Assessing the impact of diving in coralligenous communities : The usefulness of demographic studies of red gorgonian populations

Cristina LINARES[1*], Mikel ZABALA[1], Joaquim GARRABOU[2], Rafel COMA[3], David DIAZ[4], Bernat HEREU[1], Lluis DANTART[1]

[1] *Departament d'Ecologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain*

[2] *Institut de Ciències del Mar CSIC, Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain*

[3] *Centre d'Estudis Avançats de Blanes CEAB-CSIC, Accés Cala St. Francesc 14, 17300 Blanes, Girona, Spain.*

[4] *Instituto Español de Oceanografía, C/ Moll de Ponent s/n, 07015 Palma de Mallorca, Spain.*

*Corresponding author: cristinalinares@ub.edu

Résumé. **Évaluation de l'impact de la plongée dans le coralligène : L'utilité des études démographiques des populations de *Paramuricea clavata*.** Les communautés coralligènes sont considérées comme de vraies "hot spots" de la biodiversité méditerranéenne. Ces communautés se trouvent aujourd'hui menacées par divers impacts d'origine anthropique. Malgré la protection des aires marines protégées (MPAs), ces communautés subissent les impacts du changement global. Les gestionnaires de ces espaces sont demandeurs de protocoles de suivi de la biodiversité coralligène capables de déceler ces impacts. Comme il parait impossible de faire des suivis de la biodiversité dans son ensemble, il faut avoir recours à des espèces indicatrices. L'examen critique des caractéristiques que doivent réunir de telles espèces indicatrices pour que le suivi soit significatif et faisable nous a amené vers le choix d'espèces clonales, à forte densité de population, bio-ingénieurs, de grande taille, de port érigé avec des colonies isolées. L'examen sommaire des grands groupes taxonomiques présents dans le coralligène nous a conduit aux gorgonaires comme le meilleur groupe. L'effort que l'on épargne avec le suivi d'une seule espèce peut être investi dans l'acquisition des paramètres démographiques (fécondité ou recrutement, croissance et survie) des populations de cette espèce. L'acquisition de ces données structurées en classes de taille va permettre la modélisation de l'évolution future des populations et celle de sa réponse aux impacts divers, et ainsi l'orientation des mesures de gestion. Pour montrer l'intérêt de ce type d'approche, nous présentons trois cas d'étude démographique de la gorgone rouge (*Paramuricea clavata*) dans des MPAs soumises respectivement à un épisode de mortalité massive (été 1999, Port-Cros) et à la pression récurrente des plongeurs (Iles Medes, Cap de Creus). Au final, en combinant ces données, nous simulons en même temps l'effet de la mortalité massive et l'impact des

plongeurs sur l'évolution des populations de gorgone rouge. Les résultats montrent que la fréquentation des sites par les plongeurs a des effets notables sur la survie de ces populations. Cependant, ces effets sont beaucoup plus faibles que ceux des anomalies thermiques associées au réchauffement global. Les populations suivies à Port-Cros ont perdu plus du 60 % de la biomasse après l'événement de mortalité de 1999 et aucune récupération n'a été observée après 8 ans sur les placettes suivies. Ces résultats suggèrent un avenir incertain pour les populations de gorgones rouges de Port-Cros accessibles aux plongeurs. Les données démographiques acquises ont permis le développement de modèles de viabilité de populations (PVA) qui permettent la simulation des effets potentiels des perturbations, ainsi que l'effet d'une régulation de la visite des plongeurs. Ces cas d'étude démontrent l'utilité des suivis à long terme de placettes permanentes et de la modélisation. Malgré l'utilité de cette approche, il faut souligner que les gorgones ne sont pas présentes dans toutes les communautés coralligènes, et qu'il faudra trouver d'autres indicateurs, un choix qui sera difficile.

Abstract. Coralligenous communities are an important "hot spot" of Mediterranean biodiversity. These communities are presently threatened by a combination of anthropogenic impacts partly related to global change. Managers of MPAs are increasingly concerned about the capacity of coralligenous communities to endure crowds of divers, and there is a call for descriptors and for quantitative methods for estimating this capacity. A good indicator to detect the impacts on coralligenous communities should gather the following essential traits: to be a long-lived, clonal, engineering species displaying an erect shape and a large size in order to facilitate the monitoring. Among the main taxonomic groups of the coralligenous, gorgonians display several advantages and, in this study, the red gorgonian *Paramuricea clavata* was selected as a model species to evaluate the effects of diving impact and climate change on coralligenous communities. We present three cases of study about the demographic monitoring of red gorgonian populations affected by the 1999 mass mortality event (Port-Cros) and subjected to high diving activity (Medes Islands and Cap de Creus). Finally, combining all these data we simulate the interacting effects of divers damage and mass mortality events on the persistence of gorgonian populations. The results of long-term monitoring of permanent plots allowed showing that although diving activity affects significantly the red gorgonian populations, the effect of climate change has more significant effects on the populations. Port-Cros populations affected by the 1999 mass mortality suffered a 60% biomass loss that has not been recovered in the following eight years. Simulations showed that the combination of both disturbances can have large and lasting effects on the future viability of red gorgonian populations. As gorgonian assemblages are only one facies of the coralligenous communities, other species should be selected for detecting the impact on these communities. Nevertheless, the development of similar demographic approaches for other species would be more difficult than for gorgonians.

INTRODUCTION

Coralligenous assemblages: a threatened hot spot of biodiversity

The Mediterranean Sea has been identified as an important "hot spot" of biological diversity (Bianchi and Morri, 2000). A large part of this biodiversity is to be found in coastal benthic environments, mainly in shallow areas with rocky bottoms and *Posidonia* meadows (Boudouresque, 2004). Among the rocky benthic assemblages, the coralligenous stands out for its species richness (of the order of 1600 species have been identified) and great structural complexity (Pérès and Picard, 1964; Ballesteros, 2006).

Coralligenous communities are presently threatened by a combination of human impacts such as pollution, fishing (especially trawling), diving, invasive species and climate change (Ballesteros, 2006). The fragility of coralligenous communities seems to be related to both the stability of

the environment in which they have evolved and the low demographic dynamics of their inhabitants. It has been suggested (but little experimental evidence exists) that at the depths where coralligenous assemblages dwell (mainly below 20 m) environmental factors show a marked stability; there are few if any strong natural disturbances, and there has historically been an absence of excessive anthropogenic pressures (Ballesteros, 2006). Thus, environmental stability may help to explain the slow dynamics and longevity that has been observed among the species dwelling in coralligenous bottoms (Garrabou, 1999; Garrabou and Harmelin, 2002; Coma *et al.*, 2004). However, it is precisely their slow dynamics that lead to low resilience and slow recovery rate from disturbances (Holling, 1973).

Among the threats mentioned above, during the last decade, coralligenous communities have been affected by several mass mortality events (in 1999, 2003 and 2006) related to unusual climatic anomalies in the NW Mediterranean Sea (Romano *et al*., 2000; Garrabou *et al.,* 2009). Data on the immediate impact of these mass mortality events on gorgonian populations has been widely documented (Cerrano *et al*., 2000; Pérez *et al*., 2000; Garrabou *et al*., 2001; Coma *et al*., 2006). Delayed effects have also been reported in the Port-Cros National Park (France), where populations of *P clavata* showed no signs of recovery four years after the 1999 mass mortality event (Linares *et al*., 2005). However, the longer-term consequences of an increase in the frequency of these events, a likely scenario as the frequency of mass mortality episodes may increase as a result of global warming (Coma and Ribes, 2003; Garrabou *et al*., 2009), have never been assessed and remain largely unknown.

Likewise the effects of diving pose a special concern for managers of protected areas (Francour *et al.*, 2001). Due to their beauty, coralligenous assemblages are among the most attractive seascapes for scuba divers, who can have a considerable erosive impact on benthic communities (Garrabou *et al*., 1998; Wielgus *et al*., 2002; Coma *et al*., 2004). When coralligenous assemblages are located in marine protected areas (MPAs), they are generally protected from many impacts, such as dredging. However, MPAs within which diving is permitted are faced with the effects of divers frequentation. Managers of those MPAs have to cope with the problems of excessive flood of visitors in sites which theoretically are devoted to conservation of marine habitats. Such protection does not hold for the effects of frequentation: managers of marine protected areas (MPAs) must face the paradox that, although MPAs are a fundamental tool for the conservation of marine habitats (Kelleher and Kenchington, 1992), they tend to attract more tourism and associated recreational activities such as diving. Managers of MPAs where marine tourism is practised are becoming increasingly concerned about the capacity of their benthic communities to withstand intense diving frequentation. In particular, there is a call for descriptors of the impact of diving and for quantitative methods for estimating this capacity.

Selecting the best descriptor to detect the impact of diving on coralligenous assemblages

Bearing in mind that the main goal is the conservation of the whole coralligenous assemblages, it seems reasonable searching for some descriptors capable to quantitatively evaluate changes in biodiversity on these assemblages. Unfortunately, although biodiversity (Wilson and Peter, 1988) is a nice concept, it is worrisomely elusive when it comes to quantitative monitoring (Purvis and Hector, 2000; Gotelli and Colwell, 2001). Common alternatives for terrestrial ecosystems are to look for restricted "flagship" high taxa like birds (Lawton *et al*., 1998) or, more frequently, for indicator "umbrella" species (Lambeck, 1997) that are believed to act as representatives of the overall dynamics of these assemblages. However, the key question lies in the criteria that guide the selection of adequate indicator species (Lindenmayer, 2000). Beyond requirements that are common to a good indicator for any ecosystem, we propose to consider criteria specifically related to two relevant aspects of our case: 1) those linked to ecological particularities with regard to the functioning and structure of coralligenous communities; and 2) the specific impact of diving.

Biotic relationships are crucial when explaining the functioning of coralligenous assemblages. The space is completely saturated by organisms (Zabala and Ballesteros, 1989), and the largest part of the living biomass in coralligenous sessile assemblages consists of algae and suspension feeders (True, 1970; Zabala and Ballesteros, 1989), that are highly persistent, slow growing, and show low to nil seasonality in terms of space occupation (Garrabou *et al*., 2002). These species are considered engineering species because they make an important contribution to the communities in terms of structure and biodiversity (Jones *et al*., 1994).

Competition for space has probably been the selective force that has determined that most of the species that make a significant contribution to the total biomass/coverage of coralligenous assemblages are clonal organisms (Ballesteros, 2006). The ability of clonal species to recover from partial mortality, to exhibit negative growth and to undergo both fusion and fission coupled with their capacity for asexual reproduction, make it difficult to obtain good relationships between size and age, and hence, to know the age of clonal organisms. Furthermore, clonal organization offers such high morphological plasticity that most of these species lack a definite form. This poses a serious problem when looking for unambiguous measurements of size, a basic monitoring parameter. Hence, an important requirement is searching for clonal species displaying forms and sizes which facilitate monitoring.

Bearing in mind all these arguments, a suitable indicator species for the diversity of the whole coralligenous community may be a long-lived, clonal and engineering species.

In protected areas, human activities are regulated through different measures including the total prohibition on collecting animals and

plants. However, there is generally less restriction on public access. The impact of human visits to protected areas can roughly be split into two types: 1) one related to changes in behaviour of animals and 2) one related to mechanical abrasion.

The first type of impact generally affects large mobile animals and causes changes in their escape responses or reproductive behaviour (Au and Green, 2000; Corkeron, 1995). The second type affects sessile organisms and the effects of passive damage on sessile marine benthic communities have been related to intensive trampling (Liddle and Kay, 1987; Kay and Liddle, 1989; Brosnan and Crumrine, 1994), anchoring (Davis 1977) and diving (Tratalos and Austin, 2001; Wielgus et al., 2002). The main impact reported involves the breakage of tips or entire colonies of erect, rigid species while encrusting species and erect fleshy species are less affected. Therefore, the organisms selected as indicators should be erect species with rigid skeletons that are large enough to be sensitive to erosion caused by divers. There are other requirements regarding to ethical and statistical constraints that have to be considered when searching for a suitable descriptor. The ethics of working in MPAs forbids the use of extractive techniques for monitoring. Thus, sampling must be based on visual censuses or photographic/video techniques. Finally, the intrinsic natural variability of ecological systems makes it difficult to distinguish between the specific influence studied and other factors (Underwood, 1997). This difficulty should be overcome by appropriate sampling design (Fraschetti *et al.*, 2002), which, in turn, demands a great number of replicable units. In order to satisfy the statistical design requirements, our studies focus on abundant and easily identifiable species, thus allowing us to obtain several straightforwardly repeatable measurements.

Considering all these requirements, among the numerous groups of clonal organisms that make an important contribution to coralligenous communities (i.e., calcareous algae, sponges, cnidarians, bryozoans and tunicates), we contend that gorgonians are suitable to be used as indicators of disturbance impacts (Table 1).

Despite their clonal nature, gorgonians display a relatively clear morphological pattern (erect and tree-like form) and continuous growth (Coma *et al.*, 1998) which together with their large size, makes it easy to locate, map and measure individuals underwater. Furthermore, Mediterranean gorgonian species currently suffer adverse impacts from a wide variety of disturbances. These substantially increase their mortality rates above natural levels. Some of these disturbances are directly anthropogenic, such as anchors, fishing nets, diving, mucilage events and contamination (Arnoux *et al*., 1992; Harmelin and Marinopoulos, 1994; Mistri and Ceccherelli, 1996; Bavestrello *et al.*, 1997; Coma *et al*., 2004). Others, such as recent mass mortality events (Garrabou *et al.,* 2001; Linares *et al*., 2005; Coma *et al*., 2006), appear to be related to climatic anomalies, which are considered to be indirectly linked to human activities (Romano *et al*., 2000).

Table 1. Scoring the adequacy of the commonest high taxa on coralligenous assemblages as indicator species to detect diving impacts.

Criteria / Descriptors	Statistical		Ethic (Non-destructive methods)		Ecological		
	Abundance	Repeatability (definite form)	Large size	Easy taxonomy	Engineering species	Rigid skeletons	Sensible erosion
Calcareous algae	√		√		√	√	√
Fleshy algae	√		√				
Hydrozoans	√						
Scleractinian corals			√	√		√	√
Gorgonians	√	√	√	√	√	√	√
Polychaetes	√						
Mollusks		√	√	√		√	
Decapods		√	√	√		√	
Bryozoans	√		√		√	√	√
Echinoderms	√	√	√	√			
Ascidians			√				
Fishes	√	√	√	√			

Demographic approaches to assess the impacts on coralligenous communities

Monitoring the diversity of a whole community by observing just a single indicator species allows saving a considerable amount of effort. We propose to invest all of this saving in a detailed description of the population dynamics of the selected indicator species. The benefits of such an endeavour will become apparent when data from the demographic study are used as input into models which can provide not just a static or current image, but also forecast the fate of these populations; a major goal of conservation managers.

Much effort in conservation biology has been focused on studying demographic parameters and population dynamics of slow growing species and on developing quantitative models that can help environmental managers make decisions (Simberloff, 1988; Beissinger and Westphal, 1998). Several basic questions need to be addressed if we want to conserve threatened species, such as: is the population under study in decline? What are the factors that determine the viability of the population? Which management strategy offers the greatest chances for the survival of the population? (Heywood and Iriondo, 2003).

Population viability analysis (PVA) is one of the most powerful tools for answering questions such as these. PVA is based on demographic models, and the most accurate methods use the logic of matrix models (Caswell, 2001). Matrix models are mostly used to calculate the population growth rate (λ); the value of lambda indicates whether a population

would grow ($\lambda>1$), go extinct ($\lambda<1$) or remain steady ($\lambda=1$) over time (Morris and Doak 2002). They are also used to estimate the stable stage distribution, and the sensitivity and elasticity of population growth when faced with changes in the life history traits of threatened species (Caswell, 2001; Morris and Doak, 2002). The increase in threats that affect both terrestrial and marine ecosystems highlights the importance of these models for examining the future persistence of species as well as for evaluating the effectiveness of possible management strategies (Beissinger and Westphal, 1998; Reed *et al*., 2002).

To examine the resilience of the gorgonian populations facing increasing disturbances, it is essential to develop reliable PVA models and these require accurate demographic estimates (survival, growth and recruitment rates). Because of their extremely long lifespan, only long-term monitoring of permanent plots, where each colony is individually monitored every year, can provide the necessary data.

Mass mortality events, diving impact and the interactive effects: three study cases

In this study, the Mediterranean red gorgonian *Paramuricea clavata* (Risso, 1826) was selected as a representative species because was one of the species most severely affected during the recent mass mortality events (Cerrano *et al*., 2000; Pérez *et al*., 2000; Linares *et al*., 2005; Garrabou et al. 2009) and has been used as indicator of diving impacts in coralligenous communities (Coma et al. 2004). Furthermore assemblages of *P. clavata* constitute one of the most attractive landscapes in the Mediterranean benthos and recreational divers therefore target these communities (Coma *et al*., 2004).

Three case studies on *P. clavata* populations are shown to demonstrate the usefulness of demographic monitoring and modelling of red gorgonian populations to evaluate the impact of diving and of a mass mortality event; the main disturbances currently affecting red gorgonian populations, and to forecast long-term population trends under different intensity and frequency of disturbances. The first case study evaluates the impact of the 1999 mass mortality event at the Port-Cros National Park. Through the use of demographic models the data allowed us to infer the long-term effects of this disturbance and the likely scenario of increase of the frequency of such events. The second study case focuses on the effects of diving on red gorgonian populations in the Cap de Creus and Medes Islands MPAs (Fig. 1). The data obtained from these two populations can be extrapolated to other Mediterranean locations, such Port-Cros National Park, where there are similar concerns regarding the impact of diving on benthic communities. Understanding interacting effects of different disturbances that threaten the viability of disturbed populations may be essential if we are to provide criteria for effective management of these species, especially in the face of global changes.

Hence, in the third case study, we have explored the interacting effects of diving damage and mass mortality events on the persistence of gorgonian populations.
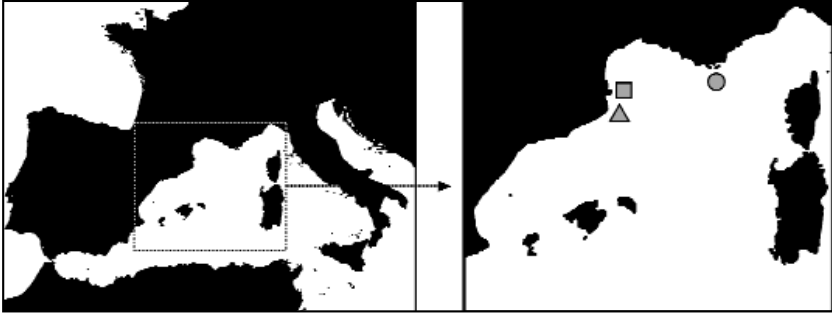

Figure 1. Location of the three studied MPAs: Medes Islands Marine Reserve (triangle), Cap de Creus Natural Park (square) and Port-cros National Park (circle). Data from demographic monitoring of red gorgonian populations located in these MPAs have been used to assess the effects of diving and mass mortality events on this species.

MATERIAL AND METHODS

We adopted a three-step procedure to develop the PVA models: sampling, model formulation and simulation of particular cases. We describe the first two steps which are common to all three case studies and finally, we present the data and simulations used for each case study.

Sampling: permanent plots

To obtain accurate demographic estimates, we selected permanent plots and monitored each colony present within these plots. Each plot was 4 m long and 0.8 m wide (3.2 m^2). To facilitate accurate mapping, each plot was partitioned into 40x40 cm quadrants. The corners of each quadrant were marked with PVC screws fixed in holes in the rocky substratum with two-component putty. Each plot was surveyed annually. In the first survey, all gorgonian colonies were mapped on a polyvinyl sheet by scuba divers. A number was assigned to each colony for purposes of recognition for the database and for use in following surveys. This procedure allowed us to monitor more than 100 colonies within each of the permanent plots.

For each gorgonian, colony height, the extent of colony injury and the nature of epibionts were recorded. Colony height was measured with a ruler as the distance between the colony base and the end of the farthest tip. Colonies were grouped for demographic analysis in size-classes in accordance with their height. The extent of colony injury was estimated as the proportion of each colony's total surface that showed no tissue (i.e., denuded axis) or was overgrowth by other organisms (as in Harmelin *et al*., 1999). We estimated colony biomass from the

colony height by using a relationship reported in a previous study: B = 0.002 H $^{2.61}$ (Coma *et al.*, 1998), where B is biomass in grams of dry mass (DM) and H is colony height in centimetres. Corrections for biomass loss caused by injury were introduced to these calculations by subtracting the percentage of biomass equivalent to the percentage of the colony surface affected by injury. Recruitment was measured as the number of new colonies that appeared in the permanent plots in each survey.

Model formulation

We analyzed the demography of red gorgonians using a set of seven age- and size-defined classes. The first class is age-based, representing the "newborn" colonies (primary polyps) that we were unable to observe directly in the field. Newly settled primary polyps are extremely small and thus are not readily observable in the field, with newly found colonies typically being between 0.3 and 3 cm in height. Given the growth rates of newly settled individuals observed in the laboratory, these newly found colonies are probably in their second year of life (Linares *et al*., 2008). Therefore, class 2 colonies are at least two years old, between 0.3 and 3 cm in height, and we assumed that all newly observed colonies in the field fall into this class. The remaining classes are all size-based: class 3 colonies are between 3 and 10 cm in height and are pre-reproductive, while classes 4 through 7 are 11-20 cm, 21-30 cm, 31-40 cm, and > 40 cm in height, respectively, and have increasing reproductive output. Further division of the larger colonies into narrower size classes would be desirable, but the small numbers of colonies at these sizes makes this impractical.

From one year to the next, each gorgonian colony had one of five fates: 1) survive and grow to the next largest size class, 2) survive and shrink by one size class, 3) survive and shrink by two size classes (only applicable to classes 6 and 7), 4) survive but remain in the same size class, or 5) die (Fig. 2). Because these overall fates are governed by combinations of survival, growth, and shrinkage rates, we performed most of our analysis on these underlying vital rates: s_i, the probability of a class i colony surviving; g_i, the probability of a class i colony growing (conditional on surviving); h_i, the probability of a class i colony shrinking by either one or two size class (conditional on surviving and not growing); and h_{i2}, the probability of a class i colony shrinking by two size classes (conditional on surviving and shrinking). These vital rates were estimated from the data for each year using all the individuals in each class. For these estimates, we grouped data across all plots within a class. Since no data are available on the demographic rates for yearling (primary) polyps, due to the difficulty of detecting them in the field, we made the optimistic assumption that their survival is equal to that of class 2, and that all surviving class 1 polyps advance to class 2. Preliminary analysis indicated that altering this assumption had no important effect on our results (Linares et al., 2007).
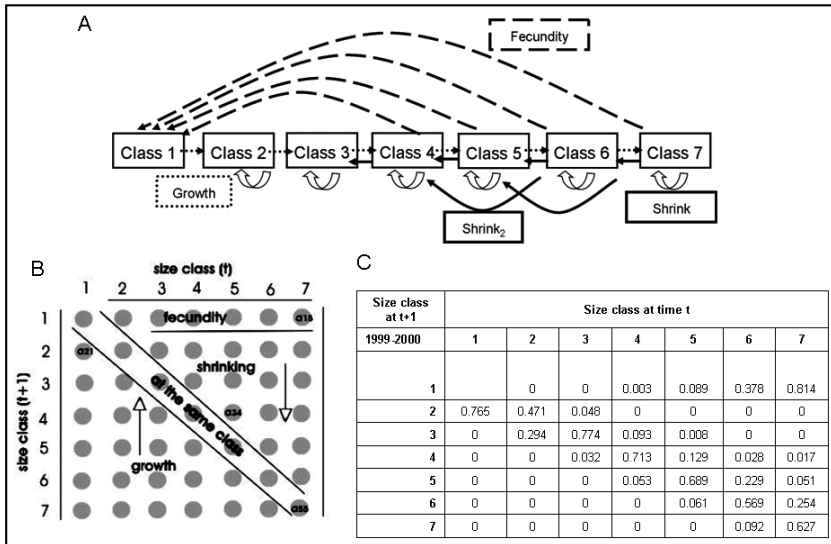
Figure 2. Diagram of the size-structured matrix model build for the red gorgonian (*Paramuricea clavata*) populations. A) Life-cycle graph. B) Schematic representation of the main elements of the projection matrix. The first row of the projection matrix represents reproduction (a15); elements along the diagonal of the matrix (a55) represent the rate of survival of pre-existing colonies without a change in size class; elements below the diagonal (a21) represent rate of survival with an "advance" in size class; elements above the diagonal represent the rate of survival with shrinking or decrease to a "lower" size class. C) Example of the matrix obtained from the first transition year (1999-2000) at Port-Cros.

Size class at t+1	Size class at time t						
1999-2000	1	2	3	4	5	6	7
1		0	0	0.003	0.089	0.378	0.814
2	0.765	0.471	0.048	0	0	0	0
3	0	0.294	0.774	0.093	0.008	0	0
4	0	0	0.032	0.713	0.129	0.028	0.017
5	0	0	0	0.053	0.689	0.229	0.051
6	0	0	0	0	0.061	0.569	0.254
7	0	0	0	0	0	0.092	0.627

To evaluate the effects of different causes of mortality on population growth and extinction risk, we constructed these models using size-structured survival, growth, and shrinkage rates that were estimated separately (see Linares et al., 2007, for a thorough description of the construction of these matrix models). For each model, we estimated deterministic lambda (λ_1), i.e. the ultimate or long-term growth rate of a structured population in a constant environment, as well as, the stochastic lambda (λ_S), i.e. the population growth rate in a stochastically varying environment, using equally-likely random draws of annual matrices.

Data and simulations for case study 1. Long-term effects of the 1999 mass mortality event on red gorgonian populations in Port-Cros National Park

In June 1999, three permanent plots were set up at each of two locations, La Gabinière (42°59'N, 6°23'E) and Montrémian (43°01'N, 6°21'E), where the plots were randomly selected at the same depth (approximately 25 m) to reduce variation in population structure and density (Fig. 3).
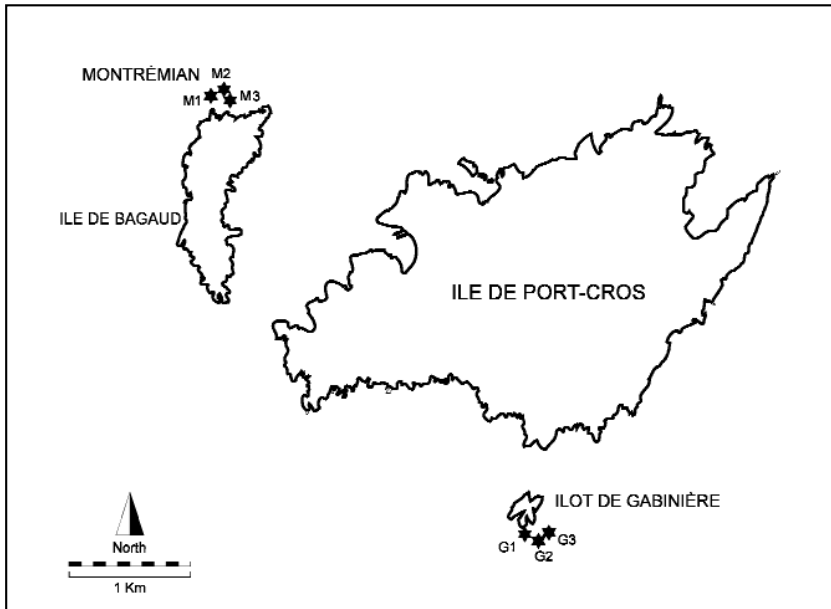
Figure 3. Location of the six permanent plots at La Gabinière (G1, G2, G3) and Montrémian (M1, M2, M3) to study the effects of 1999 mass mortality event in the Port-cros National Park.

The first survey was performed in June 1999 (before the mass mortality event), the second shortly after the event (November 1999) and the others in June 2000, November 2001, November 2002 and November 2003 (Linares *et al*., 2005). After 2005, we continued to survey the permanent plots annually until November 2007, in order to evaluate the recovery capacity of the populations.

We used data collected from the six plots just before and after the 1999 mass mortality event and an additional four years of post-event data (1999-2003) to construct matrices for the gorgonian population monitored in the Port-Cros National Park (Linares et al., 2005), From these matrices, we estimated deterministic lambda (λ), i.e. the ultimate or long-term annual growth rate of a structured population in a constant environment, as well as stochastic growth rate (λs), the average population growth rate in a stochastically varying environment, based on random draws of annual matrices (Caswell, 2001; Morris and Doak, 2002).

Data and simulations for case study 2. Diving impact on P. clavata populations in Marine Protected Areas: Cap de Creus and the Medes Islands

The demographic parameters used in this study are based on the data from a previous study (Coma et al., 2003), with the survivorship, growth, and recruitment of red gorgonian colonies estimated from annual surveys of permanent plots (see above for a thorough description of the

method used) at Cap de Creus (2 plots from 2002 to 2004) and the Medes Islands (4 plots from 2001 to 2004). Although both areas experience substantial diving activity, the Medes Islands have a higher visitation (around 70,000 divers/year) than Cap de Creus (about 30,000 divers/years) (Zabala et al., 2003; Coma et al., 2004). PVA models were used to investigate the long-term consequences of a decrease in diving activity. Since the main impact of diving was detected on total mortality, with partial mortality not significantly affected by visitation levels (Coma *et al.,* 2004) and previous modelling demographic models has shown that population growth is most sensitive to the survival of the largest colonies (Linares *et al*., 2007), we focused our simulations on the survival of the four largest size classes of colonies (i.e., higher than 10 cm).

Starting with the average matrix for each population, we created a series of new matrices, with survival rates for each of the classes increasing in tandem in 1% increments over their estimated values, up to the point when the highest class-specific survival rates equalled 99%. The long-term population growth rates of the resulting matrices (λ values) were shown as functions of these increases in survival rates.

Data and simulations for case study 3. Modelling the interacting effects of the two disturbances

The main goal of this section was to explore the interaction between the effects of diving damage and mass mortality events on the growth and persistence of gorgonian populations, and how changes in the intensity of these threats altered the viability of gorgonian populations. Specifically, we simulated the effects of mass mortality events on: 1) gorgonian populations subjected to diving activity and 2) gorgonian populations subjected to different levels of diving activity (e.g., to different survival rates)

To study whether a reduction in the impact of diving can substantially change the threat posed by mass mortality events, we used the general procedure explained in the previous section, but altered the matrices from the Medes Islands and Cap de Creus populations to reflect lower diver-induced mortality.

First, we simulated the effects of different frequencies of mass mortality events on gorgonian populations affected by different diving intensity. For these simulations we combined annual vital rates estimates for (1) Port-Cros to simulate a year of mass mortality and the following three years (see above) with (2) either the Medes Islands (high diving intensity) or the Cap de Creus (moderate diving intensity) population to simulate years when no mass mortality event was occurring and had not occurred for four years previously. Simulations were performed for four different mean frequencies of mass mortality events: every 5 (following the observations of the most recent episodes in 1999 and 2003), 10, 25, and 50 years. A total of 5000 simulations of 100 years each were run for

each frequency of mortality events using either the Medes Islands or Cap de Creus matrices for unaffected years. Results are given as the probability of quasi-extinction for each population for up to 100 years, using an extinction threshold of 10% of the initial population, and starting with a population of 300 with a stable stage distribution for the matrix of vital rates in unaffected years.

Finally, we combined two different frequencies of mass mortality events with unaffected year matrices reflecting the control of diving intensity (see above). These simulations were performed for average mass mortality event frequencies of 5 and 10 years, and using matrices for the Medes Islands (the population with the most intense diving) with survival rates for the four largest size classes increased from 0 to 7 % above their estimated values.

RESULTS

Long-term effects of the 1999 mass mortality event

After the 1999 mass mortality event, the two locations showed the same pattern of decrease in density until November 2003. After November 2005, there was a significant increase in density, due to the high recruitment of new colonies, in particular at Gabinière (Fig. 4). Density values were highly variable during the recent years due to the fact that recruits are subjected to high annual mortality rates.
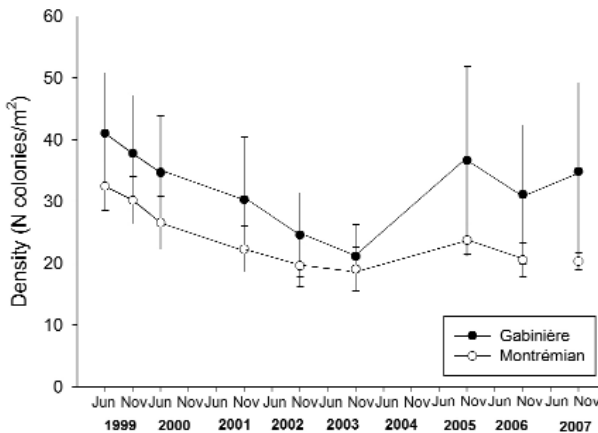

Figure 4. Changes (mean ± SE) of density (N colonies/m^2) including newborn recruits over the study period (June 1999-November 2007) at the two locations (Montrémian and La Gabinière).

The extent of injury of the colonies showed a significant decrease between November 2003 and November 2005, however, during the last

years of the study, the overall extent of injury remained constant and relatively high (up to 20%; Fig. 5). After the marked loss of biomass just after the event, from November 2001 until the last survey (November 2007) the mean biomass values remained constant at both locations (Fig. 6). The estimated long-term growth rates associated with annual matrices based on data from the Port-Cros population between 1999 and 2003 all indicate declining populations (Table 2). Furthermore, while there was some variation in survival rates and lambda values from year to year, the deterministic λ value for the mean matrix was almost identical to the λ_S value (Table 2). Although all the matrices displayed λ values under 1, the lowest value was two years after the event.
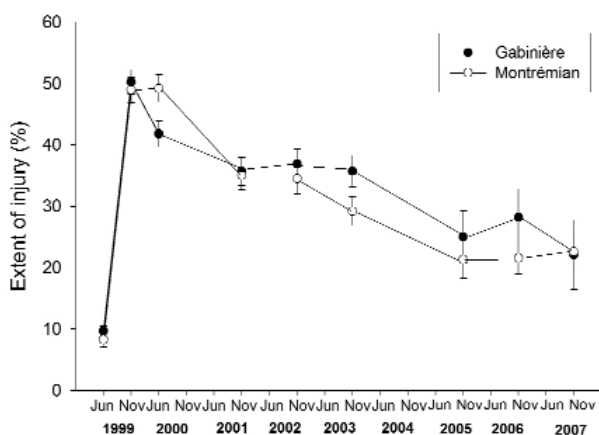
Figure 5. Changes (mean ± SE) in partial mortality (% of injured colony surface) including affected and unaffected colonies over the study period (June 1999-November 2007) at the two locations (Montrémian and La Gabinière).
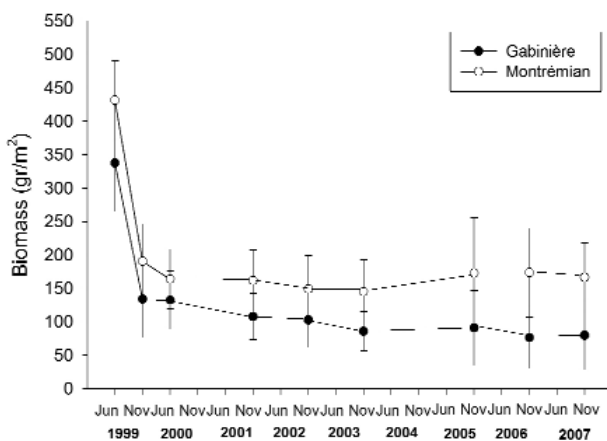

Figure 6. Changes (mean ± SE) in biomass (g DM/m²) over the study period (June 1999-November 2007) at the two locations (Montrémian and La Gabinière).

Table 2. Annual population growth rates (λ) of transition matrices for red gorgonian populations affected by a mass mortality event at the Port-Cros NP. λ_1= deterministic lambda, λs= stochastic lambda.

Site	Year	λ1	λs
Port-Cros	1999-2000	0.873	
	2000-2001	0.823	
	2001-2002	0.931	
	2002-2003	0.933	
	Mean	0.889	0.886

Diving impact on P. clavata populations

The increase in the survival of large colonies necessary to achieve a positive population growth rate varied between sites due to differences in their initial survival rates, and hence population growth rates (Medes Islands, λ=0.936; Cap de Creus, λ=0.974). At the Medes Islands, only an increase in survival of 7% or greater yielded λ values greater than 1, while at Cap de Creus, population stability or growth was achieved by an increase in survival rates of just 2% (Fig. 7). The total survival rates of large colonies needed to achieve a lambda close to 1 were similar for the two populations: 97% for Cap de Creus and 98% for the Medes Islands (Fig. 7).
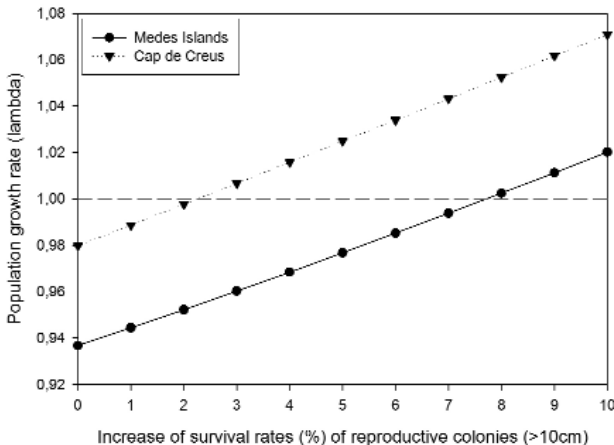

Figure 7. Sensitivity of population growth rate (λ) to changes in the survival of adult colonies (> 10 cm) for two *Paramuricea clavata* populations: Medes Islands and Cap de Creus.

Modelling the interacting effects of the two disturbances

Different extinction risks were obtained depending on the population used to estimate the unaffected year matrices. Modelling the mass

mortality effects on the Medes Islands populations (mean λ=0.936) had drastic effects on persistence. Near-certain quasi-extinction occurred after 38 to 53 years with even frequencies of between 5 and 50 years (Fig. 8a). Simulations using the Cap de Creus population (mean λ=0.974) showed near-certain quasi-extinction after 55 and 84 years with event frequencies of 5 and 10 years respectively, and substantially lower risks under less frequent disturbance regimes (the probability of extinction after 100 years was about 88% and 59% for the 25 and 50 year, respectively; Fig. 8b).
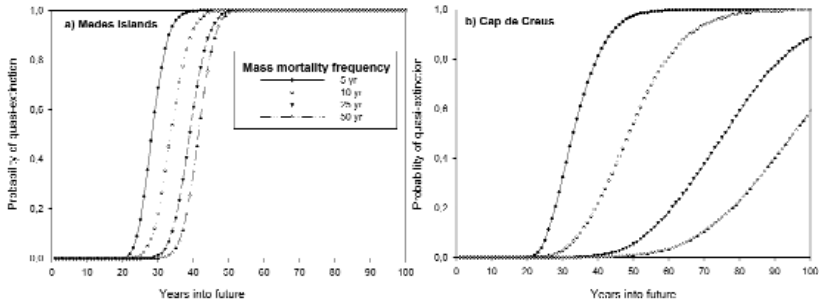

Figure 8. Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population under four mass mortality event frequencies (5, 10, 25, 50 years). (a) Simulations developed for Medes Islands population (λ = 0.936). (b) Simulations developed for Cap de Creus population (λ = 0.974).[2]

The change in the effect of mass mortality events (using frequencies of 5 and 10 years) in relation to the degree of diving control, represented as increases in survival rates from 0% to 7% is shown in Figure 8. With mass mortality events occurring every 5 years on average, the time for approximately 100% quasi-extinction was increased from 37 years (with no control: original Medes Islands matrix) to 60 years (for complete diving restriction, with survival increases of 7%; Fig. 9a). The reduction in the threat from mass mortality events that results from diving restrictions was even clearer at lower event frequencies (Fig. 9b).
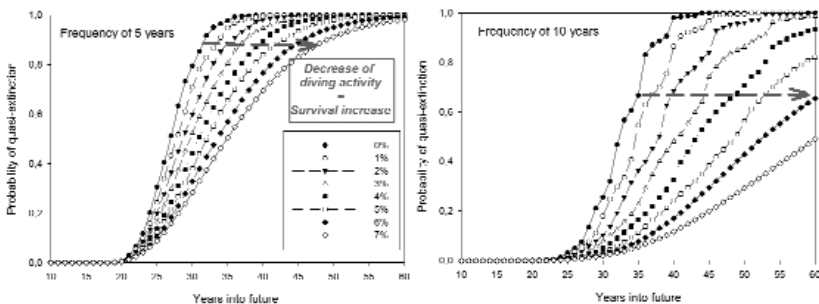

Figure 9. Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population with mass mortality event frequencies of (a) 5 years and (b) 10 years. Simulations developed for Medes Islands population under different increases in survival (from 0% to 7%) of large (>10 cm) size classes (with λ values associated with the matrices of: 0.939, 0.946, 0.954, 0.962, 0.970, 0.987, 0.996).

DISCUSSION

Our results demonstrate the usefulness of long-term demographic data and modeling approaches to improve our knowledge of the response of coralligenous communities when faced with anthropogenic disturbances such as mass mortality events and diving intensity. Our simulations, together with previous results on the sensitivity and elasticity values displayed by *P. clavata* (Linares *et al*., 2007), demonstrate the usefulness of PVA as a tool to examine a suite of hypothesized pressures and the outcomes of potential management strategies for the coralligenous communities in protected Mediterranean areas. In this study, the use of simple demographic models is robust enough to show that for some important coralligenous species even small reductions in the mortality of adults will substantially improve population viability.

Long-term effects of mass mortality events

Through long-term monitoring of red gorgonian populations in Port-Cros, we have improved understanding of the potential for recovery of red gorgonian populations when faced with powerful disturbances, such as the 1999 mass mortality event.

After eight years of monitoring, our results show a slight recovery of the red gorgonian populations affected by the 1999 mass mortality. This positive trend is only clear with regard to density (in particular at La Gabinière, due to the high recruitment rates observed there) and to the extent of injury (due to the loss of the dead apical parts of the colonies affected). However, overall biomass remains constant after the impact and at very low values in comparison to those just before the event. Our results demonstrate that the affected populations are still far from their previous state (June 1999), due to the loss of large colonies, and they suggest that the recovery time to regain the prior state of health is probably of the order of decades (in the absence of other strong disturbances). The same pattern was observed in the red gorgonian population located at La Galère between 1992 and 2004 (Harmelin and Garrabou, 2005); despite the increase in juvenile colonies, there was a significant decrease (around 45%) in biomass during this period, which can be related to the 1999 mass mortality event.

The persistent low λ values obtained from the size-structured matrices of Port-Cros populations confirm the delayed and long-lasting effects of mass mortality events described in previous research (Linares *et al*., 2005). The lowest value of λ was obtained one year after the mortality (2000-2001; $\lambda=0.823$) rather than immediately after the event (1999-2000; $\lambda=0.873$). The increase in λ values 3-4 years after the event suggests a certain ability to recover, but only after a substantial period of delayed impact. The total delayed response and eventual extent of recovery are, however, not yet clear and will only become apparent after longer-term monitoring of more events.

The impact of diving: a general concern for MPA managers

Over the last two decades the impact of diving on coastal MPAs has been a major concern for managers of tropical ecosystems (Jamelson et al., 1999; Rouphael and Inglis, 2002; Zakai and Chadwick-Furman, 2002). Research mainly focuses on systems with relatively high dynamics, such as shallow coral reefs, that may be able to persist under a moderate impact. In contrast, there is a lack of research into the effects of recreational activities on systems with low dynamics, such as those that are characteristic of Mediterranean coralligenous concretions (Sartoretto, 1996; Ballesteros, 2006; but see Sala et al., 1996; Garrabou et al., 1998; Coma et al., 2004). The lack of such studies may be explained by the practical difficulties resulting from the characteristics of many species dwelling in coralligenous habitats: longevity (Linares et al., 2007), low vital rates (Garrabou and Harmelin, 2002; Teixidó et al., 2009) and morphological plasticity resulting from their clonal nature. The observed vital rates of red gorgonian in Medes Islands and Cap de Creus suggest that these populations exposed to intense diving activity are in decline, with both deterministic and stochastic growth rates of less than one. Our modelling of simulated increases on survival of large size colonies (>10 cm) shows clear positive effects on the populations studied, and most importantly, it shows that local persistence (λ=1) of gorgonian populations can be achieved with only modest increases (3% and 7% in Cap de Creus and Medes populations, respectively) in colony (>10 cm) survival. The differences in the survival increase required to ensure the population persistence at the two sites may reasonably be related to the different levels of diving they are subjected to. Indeed, the differences in the population growth rates between the two areas seem to be directly related to differences in diving intensity, suggesting the importance of the impact of diving on population decline. While both areas experience substantial diving activity, the Medes Islands have a higher visitation (around 70,000 divers/year) than Cap de Creus (about 30,000 divers/years) (Zabala *et al*., 2003; Coma *et al*., 2004). These differences may explain the higher mortality and lower population growth rates at the first study site, however, we have to be cautious as this explanation is based on the observed correlation.

Diver "carrying capacity" has been an important issue for several studies. However, the discrepancies (ranging from 500 to 15,000 dives per year), depending on the site and species studied (Hawkins and Roberts, 1997; Dixon *et al*., 1993; Zakai and Chadwick-Furman, 2002), highlight the complexity of determining a scientifically defendable limit on the effects of diving for a particular community. Further complicating factors are the interaction of the life-history traits of the organisms and the existence of other disturbances. However, there is a large difference between the levels of diving recorded at the study sites (between 30,000 and 70,000 dives/year) and those considered suitable for coral

reefs (500 to 15,000 dives/year). Our results, which quantify the increase in survival necessary to reduce short- and medium-term extinction risks, are thus valuable for informing adjustments to management criteria to address clear biological goals. Most importantly, our work suggests that decreases in the mortality of adult colonies can be achieved through regulating diving within the MPAs, as well as through the implementation of good diving practices, as has been suggested for coral reefs suffering from intense diving (Zakai and Chadwick-Furman, 2002; Baker and Roberts, 2004).

Assessing the threat of combined disturbances

The repercussions of global warming for the recovery of endangered species are of great importance to conservation. Our findings confirm that anthropogenic activities, such as diving, together with global warming can combine to have dramatic effects on the viability of long-lived and slow-growing marine species. Our simulations clearly show that if mass mortality events affect populations with low λ values due to direct human action such as diving, as occurs for the Medes Islands population, even low frequencies of sea-water temperature anomalies will substantially compromise population viability in the short and medium term. In contrast, lambda values close to 1 reduce the short-term (though not the longer-term) risk for gorgonian populations when exposed to these global warming effects. The two different patterns are exemplified when the results obtained for Cap de Creus populations (with a mean λ of 0.974 and predicted times of quasi-extinction between 55 and 84 years) are compared with those obtained for the Medes Islands populations (38 and 45 years for a mean λ of 0.936) for event frequencies of 5 and 10 years.

Even with the less optimistic event repetition estimates (every 5 years) the time to quasi-extinction if the non-mass mortality lambda values were close to 1 was considerably longer than for those estimated for our studied populations. The effects of diving restrictions are much more pronounced at lower mass mortality event frequencies, suggesting that effective management strategies could have large and lasting effects on the population viability of long-lived and slow-growing coralligenous species facing recurrent mass mortality events.

Future viability of red gorgonian populations at Port-Cros National Park

Unfortunately, it seems unlikely that these populations will have long periods in which they suffer no disturbances. After the 1999 and 2003 summer mass mortality events, which have been related (more or less confidently) to the recent warming of the Mediterranean (Romano *et al*., 2000; Harmelin, 2004), at least two new mass mortality events have been observed at other NW Mediterranean locations during the

summers of 2006 and 2007 (Ballesteros, pers. com.; J.M. Culioli pers. com.). As these observations suggest, an increase in the frequency of these events can be expected around the NW Mediterranean as a result of global climate change (Vargas-Yáñez *et al.,* 2008). Consequently, further mass mortality events at the Port-Cros National Park in the near future seem likely.

Finally, other effects can be added to the analyses which show the prospects for species survival to be worse still. The boundary of the Port-Cros National Park (France) offered no protection from the migration of *Caulerpa racemosa* var. *cylindracea* once they were present along the coast of the French Riviera (Boudouresque and Verlaque, 2005). Since 2006, the permanent plots located at La Gabinière have been invaded by this invasive alga. The response of gorgonian populations faced with this disturbance will have to be examined in the coming years.

In summary, the results obtained during this study which combine data from different sites have revealed the fragility of the red gorgonian *Paramuricea clavata* as it faces increasing disturbances. Effective responses to the threats that many long-lived marine species face will require their life-history traits and, in particular, their low resilience to periodic disturbance, to be considered in tandem with interacting threats if effective conservation plans are to be made for their preservation.

Can this demographic approach be extrapolated to the study of other members of the coralligenous community?

Although we present these methods as one of the most promising tools for the management of coralligenous communities, this study only focuses on the viability of gorgonian populations, only one of the assemblages of coralligenous communities. The abundance of gorgonians mainly depends on average current intensity and the availability of food; in some of the richest zones gorgonians can dominate the community but in highly oligotrophic waters they are scarce or absent (Ballesteros, 2006). Moreover, several gorgonian facies are not considered coralligenous communities because they are sciaphilic communities without a basal framework of coralline algae (e.g., Pérès and Picard, 1964; Gili and Ros, 1985). In our opinion, the development of these modelling methods opens up the way for their application to the conservation of other species of coralligenous communities. However, the methods may be difficult to apply to other benthic species (sponges, bryozoans, algae, etc.), which do not display the morphological and demographic attributes detailed above. Extra effort would be necessary to select an appropriate pool of model species, and to research the particular demography of each species.

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