QUOTAS REGULATION IS NECESSARY BUT NOT SUFFICIENT TO MITIGATE THE IMPACT OF SCUBA DIVING IN A HIGHLY VISITED MARINE PROTECTED AREA

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ABSTRACT

When effectively managed, Marine Protected Areas (MPAs) can produce wide ecosystem benefits that can foster, directly and indirectly, local economies. Tourism is one of the sectors mainly benefited by the effect of conservation. SCUBA diving represents an important tourism activity, especially in the context of MPAs, where it is one of the few activities often fostered rather than limited, for its capacity to integrate environmental and socio-economic sustainability. However, SCUBA diving can also produce negative impacts on the environment when tourism frequentation exceeds a sustainable threshold, these potentially generating negative effects on the sector itself. In this study, we (1) investigated the impact of SCUBA diving in one of the most frequented diving areas of the Mediterranean Sea (Cabo de Palos – Islas Hormigas marine reserve), and (2) assessed the potential benefits over time related to the adoption of a regulation change for the diving activity (i.e., formally adoption of diving quotas). Specifically, we compared demographic (density of alive and dead colonies) and morphometric (height, width and complexity) characteristics of the false coral (*Myriapora truncata*) between dived and fully protected (non-dived) locations over four diving seasons (one before and three after the change in diving quotas). The density of alive colonies of the false coral was, on average, six times lower in dived locations compared to controls, highlighting a clear impact of SCUBA diving (consistent over time). Colonies were also significantly smaller in dived locations. The diving quotas produced a significant reduction of the ratio dead/total colonies in the dived locations soon after their adoption, but these benefits disappeared over the following years, possibly due to a gradual decline in operators' and divers' observance and concern, rather than an increasing number of dives. This suggests that the adoption of effective regulations is crucial for the environmental sustainability of diving tourism in protected areas and can provide positive effects, but an effort is needed to ensure that compliance is consistent over time, and that low-impact diving practices are adopted by this important recreational sector.

KEY WORDS

Sustainable tourism, Tourism hotspot, Recreational diving, Ecological indicator, Human impact

1 INTRODUCTION

Marine protected areas (MPAs) have been proven a powerful tool for achieving ecological conservation goals (Lubchenco and Grorud-Colvert, 2015). When properly managed, MPAs can provide many ecological benefits (Edgar et al., 2014; Gill et al., 2017) that in turn can result both in direct and indirect economic profits (Badalamenti et al., 2000; Basurto et al., 2016; Ban et al., 2019). Tourism has become one of the sectors mainly drawing benefit from MPAs, able to offer a series of services and activities, both cultural and wildlife, in a natural and healthy environment (Badalamenti et al., 2000; Sala et al., 2013; Casoli et al., 2017; Marconi et al., 2020). Among the numerous tourist sectors, SCUBA diving is one of the most important in the context of multiple-use MPAs, able to provide economic benefits both directly to the SCUBA diving industry (i.e., diving centres and dive equipment retailers), and indirectly to all other subsidiary activities (e.g., hotels, restaurants, and transport, among other sectors) (Giglio et al., 2015; Lucrezi et al., 2017). From this perspective, SCUBA diving has been generally considered an example of sustainable economic development, able to foster the economy of local communities without compromising the environmental asset, owing to its non-consumptive use of marine biodiversity (Toyoshima and Nadaoka, 2015; Flores-de la Hoya et al., 2018).

However, the continuous growth of diving tourism, especially in the context of MPAs, has raised much concern regarding its potential ecological impact (Casoli et al., 2017; Lucrezi et al., 2013; Lucrezi et al., 2020; De et al., 2020; Pagès-Escolà et al., 2020; Giglio et al., 2020). Several studies have pointed out that uncontrolled and intensive SCUBA diving activity can seriously affect reef communities both directly, through intentional (i.e. deliberate touching of living organisms) and fortuitous contact (i.e. by the equipment) of divers with benthic organisms (Luna-Pérez et al., 2010; Hammerton, 2017; Bravo et al., 2015; Terrón-Sigler et al., 2016), and indirectly, mainly due to sediment resuspension and deposition (Milazzo et al., 2002; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004; Di Franco et al., 2009). Further evidence is associated with the influence of SCUBA diving in altering fish behaviour (Titus et al., 2015; Valerio et al., 2019). Impacts are often exacerbated where the diving pressure is disproportionate compared to the surface area of the diving spots (Au et al., 2014; Hammerton and Bucher, 2015; Hasler and Ott, 2008). Based on these considerations, the control of SCUBA diving intensity, together with assessment of divers' profiles and characteristics, and their potential impact on marine ecosystems, remain a crucial aspect to consider for the proper management of recreational activities in the context of MPAs (Flores-de la Hoya et al., 2018; Hammerton, 2016; De Brauwer et al., 2018).

Multiple measures have been proposed to mitigate the impact of SCUBA diving (e.g., reduction of quotas, smaller diver groups, improvement of pre-dive briefings, etc.) (Giglio et al., 2020). However, most studies researching management strategies to reduce the impact of diving tourism have usually only recommended specific interventions, while few actually tested or assessed their effectiveness (Giglio et al., 2020).

The Cabo de Palos - Islas Hormigas marine reserve (hereafter CPMR) is considered one of the most ecologically effective MPAs in the whole of the Mediterranean Sea (García-Charton et al., 2004; Rojo et al., 2021a; Rojo et al., 2021b), hosting a disproportionally high biomass of the rocky reef fish assemblage compared to other effective Mediterranean MPAs, encompassing high densities of large-size predators around the rocky shoals and small islets characterising the reserve (Rojo et al., 2021a; Rojo et al., 2021b). For this reason, the area is considered one of the most attractive Mediterranean diving destinations, and as a result the number of diving charter businesses operating in the area increased from 1 to 9 since the establishment of the MPA, and the number of divers visiting the MPA each year increased from about 8,000 in 1998 to more than 32,000 in 2017. This makes the SCUBA diving industry in the area one of the core stakeholder groups and one of the main economic activities, especially considering the relatively small size of the town of Cabo de Palos (Hogg et al., 2017; Hogg et al., 2018). Nevertheless, the huge increase in the number of divers over the last decade has also given rise to concern, in both the scientific community and the local administration, regarding the possible deterioration of diving sites, potentially related to the overcrowding of divers unevenly distributed both temporally and spatially. As in other temperate coastal areas, diving tourism in CPMR tends to be concentrated mostly during the warm months (from June to October). Furthermore, the morphology of the CPMR contributes to the concentration of diving activity around a series of small rocky shoals. For this reason, in 2014, the management authority amended the law regulating recreational SCUBA diving activity in the CPMR, established along with the MPA, introducing new maximum daily quotas of divers for each diving spot (*Orden de 4 de junio de 2014, de la Consejería de Agricultura y Agua, por la que se regula el ejercicio de las actividades subacuáticas en aguas interiores de la reserva Marina de Cabo de Palos-Islas Hormigas (BORM nº 133, Consejería de Agricultura y Agua* (2014) - http://www.borm.es/borm/documento?obj=anu&id=703032). At the same time, two new diving sites were opened with the aim of distributing the diving pressure more evenly in the MPA over space and time while keeping the overall number of dives in the reserve roughly stable, in order to prevent a major economic loss for the local diving operators. The previously existing diving quotas, stipulated from the moment the declaration of the marine reserve was made in 1995, were not applied in practice because compliance was not enforced from the outset, so recreational diving expanded freely, to a point where these quotas were too low to accommodate the reality of the sector's requirements; it was only after the new regulations were introduced in June 2014 that quotas began to be effectively enforced.

The aims of this study were (1) to assess the impact of recreational SCUBA diving in the CPMR, using a fragile benthic species, the bryozoan *Myriapora truncata*, as indicator of the erosive effect of divers, and (2) to assess the efficacy of the diving regulations introduced to produce measurable changes in the impact indicators used, thus indicating the likely achievement of a sustainable SCUBA diving activity in the MPA.

2 MATERIAL AND METHODS

2.1 Study species

The “false coral” *Myriapora truncata* (Pallas, 1766), is a common bryozoan inhabiting shallow sheltered and shadowed rocky habitats down to 60 metres depth (Zabala, 1986) in the Mediterranean Sea and the eastern Atlantic (Lopez de la Cuadra and García-Gómez, 1994). It is a colonial species growing as tree-like bushes with a robust skeleton, reaching a maximum diameter and height of 15 cm, generally growing on hard substrates (i.e. rocks, crustose red algae and shells) (Berning, 2007; De La Nuez-Hernández et al., 2014). Colony growth starts with the formation of an encrusting base from a twinned ancestrula and proceeds with the development of alternating whorls made by undifferentiated autozooids (feeding units) and a bundle of kenozooids, formed for structural reasons (Berning, 2007; Lombardi et al, 2011). The little information available on the biology of the species suggests that, like other bryozoans, *M. truncata* has a very slow colony growth rate, with a field-estimated branch extension rate of 0.41 cm per year (Gristina and Balduzzi, 1999; Hermansen et al, 2001). This slow growth rate contributes to making it particularly sensitive to natural and human-induced environmental stressors (e.g. ocean acidification) (Rodolfo-Metalpa et al, 2010). Several studies have highlighted the likely effect of environmental factors on the morphology of this species: as pointed out by Harmelin (1988), its branching pattern (branch spacing) is largely controlled by hydrodynamics, so that with decreasing water currents (and possibly also with increasing sedimentation rate) the length between two bifurcations increases, i.e. bushier colonies are formed in high energy environments whereas colonies in lower energy conditions are more openly spaced; in addition, branch diameter has been shown to greatly vary (ranging 2.0-6.6 mm), likely caused by differences in food supply rather than other environmental factors such as temperature or current energy, although further studies are needed (Berning, 2007). Like other calcareous organisms, *M. truncata* is also very sensitive to physical damage (e.g. diver contacts while swimming), due to its fragility. Additionally, thanks to its colony size and bright orange-red colour, it can be easily identified during underwater visual censuses. All these characteristics make it a perfect indicator of the local impact of SCUBA diving (De La Nuez-Hernández et al., 2014; Casoli et al., 2017).

2.2 Study area and data collection

The study was carried out in Cabo de Palos-Islas Hormigas marine reserve (CPMR), situated along the coast of Murcia (SE Spain, Mediterranean Sea) (Fig. 1). The area is mainly characterised by rocky reefs, with extended patches of coralligenous, surrounded by detritic bottoms (García Charton and Pérez Ruzafa, 1998). The oceanographic conditions of this area are singular. On the one hand, its relative proximity to the Straits of Gibraltar and the Alboran Sea gives to this zone particular hydrodynamic characteristics, being mainly characterized by areas of intense currents from two main directions, south-west and north-east (Hernández-Molina et al., 2011). On the other hand, despite the influence of the Atlantic waters on this area, open waters off the coast of Cabo de Palos are usually warmer in summer compared to other zones (Cano, 1978). The MPA was established in 1995 and has a total surface area of 1931 ha, including a no-take zone (270 ha) surrounding two small islets (Hormiga and Hormigon) and a steep rocky shoal (El Mosquito) where only scientific research is allowed, and a buffer zone that covers a series of rocky shoals (Fig. 1) where two types of artisanal fishing (bottom longline from October to April, and trammel net from April to October) are allowed to a few boats traditionally linked to the area, and where diving spots are concentrated.

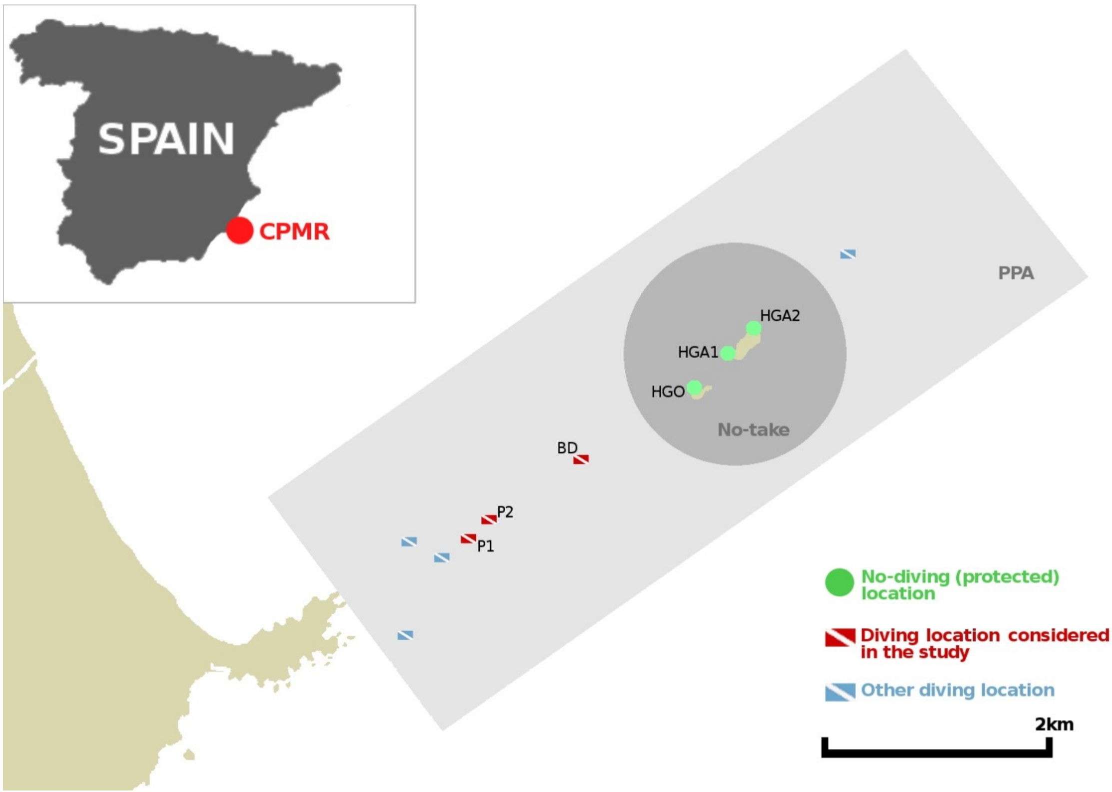

Figure 1. Study area (CPMR): green dots indicate the 3 areas of the no-take zone (where diving is prohibited) considered in the study [HGA: Hormiga Is., HGO: Hormigón Is.]; red SCUBA flags indicate the 3 diving spots of the partially protected area (PPA) considered in the study [BD: Bajo de Dentro, P1: Piles I, P2: Piles II]; blue SCUBA flags indicate other diving locations within the PPA.

Although small-scale fishing and SCUBA diving potentially compete for space in the buffer zone, this is practically never the case over the main diving sites. In fact, due to the high diver frequentation and the constant presence of dive boats around the mooring buoys of the diving sites, fishers have been gradually displaced from these fishing grounds (Hogg et al, 2017). Fishing gears are usually deployed at some distance from the shallower portion of the rocky shoals, and during summer, when there is a greater affluence of divers, fishers avoid setting their gear around the diving spots specifically in order to avoid conflict. The management body of the CPMR (Regional Fisheries and Aquaculture Service, Autonomous Community of Murcia) has been gathering data on diving frequentation in each diving spot on a monthly basis since 2002. Four sampling campaigns were conducted yearly in the winter season (i.e. between December and March), thus after the period of the year with the highest presence of SCUBA diving activity (from June to October, Fig. 2). Specifically, the first campaign (winter 2013-2014) was conducted before the implementation of the diving quotas, and the other three campaigns in the following winters after the introduction of the new regulation (officially in June 2014). The choice to carry out only one sampling campaign each year was motivated by two reasons: (1) the false coral has a long life-span without considerable seasonal fluctuations, as so often for other coralligenous builders (Garrabou et al., 1998); (2) diving impact takes place as a constant disturbance during the high season, thus within-year sampling was considered unnecessary (Garrabou et al., 1998).

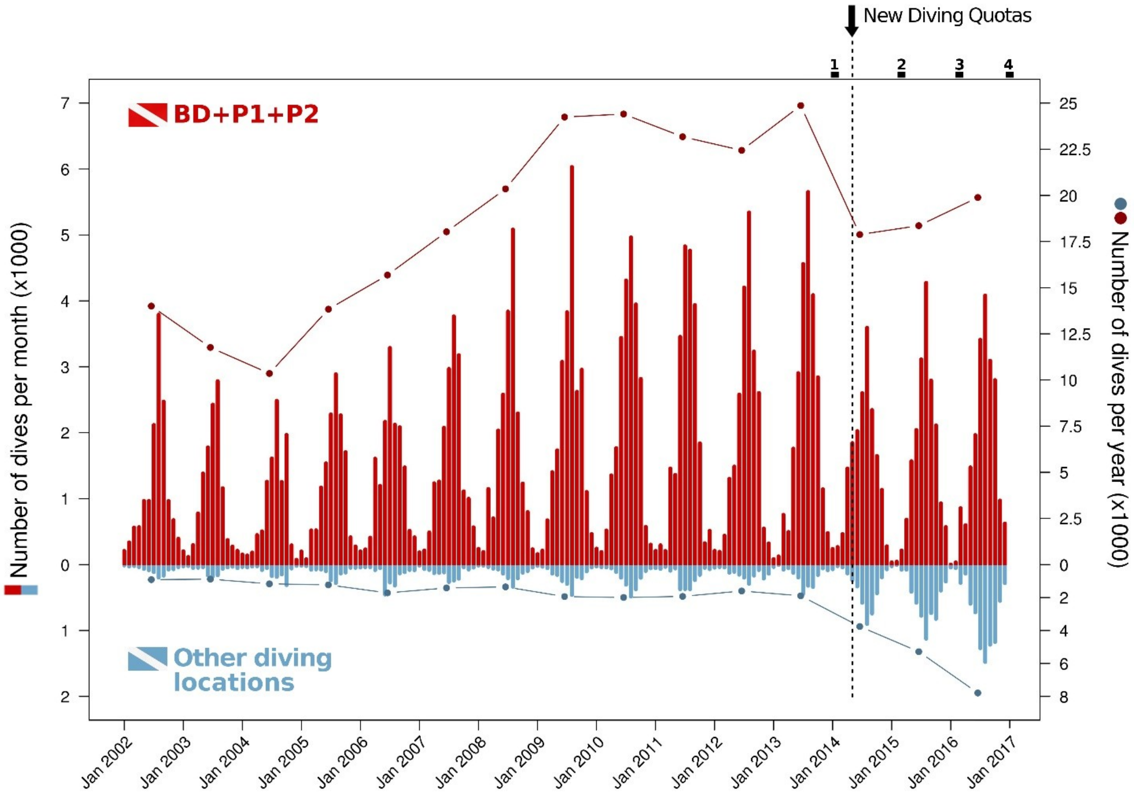

Figure 2. Distribution of total number of dives between January 2002 and December 2016. Red color represents the 3 diving spots considered in the study (BD, P1 and P2), and the blue color represents all other diving spots within the CPMR (refer to Fig.1): bars indicate the total per month (scale on left y axis), dots indicate the total per year (scale on right y axis). The dashed line indicates the month of implementation of the new diving quotas in the PPA. Numbers in the top-right corner indicate the periods in which the 4 sampling campaigns were carried out.

In order to investigate the potential impact of SCUBA diving on *M. truncata* and the eventual mitigation of this impact due to the implementation of new diving quotas, two zones associated with opposite SCUBA diving pressure were considered: the no-take zone (NTZ), in which recreational SCUBA diving is prohibited, and the buffer zone (or partially protected area, PPA), in which such activity is allowed (Fig. 1). In each of these two zones, 3 locations 500-1000 m apart were considered, both in the NTZ (two of them haphazardly positioned each year on Hormiga islet ‒ HGA1 and HGA2, respectively, and a third randomly located on Hormigon islet ‒ HGO), and in the PPA ‒ each of them located every year at a random place in the rocky shoals Bajo de Dentro (BD), Piles I (P1) and Piles II (P2), which are the most frequented diving spots. In each location, 2 depth ranges were considered: shallow (10-12 m) and deep (20-22 m), in order to represent the depths mostly frequented by SCUBA divers during their diving excursions in the CPMR, while attempting to capture a possible bathymetric variability in the population characteristics of this indicator species. For each combination of location and depth, 3 sites were randomly selected (tens to hundreds of meters apart from each other). Although there are some topographical differences between the NTZ and the PPA - namely the presence of the islets in the NTZ, potentially offering higher protection to benthic communities against strong currents or storm events, as compared to the shoals in the PPAS – these differences were controlled as much as possible by placing sites in areas with similar characteristics in both the NTZ and the PPA (i.e., site exposure to currents and waves, slope and complexity). Furthermore, by sampling at depths below 10 m and considering that all rocky shoals included are shallower than 5 m at the top, we can confidently exclude any sampling bias in the design adopted. All these factors, coupled with the scarce spatial interference between artisanal fishing and SCUBA diving described above, makes SCUBA diving the only potential impact discriminating the two zones, all other potential factors remaining essentially the same in both zones. This enabled us to design a natural experiment in which the varying factor is precisely the pressure exerted by SCUBA divers throughout the year. At each site, 5 quadrats (1×1 m) were randomly positioned during underwater visual censuses for a total of 180 quadrats for each of the four sampling campaigns. *In situ* visual census was preferred to photographic sampling (such as that used in de la Nuez-Hernandez et al (2014) and Casoli et al (2017)) because, by a preliminary survey, it was highlighted that the sampling area was not suitable for photographic sampling, due to the presence of many blocks and crevices below/inside which false coral colonies were often found, impeding the proper characterisation of false coral populations on the basis of photographs. For each quadrat, observers visually counted the total number of colonies, distinguishing between alive and dead ones, the latter being considered as such if they were completely detached from the substrate. In addition, the level of damage related to diving activity was assessed by investigating a series of morphological and morphometric characteristics of the colonies. To do so, 6 living colonies closer to the upper right corner of each quadrat were selected (when present), recording the maximum height and width of the colony (measured with a ruler to the nearest 5 mm), the presence of breaks and the complexity (i.e. the level of ramification, considered as an ordered categorical variable, taking values from 1 – low complexity to 3 – high complexity). For each colony, its level of exposure to physical damage was also recorded, distinguishing between high-exposed (i.e. more susceptible to physical damages) and low-exposed (i.e. less susceptible to damage because they were at the bottom of crevices or below rocks) colonies.

2.3 Statistical analyses

Data was collected on the total number of dives per month and year for the period between 2002 (the first year for which the official number of dives per month was available) and 2016, distinguishing between high-dived sites and recently opened low-dived sites. We focused especially on the period before and after the adoption of new diving quotas (summer 2014) with the aim of highlighting trends in the intensity of the diving activity.

The potential impact of SCUBA diving on *M. truncata* in CPMR was first assessed using the density of alive colonies as response variable. A linear mixed model (lmm) was used, implementing the 'lme4' package (Bates et al., 2015) in the statistical suite R (R Core Team, 2020), and using Wald Chi-square test to calculate P-values. The factors considered were: Year (Y, fixed and orthogonal with 4 levels), Protection (P, fixed with 2 levels – no diving *vs.* diving) and Depth (D, fixed and orthogonal with 2 levels - shallow *vs.* deep) and their respective interactions. Potential spatial variability was controlled including in the model the factors Location (L, random with 3 levels, nested in the (Y x P x D) interaction) and Site (random with 3 levels, nested in the L(Y x P x D) interaction).

Secondly, the potential impact of diving on the morphometric characteristics of the colonies (considering their height and width in mm) was investigated fitting linear mixed-effect models similar to the previous one but including the additional factor ‘Exposure’ (2 levels: ‘low’ and ‘high’), and its interaction with the other orthogonal sources of variation, to account for the effect of the vulnerability of the single colonies to diving impacts. Finally, the impact of diving on colony complexity was investigated through an ordered logistic regression, a procedure for testing categorical response variables that can assume a restricted number (more than 2) of ordered values (Agresti, 2019). To this aim, we implemented a cumulative link mixed-effect model (clmm) using the ‘ordinal’ package (Christensen, 2019) in R. The initial full model was the same as that used for morphometric characteristics.

To assess the potential SCUBA diving impact mitigation effect of the new diving quotas, and considering the slow population growth of the false coral, as of other bryozoans used as indicators, that would not produce any detectable changes in the density of alive colonies in the short term (e.g., between two consecutive years as before and after the change of diving quotas) (Giglio et al., 2020), we focused on dead (detached) colonies and the presence of breaks on alive colonies. Since the density of dead colonies was verified to be proportional to the density of alive colonies, we considered instead the ratio dead/total colonies within quadrats as the response variable. The model design represented a before-after/control-impact design with one time before and several times after the change in the number of dives, and multiple impacted and multiple control locations (multiple before-after/control-impact – MBACI design) (Underwood, 1992; 1994; Keough and Mapstone 1997; Roberts et al., 2007). The rationale of the MBACI design is that the impact (in our case the potential positive impact caused by the reduction of diving pressure) in several diving spots should cause a reduction in the dead/total ratio of *M. truncata* colonies from before to after greater than the one observed for false coral populations in the multiple control locations where diving is forbidden (Garrabou et al., 1998), causing a significant interaction between sampling year and protection (Y × P). To this aim, a binomial generalized linear mixed model (glmm) was run testing for the significant interactions (Y × P) considering the year before (2013) and the three years after the change of diving quotas (2014, 2015 and 2016). In the full model, we included all factors used for testing the density of alive colonies (see above) but dropping the factor ‘Site’ owing to model singularity problems. Tests between pairs of years before and after the change in diving quotas (i.e. 2013 *vs.* 2014, 2013 *vs.* 2015 and 2013 *vs.* 2016) were run in case of detecting a significant interaction (Y × P), in order to assess for which pairs of years a change in the ratio dead/total colonies emerged between protected and dived locations. The relation between the ratio dead/total colonies and the number of dives, relative to each year, in the dived locations was investigated through a linear model and visually inspected through a scatterplot. The MBACI approach was used also for the ratio broken/total colonies (on the total number of alive colonies selected for the morphometric characterization). However, due to the low frequency of broken colonies (less than 10% of the total), we modelled the presence *vs.* absence of broken colonies within each quadrat as response variable (instead of the ratio) to improve model fit and implementing a binomial glmm (again, factor ‘Site’ was dropped owing to model convergence problems, while keeping all factors used for the ratio dead/total). For all models, normality of residuals has been visually inspected through normal qq-plots and the homogeneity of variance by checking residuals *vs.* fitted plots (Zuur et al., 2010). Data were log-transformed (logx+1) in case of initial heteroscedasticity. None of the final models departed from homogeneity of variance, nor from normality of residuals (see Supplementary Material). All analyses were run using R software (R Core Team, 2020).

3 RESULTS

3.1 Record of diving activity

The total number of dives in the PPA of the CPMR increased overall from ~15,000 dives in 2002 to ~26,000 dives in 2009, after which the yearly amount of dives remained approximately stable (Fig. 2). Considering only the three diving spots where the random locations were selected each year in this study (P1, P2 and BD), the maximum number of dives between 2002 and 2016 was recorded in 2013 (the year before the change in quotas), with a total of 24,866 dives. In the following year (2014), the total number of dives recorded for the same spots dropped to 17,880, i.e., was reduced by 28.1% compared to the previous year due to the new regulation. In subsequent years, the number of dives slightly increased, so that, compared to 2013, the reduction in the number of dives was 26.2% in 2015 and 20.0% in 2016 (Fig. 2). The implementation of quotas mainly affected the number of dives during the high season (May-October) that passed from 20,470 ± 697 dives (mean ± SE, for the period 2011-2013) to 15,585 ± 813 (for the period 2014-2016), thus determining a mean reduction of 23.8%. For their part, the number of dives in other diving locations of the MPA, approximately stable until 2013, constantly increased after the change of quotas and passed from 1,894 dives in 2013 to 7790 in 2016, with an average increase per year of 36.9% (Fig. 2).

3.2 Impact of diving on *Myriapora truncata*

The density of alive colonies was, on average, almost six times higher in the NTZ (where diving is prohibited), harbouring on average 28.9 ± 1.39 colonies m^{-2} (mean ± SE), compared to the PPA (where diving is allowed) with 5.2 ± 0.36 colonies m^{-2} (Fig. 3), this difference being statistically significant and consistent over the four sampling campaigns and the two depth levels (Table 1, Fig. S2). The effect of depth was also statistically significant, with the density of alive colonies approximately two-fold on deeper bottoms (proportionally for each level of protection) compared to shallower ones (Fig. 3). A significant spatial variability was recorded both at medium spatial scale (among locations) and at small spatial scale (among sites within each location and depth range) (Table 1).

Table 1. Model output from the linear mixed model on density of alive colonies of *M. truncata*. Significant predictors are presented in bold.

RESPONSE	**RANDOM COMPONENT**			**FIXED COMPONENT**			
	Predictor	**Chisq**	**pvalue**	**Predictor**	**df**	**Chisq**	**pvalue**
Alive colonies lmm (log+1)	***Location***	**8.9331**	**2.80E-03**	*Year*	3	1.842	0.605
	Site	**35.095**	**3.14E-09**	***Protection***	**1**	**165.956**	**2.200E-16**
				Depth	**1**	**36.977**	**1.195E-09**

				Year × Protection	3	2.9753	0.395
				Protection × Depth	1	3.331	0.068
				Year × Depth	3	2.525	0.470
				Year × Protection × Depth	3	2.376	0.498

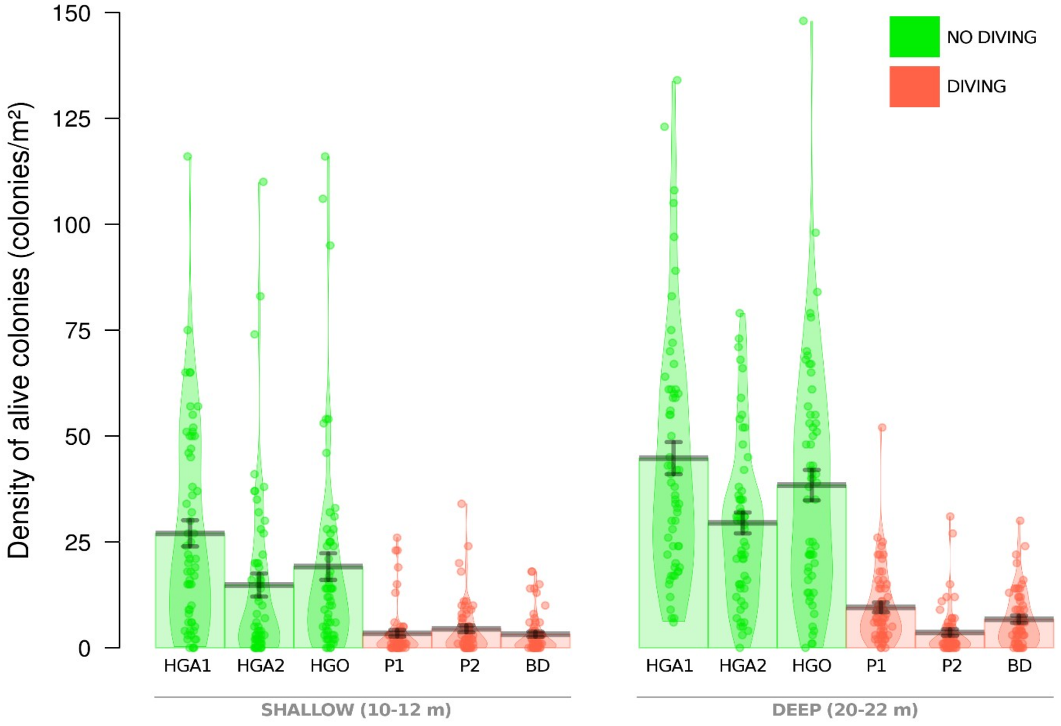

Figure 3. Combined Barplot and Violin plot reporting the density of alive *Myriapora truncata* colonies for each combination of location and depth level considered (all years pooled). Black horizontal and vertical bars represent means and standard errors, respectively. Dots represent replicates (horizontal jittering added for improving clarity) and shaded violins represent the smoothed values of density.

Regarding the morphometric characteristics of the colonies, a significant effect of protection was observed for colony height: colonies were, on average, shorter in dived than in non-dived locations (Tab. S1 and Fig. S5). A significant effect of colony exposure was also detected with high-exposure colonies shorter than low-exposure ones (Fig. S5). In the case of colony width a significant interaction Protection × Exposure was detected, together with a significant effect of Protection and Exposure: high-exposure colonies were statistically narrower in dived locations, whereas no statistical differences in colony width were detected for low-exposure colonies between protected and dived locations (this generating the significance of the interaction term) (Tab. S1 and Fig. S6).

No effect of protection on colony complexity was observed (Tab. S1). Highly complex colonies were, on average, more abundant with a low exposure, while an opposite pattern was observed for the least complex colonies, found to be more abundant in highly exposed areas (Fig. S7). All morphometric and morphological characters showed a significant spatial variability at the scale of the site (Tab. S1).

3.3 Effect of diving quotas regulation

The ratio dead/total colonies was, on average, consistently higher in the dived locations compared to the protected ones all years taken together, although, considering all the four sampling years, the interaction year × protection (Y × P) was statistically significant (Table S2), as a result of a change in the ratio through time, as follows: the tests between pairs of years yielded a significant interaction (Y × P) when comparing 2013 and 2014, so that the ratio dead/total colonies was statistically higher in dived locations in 2013 (before the adoption of the diving quotas), while no differences between protection levels were observed in 2014, regardless the depth level (Table 2); the comparison 2013 *vs.* 2015 highlighted the absence of statistical differences between protection levels only in the case of the shallow depth level (Fig. 4), which generated a Y × P × D interaction (Table 2); finally, the comparison 2013 *vs.* 2016 detected only a statistically significant effect of the factor Protection, consistent over the years compared, with higher values of the ratio dead/total colonies observed in the dived locations (Table 2, Fig. 4), regardless of the depth level. Therefore, the positive effect of the reduction in diving pressure has gradually dissipated.

Considering all combinations of years and dived locations, the relationship between the ratio dead/total colonies and the number of dives was positive, although this trend was not statistically significant (Fig. 5). The year before the reduction of diving quotas (2013) was associated with a higher number of dives and higher values of dead/total ratio, while a low ratio associated with a lower number of dives was observed for the years 2014 and 2015, almost approaching the ratio observed in no-diving locations. No significant main factors were highlighted analysing the presence/absence of broken colonies (Table S3).

Table 2. Model output (Wald chi-square test) from the generalized linear mixed model on the ratio dead/total colonies of *M. truncata* run on pairs of year before and after the reduction of quotas in the dived locations. Significant predictors are presented in bold.

RESPONSE Ratio Dead/Total colonies Binomial glmm		**2013 vs 2014**		**2013 vs 2015**		**2013 vs 2016**	
	Predictor	**Chisq**	**pvalue**	**Chisq**	**pvalue**	**Chisq**	**pvalue**
	Year	0.622	0.430	**4.580**	**0.032**	0.019	0.888
	Protection	**25.606**	**4.19E-07**	**23.274**	**1.41E-06**	**20.116**	**7.29E-06**
	Depth	0.001	0.975	0.001	0.971	0.002	0.968

Year × Protection	**6.286**	**0.012**		1.166	0.280		0.003	0.958
Year × Depth	1.551	0.213		0.065	0.799		0.254	0.614
Protection × Depth	1.86	0.173		1.658	0.198		1.395	0.237
Year × Protection × Depth	0.456	0.499		**4.072**	**0.044**		1.891	0.169

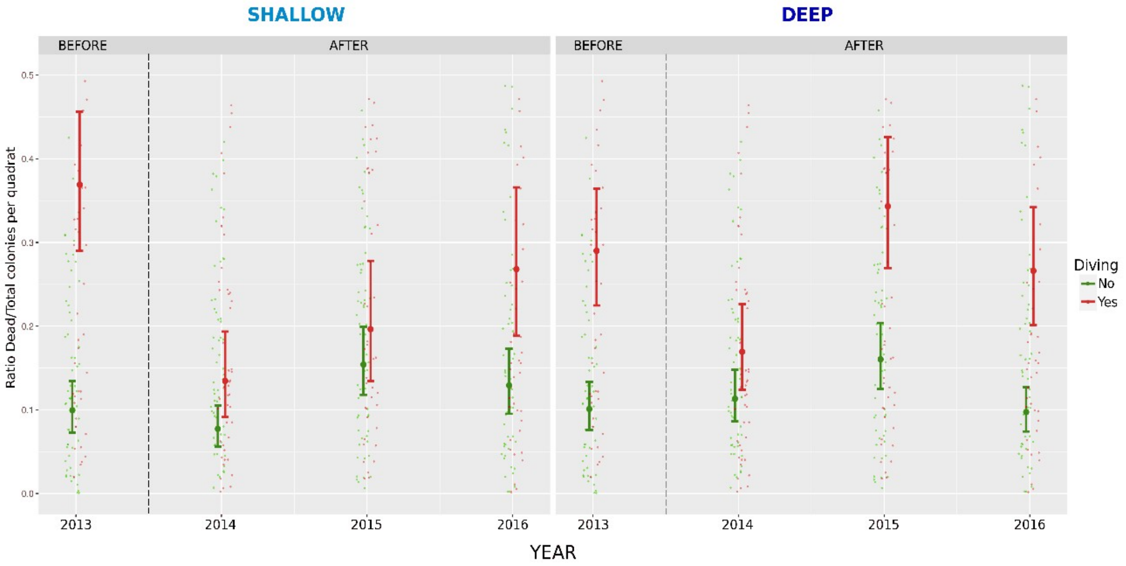

Figure 4. Ratio dead/total colonies between protected (green) and dived (red) locations in the four sampling campaigns and in the two depth levels considered: full dots and relative bars represent model predicted mean ± SE, semi-transparent dots represent field data (horizontal jittering added for improving plot clarity). The dashed line separates the campaign before and the three campaigns after the change in diving quotas.

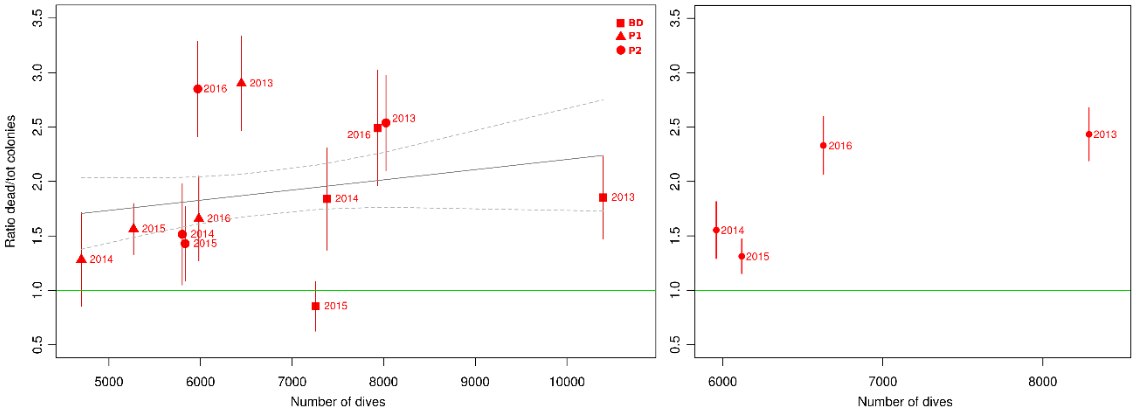

Figure 5. Relation between the ratio dead/total colonies in the dived locations and the number of dives in each year. Left panel: Red symbols and bars represent mean ± SE of dead/total colonies for each combination of dived location and year (different symbols indicate different locations over the years considered); grey lines represent the linear regression and the 95% confidence intervals (dotted lines). Right panel: values represent mean ± SE per year, dives are averaged between the diving locations considered.

In both plots, for each year, values are standardized for the relative mean dead/total colonies ratio observed in the protected locations, to take into account the natural variability (the green line represents the ratio dead/alive colonies in the protected locations).

4 DISCUSSION

Our results clearly showed that the cumulative diving pressure in the MPA determined a strong negative impact on the density and morphometric characteristics of the false coral, used here as a bio-indicator. On the other hand, the introduction of diving quotas, implemented after the first monitoring campaign, showed that a rapid mitigation of the impact is possible, but benefits can vanish quickly unless additional management measures are adopted, as discussed below.

The decline in abundance of benthic organisms related to the physical impact by divers is a well-known phenomenon occurring in intensively dived sites. In our study, total densities of living colonies of *M. truncata* in the PPA of the CPMR (diving spots) were between 3 and 12 times lower than in the NTZ, this difference being consistent over the four years. This result suggests a pronounced impact of diving activity in the PPA, which is in line with the outcomes of other studies carried out both in tropical and temperate reefs characterized by tourism over-frequentation (see Giglio et al., 2020, for a review).

The implications of prolonged and intensive SCUBA diving are multiple and concern both ecological and socio-economic aspects. The cumulative effects of intensive diving frequentation can determine a gradual decline of density and size of species composing the benthic communities of coastal habitats, potentially impairing their ecological functions, and altering ecosystem-wide ecological processes. A major consequence of the impact of diving on benthic communities is a loss of structural complexity (determined by the diversity and the architecture of the benthic organisms), considered a crucial characteristic for maintaining high biological diversity in coastal habitats (Roberts et al., 2003; Munguia et al., 2011). Highly structurally complex benthic communities, in fact, provide a variety of food and refuge resources to different species, sustaining the presence, abundance and diversity of fishes and other mobile organisms (García-Charton et al., 2004; Carminatto et al., 2020, Di Franco et al., 2021). A reduced biotic complexity can determine a negative change in the characteristics and dynamics of the community, and leave space for the invasion of opportunistic, often non-indigenous organisms, potentially causing a complete ecological phase-shift toward a less resilient costal community, with an increased susceptibility to other direct and indirect anthropogenic impacts (and, in particular, to climate change) (Garrabou et al., 1998; Lyons et al., 2015).

The pauperization of the natural environment can lead to a degradation of the quality of the diving experience (Flores-de la Hoya et al., 2018), which, in turn, will generate detrimental socio-ecological effects. These negative dynamics are especially paradoxical in MPAs: as dive tourism increases, attracted by the environmental richness of effectively managed protected sites, heavily dived areas can experience an impoverishment of the environmental resources for which they received protection status and which represent the basis of their appeal for tourists (García-Charton et al., 2008; Roncin et al., 2008; Hammerton, 2017; Giglio et al., 2018).

The available studies conducted in the Mediterranean Sea, and targeting the false coral as indicator, highlighted less evident patterns of diving impact on this species than those measured in the present study. De la Nuez-Hernández et al. (2014) showed that in locations characterised by a high frequency of divers, immediately after the peak season for tourism, colonies of *M. truncata* suffered a certain reduction in density, although not statistically significant. For their part, Casoli et al. (2017) observed a consistent effect of diving pressure on density of false coral only on relatively deep bottoms (30-40 m), but they did not observe any difference in the density of this species in the depth range considered in our study (14-25 m). Recently, the same authors found that *M. truncata* was more abundant at sites with medium/high disturbance levels (Casoli et al., 2020), but, noteworthily, their sampling sites were placed at a depth of 35-40 m and only on vertical walls, thus likely being less impacted by divers. In contrast, the outcomes of the present study highlight straightforward evidence of the impact of diving pressure on colonies of false coral, regardless of the depth level. Importantly, Casoli at al. (2017) found an evident effect of diving on bryozoan species other than *M. truncata* composing the Mediterranean coralligenous assemblage and suggested that the false coral could be actually less impacted by SCUBA diving compared to other coralligenous builders (Casoli et al., 2017). From this perspective, the impact on the false coral detected in the CPMR could be even worse for other species of the coralligenous community not considered in our study. Apart from the high absolute number of divers recorded in the diving locations, the diving pressure in the CPMR is exacerbated by the relatively small surface area of the diving spots. As a reference, the most frequented diving spot in the MPA (i.e. the rocky shoal ‘Bajo de Dentro’), hosting every year about 9,000 divers, has an available surface area for SCUBA diving of about 4,000 m^2 (considering the surface comprised between its top and the isobaths of 30 m, which is the maximum depth to which the average diver can go). This means that every square meter of the diving spot is frequented by an average of 2.25 divers each year, for the duration of a standard dive (about 50 minutes).

According to our results, the effect of diving pressure on *M. truncata* seems to also affectits morphometric characteristics. Colonies were found to be significantly smaller in the dived locations. Colony exposure to physical damage appears to also be a major driver of these two traits. In addition, low exposure colonies in the two protection levels were similar in terms of width, whereas a significant difference was observed in the case of high-exposed high exposure ones, this generating the interaction term Protection × Exposure. This result is in line with the outcomes of the study of De la Nuez Hernandez (2014) that found a non-significant trend to larger colony sizes of the false coral in sites not frequented by SCUBA divers. On the other hand, no differences in terms of colony complexity, or in terms of presence of breakages were found. Although the increase in skeletal breakage of corals is a frequently documented impact (Giglio et al., 2020), our results regarding the complexity and presence of breakages could be a consequence of the rather robust skeleton of *M. truncata* (Zabala, 1986) that would make a complete detachment of colonies due to physical collisions more frequent than single branch breaks, this action affecting all colonies regardless of their complexity.

Regarding the effect of the regulation measures introduced in summer 2014, a drop in the ratio dead/total colonies, here used as an indicator of the recent diving impact, was observed in the dived locations of the CPMR in the first year after the implementation of quotas, whereas fully protected locations did not experience any detectable change. The ratio observed in the diving sites in 2014 almost reached the values observed in the locations of the NTZ, where the presence of dead colonies is independent of direct anthropogenic disturbances. This pattern is very likely related to the clear decline in the absolute number of divers frequenting the main diving spots of the MPA recorded in the year after the introduction of the new diving quotas. From this perspective, it appears that the regulation produced a promising change in the trend of diving impacts in the MPA. This outcome is extremely important as it suggests that sustainable SCUBA diving in highly touristic MPAs is possible without compromising the socio-economic benefits generated by this activity in the area, thanks to a redistribution of the diving pressure around newly opened diving spots. Apart from being one of the few studies assessing the effectiveness of a diving management measure, to our knowledge this is the first study in which an assessment of impact reduction of SCUBA diving has been performed on a benthic bio-indicator and based on a MBACI approach, which is one of the more robust sampling designs to detect the effect of disturbing factors (Underwood, 1994; Keough and Mapstone, 1997; Roberts et al., 2007). In fact, the few studies available in the literature estimated the effect of management measures on the source of impact (e.g. the frequency of divers’ contacts with the bottom, Hammerton and Bucher, 2015), rather than its effect on the biological components of the benthic community. Additionally, the BACI approach, considered the optimal solution for isolating the effect of the anthropogenic disturbance from the natural variability, has been used for the first time to assess the effects of a SCUBA diving management measure, being implemented rather rarely so far to assess the impact of diving activity (Giglio et al., 2020).

In the second year after the implementation of the diving regulation, however, the benefits gradually diminished, only occurring on shallow bottoms, and completely vanished in the third year after implementation. Based on the available data, it is difficult to draw a solid conclusion about the factors that determined the gradual loss of benefits of the management measures over the years, but we hypothesize that this could likely be a consequence of more relaxed observance by diving operators in providing pre-dive briefings and keeping their customers' attention highly focused on maintaining a low-impact swimming while diving. In fact, although only a slight increase in the number of dives was recorded in 2015 and 2016 compared to 2014, the positive effect of the new regulation gradually vanished, suggesting that the observance of a low-impact diving might contribute more than the absolute number of divers in generating the impact on the colonies of false coral. The characteristics of single divers – encompassing, among others, their swimming ability, their experience in maintaining optimal buoyancy, their environmental awareness, and their compliance in maintaining responsible diving behaviour (Di Franco et al., 2009; Hammerton and Bucher, 2015; Casoli et al., 2017) – are considered drivers of SCUBA diving impact in protected locations equally important, or even more so, than the absolute number of visitors (Davis and Tisdell, 1995; Toyoshima and Nadaoka, 2015; Hammerton, 2016; Giglio et al., 2018; Giglio et al., 2020). In fact, the decree of 2014 establishing the daily diving quotas in the CPMR, in addition to limiting the number of divers at each diving site, included a series of obligations for divers in order to reduce impacts associated with bad diving practices, thus disturbing as little as possible the conservation status of the environment (i.e., preserving the integrity of marine individuals and communities and prohibiting the collection of both live and dead organisms, etc.). Nevertheless, while controlling the number of entries in the MPA is relatively easy to enforce and monitor, ensuring that each visitor dives with low-impact behaviour is a much harder task, often in the hands of local diving operators both in terms of pre-diving instructions provided to divers and surveillance of their underwater behaviour (Giglio et al., 2018). Proper instruction and awareness-raising that can be provided by international SCUBA schools during training (e.g., improving environmental education and buoyancy training) is certainly important (Hammerton, 2016), but it is unlikely that these macro-level management strategies could have affected the benefits produced by the regulation change. In contrast, considering the increasing attention paid by SCUBA companies to teaching environmentally responsible diving, an increase in low-impact behaviour should be expected over time (Hammerton, 2016). Considering all these aspects, we stress that further research is needed to disentangle the benefits produced by the adoption of a new regulation and those produced by its observance.

Another hypothesis, that we cannot exclude *a priori*, is that the system we considered is characterized by a phase shift when a specific threshold in the number of divers is exceeded, as proposed by Davis and Tisdell (1995). In this case, in proximity to the threshold, a small change in the frequency of divers would determine an abrupt increment of the impact on the species considered, and, potentially, a rapid loss of the management benefits provided by the new regulation. From this perspective, the relationship between the ratio dead/total colonies in the dived locations and the relative number of dives could be a hint of the occurrence of a rapid change. Our results seem to indicate that by passing a threshold of around 6,000 dives/site/year, the ratio dead/total colonies quickly increases, but remains approximately similar for a much higher number of dives (Fig. 5). Although this is a rough estimation, this threshold would be perceptibly in line with the values indicated in other studies investigating the carrying capacity of diving sites (Dixon et al., 1994; Hawkins and Roberts, 1993; Harriott et al., 1997; Zakai and Chadwick-Furman, 2002; Barker and Roberts, 2004), taking into account that a certain variability is to be expected in relation to the average divers' experience and behaviour visiting the MPA (Zhang et al., 2016; Lloret et al., 2006). This hypothesis should be further investigated through an *ad hoc* study to evaluate the carrying capacity of the diving locations, so that diving quotas could be further refined in order to ensure the sustainability of this important activity in the studied MPA.

5 CONCLUSIONS

Impacts of SCUBA diving activity on natural ecosystems are often underrated, especially in the context of MPAs, where diving is considered an activity to be fostered from the perspective of sustainable development. However, intensive diving can determine cumulative detrimental effects on the ecological and the aesthetic resources of an effectively enforced MPA, as clearly pointed out in our study. This, in turn, can potentially jeopardize the socio-ecological wellbeing of the area. The occurrence of these negative effects means that it is crucial for managers and MPA practitioners to identify and monitor the possible sources of anthropogenic impacts for coastal habitats under protection, in order to develop and adopt measures that can minimize a further worsening of the socio-ecological status of the MPA (Betti et al., 2019). In this respect, the adoption in the CPMR of a new regulation based on quotas and the redistribution of the diving pressure to newly opened sites showed promising results for the mitigation of diving impacts, potentially representing a positive example for other tourism hotspots, especially if protected. However, the mere implementation of new regulations is not sufficient to guarantee a reduction of anthropogenic impacts, and care is needed to ensure that the regulations are enforced, observed, and monitored over time. In fact, under the hypothesis that operators' and divers' compliance with rules (e.g. the adoption of a pre-dive briefing and a low impact behavior, respectively) is equally important as the implementation of quotas for reducing diving impact, the opening of new sites, as a way to redistribute the diving pressure, could turn out to be a counterproductive measure. If a relatively low number of impacting divers at the new sites were enough to determine detrimental effects for the benthic communities, the redistribution of the diving pressure to new sites would simply result in an increase in the area where diving impacts occur. Thus, while limiting the number of visitors in protected locations is an important step, a consistent reduction of the diving impact needs to also be based on the observance of low-impact diving practices, in which diving operators locally, and diving training companies at a broader scale, have a paramount role (Giglio et al., 2020). In addition, better management outcomes may be expected if regulations are not based on precautionary principles, as in the case of the CPMR, but on a proper assessment of the carrying capacity of the area in relation to recreational SCUBA diving, embedded within an adaptive and co-managed approach that would allow managers, scientists, and diving operators to identify, monitor and adjust the optimal trade-off between societal needs and the ecological objectives of MPAs (Giglio et al., 2020).

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REFERENCES

Agresti, A., 2019. An Introduction to Categorical Data Analysis, An Introduction to Categorical Analysis, 3rd Edition. Hoboken, USA.

Au, A.C. sun, Zhang, L., Chung, S. shan, Qiu, J.W., 2014. Diving associated coral breakage in Hong Kong: Differential susceptibility to damage. Mar. Pollut. Bull. 85, 789–796. https://doi.org/10.1016/j.marpolbul.2014.01.024

Badalamenti, F., Ramos, A.A., Voultsiadou, E., Sánchez Lizaso, J.L., D’Anna, G., Pipitone, C., Mas, J., Ruiz Fernandez, J.A., Whitmarsh, D., Riggio, S., 2000. Cultural and socio-economic impacts of Mediterranean marine protected areas. Environ. Conserv. 27, 110–125. https://doi.org/10.1017/S0376892900000163

Ban, N.C., Gurney, G.G., Marshall, N.A., Whitney, C.K., Mills, M., Gelcich, S., Bennett, N.J., Meehan, M.C., Butler, C., Ban, S., Tran, T.C., Cox, M.E., Breslow, S.J., 2019. Well-being outcomes of marine protected areas. Nat. Sustain. 2, 524–532. https://doi.org/10.1038/s41893-019-0306-2

Barker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biol. Conserv. 120, 481–489. https://doi.org/10.1016/j.biocon.2004.03.021

Basurto, X., Blanco, E., Nenadovic, M., Vollan, B., 2016. Integrating simultaneous prosocial and antisocial behavior into theories of collective action. Sci. Adv. 2, 1–11. https://doi.org/10.1126/sciadv.1501220

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 18637. https://doi.org/10.18637/jss.v067.i01

Berning, B., 2007. The Mediterranean bryozoan Myriapora truncata (Pallas, 1766): a potential indicator of (palaeo-) environmental conditions. Lethaia 40: 221−232

Betti, F., Bavestrello, G., Fravega, L., Bo, M., Coppari, M., Enrichetti, F., Cappanera, V., Venturini, S., Cattaneo-Vietti, R., 2019. On the effects of recreational SCUBA diving on fragile benthic species: The Portofino MPA (NW Mediterranean Sea) case study. Ocean Coast. Manag. 182. https://doi.org/10.1016/j.ocecoaman.2019.104926

Bravo, G., Márquez, F., Marzinelli, E.M., Mendez, M.M., Bigatti, G., 2015. Effect of recreational diving on Patagonian rocky reefs. Mar. Environ. Res. 104, 31–36. https://doi.org/10.1016/j.marenvres.2014.12.002

Cano, N. (1978) Hidrología del mar de Alborán en primavera-verano. Boletín del Instituto Español de Oceanografía 248:51-66

Carminatto, A.A., Rotundo, M.M., Butturi-Gomes, D., Barrella, W., Petrere Junior, M., 2020. Effects of habitat complexity and temporal variation in rocky reef fish communities in the Santos estuary (SP), Brazil. Ecol. Indic. 108, 105728. https://doi.org/10.1016/j.ecolind.2019.105728

Casoli, E., Nicoletti, L., Mastrantonio, G., Jona-Lasinio, G., Belluscio, A., Ardizzone, G.D., 2017. Scuba diving damage on coralligenous builders: Bryozoan species as an indicator of stress. Ecol. Indic. 74, 441–450. https://doi.org/10.1016/j.ecolind.2016.12.005

Casoli, E., Piazzi, L., Nicoletti, L., Jona-Lasinio, G., Cecchi, E., Mancini, G., Belluscio, A., Ardizzone, G., 2020. Ecology, distribution and demography of erect bryozoans in Mediterranean coralligenous reefs. Estuar. Coast. Shelf Sci. 235, 106573. https://doi.org/10.1016/j.ecss.2019.106573

Christensen, R.H.B., 2019. Ordinal - Regression Models for Ordinal Data. R package version 2019.12-10. https://CRAN.R-project.org/package=ordinal 2019.

Consejería de Agricultura y Agua, R. de M., 2014. Orden de 4 de junio de 2014, de la Consejería de Agricultura y Agua, por la que se regula el ejercicio de las actividades subacuáticas en aguas interiores de la reserva Marina de Cabo de Palos-Islas Hormigas.

Davis, D., Tisdell, C., 1995. Recreational scuba-diving and carrying capacity in marine protected areas. Ocean Coast. Manag. 26, 19–40. https://doi.org/10.1016/0964-5691(95)00004-L

De Brauwer, M., Saunders, B.J., Ambo-Rappe, R., Jompa, J., McIlwain, J.L., Harvey, E.S., 2018. Time to stop mucking around? Impacts of underwater photography on cryptobenthic fauna found in soft sediment habitats. J. Environ. Manage. 218, 14–22. https://doi.org/10.1016/j.jenvman.2018.04.047

De, K., Nanajkar, M., Mote, S., Ingole, B., 2020. Coral damage by recreational diving activities in a Marine Protected Area of India: Unaccountability leading to ‘tragedy of the not so commons.’ Mar. Pollut. Bull. 155, 111190. https://doi.org/10.1016/j.marpolbul.2020.111190

De La Nuez-Hernández, D., Valle, C., Forcada, A., Correa, J.M.G., Fernández Torquemada, Y., 2014. Assessing the erect bryozoan *Myriapora truncata* (Pallas, 1766) as indicator of recreational diving impact on coralligenous reef communities. Ecol. Indic. 46, 193–200. https://doi.org/10.1016/j.ecolind.2014.05.035

Di Franco, A., Milazzo, M., Baiata, P., Tomasello, A., Chemello, R., 2009. Scuba diver behaviour and its effects on the biota of a Mediterranean marine protected area. Environ. Conserv. 36, 32–40. https://doi.org/10.1017/S0376892909005426

Di Franco, E., Di Franco, A., Calò, A., Di Lorenzo, M., Mangialajo, L., Bussotti, S., Bianchi, C.N., Guidetti, P., 2021. Inconsistent relationships among protection, benthic assemblage, habitat complexity and fish biomass in Mediterranean temperate rocky reefs. Ecol. Ind. 128, 107850. https://doi.org/10.1016/j.ecolind.2021.107850

Dixon, J.A., Scura, L.F., Hof, T., 1994. Ecology and Microeconomics as ‘Joint Products’: The Bonaire Marine Park in the Caribbean 120–138. https://doi.org/10.1007/978-94-011-1006-8_8

Edgar, G.J., Stuart-smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220. https://doi.org/10.1038/nature13022

Flores-de la Hoya, A., Godínez-Domínguez, E., González-Sansón, G., 2018. Rapid assessment of coastal underwater spots for their use as recreational scuba diving sites. Ocean Coast. Manag. 152, 1–13. https://doi.org/10.1016/j.ocecoaman.2017.11.005

García-Charton, J.A., Pérez-Ruzafa, A., Marcos, C., Claudet, J., Badalamenti, F., Benedetti-Cecchi, L., Falcón, J.M., Milazzo, M., Schembri, P.J., Stobart, B., Vandeperre, F., Brito, A., Chemello, R., Dimech, M., Domenici, P., Guala, I., Le Diréach, L., Maggi, E., Planes, S., 2008. Effectiveness of European Atlanto-Mediterranean MPAs: Do they accomplish the expected effects on populations, communities and ecosystems? J. Nat. Conserv. 16, 193–221. https://doi.org/10.1016/j.jnc.2008.09.007

García-Charton, J.A., Pérez-Ruzafa, Á., Sánchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O., Moreno, D., 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Mar. Biol. 144, 161–182. https://doi.org/10.1007/s00227-003-1170-0

García Charton, J.A., Pérez Ruzafa, A., 1998. Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. Mar. Ecol. 19, 111–128. https://doi.org/10.1111/j.1439-0485.1998.tb00457.x

Garrabou, J., Sala, E., Arcas, A., Zabala, M., 1998. The impact of diving on rocky sublittoral communities: A case study of a bryozoan population. Conserv. Biol. 12, 302–312. https://doi.org/10.1111/j.1523-1739.1998.96417.x

Giglio, V.J., Luiz, O.J., Chadwick, N.E., Ferreira, C.E.L., 2018. Using an educational video-briefing to mitigate the ecological impacts of scuba diving. J. Sustain. Tour. 26, 782–797. https://doi.org/10.1080/09669582.2017.1408636

Giglio, V.J., Luiz, O.J., Ferreira, C.E.L., 2020. Ecological impacts and management strategies for recreational diving: A review. J. Environ. Manage. 256, 109949. https://doi.org/10.1016/j.jenvman.2019.109949

Giglio, V.J., Luiz, O.J., Schiavetti, A., 2015. Marine life preferences and perceptions among recreational divers in Brazilian coral reefs. Tour. Manag. 51, 49–57. https://doi.org/10.1016/j.tourman.2015.04.006

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543, 665–669. https://doi.org/10.1038/nature21708

Gristina, M., Balduzzi A., 1999. Preliminary data on the growth of *Myriapora truncata* in Ustica Island (N/W Sicily) (Bryozoa: Cheilostomatida). Biol. Mar. Med. 6: 256−258

Hammerton, Z., 2016. Low-impact diver training in management of SCUBA diver impacts. J. Ecotourism 16, 69–94. https://doi.org/10.1080/14724049.2016.1194849

Hammerton, Z., 2017. Determining the variables that influence SCUBA diving impacts in eastern Australian marine parks. Ocean Coast. Manag. 142, 209–217. https://doi.org/10.1016/j.ocecoaman.2017.03.030

Hammerton, Z., Bucher, D., 2015. Levels of intervention-reducing SCUBA-diver impact within subtropical marine protected areas. J. Ecotourism 14, 3–20. https://doi.org/10.1080/14724049.2015.1073738

Harmelin, J.G., 1988. Les Bryozoaires, de bons indicateurs bathymétriques en paléoécologie? Géologie Méditerranéenne 15(1): 49-63. https://doi.org/10.3406/geolm.1988.1394

Harriott, V.J., Davis, D., Banks, S.A., 1997. Recreational diving and its impact in marine protected areas in Eastern Australia. Ambio 26, 173–179. https://doi.org/10.1016/S0967-0653(98)80646-7

Hasler, H., Ott, J.A., 2008. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea. Mar. Pollut. Bull. 56, 1788–1794. https://doi.org/10.1016/j.marpolbul.2008.06.002

Hawkins, J.P., Roberts, C.M., 1993. Effects of recreational scuba diving on coral reefs: trampling on reef-flat communities. J. Appl. Ecol. 30, 25–30. https://doi.org/10.2307/2404267

Hermansen, P., Larsen, P.S., Riisgard, H.U., 2001. Colony growth rate of encrusting marine bryozoans (*Electra pilosa* and *Celleporella hyalina*). J. Exp. Mar. Biol. Ecol. 263: 1−23

Hernández-Molina, F. J., Serra, N., Stow, D. A. V., Llave, E., Ercilla, G., & Van Rooij, D. (2011). Along-slope oceanographic processes and sedimentary products around the Iberian margin. Geo-Marine Letters, 31(5-6), 315–341. doi:10.1007/s00367-011-0242-2

Hogg, K., Semitiel-García, M., Noguera-Méndez, P., García-Charton, J. A., 2017. A governance analysis of Cabo de Palos-Islas Hormigas and Cabo de Gata-Níjar Marine Protected Areas, Spain. Mar. Pol. 102944.Hogg, K., Noguera-Méndez, P., Semitiel-García, M., Gray, T., Young, S., 2017. Controversies over stakeholder participation in marine protected area (MPA) management: A case study of the Cabo de Palos-Islas Hormigas MPA. Ocean Coast. Manag. 144, 120–128. https://doi.org/10.1016/j.ocecoaman.2017.05.002

Hogg, K., Semitiel-García, M., Noguera-Méndez, P., Gray, T., Young, S., 2018. Perceptions of Threats Facing Cabo de Palos - Islas Hormigas MPA and Potential Solutions. Coast. Manag. 46, 58–74. https://doi.org/10.1080/08920753.2018.1405330

Keough, M.J., Mapstone, B.D. (1997) Designing environmental monitoring for pulp mills in Australia. Wat. Sci. Tech. 35: 397-404.

Lloret, J., Marín, A., Marín-Guirao, L., Carreño, M.F., 2006. An alternative approach for managing scuba diving in small marine protected areas. Aquat. Conserv. Mar. Freshw. Ecosyst. 16, 579–591. https://doi.org/10.1002/aqc.734

Lombardi, C., Cocito S., Gambi, M.C., Cisterna, B., Freer, A., Cusack, M., 2011. Effects of ocean acidification on growth, organic tissue and protein profile of the Mediterranean bryozoan *Myriapora truncata*. Aq. Bio., 13 (3), pp. 251-262. https://doi.org/10.3354/ab00376

Lopez de la Cuadra, C., García-Gómez, J., 1994. Zoogeographical study of the Cheilostomatida from the Straits of Gibraltar, in: P.J. Hayward, J.S.R. and P.D.T. (eds. . (Ed.), Biology Nad Palaeobiology of Bryozoans. Olsen & Olsen, Fredensborg, pp. 107–112. https://doi.org/10.1034/j.1600-0560.2003.00021.x

Lubchenco, J., Grorud-Colvert, K., 2015. Making waves: The science and politics of ocean protection. Science (80-.). 350, 382–383.

Lucrezi, S., Ferretti, E., Milanese, M., Sarà, A., Palma, M., 2020. Securing sustainable tourism in marine protected areas: lessons from an assessment of scuba divers’ underwater behaviour in non-tropical environments. J. Ecotourism 1–24. https://doi.org/10.1080/14724049.2020.1856122

Lucrezi, S., Milanese, M., Markantonatou, V., Cerrano, C., Sarà, A., Palma, M., Saayman, M., 2017. Scuba diving tourism systems and sustainability: Perceptions by the scuba diving industry in two Marine Protected Areas.

Tour. Manag. 59, 385–403. https://doi.org/10.1016/j.tourman.2016.09.004

Lucrezi, S., Saayman, M., van der Merwe, P., 2013. Managing diving impacts on reef ecosystems: Analysis of putative influences of motivations, marine life preferences and experience on divers' environmental perceptions. Ocean Coast. Manag. 76, 52–63. https://doi.org/10.1016/j.ocecoaman.2013.02.020

Luna-Pérez, B., Valle, C., Vega Fernández, T., Sánchez-Lizaso, J.L., Ramos-Esplá, A.A., 2010. *Halocynthia papillosa* (Linnaeus, 1767) as an indicator of SCUBA diving impact. Ecol. Indic. 10, 1017–1024. https://doi.org/10.1016/j.ecolind.2010.02.010

Lyons, P.J., Arboleda, E., Benkwitt, C.E., Davis, B., Gleason, M., Howe, C., Mathe, J., Middleton, J., Sikowitz, N., Untersteggaber, L., Villalobos, S., 2015. The effect of recreational SCUBA divers on the structural complexity and benthic assemblage of a Caribbean coral reef. Biodivers. Conserv. 24, 3491–3504. https://doi.org/10.1007/s10531-015-1009-2

Marconi, M., Giglio, V.J., Pereira Filho, G.H., Motta, F.S., 2020. Does quality of scuba diving experience vary according to the context and management regime of marine protected areas? Ocean Coast. Manag. 194, 105246. https://doi.org/10.1016/j.ocecoaman.2020.105246

Milazzo, M., Chemello, R., Badalamenti, F., Riggio, R.C., Riggio, S., 2002. The impact of human recreational activities in marine protected areas: What lessons should be learnt in the Mediterranean Sea? Mar. Ecol. 23, 280–290. https://doi.org/10.1111/j.1439-0485.2002.tb00026.x

Munguia, P., Osman, R.W., Hamilton, J., Whitlatch, R., Zajac, R., 2011. Changes in habitat heterogeneity alter marine sessile benthic communities. Ecol. Appl. 21, 925–935. https://doi.org/10.1890/09-2398.1

Pagès-Escolà, M., Hereu, B., Rovira, G., Medrano, A., Aspillaga, E., Capdevila, P., Linares, C., 2020. Unravelling the population dynamics of the Mediterranean bryozoan *Pentapora fascialis* to assess its role as an indicator of recreational diving for adaptive management of marine protected areas. Ecol. Indic. 109, 105781. https://doi.org/10.1016/j.ecolind.2019.105781

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-319-19425-7_6

Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Ruckelshaus, M., Warner, R.R., 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecol. Appl. 13, 215–228. https://doi.org/10.1890/1051-0761(2003)013[0215:aoecis]2.0.co;2

Roberts, D.A., Poore, A.G.B., Johnston, E.L. (2007) MBACI sampling of an episodic disturbance: Stormwater effects on algal epifauna. Mar. Environ. Res. 64: 514-523.

Rodolfo-Metalpa, R., Lombardi, C., Cocito, S., Hall-Spencer, J., Gambi, M.C., 2010. Effects of acidification and high temperature on the bryozoan *Myriapora truncata* at natural CO2 vents. PSZN I: Mar. Ecol. 31: 447−456

Rojo, I., Anadón, J.D., García-Charton, J.A., 2021a. Exceptionally high but still growing predatory reef fish biomass after 23 years of protection in a Marine Protected Area. PLoS One 16, e0246335. https://doi.org/10.1371/journal.pone.0246335

Rojo, I., Irigoyen, A.J., Cuadros, A., Calò, A., Pereñíguez, J.M., Hernández-Andreu, R., Félix-Hackradt, F.C., Carreño, F., Hackradt, C.W., García-Charton, J.A., 2021b. Detection of protection benefits for predatory fishes depends on census methodology. Aquat. Conserv. Mar. Freshw. Ecosyst. 1–16. https://doi.org/10.1002/aqc.3539

Roncin, N., Alban, F., Charbonnel, E., Crec'hriou, R., de la Cruz Modino, R., Culioli, J.M., Dimech, M., Goñi, R., Guala, I., Higgins, R., Lavisse, E., Le Diréach, L., Luna, B., Marcos, C., Maynou, F., Pascual, J., Person, J., Smith, P., Stobart, B., Szelianszky, E., Valle, C., Vaselli, S., Boncoeur, J. (2008) Uses of ecosystem services provided by MPAs: How much do they impact the local economy? A southern Europe perspective. J. Nature. Cons. 16: 256-270.

Sala, E., Costello, C., Dougherty, D., Heal, G., Kelleher, K., Murray, J.H., Rosenberg, A.A., Sumaila, R., 2013. A General Business Model for Marine Reserves. PLoS One 8, 1–9. https://doi.org/10.1371/journal.pone.0058799

Terrón-Sigler, A., León-Muez, D., Peñalver-Duque, P., Torre, F.E., 2016. The effects of SCUBA diving on the endemic Mediterranean coral *Astroides calycularis*. Ocean Coast. Manag. 122, 1–8. https://doi.org/10.1016/j.ocecoaman.2016.01.002

Titus, B.M., Daly, M., Exton, D.A., 2015. Do reef fish habituate to diver presence? Evidence from two reef sites with contrasting historical levels of SCUBA intensity in the Bay Islands, Honduras. PLoS One 10, 1–13. https://doi.org/10.1371/journal.pone.0119645

Toyoshima, J., Nadaoka, K., 2015. Importance of environmental briefing and buoyancy control on reducing negative impacts of SCUBA diving on coral reefs. Ocean Coast. Manag. 116, 20–26. https://doi.org/10.1016/j.ocecoaman.2015.06.018

Underwood, A.J., 1994. On Beyond BACI Sampling Designs that Might Reliably Detect Environmental Disturbances. Ecol. Appl. 4, 3–15.

Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Bio. Ecol. 161, 145–178.

Valerio, M., Mann, O., Shashar, N., 2019. “Boo! Did we scare you?”: behavioral responses of reef-associated fish, prawn gobies (*Amblyeleotris steinitzi* and *Amblyeleotris sungami*) to anthropogenic diver disturbance. Mar. Biol. 166, 1–9. https://doi.org/10.1007/s00227-018-3447-3

Zabala, M., 1986. Fauna dels briozous dels Països Catalans. Institut d’Estudis Catalans.

Zakai, D., Chadwick-Furman, N.E., 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biol. Conserv. 105, 179–187. https://doi.org/10.1016/S0006-3207(01)00181-1

Zhang, L.Y., Chung, S. shan, Qiu, J. wen, 2016. Ecological carrying capacity assessment of diving site: A case study of Mabul Island, Malaysia. J. Environ. Manage. 183, 253–259. https://doi.org/10.1016/j.jenvman.2016.08.075

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x