048.

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