Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: a case study of *Paramuricea clavata*

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ABSTRACT: The combined effects of disparate impacts on population health are a continuing problem in risk assessment and management for threatened species. Populations of red gorgonian *Paramuricea clavata* in the NW Mediterranean Sea are threatened both by chronic and localized increases in mortality due to high diving activity and by widespread but episodic mass mortality events related to climatic anomalies. Using demographic data obtained from 3 populations (2 under contrasting levels of diving and one affected by a 1999 mass mortality event), we developed size-structured matrix models to forecast the long-term consequences of both disturbances and their combined effects. When we considered only the effects of diver damage, our results showed that population stability could be achieved with an increase in the annual survival of adult colonies of between 3 and 7 %, demonstrating the need for diving reduction in the study locations, where there are estimated to be between 30000 and 70000 dives yr^{-1}. Modeling the effects of mass mortality events alone showed a low annual population growth rate (0.886) and near certain extinction risk over even short time scales. Considering these 2 types of impacts together, we found that the effects of mass mortality events aggravate the decline in gorgonian populations subjected to high diving impact, reaching the extinction threshold after 36 to 55 yr under the actual frequency of mass mortality events. Simulated reduction of diving effects dramatically increased the time to quasi-extinction for populations subjected to realistic frequencies of mass mortality events. Our simulations reveal the need of management actions to ensure the gorgonian viability in the face of climate change, and suggest that management of more controllable impacts, such as diving, can help buffer populations against the less controllable effects of climate change.

KEY WORDS: Matrix models · Population viability analysis (PVA) · Diving · Mass mortality events · Global warming · NW Mediterranean · *Paramuricea clavata*

INTRODUCTION

The increase in the magnitude and frequency of human-induced impacts on marine coastal ecosystems, including overfishing, pollution, habitat destruction, and global warming, is causing the decline in many ecological communities (Vitousek et al. 1997, Jackson et al. 2001, Harvell et al. 2004, Hughes et al. 2005). In particular, these impacts have serious consequences on sublittoral marine communities dominated by ben-

thic species, which, due to their sessile nature, cannot avoid disturbances (Solan et al. 2004). Due to this susceptibility, it is critical to better understand how seriously these species and communities are threatened by different combinations of impacts, and whether feasible management actions can be used to effectively mitigate these combined effects.

In addressing the impacts of global warming, it is especially important to pay attention to other, less intractable threats, due to additive or multiplicative

impacts from multiple stressors on individual fitness and population viability (Hughes & Connell 1999, Vilchis et al. 2005). Understanding the risks that these impacts and their interacting effects pose for the viability of disturbed populations may be essential in devising criteria for effective management of these species, especially in the face of global change. One of the main challenges for ecologists is to quantify the ways in which multiple stressors will interact. Although it is often assumed that the stressors typically act in synergy (Harley et al. 2006, Sala & Knowlton 2006), the frequency and magnitude of these interactions (by means of synergies, additive effects, or antagonistic interactions) remain unclear for most systems (Darling & Côté 2008).

Our study organism, the red gorgonian *Paramuricea clavata,* is an emblematic species of Mediterranean hard-bottom communities, increasing the biomass and the structural complexity of sublittoral communities (Ballesteros 2006). This species displays slow growth rates, low recruitment rates, and low natural mortality rates (Coma et al. 1998, 2004, Linares et al. 2007). Furthermore, the size distributions of *P. clavata* populations show that most local populations are long-established, indicating that recruitment failures or increased mortality due to disturbances in existing populations could lead to region-wide declines (Linares et al. 2008a).

The red gorgonian *Paramuricea clavata* has also been one of the species most severely affected during region-wide 'mass mortality' events (Cerrano et al. 2000, Perez et al. 2000, Garrabou et al. 2009). During 1999 and 2003, high-diversity Mediterranean marine benthic communities dominated by suspension feeders were affected by 2 unusual, regional-scale (spanning several 100s of km) climatic anomalies, with warmer water temperatures resulting in a pulse of increased mortality for multiple species across the region (Romano et al. 2000, Garrabou et al. 2009). Although similar pulses in mortality rates have also been described at local scales (several 10s of m or km) since 1983 (Harmelin 1984, Bavestrello & Boero 1986), the magnitudes of these disturbances were exceedingly large, with almost 30 sessile species affected at a regional scale in the 1999 event. For a representative set of gorgonian and sponge species, the most impacted taxa, 60 to 100% of colonies suffered damage over ≥50% of the colony surface (Cerrano et al. 2000, Perez et al. 2000, Garrabou et al. 2001, Linares et al. 2005, Coma et al. 2006).

Although the medium-term impacts of mass mortality events on red gorgonian populations have been documented (Cerrano et al. 2005, Linares et al. 2005, Cupido et al. 2008), the longer-term consequences of an increase in the frequency of these events for the popula-

tions are unknown. Making such an assessment is timely, with local-scale mass mortality events occurring during the late summers of 2005, 2006, and 2007 in several Mediterranean localities (Cigliano & Gambi 2007, Coma et al. 2009, Garrabou et al. 2009). These more recent events may indicate that the frequency of mass mortality episodes is increasing as a result of the global warming (Cerrano & Bavestrello 2008, Garrabou et al. 2009). In fact, a recent analysis of a long-term temperature series has shown warming and a consequent 40% lengthening of summer conditions between 1974 and 2006 (Coma et al. 2009). Climatic projections for the 21st century in the Mediterranean Sea indicate warmer and drier conditions, with a dramatic increase in the frequency and persistence of extreme events such as heat waves (Déqué 2007, IPCC 2007).

The second major threat to red gorgonian populations comes from the damage inadvertently inflicted by recreational diving activities. Effects of divers on gorgonians are strongest in the few areas with high levels of visitation, as is true for other systems subjected to damage from trampling or diving (Liddle & Kay 1987, Brosnan & Crumrine 1994, Garrabou et al. 1998, Tratalos & Austin 2001). Paradoxically, these areas (with high levels of visitation) are also often those with the highest theoretical protection, such as marine parks and other marine protected areas (MPAs). In Medes Island MPA (Spain, NW Mediterranean), the increase in annual mortality of red gorgonian colonies over natural mortality rates due to the increase of diving activity (from 100 to 1000 dives per location per yr) was previously estimated as 2.7 to 7.4% yr^{-1} (Coma et al. 2004).

In the present study we sought to remedy the lack of studies that simultaneously assess the different threats that are now affecting many sessile invertebrate populations. To do so, we used size-structured matrix models to forecast the long-term consequences of both diving disturbances and mass mortality events on *Paramuricea clavata* populations in the NW Mediterranean Sea. Long-lived sessile species such as red gorgonian are especially vulnerable to disturbances due to slow population dynamics (Hughes & Jackson 1985, Dayton et al. 1995, Garrabou & Harmelin 2002, Coma et al. 2004). The past, and expected future, increases in multiple anthropogenic mortality sources create the need for a joint assessment of the threats they pose to marine long-lived species, especially in MPAs (Rouphael & Inglis 2002, Barker & Roberts 2004). One approach to such an assessment is to conduct long-term monitoring to examine the response capacity of the species facing increasing disturbances. Alternatively, the use of matrix models (Caswell 2001, Morris & Doak 2002) can be helpful to examine the future persistence of these species, as well as to evaluate the effectiveness of possible

management measures. In conservation studies, matrix models are mostly used to calculate the annual population growth rate λ with $\lambda = N(t + 1)/N(t)$, where t is time and $N(t)$ is population size at time t, or quasi-extinction probabilities (the probability that a population fall below a threshold population size by different times into the future). In the present study, we make use of both these outputs in a series of analyses using size-structured matrices parameterized with demographic data from 3 MPAs to project *P. clavata* population growth rate under different scenarios of diver damage and different frequencies of mass mortality events.

MATERIALS AND METHODS

Study species and anthropogenic threats. The populations studied were located within MPAs heavily visited by divers, where there is a large and well-documented increase in red gorgonian mortality rates (Coma et al. 2004). A demographic model we previously developed for *Paramuricea clavata* showed that annual population growth is far more sensitive to changes in survival rates than to growth, shrinkage (negative growth) or reproductive rates (Linares et al. 2007). The previous modeling also revealed the fragility of 2 of our 3 study populations (Medes Islands and Cap de Creus, Spain), both of which are predicted to decline rapidly, with a high risk of extinction over moderate time horizons (Linares et al. 2007). The differences in the population growth rates predicted by our models for these 2 populations also correlate with differences in diver impacts, further suggesting the importance of diving effects for population decline. Medes Islands experiences an estimated 70 000 dives yr^{-1}, while Cap de Creus experiences an estimated 30 000 dives yr^{-1} (Zabala et al. 2003).

The second major threat to red gorgonian populations that we investigate here comes from a far less controllable source than diving. As we noted above, during the last several years, the Mediterranean hard-bottom communities have been affected by 2 mass mortality events. The monitoring of red gorgonian populations affected by the 1999 massive mortality event showed a large delayed effect on total mortality from 9% mortality in populations just after the event to a total of 48% of all colonies dead by 4 yr after the event. Moreover, red gorgonian populations displayed a high increase of the degree of injury of the colonies (partial mortality), and the integrated effect on lost of biomass was estimated to be on the order of 60% of the total initial biomass (Linares et al. 2005).

Demographic data. We used demographic parameters previously obtained from 3 red gorgonian populations located along the NW Mediterranean coast and studied for 2 to 4 yr: Cap de Creus (2002–2004), Medes Islands (2001–2004), and Port-Cros (1999–2003). All 3 populations occur in areas where well-developed red gorgonians populations can be found and are located at the same depth range (15 to 25 m) in Mediterranean MPAs with substantial levels of diving activity.

To obtain accurate demographic estimates, we set up between 3 and 6 permanent plots in each population and monitored each colony present within these plots. Each plot was 4 m long and 0.8 m wide (total 3.2 m^2) and to facilitate accurate mapping were partitioned in 40×40 cm quadrats. Each plot was surveyed annually. During the first survey, all colonies present in each subquadrat were mapped on a polyvinyl sheet by SCUBA divers to facilitate their monitoring during the following surveys. This procedure allowed us to monitor more than 100 colonies with each of the permanent plots. The periodical surveys of the permanent plots allowed the monitoring of total mortality, partial mortality, colony size (height), and recruitment rates.

Model formulation. To examine the viability of red gorgonian populations under different threat scenarios, we employed size-structured matrices. We analyzed the demography of red gorgonians using a set of 7 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 (Linares et al. 2008b). Class 2 colonies are at least 2 yr old (between 0.3 and 3 cm), and we assumed that all newly observed colonies in the field fall into this class. The remaining classes are all size-based and were chosen to match those used in previous work on this species (Coma et al. 1995): Class 3 colonies are between 3 and 10 cm in height and are pre-reproductive, while Classes 4 through 7 are 11 to 20, 21 to 30, 31 to 40, and >40 cm in height, respectively, and have increasing reproductive output.

We constructed the matrices using separately estimated, size-specific survival, growth, and shrinkage rates. 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 in each study site within a class. Since no data are available for the Class 1, we made the optimistic assumption that their survival is equal to that of Class 2. We assume that all surviving Class 1 colonies advance to Class 2, because preliminary analysis indicated that altering this assumption had no important effect on our results (see Fig. S1 in the supplement for details of how demographic rates are combined to form the population matrices; available at www.int-res.com/articles/suppl/m402p059_app.pdf).

As baseline descriptions of gorgonian demography for the current study, we used the matrix models developed during a previous study for 2 plots monitored at

Cap de Creus and 4 plots monitored at Medes Islands (Linares et al 2007). Following the same methods, we constructed matrices for the gorgonian population at Port-Cros National Park, which was affected by the 1999 mass mortality event (Linares et al. 2005). Because the data taken at Cap de Creus and Medes Islands populations did not encompass a mass mortality event, this additional population is the key to forecasting how these events may influence the persistence of the gorgonian populations. Unfortunately, in the Port-Cros National Park, no demographic studies were conducted prior to the occurrence of the 1999 mass mortality event. Data were collected during a monitoring of 6 plots just before and after the 1999 mass mortality event and during the following 4 yr (1999–2003) (Linares et al. 2005). As with other types of disturbances (e.g. fires; Gross et al. 1998) following a mass mortality event, demographic rates remain altered, with elevated total mortality rates and high shrinkage rates, caused by partial mortality, for at least 4 yr after the event.

We calculated several outputs from these matrix models. First, 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 (λ_s), the average population growth rate in a stochastically varying environment, based on random draws of annual matrices (Caswell 2001, Morris & Doak 2002). These random-draw simulations were also used to estimate the probabilities of quasi-extinction for each impact scenario for up to 150 yr, using an extinction threshold of 10% of the initial population size and starting with a population size of 300 colonies at stable stage distribution; below this size, we expect that low recruitment rates would result in rapid population extirpation.

Population viability under different impact scenarios. The main goal of the present study was to explore the separate and combined effects of diving damage and mass mortality events on the growth and persistence of gorgonian populations and to ask how changes in the intensity of these threats will alter viability of gorgonian populations. To this end, we conducted sets of analyses to address the following 3 questions:

(1) How effective must management of diving become in MPAs to substantially reduce the risk of gorgonian extirpation?

To simulate the reduction in diving effects we used separate time-averaged matrices for the Cap de Creus and Medes Islands populations (Linares et al. 2007). Diving can have effects on both partial and total mortality of all colonies due to partial colony breakage or whole colony detachment after contact with divers (Liddle & Kay 1987, Zakai & Chadwick-Furman 2002).

However, previous work has shown that intense recreational activity results in an increase in total mortality rates (due to the detachment of entire gorgonian colonies), while the degree of injury of the colonies is not significantly affected by visitation level (Coma et al. 2004). In addition, population growth is most sensitive to survival of these largest, otherwise long-lived, and most fecund colonies (Linares et al. 2007).

Given these previous observations, we focused our simulations on diver-driven effects on the survival of the 4 largest size classes of colonies, classes 4 to 7 (i.e. greater than 10 cm height and including all reproductive colonies). Starting with the average matrix of the available annual transitions for each site (2001–2002, 2002–2003, 2003–2004 for Medes Islands and 2002–2003, 2003–2004 for Cap de Creus; Table S1, www.int-res.com/articles/suppl/m402p059_app.pdf), we created a series of new matrices, with survival rates for each of the 4 largest classes increasing in tandem in 1% increments over their estimated values, up to the point of the highest class-specific survival rates equaling 99%. Since only small differences in survival rates among all sizes of adult colonies were found in previous studies (Coma et al. 2004, Linares et al. 2007), it seems reasonable to model similar diver-caused effects on all sizes of adult colonies. We present the long-term average annual population growth rates of the resulting matrices (λ values) as functions of these increases in survival rates. Note that our previous analyses show little annual variation in vital rates, so use of deterministic analyses to address this question is warranted (Linares et al. 2007).

(2) How will increases in mass mortality events impact viability of gorgonian populations?

To answer this question we performed a series of stochastic simulations to model different random frequencies of mass mortality events. Simulations were performed for 4 different mean frequencies of mass mortality events: on average every 5, 10, 25, and 50 yr. These frequencies were chosen to accord with the following observations and reasoning: first, the most recent large-scale episodes occurred in 1999 and 2003 (5 yr apart); second, the Port-Cros population has not been affected by another event since 1999 (10 yr); and third, even if the most infrequent estimates from field observations are an overestimate of the frequency in the long term, warming trends suggest that events will occur at relatively low rates in the future (25 and 50 yr).

As vital rates estimates for the Port-Cros population were not obtained before the mass mortality event occurred (see above), for these simulations we used sets of annual vital rate estimates from either the Medes Islands or the Cap de Creus population to simulate years when no mass mortality event was occurring or had occurred within 4 yr. We used the vital

rates from Port-Cros during 1999–2000 to simulate a year of mass mortality and the vital rates estimated from this site for 2000–2001, 2001–2002, and 2002–2003 to simulate vital rates 1, 2, and 3 yr following an event, respectively (Table S1). For each year of these simulations, a pseudo-random number was first drawn to determine whether a mass mortality event would occur. If so, the 1999–2000 Port-Cros matrix was used to project the population. Otherwise, if an event had occurred within the last 4 yr, the appropriate Port-Cros matrix was used. A total of 5000 simulations of 100 yr each were run for each mortality event frequency and using either Medes Islands or Cap de Creus matrices for unaffected years. Results are shown as the probabilities of quasi-extinction for each population for up to 100 yr, using an extinction threshold of 10% of the initial population size and starting with a population size of 300 at the stable stage distribution for the matrix of vital rates in unaffected years.

(3) Can reductions in diving impacts substantially change the threat posed by mass mortality events?

To address this question we performed simulations of 5 and 10 yr average frequencies of mass mortality events, using matrices for the Medes Islands (the population with the highest diving impact) for non-event years. We ran simulations with survival rates for the 4 largest size classes increasing from 0 to 7% over their estimated values in accordance with the increase of natural mortality rates from 2.7% to 7.4% yr^{-1} previously reported in Medes Islands MPA due to the high diving activity (Coma et al. 2004). Starting with the average matrix, we created a series of new matrices, with survival rates for each of these classes increasing in tandem in 1% increments over their estimated values, up to the point of the highest class-specific survival rates equaling 99% (bearing in mind that natural mortality rates are about 1%; Coma et al. 2004). For each set of assumptions regarding diver-caused mortality and mortality-event frequency, we performed 5000 replicate simulations and report quasi-extinction risks, as described under question (2) above.

RESULTS

Management of diving effects to reduce the decline in gorgonian populations

The 2 sites impacted only by diving differed in their baseline adult survival rates and hence in their baseline population growth rates, with Medes Islands having a considerably lower growth rate, λ = 0.936, than did Cap de Creus, with λ = 0.974 (Linares et al. 2007). These different baselines resulted in substantial differences in the absolute increases in survival of large

colonies necessary to achieve positive population growth rates. For the Medes Islands, only the matrices with increases in annual survival of 7% or greater yielded λ values >1, while in Cap de Creus, population stability or growth was achieved by an increase in survival rates of just 2% (Fig. 1). However, the final survival rates of large colonies needed to achieve a λ close to 1 were very similar for both populations: 97% for Cap de Creus and 98% for Medes Islands.

The threat of increasing mass mortality events

The long-term estimated growth rates associated with annual matrices based on data from Port-Cros between 1999 and 2003 all indicate a declining population (Table 1, Fig. 2). Although all the matrices displayed λ values <1, the lowest value was obtained 2 yr after the event. The annual size-specific survival rates in the years following the event showed the same trend (Fig. 2). Although the smaller size classes suffered the
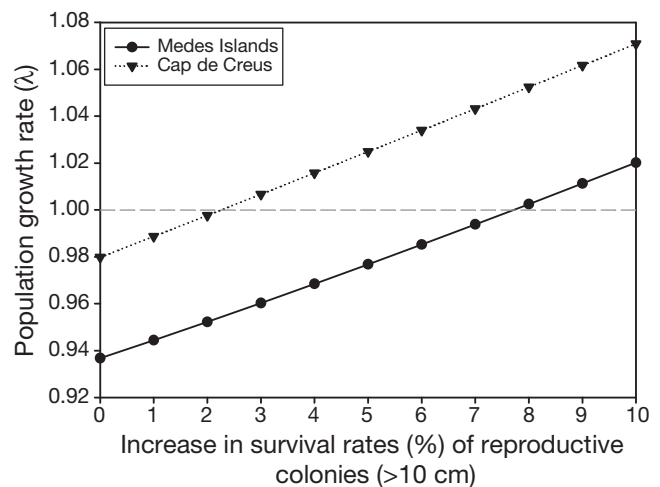

Fig. 1. *Paramuricea clavata*. Sensitivity of the population growth rate (λ) to changes in the survival of adult colonies (>10 cm) for 2 populations: Medes Islands and Cap de Creus

Table 1. Annual population growth rates (λ) of transition matrices for red gorgonian *Paramuricea clavata* population affected by a mass mortality event during late summer of 1999 at the Port-Cros National Park. λ: annual lambda values and arithmetic mean lambda, λ$_s$: stochastic lambda

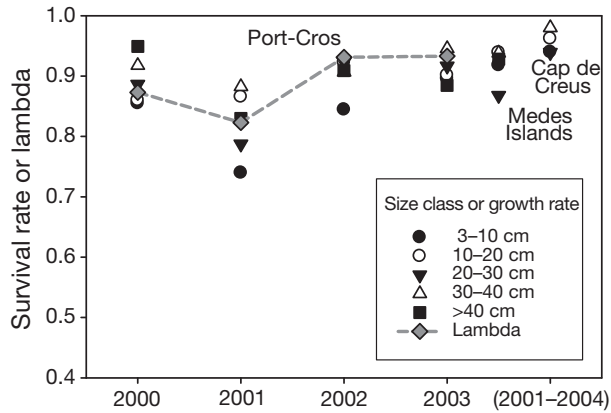| Years	λ	λ$_s$
1999–2000	0.873	
2000–2001	0.823	
2001–2002	0.931	
2002–2003	0.933	
Mean	0.889	0.886

Fig. 2. *Paramuricea clavata.* Annual population growth rates (λ) and survival rates of different size classes obtained from 1999 to 2003 at Port-Cros National Park and mean survival rates of the different size classes obtained from Medes Islands populations (2001–2004) and from Cap de Creus populations (2002–2004)
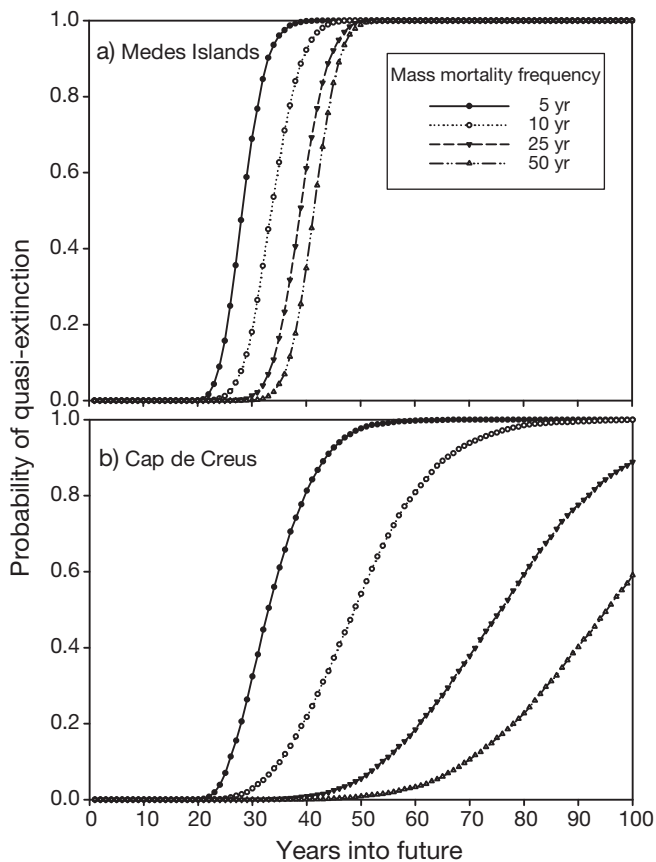

Fig. 3. *Paramuricea clavata.* Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population under 4 frequencies of mass mortality events (5, 10, 25, 50 yr). (a) Simulations using the Medes Islands population matrix in years with no mass mortality effects (growth rate [λ] = 0.936). (b) Simulations using the Cap de Creus matrix for years with no mass mortality effects (λ = 0.974)

highest mortality just after the event, at the end of the 4 yr the largest colonies displayed the lowest survival rate. Despite the slightly positive trend of increasing λ values after 2001, even at the end of the study λ was <1. The arithmetic mean λ value for the mean matrix over these years was almost identical to the λ_s value, with both predicting >10% decline in numbers per yr (Table 1). However, survival rates at Port-Cros 4 yr after the mortality event were similar to those for Medes Islands and Cap de Creus populations, suggesting the comparability of demographic patterns across the sites in the absence of mass mortality events (Fig. 2), and that some recovery following the event was possible.

We obtained different extinction risk results depending on the population used to estimate the unaffected year matrices. Modeling the mass mortality effects using the Medes Islands matrices showed important effects on persistence, with near-certain quasi-extinction after 36 to 51 yr with frequencies of events between 5 and 50 yr (Fig. 3a). On the other hand, simulations using the more optimistic Cap de Creus matrix as a baseline showed near-certain quasi-extinction at 55 and 84 yr, with frequencies of events of 5 and 10 yr, respectively, and substantially lower risks under less frequent disturbance regimes (the probability of extinction at 100 yr was about 88 and 59% for 25 and 50 yr frequencies, respectively; Fig. 3b).

Management measures to reduce the threat of mass mortality events

Fig. 4 shows the combined effects of mass mortality events (using frequencies of 5 and 10 yr) and the degree of diving control, represented as increases in survival rates from 0 to 7%. If mass mortality events occur at 5 yr frequencies, the predicted time until approximately 100% quasi-extinction was increased from 36 yr (using the baseline Medes matrix) to 65 yr if survival rates are increased by 7%, simulating complete diving control (Fig. 4). The effects of diving control in reducing the threats from mass mortality events were even more obvious under a lower frequency of these events (Fig. 4).

DISCUSSION

How effective must management of diving become in MPAs to substantially reduce the risk of gorgonian decline?

One of the main concerns of managers of several of the MPAs in our study region, as well as in other parts
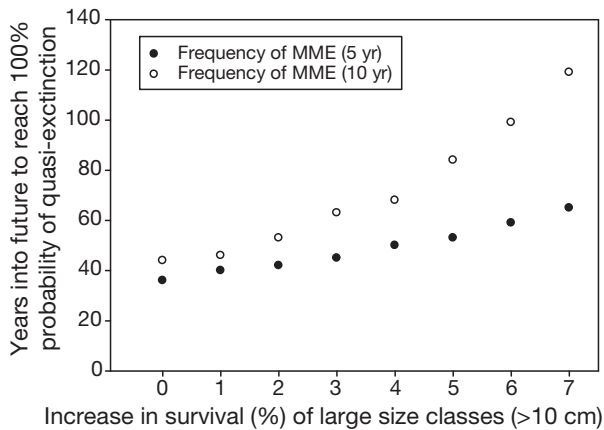
Fig. 4. *Paramuricea clavata.* Number of years to reach 100 % probability of quasi-extinction (10 % of initial population) under frequencies of mass mortality events (MME) of 5 and 10 yr, under different increases in survival (from 0 to 7 %) of large (>10 cm) size classes. Simulations were developed using only the Medes Islands population matrix for years not influenced by MME

of the world, is the intensity of diving activity and its impacts on benthic communities, especially on those dominated by long-lived and slow-growing species that can display an extreme sensitivity to increasing mortality rates. Thus, the examination of diver 'carrying capacity' has been an important issue. However, different studies have suggested dramatically different tolerable levels of diving, ranging from 500 to 15 000 dives yr^{-1} depending on the site and species studied (Dixon et al. 1993, Zakai & Chadwick-Furman 2002). These differences point to the complexity of determining a scientifically defendable limit of diving effects for any particular community, as well as the interacting effects of the life history traits of the organisms and the existence of other disturbances.

The application of population viability analysis (PVA) to detect impacts on threatened populations as well as to examine the effectiveness of potential management actions has been demonstrated in many systems (e.g. Crowder et al. 1994, Doak et al. 1994, Pfister & Bradbury 1996, Holmes & York 2003, Bakker & Doak 2009). Our modeling of the effects of increased survival of reproductive colonies allows a clear definition of the reduction in mortality needed to meet conservation goals and, most importantly, shows that the local persistence ($\lambda = 1$) of gorgonian populations can be achieved with biological feasible increases in colonies (>10 cm) survival (3 and 7 % in Cap de Creus and Medes Islands populations, respectively). These goals for increased survival should only be considered approximations, and therefore long-term monitoring is needed, especially in Cap Creus, to verify the results obtained for 3 yr (note that Coma et al. 2004 examined

the mortality rates in Medes Islands over 9 yr). The necessary reductions in mortality caused by diving could feasibly be achieved either by restrictions on diver visits or by tighter control of diving activities. Further bolstering the link between diving and population health of gorgonians is the correlation between baseline population growth rates and current estimates of diving activity (about 70 000 and 30 000 dives yr^{-1} in Medes Islands and Cap de Creus, respectively; Zabala et al. 2003).

The increase in mortality rates of adult colonies over natural rates that is caused by high diving activity was previously estimated as 2.7 to 7.4 % yr^{-1} (Coma et al. 2004). However, in the absence of a modeling effort to translate these changes into effects on population persistence, the long-term consequences of the apparently slight differences between λ found between Medes Islands and Cap de Creus (ranging between 0.936 and 0.976) as well as the relevance of these values for management was difficult to evaluate. Our results, quantifying the necessary increases in survival to reduce short- and medium-term extinction risk (on the order of 25 and 50 yr) are thus valuable for adjusting management criteria to address clear biological goals (Bakker & Doak 2009). Most importantly, our work points out that biologically relevant decreases in the mortality of adult colonies could be achievable through the reduction of divers within the MPAs, as well as through better implementation of good diving practices, as has been suggested for coral reefs with high diving activity (Zakai & Chadwick-Furman 2002, Barker & Roberts 2004). Nevertheless, it is noteworthy that the levels of diving recorded at our study sites are vastly greater than any suggested as suitable for coral reefs (500 to 15000 dives yr^{-1}; Dixon et al. 1993, Zakai & Chadwick-Furman 2002).

These results, together with the sensitivity and elasticity values displayed by this species (Linares et al. 2007), corroborate the applicability of PVA as a helpful management tool to examine a suite of hypothesized threats and potential management strategies (Heppell et al. 2000, Gerber & Heppell 2004, Bakker et al. 2009). In the present study, the use of simple demographic models confirms that for some species even small reductions in mortality of adults will substantially improve population viability.

How will increases in mass mortality events translate into decreased viability of gorgonian populations?

The persistent low λ values obtained from the size-structured matrices of the Port-Cros population confirmed the delayed and long-lasting effects of mass mortality events, also described in a previous study

about this event (Linares et al. 2005). The lowest λ value was obtained 1 yr after the occurrence of the event (2000–2001; λ = 0.823), not just after the event (1999–2000; λ = 0.873). The increase in λ values 3 to 4 yr after the event suggests a certain ability to recover, but only after a substantial period of delayed impact. The total delayed response and eventual recovery are, however, not yet clear and will require longer-term monitoring after more events.

The effects of mass mortality events can aggravate the decline of gorgonian populations found in sites with high diving activity. Our simulations clearly show that if impacted populations also have low λ values in the absence of mortally events, as occurs for the Medes Islands population, even low frequencies of seawater temperature anomalies will substantially compromise population viability over the short to medium term. In contrast, λ values close to 1 in unaffected years can reduce the short-term (though not the longer-term) risk of extinction that results from these global warming effects. This difference is demonstrated by the results using the Cap de Creus data, generating times to certain quasi-extinction of 55 to 84 yr, in comparison to 38 to 45 yr to quasi-extinction when using the Medes Islands data (for frequencies of event repetition of 5 and 10 yr).

Management and climate change on gorgonian populations

Modeling the effects of mass mortality events on populations under high diving activity suggests that management actions are necessary to prevent extreme, short-term extinction risks. For the most pessimistic scenario of 5 yr frequencies of events, the time of quasi-extinction increased from 37 to 60 yr with increasing adult survival in normal years, equivalent to reduced diver impacts. The effects of diving control are much more pronounced at lower mass mortality frequencies, further indicating their feasibility as an indirect and temporary, but effective, management tool in the face of global change.

The repercussions of global warming on the recovery of endangered species are of strong importance to conservation (Hoyle & James 2005, Vilchis et al. 2005). Our findings corroborate that the combined effects of local human impacts (in this case diving activity, but in other areas pollution, fishing, and other localized impacts), together with the global warming effects, can dramatically reduce the viability of long-lived and slow-growing marine species. Faced with these risks, managers of MPAs may nonetheless have some effective ways to forestall population collapse. The use of PVA to explore the separate and interacting effects of

disturbances on threatened species can help managers to determine guidelines of efficient conservation and to set biologically-based management criteria to at least partially mitigate these effects. This is one approach to at least temporarily stave off the most dramatic impacts of climate change while longer-term solutions are found to climate change problems. As the present work shows, effective responses to the important threats affecting many long-lived marine species will require that their life-history traits and, in particular, their low resilience to periodic disturbance, be considered in tandem with the interacting threats facing them if effective conservation plans are to be made for their preservation.

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