# Population ecology and conservation of a long-lived marine species: the red gorgonian *Paramuricea clavata*

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Provem altra vegada
provem d'aixecar el front
tornem a veure el món
amb llum de matinada.

La vida no s'acaba
el mar encara es mou
l'onada no diu prou
ni es cansa de ser blava.

Això que volem
i hi donem la cara.

Si tot ens diu que no,
provem altra vegada.

(Poema de Joan Vergés. Cantat per UC)

Als meus pares

i al Joseba

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# ☐ General introduction

"Science and management demands that complex systems be simplified,
but the art of appropriate simplification depends
on a basic understanding of the important natural history"
(Paul Dayton, 2003)

# Conservation biology facing increasing threats

Many ecosystems are being affected by the human influence and, as the human population and the technology grow the scope and nature of this human modification changes drastically (Vitousek et al 1997). The scale and intensity of human activities have led to a progressive habitat loss and degradation with subsequent loss of species and genetic variability (Fahrig 1997, Scheffer et al 2001). In front of this context, conservation biology emerged as a response of the scientific community to the wave of global environmental change that is threatening to extinguish a very large fraction of the world's biological diversity (Soulé and Kohm 1989). Hence, a key challenge for scientists, especially ecologists, is to the understanding of the consequences of human activities and to guide environmental managers towards strategies oriented to preserve critical natural ecosystems (Peterson and Estes 2001).

Since long, there is a general appreciation that human activities are causing larger alterations on the structure and the functioning of terrestrial ecosystems than in marine ones (Ehlrich 1995, Vitousek et al 1997, Fahrig 2001). However, this appreciation is rapidly changing since recent reports pointed out large-scale impacts of anthropogenic activities on marine ecosystems (Roberts and Hawkins 1999, Jackson et al 2001, Myers and Worm 2003, Pandolfi et al 2003). Although shifts in marine ecosystems are more difficult to quantify than in terrestrial ecosystems, numerous studies have confirmed the alteration of a wide range of marine ecological systems showing significant diversity losses and changes in ecosystem functioning (Botsford et al 1997, Vitousek et al 1997, Gray 1997, Roberts and Hawkins 1999, Sala 2004).

In contrast to terrestrial ecosystems, where habitat loss is the main threat driving population decline and extinction of terrestrial species, overexploitation has been recognized as the major threat to marine ecosystems causing the decline of several target species and changes in the structure of food webs (Dayton et al 1995, Jennings and Kaiser 1998, Pauly et al 1998, Jackson et al 2001). However there are other important factors that have significant effects in marine communities and species such as pollution, invasive species, diseases, alteration and loss of habitats and global climate change (Harvell et al 2002, Steneck and Carlton 2001, Hughes et al 2003, Kappel 2005, Harley et al 2006).

In both marine and terrestrial ecosystems, global warming is an important additional source of stress for species and communities that is affecting all levels of ecological organization: from population and life-history changes to shifts in the species composition and in the structure and function of ecosystems (McCarty 2001, Walther et al 2002, Harley et al 2006).

According to their life history traits, species can be placed along a fast-slow dynamics continuum. Large, slow-growing and late-maturing species with low fecundity (k-selected species) that display high vulnerability in front of human activities are at the end of the continuum. In contrast, small, fast-growing and early maturing species with high fecundity (r-selected species) are at the beginning of the continuum (Mac Arthur and Wilson 1967, Pianka 1970).

In unstable or unpredictable environments r-selection predominates, because the ability to reproduce quickly is crucial, and there is little advantage in adaptations that permit successful competition with other organisms (since the environment is likely to change again). In stable or predictable environments K-selection predominates, because the ability to compete successfully for limited resources is crucial, and populations of K-selected organisms are typically very constant and close to the maximum that the environment can bear (Pianka 1970). Therefore, as occurs on land, anthropogenic impacts are particularly severe on K-selected species with slow dynamics because of their low resilience and slow recovery from perturbations (Holling 1973). Thus, knowledge of their life history traits should be a priority for better understanding the effect of human-induced mortalities on long-lived species, and to predict population recovery/extinction risks and trajectories (Halpern 1989, Musick 1999).

Furthermore, some long-lived species can be considered as "ecosystems engineers" because they play a central role in the structure and functioning of many communities through their trophic activity, biomass and structure that may increase the biological diversity of the communities they inhabit (Jones et al 1994). The conservation of these species is essential, and their study should be considered as a priority to translate the effects of direct impacts on individuals into their ultimate ecological outcomes, linking individuals, populations and communities (Mills et al 1993).

It seems coherent to accept that these demographic characteristics evolved as mature ecosystems under low and infrequent strong environmental fluctuations, often displaying high structural complexity and low energy flow per unit of biomass (Margalef 1963). However, growing human activity, by increasing the frequency and intensity of disturbances, has revealed the high fragility of some of these "mature" ecosystems (Margalef 1997).

It is not surprising that the major efforts on conservation biology have focused on the study of demographic parameters and population dynamics of slow growing species and on the development of quantitative models that can help environmental managers to make decisions (Simberloff 1988, Beissinger and Westphal 1998). Several basic questions need to be addressed for the conservation of threatened species such as, is the population under study in decline? What are the factors that determine the viability of the population? What life stage is most critical for the viability of the population? Is legal protection of the habitat alone a sufficient measure to maintain population viability or is a more active intervention needed? Which management strategy offers the greatest chances for facilitating the survival of the population?

What may be the consequences on the population of particular human-induced environmental changes on the habitat? (Heywood and Iriondo 2003).

Population viability analysis (PVA) appears to be one of the most powerful tools in conservation biology in front of these questions. Although there is no consensus about the definition of PVA, and despite the use of the term has ranged from qualitative, verbal processes without models to mathematically sophisticated, spatially explicit, stochastic simulation models, one of the most accurate definitions narrowed is related to quantitative modeling (Boyce 1992, Reed et al 2002). In the words of Boyce (1992): "PVA entails the process of synthesizing information about a species or a population, and developing the best possible model for the species given the available information". This involves working closely with natural resource managers to develop a long-term iterative process of modeling and research that can reveal a great deal about how best to manage a species.

Population viability analyses are based in demographic models and the most accurate are matrix models (Caswell 2001). Matrix models are mostly used to calculate population growth rate ($\lambda$), the stable stage distribution, and the sensitivities and elasticities of population growth to changes in life history parameters of threatened species (Caswell 2001, Morris and Doak 2002). The increasing threats that are affecting both terrestrial and marine ecosystems highlight the importance of these models to examine the future persistence of these species as well as to evaluate the effectiveness of possible management measures (Beissinger and Westphal 1998, Reed et al 2002).

While demographic models are widely used to assess the population viability and life history patterns of many terrestrial plant and animal species (Doak et al 1994, Silvertown et al 1996, Menges 2000, Caswell 2001, Beissinger and McCullough 2002), they have been applied disproportionately to different ecosystems and taxonomic groups. In particular, they have been used less commonly in marine conservation than in other fields of population ecology (Gerber and Heppell 2004). Moreover, matrix models have been influential in assessments of the demography and population viability of some emblematic large marine mammals, sea turtles, and other marine vertebrates (Crowder et al 1994, York 1994, Holmes and York 2003), contrasting with their less common use in demographic studies of others representative organisms, such as long-lived marine invertebrates.

Several groups of marine invertebrates (sponges, bryozoans, anthozoans...) show a clonal organization which provides them with extremely high characteristic growth plasticity, and ability to recover from partial mortality (Hughes and Cancino 1985, Hughes and Jackson 1985). Together with the supplementary difficulty of conducting underwater studies on relevant temporal and spatial scales (Hughes and Connell 1999) these particular characteristics make difficult the application of classic demographic models (Hughes and Cancino 1985).

# III   The Mediterranean coralligenous community: the reference framework

The Mediterranean Sea has been identified as an important "hot spot" of biological diversity (Bianchi and Morri 2000). Most of this biodiversity occurs in coastal benthic environments, mainly in shallow rocky bottoms and Posidonia meadows (Boudouresque 2004). Among the rocky benthic assemblages, the "coralligenous community" stands out for its species richness (on the order of 1600 species have been identified) and great structural complexity (Ballesteros 2006).

The term "coralligenous" was coined by Marion in 1883 and means 'producer of coral' (it is related to the abundance of red coral *Corallium rubrum*). The coralligenous is a hard substratum of biogenic origin that is mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions. Although more extensive in the circalittoral zone, it can also develop in the infralittoral zone when light is dim enough to allow growth of the calcareous algae that produce the biogenic framework. Infralittoral coralligenous concretions always develop on almost vertical walls, in deep channels, or on overhangs, and occupy small surface areas (Ballesteros 2006).

Scientists studying the coralligenous have mainly focused their efforts on descriptive and qualitative studies (Pérès et Picard 1964, Laubier 1966, True 1970, Gili and Ros 1984) rather than on functional and dynamics aspects (Coma 1994, Garrabou 1997, Ribes 1998). The scarcity of research on the dynamics of the coralligenous may be explained by some of the main characteristics of these communities. First, it is impractical to study all species and even a pool of model species in a diverse community. In addition, most of the species with a relevant contribution to the total biomass/coverage are clonal, and the study of their dynamics involves all the methodological problems explained above. The ability of clonal species to recover from partial mortality, the negative growth due to possible losses of apical parts of the colonies, the fusion and fission of different specimens and the capacity of asexual reproduction make it difficult to know the age of clonal organisms and to obtain a significant relationship between size and age. The theoretically unlimited growth also makes it difficult to link the size with demographic characteristics such as fertility and survival.

The stability of environmental factors at the depths where these assemblages dwell, (mainly below 20 m depth), the lack of frequent strong natural disturbances, and the absence of excessive anthropogenic pressures in the past, may also contribute to explaining the scarcity of studies concerning to the conservation of the coralligenous (but see Garrabou and Harmelin 2002, Coma et al 2004). Nevertheless, the coralligenous is presently under the combined pressure of human-induced impacts such as pollution, fishing (especially trawling), diving, the expansion of invasive species and climate change (see Ballesteros 2006 for a review).

Probably one of the most worrying threats among all these disturbances is the inevitable warming of the Mediterranean Sea that is associated to global climate change (Bethoux and Gentilli 1996, J Pascual *unpublished data*). Recently, the Western Mediterranean Sea has

witnessed the repetition of mass mortality events which negatively affected several species of suspension feeders dwelling at the shallower coralligenous communities (down to 35-40 m). Although the direct cause of these episodes has not been totally elucidated, it seems to be related to summer high water column stability and high temperatures (Romano et al 2000, Coma and Ribes 2003).

The first large-scale mass mortality event occurred at the end of the summer of 1999, when about 30 species of invertebrates from 5 different phyla were severely affected over more than 500 km of coast stretching between the Ligurian sea (Italy), the Provence coast (France) and the Balearic Islands (North coast of Menorca; Spain) (Cerrano et al 1999, Perez et al 2000, Garrabou et al 2001, Coma et al *in press*). Another mass mortality event was observed in summer 2003, associated with high water temperatures resulting from the heat-wave observed in Europe (Harmelin 2004, Benssoussan et al *unpublished data*). In this event a similar set of species was affected but at larger spatial scales including, besides the areas impacted in 1999, areas of Spain, central Italy and the Corsica and Sardinia islands (Coma et al *unpublished data*, Garrabou et al *unpublished data*).

## Gorgonians as a case study

In this thesis, the Mediterranean red gorgonian *Paramuricea clavata* (Risso, 1826) was selected as a representative species to assess the viability of coralligenous communities under the current scenario of increasing disturbances (Fig. 1). In other words, the idea was to test in this "easy-to-study-species" the feasibility of different tools common in terrestrial conservation biology that in a next future might be applied to other marine, "more-difficult-to-study" long-lived species.

Among the numerous groups of clonal organisms that make an important contribution to the coralligenous community (i.e. calcareous algae, sponges, cnidarians, bryozoans and tunicates), gorgonians display several advantages for demographic studies. Their erect tree-like growth-form allows assimilating each colony to separate individuals; this feature, added to their large size, makes it easy to locate, map and measure individuals underwater. Despite their clonal nature, gorgonians display a relatively clear morphological pattern and continuous growth (Coma et al 1998a). Moreover, populations of some Mediterranean gorgonians show strongly patchy distributions with high density of colonies within the patches (Gili et al 1989, Gili and Ballesteros 1991) that resemble "miniature" forests. In this sense, most of the techniques developed by tree ecologists can be adapted to their study.

Considering *P. clavata* as indicator of the fate of the whole coralligenous community may seem abusive, but several arguments make this assumption reasonable.

First, given its contribution to the community in terms of both structure and biomass (Gili and Coma 1998), the survival of the whole community may be closely linked to that of this habitat-for-

ming species. As noted by Soulé et al (2003), the absence or scarcity of highly interactive species can leave a functional void that can cause the degradation or simplification of the ecosystems.

Second, the slow annual growth rate (about 0.8 cm in height/yr) obtained for *P. clavata* in the Medes Islands (Coma et al 1998a, R. Coma *unpublished data*) is in good agreement with the slow growth dynamics displayed by other species of the coralligenous (Turon and Becerro 1992, Garrabou 1999, Garrabou and Zabala 2001, Garrabou and Harmelin 2002). This supports the hypothesis that the some of main representative species of the coralligenous appear to display similar dynamics, which in fact can be considered as a rough estimate of the dynamics of the whole community.

Finally, the red gorgonian *P. clavata* can be considered a good sensitive indicator to the magnitude and intensity of the disturbances that are affecting to the whole community. This species has displayed high vulnerability facing to increases of human induced impacts (Harmelin and Marinopoulus 1994, Mistri and Cecherelli 1996, Bavestrello et al 1997, Coma et al 2004, Guliani et al 2005) and was one the strongly affected species during the two mass mortality events mentioned above (Cerrano et al 1999, Perez et al 2000).

Furthermore, two other reasons influenced this choice: the previous knowledge of several key aspects of its natural history (Coma et al 1994, 1995a,b, 1998a,b, Ribes et al 1999) and its extremely patchy distribution that seems restricted to small relict areas and is suggestive of some degree of vulnerability.
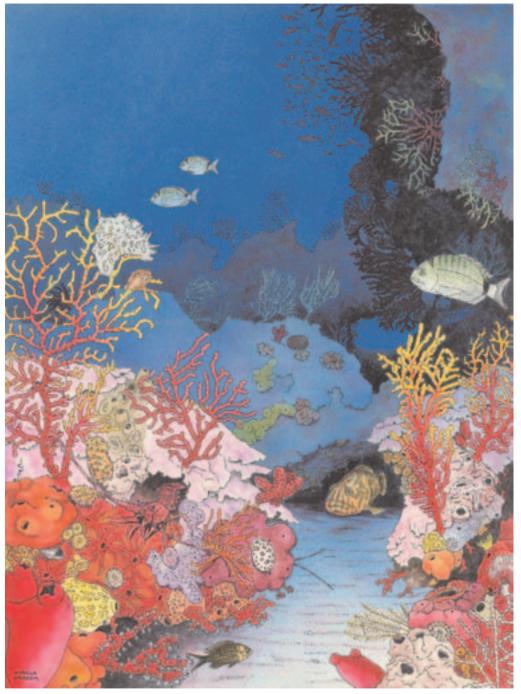
Figure 1    Drawing of a coralligenous assemblage in the Medes Islands (NE Spain). (Drawing by M. Zabala and J. Corbera in *Els Sistemes Naturals* de les Illes Medes, Ros et al 1984)

# Background on *Paramuricea clavata* natural history

This box is an attempt to summarize the current knowledge of the red gorgonian *Paramuricea clavata*. Almost certainly, it is not a complete revision of the existing literature; we have tried to show the most available information. The aspects remarked here are those dealing with the biology of the species especially concerning to conservation of the species.

The gorgonian *P. clavata* (Risso 1826) (Cnidaria, Anthozoa, Octocorallia) forms erect arborescent colonies up to about 130 cm in height and their assemblages constitute one of the most attractive landscapes in the Mediterranean benthos (Harmelin and Marinopoulus 1994, Ballesteros et al 2006).

## Distribution

The distribution of the red gorgonian *P. clavata* in the NW Mediterranean Sea shows a patchy distribution where populations are often isolated from one another and separated by large distances. The map (Fig. 2a) represents the distribution of shallow populations (<50 m) at a regional scale, and although probably other populations exist, the number of populations can be considered relatively low. The spatial scale of these populations (regardless of the fact that defining a population can be tricky) is smaller than 500 m, and the distances between them are higher than 3 km (see Table 1).

At a small scale, red gorgonian populations showed a patchy and asymmetric distribution due to their environmental requirements (Fig. 2b). Distribution ranges and abundance of gorgonians depend upon environmental factors such as the type of substrate, light, temperature and exposure to flow (Weinberg 1975, 1980). *P. clavata* populations can be found at a narrow band of light conditions (irradiance values ranging between 0.12 and 27.6%), inhabiting mostly vertical walls in the circalittoral zone (15-80 m) (Fig. 2c). Populations of *P. clavata* are abundant in steep rocky walls, exposed to strong currents (like other suspension feeders), but they also grow in horizontal to subhorizontal surfaces with dim light conditions and sediment-free bottoms (Weinberg 1975, 1980, Ballesteros 2006).

## Reproduction

The persistence of a population is based on sexual reproduction and asexual regeneration because asexual reproduction by partition has been described as negligible. *P. clavata* is a dioecious species. The sex ratio has been described as 1:1 but it seems to be variable. Sperm development is much faster (between 6 and 7 months) than oocyte development. Oogenesis lasts between 13 and 18 months, beginning between February and July and culminating in the release of the mature eggs in June. Spawning occurs with increasing seawater temperature and it is correlated with the lunar cycle. Spawned eggs are attached to the outer surfaces of the female colonies through the action of a mucus coating (Coma et al 1995a).

Sexual maturity is attained at a size about 20 cm (from 11 to 30 cm). The minimum age at first reproduction in *P. clavata* has been estimated to be around 7-13 yr on average (Coma et al 1995a). Reproductive effort is highest for polyps on first-order branches, which contribute to about 85% of the production of gametes of the colony. Reproductive output increases exponentially with colony size due to the increase in the percentage of fertile colonies and polyps and to the increase in the number of gonads per polyp (Coma et al 1995b).

## Feeding

*P. clavata* is a passive suspension feeder. The species has a broad and heterogenous diet that ranges from nano-eukaryotes (3.8 $\mu$m) to copepods (700 $\mu$m), and includes prey as diverse as ciliates, dinoflagellates, diatoms, zooplankton (nauplii, copepod eggs, other invertebrate eggs, calanoid copepods) and suspended detrital organic matter (Coma et al 1994, Ribes et al 1999). Peak prey capture levels are recorded in spring and at the end of autumn when the proportion of colonies with contracted polyps is very high (Coma et al 1994). The ingestion of carbon of detrital origin also shows a marked seasonal pattern in which winter and spring were are the seasons with the highest ingestion rates (Ribes et al 1999).

Figure 2  a) Distribution of most of the well-known *Paramuricea clavata* populations along Western Mediterranean coasts (note that the goal of this figure is to characterize, through a rough estimation, the patchy distribution of this species at a large scale). b) Distribution of red gorgonians at Medes Islands. c) Schematic view of the vertical zonation between 0 and 35 m in a submarine wall at the Medes Islands with *P. clavata* colonies restricted approximately to the 15-30 m range. (From Garrabou 1997)

| | Porquerolles | Embiez | Marseille 1 | Marseille 2 | Banyuls | Cap Creus N | Cap Creus S | Montgri | Medes | Begur | Llafranc | Palamós | Columbretes | Mallorca | Cabrera | Eivissa | Cabo Palos |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Port Cros | 48 | 50 | 84 | 86 | 282 | 281 | 284 | 280 | 280 | 283 | 289 | 292 | 638 | 514 | 540 | 662 | 807 |
| Porquerolles | | 61 | 89 | 92 | 255 | 252 | 253 | 249 | 249 | 250 | 255 | 258 | 599 | 466 | 494 | 617 | 762 |
| Embiez | | | 34 | 36 | 238 | 237 | 241 | 239 | 239 | 243 | 249 | 252 | 601 | 497 | 520 | 636 | 780 |
| Marseille 1 | | | | 3 | 213 | 213 | 216 | 217 | 217 | 222 | 230 | 232 | 581 | 493 | 513 | 625 | 768 |
| Marseille 2 | | | | | 212 | 213 | 217 | 216 | 216 | 222 | 229 | 232 | 581 | 494 | 514 | 626 | 768 |
| Banyuls | | | | | | 10 | 17 | 26 | 29 | 39 | 46 | 48 | 373 | 357 | 359 | 445 | 581 |
| Cap Creus N | | | | | | | 8 | 16 | 19 | 29 | 37 | 39 | 370 | 348 | 351 | 439 | 575 |
| Cap Creus S | | | | | | | | 10 | 13 | 22 | 29 | 31 | 365 | 340 | 343 | 431 | 568 |
| Montgri | | | | | | | | | 3 | 13 | 21 | 24 | 365 | 333 | 337 | 427 | 565 |
| Medes | | | | | | | | | | 10 | 18 | 22 | 364 | 330 | 334 | 425 | 563 |
| Begur | | | | | | | | | | | 9 | 11 | 358 | 320 | 325 | 417 | 555 |
| Llafranc | | | | | | | | | | | | 3 | 352 | 311 | 316 | 408 | 547 |
| Palamós | | | | | | | | | | | | | 349 | 309 | 313 | 405 | 544 |
| Columbretes | | | | | | | | | | | | | | 289 | 244 | 178 | 251 |
| Mallorca | | | | | | | | | | | | | | | 48 | 184 | 320 |
| Cabrera | | | | | | | | | | | | | | | | 139 | 278 |
| Eivissa | | | | | | | | | | | | | | | | | 144 |
| Cabo de Palos | | | | | | | | | | | | | | | | | |

**Table 1** Distances (Km) between some of the known shallow (<45 m) *Paramuricea clavata* populations in the North-Western Mediterranean Sea between Hyères Archipielago (France) and Cabo de Palos (Spain). We are considering as a unique "population" either the continuous populations or those separated approximately less than 1 km. The selected populations have been: Porquerolles (Le grand Serranier), Port-Cros (Gabinière), Île des Embiez , Marseille 1 (Île de Riou), Marseille 2 (Île de Plane), Banyuls (Rederis), Cap de Creus N (Pta de la figuera), Cap de Creus S (Pta falconera), Montgrí (Puig de la Sardina), Medes (Pedra de Deu), Begur (Furió Fitó), Llafranc (Ullastres), Columbretes (El cementeri), Mallorca (Formentor), Cabrera (Imperial), Eivissa (Illes Bledes), Cabo de Palos (Hormigón).

## Metabolic activity

*P. clavata* exhibits a marked seasonality in all activities (Coma et al 1998a, Coma et al 2000). Respiration rate of this species varies two- to three-fold across the annual cycle, exhibiting a marked seasonal pattern but showing no daily cycle or significant day-to-day variability within months (Coma et al 2002). The low rate of new tissue synthesis during summer, together with the contraction of polyps and a low $Q_{10}$ explains the low respiration rates of *P. clavata* observed during the period of highest temperature. These low respiration rates and the low ingestion rates observed during the summer period support the hypothesis that energy limitations may underlie summer dormancy in the activity of the species (Coma et al 2000, Coma and Ribes 2003).

## Growth

Red gorgonian colonies display a slow annual growth in height (ranged between 1.8-3 cm/yr) with a turnover time of around 8-9 years (Mistri and Cecherelli 1994, Coma et al 1998a). A long-term monitoring of the growth rates of this species showed that the mean annual growth rate is about 0.8 cm/year (R. Coma *unpublished data*). Primary branches account for 90% of the production, although the growth rates are highly variable. The gross growth rate of primary branches in colonies <20 cm (0.8 cm/yr) is higher than that of colonies >20 cm (0.5 cm/yr). Net growth of primary branches (0.4 cm/yr) is approximately 60% of positive growth. Seasonality of growth in *P. clavata*, showing a high growth period in spring, is also consistent with the seasonal fluctuation in food sources (Coma et al 1998a).

## Mortality

Mortality of red gorgonian colonies is usually very low when populations are not subjected to human-induced distur-bances. The causes of red gorgonian mortality, both total and partial, are not easily distinguished. Partial mortality occurs after the exposure of colonies to different kinds of physical injuries (e.g. storms, predation) or after physiolo-gical decay. Small naked skeletons are rarely observed because they are either recovered by the coenenchyme or quickly colonized by epibionts. Total mortality of a colony appeared to be either to detachment (by failure of the subs-tratum or holdfast) or injury. The main human-induced sources of detachment include anchors, fishing apparatus, pre-dation and divers (Harmelin and Marinopoulus 1994, Bavestrello et al 1997, Coma et al 2004).

Diving effects on red gorgonian populations have been estimated at the Medes Islands by comparing protected and unprotected areas. High levels of diving affect total mortality but not the degree of injury of the colonies. Natural mor-tality rate in sites with low diving activity has been estimated about 2.7%/yr whereas high diving activity can cause an increase of the natural mortality up to 7.4%/yr (Coma et al 2004).

At regional scale, the most important impacts for this species are the mass mortality events recorded during the last years in the NW Mediterranean Sea (Fig. 3). These events affected gorgonians from 60 to 100% of the population in distinct localities over more than 500 km from Italian coast to Balearic Islands (Cerrano et al 2000, Perez et al 2000, Coma et al *in press*). The monitoring of affected populations over time showed that the delayed impacts of these events are much higher than the immediate ones (see Chapter IV).
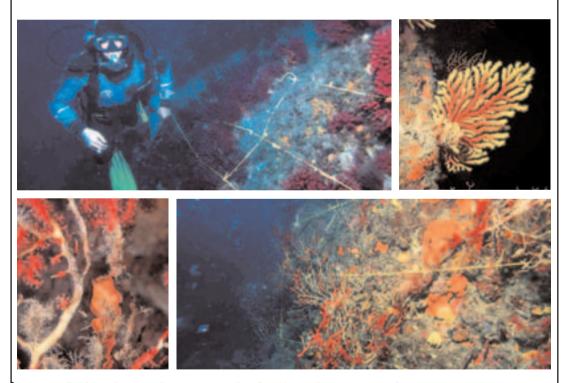


**Figure 3** Top from left to right. Permanent plot at Port-Cros National Park (June 1999). *Paramuricea clavata* "healthy" colony. Bottom from left to right. Partial mortality of a *Paramuricea clavata* colony. Permanent plot affected by the 1999 morta-lity event at Port-Cros National Park (November 1999)

# ▌▌▌ Objectives and structure of the thesis ▌

The objective of this thesis was to study the demography of the red gorgonian *Paramuricea clavata* in order to assess the resilience of their populations in front of the increase of human and environmental threats that are challenging their persistence. To achieve this objective, different studies were performed using descriptive, experimental and modeling approaches.

**Chapter I** focused on the current status of the gorgonian populations on the Spanish Mediterranean coast from Cap de Creus to Cabo de Palos, with special attention on the two most common gorgonian species *Paramuricea clavata* and *Eunicella singularis*. The study was prompted by the mass mortality event detected in the 1999 summer along the Italian and French coasts and the aims were twofold: to assess whether the event affected the study area and to draw a baseline of the distribution and health of the Spanish Mediterranean gorgonian populations facing the eventuality of future catastrophic events. This study also allowed us to address other questions. Having in mind the absence of demographic studies on Mediterranean gorgonians, in particular studies undertaken at the spatial scales that are relevant for conservation purposes (regional; $10^3$ Km), the quantitative data collected during this study allowed us to determine the existence of regional differences in the distribution and demography of these two representative Mediterranean gorgonian species. In parallel, the comparison of the demographic structure of these two species as well as their response to disturbances, allowed us to point out which species may be affected by disturbances and therefore it deserves a major conservation effort.

**Chapter II** focused on the study of the early life history of red gorgonians. Early life history encompasses some of the most critical steps for the survival of species, and this is especially true for sedentary (benthic) marine organisms to which the ability to disperse, to colonize new habitats and to maintain local populations (into a metapopulation structure) largely depends on the success of larval stages. Despite our knowledge about sexual reproduction of *Paramuricea clavata* (Coma et al 1995a, Coma et al 1995b), an important gap remained on the understanding of the early life history of this species, namely for the stages following the release of eggs.

The importance of this gap emerged when the high investment in reproductive output was compared to the low recruitment rates observed in the field. The study of the early life history of red gorgonians has been approached from different ways both qualitative and quantitative: first, by describing for the first time the early life-history stages from eggs to polyps; and second, by quantifying the survivorship of these stages and showing the implications for the population dynamics of this species. Moreover, the results obtained in this chapter were essential for building the size-structured matrix model developed in next chapter (**Chapter III**) to study the future viability of this species.

In **Chapter III**, the demographic attributes of two red gorgonian populations were compared by means of size-structured matrix models (Caswell 2001). Although the two populations were located at two marine protected areas of the North-western Mediterranean (Cap de Creus,

and Medes Islands) both were subject to considerable levels of diving activity (Coma et al 2004, Zabala et al 2003).

Both deterministic and stochastic size-based matrix models were developed to address three goals. First, to estimate the basic life history traits of this species and to use the resulting models to evaluate the sensitivity of population growth to different vital rates. Second, to ask how population structure will develop through time and to analyze the viability of the red gorgonian populations we studied. Third, to compare the life history patterns of red gorgonians to those of other species both sessile invertebrates and terrestrial plants in order to highlight both the significance of their reproductive strategy and the resemblance with species displaying similar life-history traits.

As commented above, some coralligenous communities from the NW Mediterranean were affected by recent mass mortality events apparently linked to global warming. Among them, there were "gorgonian forests" or communities dominated by long-lived gorgonian species. **Chapter IV** and **Chapter V** have been devoted to a quantitative assessment of the effects of the 1999 mass mortality event on the red gorgonian populations at the Port-Cros National Park (France). In order to understand their resilience in front of these disturbances they were assessed before and just after the event, and they were also monitored over the following four years (**Chapter IV**). To achieve a complete knowledge of the consequences of these disturbances, the effects on the reproductive output of this species were also studied (**Chapter V**).

The last part of this thesis was devoted to applied aspects of the management and conservation of this species. Two different tools, the strictly theoretical PVA (Population Viability Analysis) models (**Chapter VI**) and an experimental approach to restoration techniques (**Chapter VII**), were used to understand and to enhance the long-term stability of red gorgonian populations, respectively.

The increasing concern about the vulnerability of red gorgonian populations in the face of several causes of human-induced mortality emphasizes the importance of obtaining accurate demographic estimates to examine the resilience of this species facing to rising disturbances. Because of his extremely long life span, only long-term monitoring can provide the necessary data. Because such a monitoring could take too long, models can be helpful to forecast the future persistence of these species as well as to evaluate the effectiveness of possible management measures.

In **Chapter VI**, the size-structured matrix models build in **Chapter III** were used to investigate the long-term consequences of the two main disturbances that are currently affecting *P. clavata* populations in the NW Mediterranean Sea: global warming and diving. Simulations were specifically designed to provide criteria to the managers of the two Marine Protected areas whose populations were analyzed in **Chapter III**. Departing from the size-structured matrices obtained in this chapter, we first explored the projection of the *P. clavata*'s population growth rate under different increases of survival rates (here we assume that these increases may be the result of reductions on the number of divers in the area, a feasible measure to be promoted by the managers of these MPAs). In a second simulation, we used the size-structured matrices obtained in

**Chapter IV** from populations affected by 1999 mass mortality event, to explore the expected response of *P. clavata* populations under different increases of the frequency of mass mortality events.
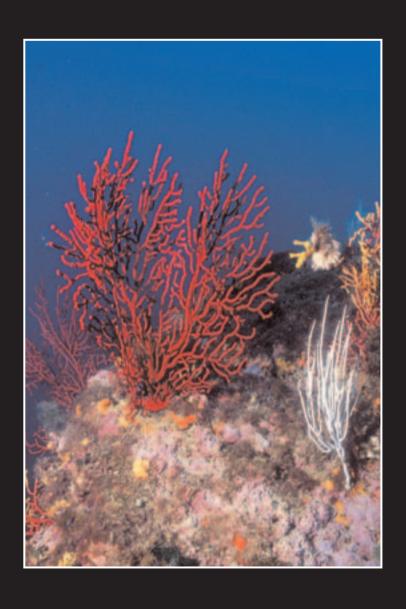
Finally, if a corollary summarizes all of the precedent arguments, it is the need for active restoration of the damaged populations. Conservation biology could be a disappointing discipline when reduced to mere techniques for prediction of repeatedly negative impacts or extremely short extinction times. When possible, the knowledge resulting from our studies must be translated to applied measures to avoid the negative effects of these disturbances, or to restore the disturbed populations.

In **Chapter VII**, the transplantation of gorgonians is proposed as a useful management technique to improve the conservation of this species at least for the managers of small areas with both valuable marine biodiversity and intense diving activity. The main goals of this study were first to examine transplanting techniques that require low labor effort and low economic costs; second, to estimate the survival of transplanted colonies regarding to the selected technique and to abiotic and biotic factors such as the irradiance values and the competition with filamentous algae; and third, to predict the survival of the transplanted colonies using a matrix model, and the intensity and magnitude of the transplanting effort necessary to obtain values of annual population growth rates close to 1, which would ensure the long-term persistence of these populations.

Despite the study has been conceived as a whole, each chapter has been or will be submitted as separated papers for publications in scientific journals (**Chapter III** and **IV** have been already published*), and it thus contains sufficient information to be considered independently. This is the reason why the main points have to be repeated along the introduction and discussion of all chapters, somewhat than can produce an annoying sense of redundancy. We sincerely apologize for all these inconveniences.

*\***Chapter III**. Linares C, Doak D, Coma R, Diaz D, Zabala M (2006). Life History and Viability of a Long-Lived Marine Invertebrate: the Octocoral *Paramuricea clavata*. Ecology, *in press*.

*\***Chapter IV**. Linares C, Coma R, Diaz D, Zabala M, Hereu B, Dantart L (2005). Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean. Marine Ecology Progress Series 305: 127-137.

Size distribution, density and disturbance
in two Mediterranean gorgonians:
*Paramuricea clavata* and *Eunicella singularis*

## Abstract

As ecosystems engineers, gorgonian species play an important role in the structural complexity, and hence, their conservation may be essential to maintain the biodiversity of the communities where they inhabit. Using the ability of classic plant ecology approaches by means of examining density, size distribution and the existence of density-dependence, the aim of this study was to determine differences in the distribution and demography of two representative Mediterranean gorgonian species, the red gorgonian *Paramuricea clavata* and the white gorgonian *Eunicella singularis* along a regional spatial scale, as well as to examine their response to disturbances. The distribution patters suggested that while *E. singularis* is more torelant to a wide range of environmental conditions, *P. clavata* seems to be more vulnerable to the variability of abiotic factors. *E. singularis* was more or less regularly distributed along the examined spatial scale, whereas *P. clavata* showed a clearly contagious, asymmetric distribution, being their populations much more common in the Northern than in the Southern areas. The upper limit of *P. clavata* decreased along the examined North-South gradient. The size distributions obtained for both species suggest that they have differing recruitment and survival dynamics, showing *E. singularis* a high dynamic pattern that clearly contrasts with *P. clavata* populations which show a clear scarcity of the initial states of population dynamics. Furthermore, regarding to the relation between density and biomass, unlike *E. singuralis* populations, red gorgonian populations displayed a strong negative correlation with a slope close to -3/2 demonstrating different carrying capacity and the existence of a self-thinning mechanism in this species. The robustness of this result and the trajectories of disturbed populations over this line revealed this approach as a useful method to identify the effects of biological or physical disturbance for vulnerable species. This study shows different vulnerability to disturbances exhibited by both species owing to their population dynamics and life-history traits, pointing out that a major effort on the conservation of red gorgonian populations is necessary.

Keywords: octocoral, spatial distribution, partial mortality, self-thinning, size distribution, disturbances

# ▎▎▎ Introduction

The increase of anthropogenic disturbances is leading to a progressive alteration of a wide range of marine ecosystems causing significant diversity losses and changes in ecosystem functioning (Botsford et al 1997, Vitousek et al 1997, Gray 1997, Roberts and Hawkins 1999). Long-lived species displaying slow-growing, late-maturing, low fecundity are one of the most affected species facing strong disturbances (Musick 1999) and moreover, their presence is often essential for maintaining the organization and diversity of communities where they dwell (Mills et al 1993, Jones et al 1994).

In marine habitats, gorgonians are generally long-lived structural species that have evolved in environments without intense and frequent disturbances and their slow population dynamics provide them of a high fragility facing to the rising anthropogenic menaces (Lasker and Coffroth 1999, Garrabou and Harmelin 2002, Coma et al 2004, Kim and Harvell 2004). Thus, a complete knowledge of the functioning of their populations may be the first step to develop reliable conservation planes. Obtaining demographic data on large temporal and spatial scales could allow us establish a baseline to determine the magnitude and intensity of disturbances as well as to anticipate the future trajectories of the disturbed populations. Unfortunately, data about the life-history traits of most marine long-lived species are difficult to acquire, especially on those temporal scales that would be appropriate to their long life span (Hughes and Connell 1999).

Population ecology provides useful tools for understanding the life-history processes, as has been largely demonstrated in terrestrial ecosystems (Begon et al 1996, Vandermeer and Goldberg 2003). The sessile nature and structural role of gorgonian species offer ecological similarities between gorgonian communities and forests; hence, the application of several theoretical and methodological advancements developed by Plant Ecology studies could be really useful to the study of disturbances that are affecting these marine species.

Plant ecologists have learned to overcome the constraint of waiting long-time scales to collect valuable dynamic data by using static size distributions to provide useful insights into many important macro-ecological phenomena (Niklas et al 2003). Although they cannot be used to predict accurately future growth or health (Condit et al 1998), size distributions coupled with density of plants have been used to explore the responses of specific demographic dynamics to the occurrence of past disturbances (Niklas et al 2003). Furthermore, by assuming the adequacy of the substitution of space for time (Pickett 1989), they allow the reconstruction of expected dynamics. The main demographic parameters can be reconstructed by examining the size structure of a large array of populations scattered along a large spatial scale, which may represent different stages of the temporal sequence of a single population.

Another approach extensively used in plant ecology has been the role of density-dependence on population dynamics through the negative linear relationship found between size/biomass and density. Since long, ecologists have recognized the effects of competition, both intra and inter-species, deeply in the alteration of shape of populations in saturated landscapes approa-

ching the carrying capacity of the ecosystem (Shinozaki and Kira 1956). When populations became sufficiently dense, competition emerges in the form of negative denso-dependent effects, inevitably some individuals come to "dominate" (grow larger) while others become "suppressed", when the suppressed individuals die, the population has been thinned (Yoda et al 1963, Silvertown and Charlesworth 2001).

The severe affectation of Mediterranean gorgonian populations, among other suspension feeders, by two mass mortality events during the summer 1999 and 2003 (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Linares et al 2005, Coma et al in press) has evidenced the urgent necessity to implement methodologies to detect easily the magnitude and severity of the disturbances. The magnitude of these events is reflected in the occurrence of these episodes and their relation to thermal anomalies pointing out that the frequency of these events may be increasing as a result of global climate change and therefore, a repetition of mass mortality events would be expected. The exploration of self-thinning mechanisms in gorgonian populations as well as their size distribution curves can allow us to obtain useful tools to reveal consequence of small changes on the environment in life-history processes and to predict population responses to environmental changes in the case of long-term monitoring can not be developed.

An extensive survey was launched in order to evaluate the health of the shallowest gorgonian populations along the Mediterranean Spanish coast after the 1999 mass mortality event as well as to collect qualitative and quantitative demographic data about Mediterranean gorgonian populations along a relevant spatial scale.

The goals of this study was first, to obtain reference data of density, size and injuries about the shallowest populations (more vulnerable to suffer mortalities related to thermal anomalies) of two of the more abundant gorgonian species in the NW Mediterranean, red gorgonian *Paramuricea clavata* (Risso, 1826) and white gorgonian *Eunicella singularis* (Esper, 1791) along a large spatial scale. Secondly, to assess the characterization of gorgonian populations to explain the current distribution patterns, especially the depth distribution. Finally, to explore the ability of classic plant ecology approaches, examining size distribution and self-thinning mechanisms, to obtain some insights of the occurrence of recent or past disturbances in the populations as well as to predict future population trajectories.

# ▌▌▌ Material and methods

## ▌ Distribution surveys

The presence of both species of gorgonian populations was determined in a total of 120 locations distributed along the Spanish coast (more than 600 km) from Cabo de Gata (36° 51' N, 2° 6' O) to Port-Bou at the French border (42° 25' N, 3° 10' E) between 2002 and 2003. The depth distribution was studied by noting the presence of gorgonians at 5 meters intervals between 5 and 45 meters (in general the deepest limit corresponded to the end of the rocky walls and/or a change of substrate, and thus coincided with the lower limit of populations).

In order to provide an estimation of abundance of populations, a minimum of five 50 x 50 cm haphazard quadrats were randomly sampled in each range depth where gorgonians were present. The abundance was noted as one of five categories that we selected: 0,1 (>0-1 col/m$^2$), 2, 3 (>5-10 col/m$^2$) and 4 (>10 col/m$^2$). To explore the existence of a latitudinal pattern on the upper limit distribution we only used as representative populations those with a density category equal or major than 2 (>1-5 col/m$^2$).

## Quantitative surveys

After the extensive survey, nineteen populations of *Paramuricea clavata* and twenty-one populations of the white gorgonian *Eunicella singularis* were selected to carry out a quantitative demographic study. The development of populations with an abundance approximately larger than category 1 (>0-1 col/m$^2$) within a depth range of 15 to 35 meters and logistic constraints were the reasons to select these populations.

The standard error (SE)-sample size function was used to determine the minimum sample size needed to examine the density and extent of injury of the colonies at each site. Thus, preliminary sampling was conducted at one of the sites by examining 17 square meters using 50 x 50 cm quadrats randomly placed on the substrate between 17 and 22 m depth. A plot of repeated measures of SE for various samples sizes was used to examine the degree of variation in sample estimates of *P. clavata*. Minimum sample size for *E. singularis* was estimated in a previous study at a sample size of 1.75 m$^2$ and 50 colonies when the variance was stabilized at about 5-10% of the mean (Coma et al *in press*).

Density of colonies was estimated using SCUBA diving by means of examining all colonies within 50 x 50 cm quadrats or in a belt transect randomly placed. The use of one or another method was determined by the extreme variability on densities (mainly in *E. singularis*), being the goal to measure at least the minimum sample size. For each colony, we measured maximum height and the proportion of injured surface (i.e. denuded axis or overgrowth by other organisms, as in Nalgelkerken et al 1997, Harmelin et al 1999). For the red gorgonian, both descriptors were used to estimate the live biomass of each colony following a previously adjusted function relating maximum height and biomass (Coma et al 1998) and after correction for the proportion of injured surface (Linares et al 2005, Chapter IV).

## Size distribution and self–thinning analysis

The size distribution curve was analyzed in terms of descriptive statistics such as skewness and kurtosis. Skewness ($g_1$) is a measure of the symmetry of a distribution about its mean. If skewness is significantly nonzero, the distribution is asymmetric. The positive values of skewness

indicate size-distributions with a prevalence of smaller size classes and relatively fewer colonies in the larger colonies. A skewness coefficient is considered significant if the absolute value of skewness/SES (standard error of skewness) is greater than 2. Kurtosis ($g_2$) is a measure of the peakedness of a distribution near its central model. A value of kurtosis significantly greater than 0 indicates that the variable has longer tails than those for a normal distribution; less than 0 indicates that the distribution is flatter than a normal distribution. A kurtosis coefficient is considered significant if the absolute value of kurtosis/SEK (standard error of kurtosis) is greater than 2 (Sokal and Rohlf 1995).

The -1/2 or the -3/2 values of the slope of the self-thinning line (Yoda et al 1963, White 1981), have showed such a wide applicability that they may be used in the reverse sense (i.e., that some degree of proximity to the carrying capacity, saturation, due to the occurrence of self-thinning may be presumed for these populations). In contrast, those populations whose density-biomass regression represent sparse clouds of scattered points, far below the expected line, must be distant from reaching the ecosystem carrying capacity, probably because they are too young, or because they have been recently disturbed (note that both reasons may be entwined).

To find some evidence of self-thinning, we plotted the log mean biomass (in the case of *Eunicella* we used the log mean height) versus the log of density. These plots also allow exploring the existence of past or current disturbances. In non-disturbed populations subjected to shelf-thinning by intraspecific competition, an ideal trajectory may be traced from the foundation to the mature state: starting in the lower right corner of the plot with a large number of colonies of small size, first moving right-up (growing without loss of density) to reach the saturation point, next moving to the upper-left corner along the expected line (slope=-3/2) under shelf-thinning process by means of colonies growing but density declining (Adler 1996). But if these populations are affected by some disturbance, we expect both their position to be displaced far below the self-thinning line and their trajectories to follow lines with smoother (or even positive) slopes because they loss both density and biomass (Fig. 1).

In order to test the validity of these assumptions, we added for *P. clavata* analysis two localities which were repeatedly sampled before, just after and 4 years after they were affected by the 1999 mass mortality event at Port-Cros National Park (France) (Linares et al 2005, Chapter IV).

# ▌▌▌ Results

## ▌ Latitudinal distribution

Figure 2 shows sampling points along the studied area (approximately 600 Km), and all points where *Paramuricea clavata* and *Eunicella singularis* were present. Among 120 explored locations, we found *E. singularis* populations in 67 locations and *P. clavata* populations in 23 locations, moreover both species were found together in 18 locations
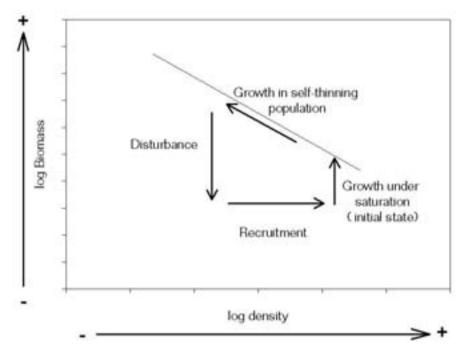
**Figure 1**    Pattern of growth and mortality under natural conditions and the expected effects of disturbance in a self-thinned population. Log of biomass refers to the logarithm of the biomass of the total population.

Differences in the pattern of distribution of both species along the latitudinal gradient can be observed in the Figure 2. *E. singularis* was more or less regularly distributed along the examined spatial scale, whereas *P. clavata* showed a clearly contagious, asymmetric distribution, being their populations much more common in the Northern than in the Southern areas.

### Upper depth distribution limit

The upper limit of *P. clavata* varied substantially along the examined North-South gradient (Fig. 3a). Shallowest populations were found in the Northern part of the Iberian Mediterranean coast (10-15 m), including a location where red gorgonian colonies were found at only 5 meters depth. In the southern part, the upper limit of distribution was situated deeper, between 25-30 m.

The upper limit of distribution of *E. singularis* (Fig. 3b) also ranged between 10 and 30 meters, but in contrast to *P. clavata*, it did not show a clear pattern along this latitudinal scale.
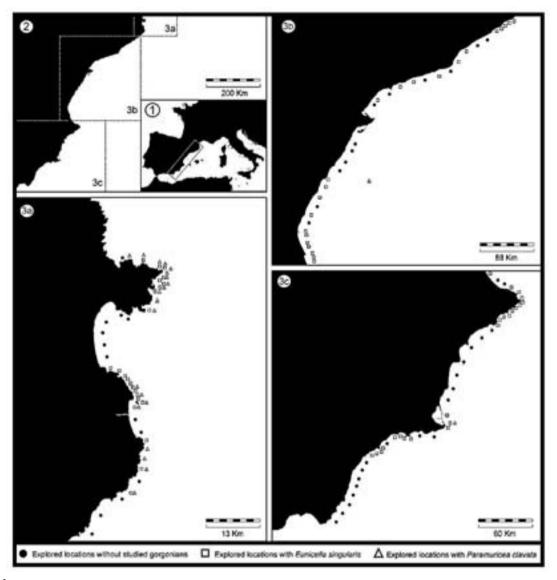
**Figure 2**  Map of the study area. Explored locations without gorgonians (black circles), *Paramuricea clavata* popula-
tions (white triangles), *Eunicella singularis* populations (white squares).

## Minimum sample size

The plot of repeated measures of SE with increasing sample size was used to examine the
degree of variation in sample estimate for the assessment of both density and extent of injury
of the colonies (Fig. 4). The SE as a proportion of the mean of density decreased quickly with

increasing sample size and the curve flattens out at a sample size of 1.5 m$^2$ where the variance becomes about 10% of the mean (Fig. 4a). The SE as a proportion of the mean of the extent of injury of the colonies also decreased quickly with increasing sample size, remaining at a variance about 15-20% of the mean from a sample size of 50-60 colonies (Fig. 4b).
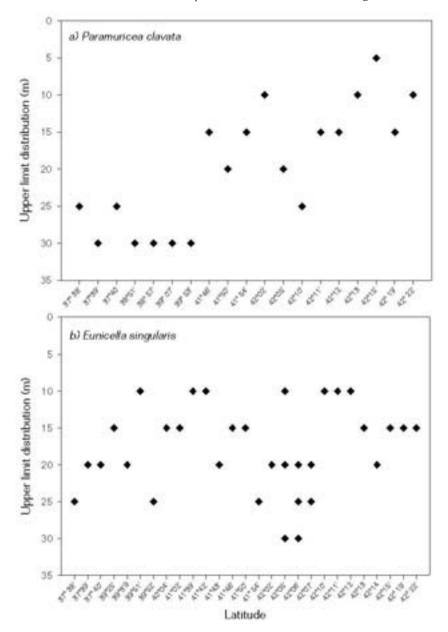


Figure 3    Variation of upper depth limit distribution along the explored latitudinal range. (a) *Paramuricea clavata* populations (b) *Eunicella singularis* populations.

## Partial and total mortality

The mean percentage of injuries of the *P. clavata* colonies tissue was variable among populations (ranging between values of 0.6 to 19%; one-way ANOVA $F_{18, 1938}$=7.20, p<0.001), but in average red gorgonian populations showed a mean % of injuries of 10.1 ± 6.2 (mean ± SD) (Table 1a). The mean percentage of injury of the colonies of *E. singularis* populations was 4.7 ± 5.4% (mean ± SD), ranging among populations from 0 to 24% (one-way ANOVA $F_{20, 2164}$=8.75, p<0.001; Table 1b). The mean % of injuries of both species did not show a significant correlation with the depth (*E. singularis*, $r^2$=0.136, p=0.099; *P. clavata*, $r^2$=0.1605, p=0.089) within the examined 15 to 35 m depth range, nor with the latitude (*E. singularis*, $r^2$=0.062, p=0.274; *P. clavata*, $r^2$=0.104, p=0.177) over the examined latitudinal range.

In average, *P. clavata* populations exhibited a lower proportion of non injured colonies (about 78% of colonies) than for *E. singularis* (about 89% of colonies). Moreover, red gorgonian populations exhibited higher proportions of affected and dead colonies (19% and 3% for *P. clavata* in contrast to 9% and 1% for *E. singularis* respectively, Table 1a,b).

## Density

Red gorgonian populations showed values of density between 11 and 53 colonies/m$^2$ with a mean density of 33.3 ± 13.91 (mean ± SD) (Table 2). The density for *Eunicella singularis* ranged from 0.3 to 56.4 colonies/m$^2$ with a mean density of 19.87 ± 17.63 (mean ± SD) (Table 3). Within the examined depth range (15-35 m), no significant correlation was found between density and depth for any of both species (*E. singularis*, $r^2$=0.173, p=0.060; and *P. clavata*, $r^2$=0.056, p=0.328). Similarly, density was not correlated with latitude for any of the two species (*E. singularis*, $r^2$=0.021, p=0.525; *P. clavata*, $r^2$=0.002, p=0.95).

## Mean colony height

The mean colony height of *P. clavata* (24.2 ± 7.7 cm) was higher than *E. singularis*, (15.1 ± 6.1 cm, Table 2 and 3). These differences were also evident for the maximum values recorded (98 cm for *P. clavata* and 67 cm for *E. singularis*); in both cases, within the studied populations, the number of colonies reaching the largest height was a small fraction of the whole (Fig.5 and 6).

As occurred for density, there was a no clear correlation between mean colony height and depth (*E. singularis*, $r^2$=0.116, p=0.132; and *P. clavata*, $r^2$=0.046, p=0.376) or latitude (*E. singularis*, $r^2$=0.004, p=0.782; and *P. clavata*, $r^2$=0.011, p=0.656) for any of both species. In contrast, significant correlations were obtained between the maximum height and depth (*E. singularis*, $r^2$=0.926, p<0.05; and *P. clavata*, $r^2$=0.904, p<0.05).

| 1a) P. clavata | | | % injury | | % colonies | | |
|---|---|---|---|---|---|---|---|
| | Depth | N | %-mean | %-SD | <10% | 10- 99% | 100% |
| Els 3 frares | 20-25 | 87 | 19.24 | 33.42 | 64.37 | 29.89 | 5.75 |
| El bau de fora | 15-20 | 116 | 6.57 | 20.73 | 86.21 | 10.34 | 3.45 |
| El gat | 20-25 | 130 | 23.46 | 37.23 | 60.00 | 23.85 | 16.15 |
| Bau Cap trencat | 20-25 | 138 | 15.65 | 26.03 | 62.32 | 36.23 | 1.45 |
| Els forcats | 25-30 | 46 | 7.50 | 16.18 | 76.09 | 23.91 | 0.00 |
| Massa d'Or | 25-30 | 108 | 5.23 | 13.33 | 79.63 | 20.37 | 0.00 |
| Pta falconera | 25-30 | 50 | 5.00 | 14.74 | 82.00 | 18.00 | 0.00 |
| Medallot | 15-20 | 168 | 13.30 | 27.51 | 71.43 | 23.81 | 4.76 |
| Tascons | 15-20 | 79 | 3.32 | 13.27 | 91.14 | 7.59 | 1.27 |
| Carall Bernat | 15-20 | 108 | 11.61 | 29.72 | 84.26 | 7.41 | 8.33 |
| Pedra de Deu | 30-35 | 141 | 13.30 | 27.51 | 80.85 | 17.73 | 1.42 |
| Pota del Llop | 30-35 | 154 | 7.80 | 20.33 | 77.27 | 19.48 | 3.25 |
| Tasconsf | 30-35 | 56 | 18.48 | 29.66 | 57.14 | 35.71 | 7.14 |
| Canons tamariu | 25-30 | 131 | 11.01 | 26.39 | 90.84 | 9.16 | 0.00 |
| Columbretes-1 | 30-35 | 55 | 0.63 | 3.05 | 96.36 | 3.64 | 0.00 |
| Columbretes-2 | 30-35 | 170 | 5.85 | 19.61 | 87.06 | 10.59 | 2.35 |
| Columbretes-3 | 30-35 | 91 | 11.90 | 23.31 | 67.03 | 31.87 | 1.10 |
| Hormigon | 25-30 | 76 | 11.38 | 20.52 | 71.05 | 27.63 | 1.32 |
| Bajo mosquito | 25-30 | 56 | 0.98 | 2.59 | 94.64 | 5.36 | 0.00 |
| Mean | | | 10.12 | | 77.88 | 19.08 | 3.04 |

| 1b) E. singularis | | | | | | | |
|---|---|---|---|---|---|---|---|
| Tres frares | 27 | 79 | 4.37 | 19.39 | 93.67 | 2.53 | 3.80 |
| Bau de fora | 18 | 141 | 5.21 | 21.16 | 93.62 | 2.13 | 4.26 |
| Els forcats | 13 | 47 | 0.43 | 2.04 | 95.74 | 4.26 | 0.00 |
| Cala Bona | 15-20 | 101 | 4.41 | 14.01 | 89.11 | 10.89 | 0.00 |
| La reparada | 15-20 | 181 | 1.71 | 8.42 | 94.48 | 5.52 | 0.00 |
| El gat | 15-20 | 90 | 0.56 | 5.27 | 98.89 | 1.11 | 0.00 |
| Rossinyol | 17 | 136 | 1.18 | 9.67 | 98.53 | 1.47 | 0.00 |
| Pta Salines | 21 | 56 | 24.43 | 37.82 | 60.71 | 25.00 | 14.29 |
| Arquets | 15-20 | 75 | 0.00 | 0.00 | 100.00 | 0.00 | 0.00 |
| Tascons | 18 | 241 | 1.33 | 10.04 | 97.51 | 1.66 | 0.83 |
| Reina | 18 | 86 | 0.00 | 0.00 | 100.00 | 0.00 | 0.00 |
| Medallot | 13 | 65 | 6.85 | 12.86 | 75.38 | 24.62 | 0.00 |
| Pedra de Deu | 13 | 106 | 2.74 | 8.40 | 86.79 | 13.21 | 0.00 |
| Tarragona | 20 | 107 | 6.70 | 20.98 | 85.98 | 14.02 | 0.00 |
| Gandia T74 | 15-20 | 93 | 9.73 | 20.28 | 74.19 | 25.81 | 0.00 |
| Gandia T52 | 12 | 73 | 2.90 | 10.83 | 91.78 | 8.22 | 0.00 |
| Gandia T57 | 15 | 85 | 10.52 | 25.10 | 80.00 | 16.47 | 3.53 |
| Valencia T5 | 15 | 109 | 4.79 | 15.28 | 88.07 | 11.93 | 0.00 |
| Hormigon-1 | 27 | 63 | 4.21 | 11.30 | 85.71 | 14.29 | 0.00 |
| Hormigon-2 | 29 | 123 | 2.11 | 10.79 | 94.31 | 5.69 | 0.00 |
| Hormiga-1 | 29 | 132 | 4.96 | 19.11 | 90.15 | 8.33 | 1.52 |
| Mean | | | 4.71 | | 89.27 | 9.39 | 1.34 |

Table 1    *Paramuricea clavata* (1a) and *Eunicella singularis* (1b). Mean percentage of injured tissue and percentage of healthy colonies (<10% injured), affected colonies (≥10-≤99%) and totally dead colonies (100% injured).

**Figure 4**  *Paramuricea clavata*. (a) Variation of the standard error (SE) as a proportion of the mean with sample size (area in square meters) to determine minimum sample size for colony density. (b) Variation of the standard error (SE) as a proportion of the mean with sample size (number of colonies) to determine minimum sample size for the extent of injury of the colonies.

## Size distributions curves

All size frequency distributions studied for both *P. clavata* and *E. singularis* populations showed unimodal, more or less bell-shaped structures, but some differences appear both between species and among populations (Fig. 5 and 6). In *P. clavata*, the proportion of the smaller

and non-reproductive colonies (<10 cm) was low, a peak always existed in the size-class 2 (>10-20 cm) and again there was a low proportion of colonies larger than 30-40 cm (Fig. 5). In contrast, most of the *E. singularis* populations showed a high proportion of colonies, a similar frequency of all the other classes or a peak in the class 20-30 cm, and a decrease of the proportion of large size classes (Fig. 6).

Regarding to skewness coefficients, in *P. clavata*, most of the size-distributions (n=12) were positively skewed and the others (n=7) were not significantly asymmetrical (Fig. 5, Table 2) Non symmetrical, positively skewed distributions were found among all the shallower populations (<25m), while mostly symmetrical (although both types were present) distributions were found among the deeper ones (>25m). Likewise in *E. singularis*, most size distributions were positively skewed (n=15) and the rest (n=6) were symmetrical (Fig. 6, Table 3). Nevertheless, grouping the populations in relation to their skewness, several differences appeared regarding to the shape of the distributions of the two species.

Comparing the symmetric and non-symetryc distributions of *P. clavata*, although the shape of both distributions were really similar, some differences were evident such as a bigger proportion of colonies between 10 and 20 cm, and a lower proportion of larger colonies (>40 cm) among the populations displaying positive skewness than among symmetric populations (Skewness 0) (Fig. 7a). In contrast, in the comparison for *E. singularis* populations two contrasted distribution shapes can be observed. Populations with positive values of skewness displayed a distribution with most of colonies in an initial, "young" phase while the populations with skewness significantly symmetric involved a next step, displaying a similar proportion of colonies in the first size classes (0-10, 10-20 and 20-30 cm) and a higher number of colonies reaching the larger size classes (Fig.7b).

Conversely, kurtosis was quite variable between species and among populations. While in *P. clavata*, 7 populations displayed positive kurtosis and 12 populations showed values no significantly different than 0, in *E. singularis* 10 populations displayed positive kurtosis, 3 populations displayed negative kurtosis and the rest of the populations showed non significant values different than 0. Average kurtosis was 0.74 for *P. clavata* and 1.16 for *E. singularis*, indicating that, in general, the distributions for both species were slightly more peaked or overcentralised than normal distributions (Table 2 and 3).

| | Depth | N | Density m² | Density col/m² | Biomass gr/m² | Size Hmean | H-SD | Min | Max | g1 | SE g1 | sig(>2) | g2 | SE g2 | sig(>2) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Els 3 franes | 20-25 | 87 | 2.5 | 34.60 | 475.12 | 24.39 | 16.31 | 4 | 96 | 1.36 | 0.26 | 5.27 | 3.02 | 0.51 | 5.90 |
| El bau de fora | 15-20 | 116 | 2.5 | 46.40 | 506.63 | 23.65 | 12.11 | 2 | 67 | 0.80 | 0.23 | 3.54 | 0.70 | 0.45 | 1.57 |
| El gat | 20-25 | 130 | 2.5 | 52.00 | 304.96 | 18.40 | 11.05 | 1 | 52 | 0.78 | 0.21 | 3.69 | 0.70 | 0.42 | 1.67 |
| Bau Cap troncat | 20-25 | 138 | 3.2 | 43.13 | 514.58 | 22.17 | 16.13 | 0.5 | 96 | 1.45 | 0.21 | 7.06 | 3.34 | 0.41 | 8.19 |
| Els forcats | 25-30 | 46 | 2.5 | 18.40 | 364.15 | 28.27 | 16.92 | 4 | 63 | 0.37 | 0.35 | 1.06 | -1.10 | 0.69 | -1.59 |
| Massa d'Or | 25-30 | 108 | 4.8 | 22.90 | 73.41 | 14.07 | 6.88 | 2.5 | 36 | 1.08 | 0.23 | 4.65 | 1.41 | 0.46 | 3.05 |
| Pta halconera | 25-30 | 50 | 4.3 | 11.76 | 574.53 | 41.48 | 21.07 | 5 | 90 | 0.20 | 0.34 | 0.58 | -0.80 | 0.66 | -1.20 |
| Medallot | 15-20 | 168 | 3.2 | 52.50 | 303.68 | 17.52 | 10.67 | 0.5 | 60 | 1.00 | 0.19 | 5.32 | 1.09 | 0.37 | 2.92 |
| Tascons | 15-20 | 79 | 3.2 | 24.69 | 542.93 | 31.41 | 14.08 | 3 | 68 | 0.59 | 0.27 | 2.19 | -0.24 | 0.54 | -0.44 |
| Caroll Bernat | 15-20 | 108 | 3.2 | 33.75 | 190.42 | 17.05 | 10.42 | 1 | 56 | 0.78 | 0.23 | 3.34 | 0.84 | 0.46 | 1.81 |
| Pedra de Deu | 30-35 | 141 | 3.2 | 44.06 | 366.65 | 18.19 | 14.07 | 1 | 89 | 1.83 | 0.20 | 8.95 | 5.06 | 0.41 | 12.44 |
| Pota del Llop | 30-35 | 154 | 3.2 | 48.13 | 269.83 | 17.54 | 11.44 | 2 | 52 | 1.15 | 0.20 | 5.84 | 0.97 | 0.39 | 2.49 |
| Tasconsf | 30-35 | 56 | 3.2 | 17.50 | 187.23 | 24.40 | 14.17 | 0.5 | 50 | 0.30 | 0.31 | 0.96 | -0.97 | 0.61 | -1.59 |
| Canons tamanu | 25-30 | 131 | 4.3 | 30.62 | 376.52 | 23.15 | 12.76 | 4 | 71 | 1.40 | 0.21 | 6.58 | 2.49 | 0.42 | 5.93 |
| Columbretes-1 | 30-35 | 55 | 3.2 | 17.19 | 811.67 | 37.09 | 24.24 | 1 | 91 | 0.45 | 0.32 | 1.39 | -0.79 | 0.63 | -1.25 |
| Columbretes-2 | 30-35 | 170 | 3.2 | 53.13 | 1762.39 | 33.75 | 20.51 | 1 | 98 | 0.61 | 0.19 | 3.27 | 0.06 | 0.37 | 0.15 |
| Columbretes-3 | 30-35 | 91 | 3.2 | 28.44 | 636.37 | 30.02 | 20.37 | 1 | 82 | 0.49 | 0.25 | 1.93 | -0.30 | 0.50 | -0.61 |
| Hormigón | 25-30 | 76 | 3.2 | 23.75 | 134.85 | 18.24 | 10.65 | 2 | 44 | 0.31 | 0.28 | 1.12 | -0.75 | 0.55 | -1.37 |
| Mosquito | 25-30 | 56 | 1.5 | 37.33 | 194.83 | 18.69 | 6.54 | 3 | 54 | -0.02 | 0.32 | -0.07 | -0.59 | 0.63 | -0.94 |

**Table 2** *Paramuricea clavata*. Characteristics of studied populations: depth, number of colonies (N), area (m2), density, biomass, height (H) and distribution parameters (skewness (g1) and kurtosis (g2)). Sig (>2): Skewness and kurtosis are considered significant if the absolute value of coefficient/SE is greater than 2

| | Depth | N | Density m² | Density col/m² | Size H-mean | H-SD | Min | Max | g1 | SE g1 | sig(>2) | g2 | SE g2 | sig(>2) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tres franes | 27 | 79 | 2.5 | 31.60 | 14.26 | 11.05 | 2 | 46 | 0.97 | 0.27 | 3.58 | 0.07 | 0.54 | 0.12 |
| Bau de fora | 18 | 141 | 2.5 | 56.40 | 7.22 | 7.53 | 2 | 43 | 2.82 | 0.20 | 13.80 | 8.13 | 0.41 | 20.01 |
| Els forcats | 13 | 47 | 2.5 | 18.80 | 12.58 | 9.10 | 2 | 47 | 1.69 | 0.35 | 4.86 | 3.63 | 0.68 | 5.33 |
| Cala Bona | 15-20 | 101 | 50 | 2.02 | 12.25 | 8.44 | 3 | 41 | 1.41 | 0.24 | 5.87 | 1.69 | 0.48 | 3.56 |
| La naparada | 15-20 | 181 | 50 | 3.62 | 24.53 | 11.89 | 2 | 61 | 0.50 | 0.18 | 2.75 | 0.34 | 0.36 | 0.94 |
| El gat | 15-20 | 90 | 50 | 1.80 | 14.70 | 8.89 | 3 | 50 | 1.13 | 0.25 | 4.46 | 2.21 | 0.50 | 4.39 |
| Rossinyol | 17 | 136 | 50 | 2.72 | 19.43 | 11.03 | 1 | 40 | -0.03 | 0.21 | -0.13 | -0.96 | 0.41 | -2.33 |
| Pta Salines | 21 | 56 | 11.75 | 4.76 | 21.43 | 13.44 | 3 | 65 | 1.23 | 0.32 | 3.85 | 1.83 | 0.63 | 2.91 |
| Arquets | 15-20 | 75 | 50 | 1.50 | 17.63 | 14.16 | 1.5 | 67 | 1.31 | 0.28 | 4.72 | 1.61 | 0.55 | 2.93 |
| Tascons | 18 | 241 | 5.75 | 41.91 | 16.36 | 13.61 | 0.1 | 56.5 | 0.44 | 0.16 | 2.81 | -0.76 | 0.31 | -2.43 |
| Reina | 18 | 86 | 5 | 17.20 | 15.87 | 12.82 | 1 | 51 | 0.70 | 0.26 | 2.68 | -0.43 | 0.51 | -0.83 |
| Medallot | 13 | 65 | 3.2 | 20.31 | 20.99 | 10.05 | 1.9 | 42.5 | -0.46 | 0.30 | -1.54 | -0.55 | 0.59 | -0.93 |
| Piedra de Deu | 13 | 106 | 3.2 | 33.12 | 7.49 | 6.22 | 0.6 | 31 | 1.61 | 0.24 | 6.86 | 2.32 | 0.47 | 5.00 |
| Tarragona | 20 | 107 | 2.25 | 47.55 | 5.52 | 3.84 | 0.3 | 20 | 1.25 | 0.24 | 5.25 | 2.04 | 0.47 | 4.33 |
| Gandia T74 | 15-20 | 93 | 5 | 18.60 | 6.95 | 3.34 | 1.5 | 23.5 | 1.47 | 0.25 | 5.90 | 5.22 | 0.50 | 10.55 |
| Gandia T52 | 12 | 73 | 100 | 0.73 | 8.97 | 4.01 | 2.5 | 21 | 1.01 | 0.28 | 3.60 | 0.79 | 0.56 | 1.42 |
| Gandia T57 | 15 | 85 | 6.25 | 13.60 | 11.20 | 4.54 | 3 | 23 | 0.44 | 0.26 | 1.69 | -0.43 | 0.52 | -0.84 |
| Valencia T5 | 15 | 109 | 65 | 1.67 | 11.72 | 6.10 | 2.5 | 28 | 0.57 | 0.23 | 2.48 | -0.61 | 0.46 | -1.33 |
| Hormigon1 | 27 | 63 | 3.2 | 19.68 | 22.66 | 10.06 | 2 | 41 | -0.33 | 0.30 | -1.10 | -0.47 | 0.60 | -0.79 |
| Hormigon2 | 29 | 123 | 3.2 | 38.43 | 25.38 | 10.36 | 1 | 47 | -0.42 | 0.22 | -1.93 | -0.39 | 0.43 | -0.89 |
| Hormiga | 29 | 132 | 3.2 | 41.25 | 20.70 | 11.41 | 1 | 49 | 0.17 | 0.21 | 0.82 | -0.90 | 0.42 | -2.15 |

**Table 3** *Eunicella singularis*. Characteristics of studied populations: depth, number of colonies (N), area (m2), density, height (H) and distribution parameters (skewness (g1) and kurtosis (g2)). Sig (>2): Skewness and kurtosis are considered significant if the absolute value of coefficient/SE is greater than 2.

Figure 5    *Paramuricea clavata*. Size-frequency distributions of nineteen populations along the explored spatial scale.

Figure 6  *Eunicella singularis*. Size-frequency distributions of twenty-one populations along the explored spatial scale.

**Figure 7** Size-frequency distributions grouping the populations according their skewness coefficient. (a) *Paramuricea clavata* b) *Eunicella singularis*.

## Evidences of self–thinning mechanism in gorgonian populations?

When *P. clavata* mean biomass was plotted against density a clear trend emerged: there was a significant (p<0.01) negative correlation where most populations were placed near of a straight line with a -3/2 slope (Fig. 8a). Both the unexpected robustness of this plot and the proximity of the slope to the predicted value (-3/2) by plant ecologists seem to suggest some true evidence

of negative denso-dependence or intra-specific competition among red gorgonian populations. The population Columbrets-2 (top-right corner in Figure 8a) was not considered in the regression due to their extraordinary values of biomass in relation to the rest of examined populations, taking into account possible problems in the measurements obtained in the field. Furthermore, there were 3 populations (Massa d'Or, Tascons, Hormigon) further separated from a theoretical self thinning line (estimated using an exact -3/2 slope) that were discarded to perform the correlation of gorgonian populations which might have higher values of biomass in accordance with their present values of density.

Under our hypothesis, the populations placed under the line might be disturbed populations, but to confirm this hypothesis, we added to the plot two populations that were affected by the 1999 mass mortality event, before and after it occurred.

As we observe in the plot (Fig. 8b), both populations sampled before the event were placed near the self-thinning line; but, as we expected, just after the disturbance populations appeared far down this line and the time-arrow pointed left-down indicating that they have lost both density and biomass. In the last years, both populations followed the same pattern to return slowly to the self-thinning line, still losing density but gaining slowly in biomass.

In contrast, *E. singularis* populations did not show any clear pattern of size-density relationship (Fig. 9).

Figure 8  *Paramuricea clavata.* (a) Relationship between the density and biomass of the nineteen studied populations, expressed in logarithmic terms. (b) Trajectory of two populations affected by 1999 mass mortality event, before (june 1999), just after (November 1999) and four years (November 2003) after the event; the line represents the self-thinning line obtained for the studied populations in this study.

Figure 9    *Eunicella singularis*. Relationship between the density and mean size of the twenty-one studied populations, expressed in logarithmic terms.

# ▌▌▌ Discussion

The demographic study along a relevant spatial scale of the two more abundant gorgonian species in the Western Mediterranean has allowed us to obtain essential baseline data about both species as well as it has revealed a contrasting population dynamics and different vulnerability facing to different biological and physical disturbances.

## ▌ Distribution patterns

It has been argued that species distribution synthesizes the responses of species capacity to survive and reproduce under particular conditions (MacArthur 1972). The extensive distribution of *E. singularis* in a spatial scale may be related to its tolerance to a wide range of environmental conditions in contrast to *P. clavata* that seems to be more vulnerable to the variability of abiotic factors.

This contrasting distribution agrees with previous studies that showed the relation of octocorallian communities with different abiotic factors. While *P. clavata* populations were found at a narrow band of light conditions (irradiance values ranging between 0.12 and 27.6%) and typi-

cally in vertical surface, although it can be found on other slope types with sediment-free bottoms; *E. singularis* is a common species on horizontal or sloping sediment-covered bottoms in irradiance conditions ranging from 3 to 60%. Both species seem to be quite tolerant to temperature but while *E. singularis* populations were found in localities with summer temperatures from 20° to 14°, *P. clavata* populations were placed in sites with an average summer temperature under 19° (Weinberg 1975,1979, 1980).

With regard to this last parameter, the punctual measures of these previous studies as well as the current development of new technologies that allow continuous measures reinforce the need of further studies to improve the knowledge about the relation of this species with the temperature, especially in front the increasing threat of new mass mortality events linked to Mediterranean warming (Bethoux and Gentilli 1996, J. Pascual *unpublished data*).

The upper limit of distribution displayed by both species along the explored coast also exhibited a different pattern. While *E. singularis* did not show any pattern in depth, a decrease along the latitudinal gradient was observed in *P. clavata* populations. This pattern may be related to the variability of the abiotic factors along this latitudinal scale. Changes on the limits of distribution of different NW Mediterranean benthic communities have been previously related to differences on the abiotic factors, such as light, temperature and hydrodynamism along a comparable spatial scale (Zabala and Ballesteros 1989). This spatial variation of abiotic factors and their relation with the species distribution (Weinberg 1975, 1980) determine the existence of areas where the range depth of distribution is compressed; i.e the biological zonation pattern that occurs in the first 40 m at Northern localities of the NW Mediterranean Sea corresponds to the 40-70 m in the most oligotrophic areas, such as the Mediterranean islands or southern coast localities, explaining the changes of the upper depth limit of *P. clavata* along the latitudinal gradient explored in this study (Weinberg 1979, Ballesteros 2006).

In contrast to species presence, density and mean colony size did not show a clear pattern along geographic and depth scales in both studied species. Only in *P. clavata*, maximum height showed a positive correlation with depth as it had been noted in a previous study (Harmelin and Marinopoulos 1994). Although changes of population structure along a depth gradient have been described in Mediterranean marine ecosystems (Ballesteros 1991, Garrabou et al 2002), the absence of these patterns may be related to the narrow depth range of the populations explored (15-35 m) because the main goal was to study the shallowest gorgonian populations that are more exposed to suffer mortalities associated to thermal anomalies.

## Baseline data for future disturbances

The results of the examination of the impacts of 1999 mass mortality event on the gorgonian populations along the Mediterranean Spanish coast, that affected a wide range of marine benthic invertebrates along a great regional scale (approximately until 1000 km) (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Linares et al 2005, Coma et al *in press*) showed

that this event did not have any effect on the examined populations. Nevertheless, data about partial and total mortality of these two gorgonian populations as well as the data about other demographic parameters provide useful baseline data to detect and quantify future impacts on these populations.

The partial mortality rates exhibited by these populations were extremely different that those obtained in the assessment of the mass mortality impact over these two species, where the proportion of injured gorgonians and the mean percentage of injured tissue were estimated around 60 to 100% of the colonies and about 50% of injured tissue (Cerrano et al 2000, Perez et al 2000, Linares et al 2005, Coma et al *in press*). In our study, the mean percentage of injured tissue and the proportion of totally injured colonies was lower in *E. singularis* than *P. clavata* (5% injured tissue and 1% of colonies totally dead versus 10% injured tissue and 3% of colonies, respectively), moreover a larger proportion of healthy colonies was observed in *E. singularis* (90% vs. 78%). These results suggest a major resistance of *E. singularis* in front of disturbances (accepting that disturbances increase the partial mortality rates), although these results contrast with the same level of affection displayed by both species facing the 1999 mass mortality event (Linares et al 2005, Coma et al *in press*).

## The application of plant ecology approaches to gorgonian populations

Analogous to distribution patterns, divergences between both species were also discernible exploring the size distribution curves and the carrying capacity (and the existence of a mechanism of self-thinning) of the populations studied.

Size distributions of both gorgonian species suggest that they have differing recruitment and survival dynamics. In both species, most of the populations showed distributions skewed to right (positive values) where large colonies were relatively rare, pointing out that gorgonian mortality may be high at most of the sites, where the colonies are not capable of reaching large size classes. But whereas in *P. clavata* the first size class never was the predominant one, being the class 2 (10-20 cm, first reproductive colonies) the most abundant one, in *E. singularis* most of populations (14 out 21) showed an exponential distribution with a largest predominance of smallest and non-reproductive colonies (0-10 cm).

Indeed, *P. clavata* distributions agree with the great variability of size distributions obtained for gorgonian species displaying distributions with a peak on the intermediate classes or with all size-classes represented on the same proportion (Jordán-Dahlgren 1989, Yoshioka 1994, Jordán-Dahlgren 2002, Bastidas et al 2004, Tsounis et al 2006), while *E. singularis* distributions were more similar than other coral species that generally display distributions extremely skewed to the right having most colonies in the smallest size class (Hughes and Jackson 1980, 1985, Babcock 1984, Soong 1993, Lewis 1997, Bak and Meesters 1998). Moreover, the fact that largest colonies were abundant in pristine conditions agree with other soft-coral species (Yoshioka 1994, Bastidas et al 2004, Bianchimani 2005), but contrast with the idea that under

environmental deterioration coral populations display negative skewness coefficients (Bak and Meesters 1998, Meesters et al 2001).

The Figure 7 showed that skewness coefficient also revealed a higher dynamic pattern for *E. singularis*. In this species two temporal stages could be distinguished, one with a largest predominance of smallest colonies and a second state with a bigger presence of large colonies. In contrast, for *P. clavata* these two groups showed the same distribution shape with the only difference of a higher presence of large colonies in symmetric populations, basically found in the populations placed below 25 m.

The fact that along the large explored area none of the *P. clavata* populations corresponded to a young or expanding population, points out that first, all explored populations are at about the same state or/and age, and second, the scarcity of the initial population stages involving a general failure of the recruitment. The larger proportion of small colonies observed in *E. singularis* may be the result of high rates of mortality of larger colonies related to the changes of abiotic factors in a unstable environment (at 10-20 m of depth) being adequately compensated for high recruitment rates. Moreover, the differences observed between both species may be explained by different reproductive strategies, *P. clavata* is a surface brooder (Coma et al 1995) whereas *E. singularis* has an internal brooding (Weinberg and Weinberg 1979). This last strategy may contribute to reduce mortality during the first stages of the colonies and increase local recruitment rates in unstable habitats.

Examining the approach to the carrying capacity (and the existence of a mechanism of self-thinning) both species displayed also a contrast dynamics. In *Eunicella singularis*, the disperse points scattered across the size-density plot confirm that other factors than intra-specific competition are governing the structure of white gorgonians populations. For red gorgonian species, there was a strong negative correlation between the biomass and density of colonies in some populations, whereas other populations were placed under this line. The robustness of this pattern points out that this significant correlation is something else that a simple coincidence. Although the mechanism remains unclear, because in these thinned populations we should find more colonies remaining extant completely dead (100% dead), and a deep study should be achieved, nevertheless the inverse relationship between biomass or height and density remains interesting.

Following our hypothesis, the populations found under the self-thinning line may correspond to young populations or populations affected by some kind of disturbance. As noted by Niklas et al (2003), it is reasonable to postulate that maximum colony size and community age should be positively correlated such that the presence of old and large individuals denotes the relative absence of recent disturbances. The results about the effects of a mass mortality event (Fig. 8b) confirm the relation between the populations placed under the self-thinning line and disturbance events. In our study, the gorgonian populations placed under the self-thinning line were probably populations (Tascó) subjected to high levels of mortality due to the high frequency of divers in a marine protected area (Coma et al 2004) or populations where probably the environmental characteristics of these sites do not allow red colonies reaching to larger classes (Massa d'Or and Hormigon).

The finding of three young population of *P. clavata* during posterior surveys of gorgonian populations in the NW Mediterranean Sea examining a wider spatial range (about 60 populations have been examined) demonstrates the low frequency of appearance of these young populations. The colony sizes and density values displayed by these young populations were really variable pointing out the fact that the establishment of red gorgonian populations could be more variable: from a unique strong recruitment to continuous and low recruitments episodes. Data about the initial stages of red gorgonian populations are really essential to predict the future trajectories of these populations using demographic models as well as to understand the dynamics and persistence of this species (Linares et al *in press*, Chapter III).

In summary, the application of these demographic approaches to gorgonian populations, has allowed us to identify two contrast population dynamics. *E. singularis* shows a high dynamism, corroborated by the high variability on population structure suggesting high recruitment rates. Roughly attributable to r-strategists (Pianka, 1970), there is a common agreement about the ability of these populations to adapt to changing environments. On the contrary, *P. clavata* shows stable bell-shaped distributions, where the low proportion of small colonies suggests they suffer short supply of recruits and/or higher mortality rates at the first classes after recruitment. As typically associated to long-living and slow-growing species, these populations use to be near to the carrying capacity, as demonstrate the fact that most populations were placed in the self-thinning line. They are roughly referred to as k-strategists and they are poorly adapted to unstable environments (Pianka 1970). Consequently, although further studies are required to achieve a whole understanding of demographic characteristics of these species, our study evidence that a major effort on the conservation of red gorgonian populations are needed in this Mediterranean hard-bottom community (Ballesteros 2006).

Finally, the relationship between density and biomass observed in this study reveals that this approach would be really useful to identify the effects of biological or physical disturbances, especially in the case of species, such as *P. clavata*, displaying a high vulnerability according to their demographic characteristics.

## Acknowledgements

**Early life history of the Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics**

## ▯▯▯▯ Abstract

Knowledge about early life stages of marine sessile invertebrates dispersing by means of free swimming propagules is fundamental towards understanding their population biology. In this study we describe the different early life-history stages, quantify their survivorship, and analyze possible implications for population dynamics the Mediterranean gorgonian *Paramuricea clavata*. Spawning was recorded in June for the three years studied (2001, 2002, and 2003). Three facts may account for fertilization to be external in this species. First, most of the eggs were not fertilized just after the spawning. Second, the increase in fertilization rates depended on the time the eggs remained on the surface of female colonies. Third, the great variability in fertilization rates recorded for the different spawning events. The blastula and the planulae appeared after 48 hours and 48-72 hours, respectively, and the complete metamorphosis into polyp was achieved between 10-18 days after the spawning. Three-four days old planulae showed negative response to light in the laboratory. Only 60% of eggs transformed into planulae and 40% of larvae survived. Survival was low (5% in the laboratory) during the metamorphosis. After settlement, none of the polyps from a field experiment survived for more than seven months. The low survival displayed by the early life-history stages may contribute to explain the low recruitment rates observed in the field and demonstrates the ecological fragility of this emblematic species. This has implications for local population persistence and possible colonization of new areas especially under human-induced disturbances.

Keywords: Cnidaria, Octocorallia, invertebrate larvae, development, recruitment

# ▐▐▐ Introduction

Most marine benthic invertebrates exhibit a complex life cycle that includes more or less mobile larval stages and sessile juvenile and adult stages (Thorson 1950, Eckman 1996). Hence, the interest to study ontogenetic processes such as gamete production, fertilization, and metamorphosis as well as ecological patterns such as larval release, behavior, dispersal, survival, and settlement (Lasker et al 1998, Morgan 2001, Underwood and Keough 2001).

The red gorgonian *Paramuricea clavata* (Risso 1826) is a long-lived, slow-growing octocoral (Coma et al 2004). It plays an important role in the maintenance of biomass and structural complexity in the highly diverse Mediterranean coralligenous community (True 1970, Ballesteros 2006).

*P. clavata* is a surface brooder, showing substantial annual investment in sexual reproduction (Coma et al 1995a,b) and a dioecious species, with a sex ratio not significantly different from 1:1. While oocyte development lasts between 13 and 18 months, sperm development is much faster (between 6 and 7 months). Reproduction and spawning co-occur every year in June in the populations studied (Coma et al 1995a). There is a high investment in reproduction, which contrasts with the low recruitment rates observed in the field (R. Coma *unpublished data*). In spite of that, there are still gaps in the scientific knowledge especially in the description of the different early life-history stages and their timing of development as well as the fertilization rates and the behavior of larvae and settlers.

In this study we describe the early life history traits of *P. clavata*, i.e. the development from the egg to the first polyp and the main behavior of larvae in the laboratory. We quantify the fertilization rates in eggs and the mortality of larvae and polyps in the laboratory; we also quantify the mortality of settlers in the field. This study may also provide knowledge on the population dynamics of the species with special regard to the success of recruitment in the habitats where *P. clavata* lives.

# ▐▐▐ Material and methods

We conducted the fieldwork in the Medes Islands Marine Protected Area (NW Mediterranean Sea, 42° 02' N, 3° 13' E) between June 2001 and June 2003. At the study site, well-structured populations of *Paramuricea clavata* are located on both overhanging walls and north-exposed sides of large boulders between 15 and 40 meters depth.

We recorded the timing of spawning in June 2001, 2002 and 2003 by daily SCUBA dives aimed at spotting the presence of egg masses over the surface of female colonies. The goal of these surveys was twofold. First, to obtain early life history stages for both their description and experiments and second, to confirm the timing of possible spawning events and its relationship with the temperature and the lunar phase, which are known as the main factors triggering spawning in this species (Coma et al 1995a).

## Description of embryonic and larval development

During the spawning of June 2002 and 2003 (see later), eggs were collected from the surface of female colonies using hypodermic syringes while SCUBA diving. Once in the laboratory, the eggs were transferred into polyethylene containers with 0.5 $\mu$m-filtered seawater (FSW) to describe the time-course of the developmental process for the different early life history stages. Stock cultures of embryos and larvae were maintained in 2-l glass jars with FSW at 16°C (June seawater temperature). The water was replaced everyday.

Some of the eggs were kept into large Petri dishes (10cm diameter) with seawater to observe and document by photographic images (a digital camera connected to the dissecting microscope) the main features of the different developmental stages as well as the main behavior of larvae. When a particular stage was achieved (e.g. embryo, larva), we collected and preserved it into 2.5% glutaraldehyde for scanning electron microscope (SEM) examination. The samples were dehydrated through a graded series of ethanol and then critically point dried from liquid $CO_2$. The preparations were coated with gold-palladium and examined with a HITACHI S3500N at 10 Kv SEM.

## Larval response to light

To assess whether the larvae of *P. clavata* display photophilic or photophobic behavior we put 30 actively swimming larvae into an especially designed device. This consisted of two polyethylene boxes (8 cm diameter) connected by a 20-cm pipe of 3-cm section. The device was filled up with seawater and one of the boxes and the adjacent half portion of the pipe were wrapped with a black plastic bag. The larvae (3-4 days old planulae) were inserted through a tiny tube connected to the middle of the connection pipe and left for 24hrs under natural conditions of daylight and darkness. After this time, the black plastic was removed and the presence of the larvae in either of the chamber recorded. The experiment was repeated three times with larvae belonging to the first spawning and twice with larvae from the second episode of June 2002.

## Fertilization

The fertilization rates were assessed counting the number of planulae present after 72 h among the eggs in the stock cultures. We used 50 eggs collected on 14 June 2002 from 10 different colonies and 100 eggs collected on 21 June 2002 from 14 colonies.

In order to determine whether the fertilization was internal or external, in June 2003 samples of eggs (100 eggs from 10 different colonies) were collected in the field from the surface of female colonies short after their release (<12 h). Sampling was repeated every 12h for 3 days until no colonies bearing eggs were detected. The fertilization rates were estimated as above taking into account the different time of collection. Fertilization rates could not be estimated during the second spawning episode in 2003.

## Survivorship

We conducted both experiments in the laboratory and in the field in order to assess the survival rates for the different developmental stages of *P. clavata*. In June 2002, 25 embryos from 10 different colonies were transported to the laboratory and reared into 0.5 l polyethylene containers with FSW. We placed small fragments of calcareous rock into the containers to simulate a natural substratum. Every 2-3 days we checked the surviving embryos under a dissecting microscope and recorded their developmental state. The water in the containers was replaced every 2-3 days to avoid, as much as possible, bacterial growth. The experiment lasted 30 days.

To assess the survival and growth of primary polyps in the field, in June 2001 and 2002 we placed three PVC cages (three cages in vertical walls and three over horizontal bottoms fastened using two-component putty) onto a rocky substrate at 15-20 meters depth within the well-developed gorgonian community. The walls of each box were made on 250 $\mu$m plankton net to allow water circulation and prevent the exit of larvae. We collected about 2000 planulae from the laboratory cultures and distributed them into the cages. Our aim was to ensure the maximum numbers of settlers in each of the cages. After one month, we removed the cages and counted the polyps, which were then used to record growth and mortality under natural conditions. Once a month and until all polyps died, we checked the numbers of surviving recruits and their possible increase in number.

# ▌▌▌ Results

Eggs surrounded by mucus were observed on the surface of female colonies in June in the three years studied. We recorded two different spawning episodes each year, lasting 2-3 days and separated each other between 7 and 13 days: on June 10th and 23rd in 2001, on June 13th and 20th in 2002, and on June 13th and 26th in 2003. The first spawning episodes started respectively four and two days after and one day before June's full moon in the three years. The second spawning started respectively two days after and four and three days before June's new moon. Water temperatures in these periods were ~16°C (J. Pasqual *unpublished data*).

## Embryonic and larval development

While the majority of eggs examined with the SEM were unfertilized (Fig. 1a), some of them were at the first division of the cleavage (Fig. 1b). The eggs collected at the beginning at the spawning were more or less spherical, from 250 to 350 $\mu$m in diameter after their fixation with glutaraldehyde (Fig. 2) .The cleavage was holoblastic and equal, although in some embryos the cell divisions became unequal and development ceased. Different developmental stages were observed at eight hours after collection, from first-cleavage to 16-cell embryos (Fig. 1c).

On the following day (24 h after collection), the embryos achieved the stereoblastula stage (Fig. 1d) when cell divisions became less regular and the embryos gradually showed jagged (irregular) shapes (Fig. 1e). At this stage, short mircrovilli were observed on the surface of the embryos (Fig. 1f). After 48h the embryos acquired more regular and spherical shapes (Fig. 1g, 1h) and between 48-72 hours the embryogenesis ended when a premature pear-shaped planula appeared. At this time eggs at a late embryonic stage and premature planulae could be observed simultaneously (Fig. 1i).

The premature planulae (Fig. 3a) were uniformly flagellated and swam actively into the petri dishes. They became more elongated in time (Fig. 2), from approximately 500 to 800 $\mu$m in length (max. length 1mm in older planulae) and more pear-shaped with a wider anterior pole (Fig. 3b). The mature planulae had a flagellated surface, with the oral pole (anterior) displaying greater density of flagella (Fig. 3c) than the aboral pole (posterior) (Fig. 3d). The mature planulae were observed swimming slowly as well as crawling or standing over the bottom of the petri dishes. They displayed an anti clockwise corkscrew rotation on their median axis whilst forward swimming.

The time at which the metamorphosis into polyp started was variable. The planulae started to metamorphose 8 days after collection, although this process did not start before 25 days in some of them. The metamorphosis into polyp did not require the attachment of the planula to

the substrate. The planulae (Fig. 4a) became progressively shorter (Fig. 2) and their anterior pole showed short tentacles (Fig. 4b). At the end of this process the primary polyps had 8 tentacles which became elongated and pinnate after 24 hrs (Fig. 4c). This process lasted about 2-3 days. The primary polyps were around 1.2 mm in length (Fig. 2) and survived in the laboratory for 1 month. None of the polyps (N=13) was capable to permanently attach to the bottom of the Petri dishes nor any divided into more than one polyp. Some polyps were observed whilst actively feeding on the ciliates in the dishes using the tentacles to trap the food and bring it into the mouth (Fig. 4d).



**Figure 1**   SEM images of embryogenic development. (a) Spawned eggs. (b) Egg undergoing first cleavage. (c) Sixteen-cell embryo. (d) Stereoblastula. (e) Bizarre form embryos (f) Flagellated surface of stereoblastula (g,h) Late spherical embryos (i) Premature pear shaped planulae (left) and embryo (right). Notice the variation of scale bar (2 $\mu$m - 300 $\mu$m) between the images.

Figure 2    Evolution in size of the different developmental stages (mean ± SD; n=10).



Figure 3    SEM images of planula development. (a) Premature pear shaped planulae. (b) Mature flagellated planulae. (c) Enlarged flagellated patch of the oral pole. (d) Enlarged flagellated of the aboral posterior pole. Note the variation of scale bar (10 $\mu$m - 200 $\mu$m) between the images.

Figure 4    Metamorphosis of the planula. (a) A mature planula. (b) Tentacled primary polyp (c) Primary polyp showing pinnulated tentacles (day 10). (d) Polyp whiles feeding on ciliates.

## Larval response to light

The vast majority of the larvae showed negative phototaxis. More than 92% of the larvae in the first experiment and all the larvae from the two trials of the second experiment were found in the dark box after 24h (Table 1).

| Experiment | Trial | Nº. planulae | | Dark side | Bright side |
|---|---|---|---|---|---|
| 13/06/02 | 1 | 30 | | 27 | 3 |
| | 2 | 30 | | 28 | 0 |
| | 3 | 30 | | 28 | 1 |
| | | | mean % | 92.22 | 4.44 |
| 20/06/02 | 1 | 30 | | 30 | 0 |
| | 2 | 30 | | 30 | 0 |
| | | | mean % | 100 | 0 |

**Table 1**     Larval positions in the bright-dark chamber after 24 hours.

## Fertilization

The fertilization rates were measured in both the 2002 spawning episodes and only for the first episode of 2003. All the eggs collected from the surface of the colonies were either unfertilized or commencing the first divisions of the cleavage.

In the first spawning event of 2002, 68.6 ± 20.91% (mean ± SD) of the eggs were fertilized (Table 2a), whereas in the second event fertilization was much lower (22.78 ± 18.76%; mean ± SD). In the first spawning of 2003 the eggs fertilized were 61.90 ± 24.93% (mean ± SD) (Table 2a).

In 2003, the fertilization rates varied depending on the time the eggs remained onto the surface of female colonies (Table 2b). Although the fertilization rates measured on the first day of the spawning were high (61.90%; Table 2a), they increased up to 96% with low variation (SD=4.07%) in the subsequent samples collected (Table 2b). In the last day of sampling a low number of colonies bearing eggs was observed due to an increase of sea current strength. No colonies bearing eggs were detected in the following days.

## Survivorship

The survivorship rates of planulae in the laboratory are shown in Figure 5. Survival of embryos in the laboratory was relatively high (about 50%) until the metamorphosis into polyp took place.

At this stage the mortality increased and after one month only 5% of the embryos reached the primary polyp stage (13 among 250 eggs). The first metamorphoses were recorded after eight days from the start of the experiment, and, after one month, all the surviving planulae transformed into polyps (Fig. 5). In spite of the presence of the rocks in the aquariums, the polyps did not establish permanent attachment to any substrate.

The total numbers of settlers were 150 in 2001 and 80 in 2002. In both years, all the polyps were found into the crevices underneath only one of the cages positioned on the vertical walls. All the settled polyps died before 6-7 months from the start of the experiment (Fig. 6). Only one polyp survived up to December 2001 and three polyps until January in 2002. None of the settlers developed into more than one polyp during the study period (Fig. 7).

| Spawning | Date | Time | N° colonies | N° eggs/colony | Fertilization rates % | SD | Min | Max |
|---|---|---|---|---|---|---|---|---|
| a) | | | | | | | | |
| 1° 2002 | 14/06/02 | | 10 | 50 | 68.6 | 20.91 | 30 | 98 |
| 2° 2002 | 27/06/02 | | 14 | 100 | 22.78 | 18.76 | 0 | 75 |
| 1° 2003 | 13/06/03 | | 10 | 100 | 61.9 | 24.93 | 14 | 88 |
| b) | | | | | | | | |
| 1° 2003 | 14/06/03 | 8h | 10 | 100 | 78.4 | 19.68 | 41 | 93 |
| 1° 2003 | 14/06/03 | 20h | 10 | 100 | 80.2 | 21.28 | 61 | 100 |
| 1° 2003 | 15/06/03 | 8h | 10 | 100 | 96.2 | 4.07 | 90 | 100 |

**Table 2** Results of the fertilization rates showing the number of eggs that developed into planulae after 72h. a) Variation in the fertilization rates between spawning events. b) Temporal variation of eggs embedded in mucus surface.



**Figure 5** Survival rates (mean ± SD) of the larval stages from eggs to polyps in the laboratory (dark circles) (10 replicates of 25 eggs). In the left axis, proportion of the primary polyps observed (N total=13).

**Figure 6**  Survival of primary polyps of *Paramuricea clavata* recently settled in the field in 2001 and 2002. Initials numbers were 150 polyps in 2001 and 80 polyps in 2002.



**Figure 7**  Primary polyps of *Paramuricea clavata* recently settled in the field in August 2001.

# ▌▌▌ Discussion

The lack of knowledge about the timing of spawning in corals is one of the main issues preventing the study of early ontogenetic stages (Spaulding 1974, Dahan and Benayahu 1998). Nevertheless, various studies have demonstrated the predictability of spawning in octocoral species (Brazeau and Lasker 1989, Lasker and Kim 1996; Guiterrez-Rodríguez and Lasker 2004).

Here we confirm that spawning in the gorgonian *Paramuricea clavata* is a predictable event which occurs twice each year in the same periods from one to four days before or after the full and new moon of June and when water temperatures are near 16°C.

Our results support the hypothesis that fertilization is external in *P. clavata*. In fact most of the eggs were not fertilized right after the spawning and the more the eggs remained over the surface of female colonies the higher the fertilization rates. Under conditions of reduced water movement, fertilization increased from 62 to 96% (percent of fertilized eggs) over two days.

There was also remarkable variability in the fertilization rates and timing depending on the spawning event observed. The proportion of eggs that developed into planulae was relatively high (average 68% and 62% in 2002 and 2003 respectively) in the first spawning episodes whereas it was low and variable in the second event (from 0 to 75%, mean 22%).

Experimental studies on tropical gorgonians have indicated that the variability in the fertilization rates may depend upon different factors: different sperm release rates, different flow regimes during spawning, the respective positions of female and male colonies, and the variation in the numbers of colonies which spawned (Lasker et al 1996, Coma and Lasker 1997a,b). Further experimental study is needed to ascertain what factors are responsible for the variability in fertilization rates observed in *P. clavata*.

Some authors have argued that higher fertilization rates in the first spawning episodes may guarantee a significant source of larvae to the population (Coma and Lasker 1997a). This seems to account for a mechanism to achieve high fertilization rates at low sperm density, avoiding both sperm limitation and polyspermy in surface brooders (see Lasker 2006). Overall, the high fertilization rates recorded for *P. clavata* contrast with the low rates recorded for the broadcast spawning Caribbean gorgonian *Plexaura Kuna* (<20%; Lasker et al 1996, Coma and Lasker 1997b).

*P. clavata* shows an ontogenic development similar to that of other octocoral species (Benayahu 1989, Benayahu et al 1989; Lasker and Kim 1996, Dahan and Benayahu 1998). However and despite such similarity, the developmental timing seems to be slightly delayed with respect to other species. Both the blastula and the planulae of *P. clavata* appear after 48 hours and between 48-72 hours respectively from the beginning of the spawning. In other octocoral species the first planulae appear from 12-24 hours to 36-60 hours after the spawning (Weinberg and Weinberg 1979 for *Eunicella singularis*; see Table 5 in Lasker and Kim 1996 for other octocoral spe-

cies). There seems to be a short delay also in metamorphosis which takes place between 10-18 days after the spawning in *P. clavata*, disregarding the presence of a suitable substrate on which to settle, and after 4-15 days in other gorgonian species (Lasker and Kim 1996).

To some extent, the larvae of *P. clavata* seemed capable to swim and crawl in an apparent exploratory behavior. In our laboratory experiments the time required for the metamorphosis into primary polyps (minimum 10 days) suggests rather high dispersal potential. Transport over long distances by mainstream flows has been proposed for the gorgonian *Pseudopterogorgia elisabethae* (Gutiérrez-Rodríguez and Lasker 2004).

Nevertheless, possible retention mechanisms exist in *P. clavata*. First, the eggs are kept together within a mucus which may favor both sinking and adhering to the substrates near maternal colonies. Second, the larvae are rather efficient crawlers and tend to keep contact with the substrate in artificial containers. This coupled with the negative phototaxis recorded in the laboratory may allow the larvae to seek crevices and other dark habitats. The negative phototaxis may also represent a strategy of larvae to avoid the competence with fast-growing algae especially in photophilic habitats. Both filamentous and fleshy algae can easily overgrow juvenile individuals and represent the main source of mortality during post-settlement (Mariani et al 2005). Nevertheless, we may need to take into account that to ensure the highest motility of larvae, our experiments on larval response to light were conducted only on 4-5 days old planulae. Larvae of different ages may respond differently to light stimuli.

Studies on dispersal in other octocoral species have pointed out that most larvae settle near parental colonies (Benayahu and Loya 1983, Brazeau and Lasker 1989, Lasker and Kim 1996), hence a similar pattern may occur in *P. clavata*. The extent of connectivity among populations in this species will possibly elucidate with the aid of molecular approaches.

In spite of the high fertilization rates, larval survivorship was extremely low in the laboratory. After fertilization, an average of 60% of the eggs became planulae and during the larval phase the survivorship decreased until 40%. But it was during the metamorphosis when the mortality was highest and only 5% of the initial eggs achieved the primary polyp stage.

Mortality was notably high among polyps in the field (Fig. 6). High mortality and the lack of growth among primary polyps have been described for the tropical gorgonian *Plexaura kuna* (Lasker et al 1998). In the alcyonacean Alcyonium siderium, in contrast, in spite of the low survival, polyps are known to start growing after 3-4 months (Sebens 1983).

The recruitment failure shown in this study is in accordance with the extremely low survival of juvenile stages recorded in an extensive monitoring carried out from 1991 to 2005 in the Medes Islands (R. Coma *unpublished data*). According to the bet-hedging theory (Stearns 1992), sporadic recruitment episodes may be sufficient to ensure the persistence of local gorgonian populations in the absence of strong and frequent disturbances. Nevertheless, the low success, in terms of survivorship, of the first life-history stages, in spite of the great investment in gametes production displayed by *P. clavata* (see also Coma et al 1995b), confirms the species' fragility especially facing anthropogenic disturbances (Coma et al 2004, Linares et al 2005, Chapter IV

and VI). These traits are common among long-lived octocoral species (Lasker 1990, Gotelli 1991, Yoshioka 1998, Garrabou and Harmelin 2002) and reveal severe limitations for local population persistence and colonization of new areas through sexual reproduction.

### Acknowledgements

[] Life History and Viability of
a Long–Lived Marine Invertebrate:
the Octocoral *Paramuricea clavata*

## Abstract

The red gorgonian *Paramuricea clavata* is a long-lived, slow-growing sessile invertebrate of ecological and conservation importance in the North-Western Mediterranean Sea. We develop a series of size-based matrix models for two *Paramuricea clavata* populations. As for many other slow-growing species, sensitivity and elasticity analysis demonstrate that gorgonian population growth is far more sensitive to changes in survival rates than to growth, shrinkage, or reproductive rates. The slow growth and low mortality of red gorgonians results in low damping ratios, indicating slow convergence to stable size structures (at least 50 years). The stable distributions predicted by the model did not differ from the observed ones. However, our simulations point out the fragility of this species, showing both populations in decline and high risk of extinction over moderate time horizons. These declines appear to be related to a recent increase in anthropogenic disturbances. Relative to their lifespan, the values of recruitment elasticity for *Paramuricea clavata* are lower than those reported for other marine organisms but are similar to those reported for some long-lived plants. These values and the delayed age of sexual maturity, in combination with the longevity of the species, show a clear fecundity/mortality trade-off. Full demographic studies of sessile marine species are quite scarce, but can provide insight into population dynamics and life history patterns for these difficult and under-studied species. While our work shows clear results for the red gorgonian, the variability in some of our estimates suggest that future work should include data collection over longer temporal and spatial scales to better understand the long-term effects of natural and anthropogenic disturbances on red gorgonian populations.

Keywords: life-history, population viability analysis, gorgonian, matrix models, size-structured populations, sensitivity, elasticity, longevity, recruitment, NW Mediterranean

# ▌▌▌ Introduction

Matrix population models are a powerful tool for quantifying the population dynamics of diverse organisms and for comparing life history patterns across taxa. These models are most often used to calculate population growth rate ($\lambda$), the stable stage distribution, and the sensitivities and elasticities of population growth to changes in life history parameters (Caswell 2001). While demographic models are widely used to assess the population viability and life history patterns of many terrestrial plant and animal species (Silvertown et al 1996, Caswell 2001, Beissinger and McCullough 2002, Doak et al 2002), they have been applied quite disproportionately to different taxonomic groups, and in particular have been used less commonly in marine conservation than in other fields of population ecology (Gerber and Heppell 2004).

Age or stage-based matrix models have been influential in assessments of the demography and population viability of some large marine mammals, sea turtles, and other vertebrates (Crowder et al 1994, York 1994, Thompson et al 2000, Holmes and York 2003). In contrast, these models have been less commonly used in demographic studies of marine invertebrate taxa. In fact, these studies have been conducted on only a few groups of marine invertebrates including sea urchins (Pfister and Bradbury 1996), bivalves (Nakaoka 1993, 1997), bryozoans (Hughes 1990), hard corals (Hughes 1984, Done 1988, Babcock 1991, Hughes and Tanner 2000), and soft corals and gorgonians (Gotelli 1991, McFadden 1991, Lasker 1991).

In this study, we develop a demographic matrix model for populations of the long-lived, slow-growing Mediterranean red gorgonian coral, *Paramuricea clavata* (henceforth, red gorgonian). In common with other clonal species, both plants and marine invertebrates (Cook 1985, Hughes 1984, Hughes and Jackson 1985), gorgonians have low recruitment rates, high longevity, and low mortality rates (Lasker 1991, Yoshioka 1994, Coma et al 1998, 2003, 2004). In the case of the red gorgonian, these traits have resulted in both extreme local endangerment due to disturbance by increasing SCUBA-based tourism in marine reserves (Coma et al 2004) and in regional endangerment due to mass mortality events (Cerrano et al 2000, Perez et al 2000, Linares et al 2005). Therefore, studying the population dynamics of the species has profound implications for the conservation of the species and more generally for the management of marine protected areas; in Mediterranean marine hard-bottom communities, long-lived species, such as red gorgonian, serve as "ecosystem engineers" (Jones et al 1994), with significant effects on the structure and biodiversity of their communities.

We have developed both deterministic and stochastic size-based matrix models for two red gorgonian populations in the North-Western Mediterranean Sea. We use these models to address three goals. First, we estimate basic life history traits for this species and use the resulting models to evaluate the sensitivity of population growth to different vital rates. Second, we ask how population structure will develop through time and analyze the viability of the red gorgonian populations we studied. Third, we compare the life history patterns of red gorgonian to those of other sessile species of invertebrates and of terrestrial plants to highlight the significance of their reproductive strategy and the resemblance with species

displaying similar life-history traits despite having very different environments and evolutionary histories.

# ||| Material and methods

## ▌ The Natural history of *Paramuricea clavata*

*Paramuricea clavata* (Anthozoa, Octocorallia) is one of the key species of the highly diverse Mediterranean coralligenous communities, playing an important role in the maintenance of biomass and the structural complexity in these habitats (Ballesteros 2006, True 1970). Red gorgonian can be found in rocky substrates from 10 m to at least 110 m, in locations subjected to strong currents (Weinberg 1991), and is widely distributed in the western basin of the Mediterranean and in the Adriatic Sea. In spite of its broad geographic range, red gorgonian has a strikingly patchy distribution.

Red gorgonian colonies are discrete and generally assume a two-dimensional arborescent form, reaching heights of up to 1.5 meters. At present, there is no method available to directly estimate the age of gorgonian colonies. Past studies have estimated mean growth rates of about 0.8 cm/year in colony height (Coma et al 2001 and R. Coma, *unpublished data*), suggesting ages of up to 50 to 100 years for individual colonies. However, breakage of branches on the main stalk is relatively common, so colonies may be much older than they appear. Due to variation in growth rates between individuals and the possibility that individuals can undergo "partial mortality" (loss of living tissue, in part due to branch breakage), two colonies of the same size may be very different in age. As for many other species with indeterminate growth, the demographic characteristics of gorgonian colonies (survival, growth, and fecundity) appear to be influenced more by size than by age. Consequently we classify colonies by size in all of our models.

Gorgonians suffer high mortality rates as recruits and juvenile colonies (Coma et al 2001) and low natural mortality as adults (Coma et al 2004). While partial mortality due to strong currents occurs at low rate, this damage can be dramatically increased by diving activity, fishing nets and lines, and recently by mass mortality events (Coma et al 2004, Bavestrello et al 1997, Linares et al 2005). Colonies can survive and potentially regrow following the loss of living tissue, but past data indicate that regeneration depends on the extent of injuries, and is often fairly low (Bavestrello and Boero 1986, Linares et al 2005).

The reproductive biology of this species has been well studied. The red gorgonian is dioecious, with a sex ratio not significantly different from 1:1 in the studied populations (Coma et al 1995a and R. Coma, *unpublished data*). Spawning is synchronous and occurs two times each year in June, apparently related with the new and full moons. The fertilization is external and embryogenesis takes place on the surface of the colony (Coma et al 1995a). The planulae of red gorgonian have little potential for dispersal and most settle near the parental colony (Coma et al 1995a). Similar characteristics have been observed in other gorgonian species (Gutiérrez-

Rodríguez and Lasker 2004). While this long-lived species has a substantial investment in sexual reproduction each year (Coma et al 1995a), low recruitment rates are typically observed (Coma et al 2001). This pattern is due to high mortality rates during all reproductive stages: fecundity, embryogenesis, and settlement (C. Linares, *unpublished data*). Consequently, the high numbers of eggs produced by female colonies result in only low numbers of primary polyps (the first observable settled stage).

## Data

We analyzed the demographic parameters of the red gorgonian populations located at two marine protected areas of the North-western Mediterranean coast: Cap de Creus, and Medes Islands, separated by more than 25 km. Both localities are typical of the habitats where well-developed red gorgonian populations are found along the North-western Mediterranean coast, and the studied populations are located at the same depth range (15-25 meters). Due to their beauty, red gorgonian populations are among the most attractive areas for scuba divers, making it difficult to study populations that are not subjected to diving impacts. Although our study sites are located within marine reserves, both are subject to considerable levels of diving activity (Coma et al 2004).

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 monitoring of six 4 m long and 0.8 m wide permanent plots at Cap de Creus (2 plots from 2002 to 2004) and Medes Islands (4 plots from 2001 to 2004). All colonies present in a plot were individually identified and mapped at the start of the study and relocated in each year to record their fates. Each of the six plots contained between 80 and 200 colonies in each year of the study. The size of each colony was measured as maximum height in centimetres, and mortality was estimated both through the disappearance of whole colonies and by the presence of the standing dead skeletons of colonies. Reproduction is extremely difficult to quantify in the field, so neither the sex nor reproductive effort was measured in this study. Previous work indicates that the size distributions and hence the demography of male and female colonies are similar (Coma et al 1994). Newly settled primary polyps are extremely small and thus are not readily observable in the field, with newly found colonies typically between 0.3 cm and 3 cm height. Given the growth rates of newly settled individuals observed in the lab (C. Linares, *unpublished data*), these newly found colonies are likely to be in their second year of life.

## Model formulation

We analyzed the demography of red gorgonians using a set of seven age- and size-defined stage classes. The first class is age-based, representing the "newborn" colonies (primary polyps) that

we were unable to directly observe in the field. Class 2 colonies are at least two-year olds 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 colonies 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. These classes are chosen to match those used during previous work on this species (Coma et al 1995b). Further division of the larger colonies into narrower size classes would be desirable, but the low numbers of colonies at these sizes prevent their use.

Across each annual transition period, each gorgonian colony could have 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. 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). The matrix model we used, defined in terms of these vital rates, is shown in Table 1. These rates were directly estimated from the data for each annual transition using all individuals in either population. For these estimates, we grouped data across all plots within a population. Separate likelihood ratio Chi-square (G) tests for each of the five site by annual transition combinations (estimated with all zero frequency cells defined as structural zeros in increase power) showed significant plot effects on transition probabilities only for the Medes population from 2002-2003 (p=0.012). We also tested G-tests to check the assumption that demographic rates can be modelled as first-order Markov processes (Caswell 2001) and found no significant second-order effects for either population.

| Size class t+1 | Size class at time t | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 | 0 | 0 | 0 | $f_a$ | $f_a$ | $f_a$ | $f_a$ |
| 2 | $s_2{}^*g_1$ | $s_2{}^*(1-g_2)$ | $s_3{}^*(1-g_3)^*h_3$ | 0 | 0 | 0 | 0 |
| 3 | 0 | $s_3{}^*g_2$ | $s_3{}^*(1-g_3)^*(1-h_3)$ | $s_4{}^*(1-g_4)^*h_4$ | 0 | 0 | 0 |
| 4 | 0 | 0 | $s_3{}^*g_3$ | $s_4{}^*(1-g_4)^*(1-h_4)$ | $s_5{}^*(1-g_5)^*h_5$ | $s_6{}^*(1-g_6)^*h_{6a}{}^*h_{6a}$ | 0 |
| 5 | 0 | 0 | 0 | $s_4{}^*g_4$ | $s_5{}^*(1-g_5)^*(1-h_5)$ | $s_6{}^*(1-g_6)^*(1-h_{6a})^*h_6$ | $s_7{}^*h_7{}^*h_{7a}$ |
| 6 | 0 | 0 | 0 | 0 | $s_5{}^*g_5$ | $s_6{}^*(1-g_6)^*(1-h_6)$ | $s_7{}^*(1-h_{7a})^*h_7$ |
| 7 | 0 | 0 | 0 | 0 | 0 | $s_6{}^*g_6$ | $s_7{}^*(1-h_7)$ |

**Table 1**    Size-class transition matrix, matrix elements represents tour types of variables ($f_i$, $g_i$, $h_i$, $h_{i2}$, $s_i$); $f$, fecundity; $g$, growth; $h$, shrink in to one smaller class; $h_2$, shrink in two smaller class; $s$, survival.

With the classes we used, the median and minimum number of colonies starting each transition in each year were 99 and 16, respectively, giving reasonable sample sizes for vital rate estimation (the minimum number of colonies were all for size class 2, newly found colonies). As a check, we also used logistic regression to estimate survival as a continuous function of size (-2LL=793.434, Chi square=33.788, df=3, p<0.001); this resulted in survival estimates extremely similar to those found with direct estimation. Since no data are available on the demogra-

phic 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 size class 2, and that all surviving class 1 polyps advance to class 2. Preliminary analyses indicated that alterations of this assumption had no important effects on our results.

To estimate reproduction, we used the relationship between the colony size and the gonadal production described in a previous study of this species (Coma et al 1995b). Based on these data, we assume that the reproductive terms $f_i$ can be estimated as the product of: 1) the size-dependent gonadal production of oocytes from female colonies (assuming a 1:1 sex ratio; Coma et al 1995) and 2) the fecundity of the gonads (fraction of gonads converted to eggs (C. Linares, *unpublished data*) ; 3) the annual survival rate from eggs to primary polyps that would be seen during the census just before the reproductive pulse in June (C. Linares, *unpublished data*; note that we do not include a correction of ½ in this estimation of f to account for dioecy: while only half of colonies are female, our model is for the entire population of male and female colonies, such that the halving of colony number to estimate the number of female colonies is offset by the doubling of reproduction to account for male offspring). The resulting size-dependent estimates of total production of class 1 polyp were then used in each matrix estimated, but did not vary with population or year.

From these vital rate estimates we constructed transition matrices for each time interval for each population (see Table 2), and also a mean matrix for each population. We calculated several outputs from these matrix models. First, we determined the long-term deterministic growth rate, $\lambda_1$, predicted by each matrix. Second, we calculated the damping ratio for each matrix, $\rho = \lambda_1/\lambda_2$ (Caswell 2001), which provides a measure of how fast a population will converge to the stable stage distribution. Third, we quantified patterns of importance to $\lambda_1$ of changes in each vital rate for the mean matrix for each population; given that there is no single correct scaling for measures of relative importance different vital rates (Caswell 2001, Morris and Doak 2002), we present both sensitivity and elasticity values as measures of importance. Finally, we asked how size structure will develop following population establishment, a critical question in interpreting observed population structures. To explore the development of a newly founded population, we used the mean matrix of each population to simulate 100 years of population growth, starting with 100 colonies of class 1 polyp. At each time step the size distribution was recorded, and the results were compared with the observed distribution of each site. To compare the observed and predicted size distributions, the class 1 (primary polyps) were not used, since this class is not observable in the field.

We also conducted a series of stochastic analyses. First, we estimated the stochastic population growth rate, $\lambda_s$ for each population using equally-likely random draws of our annual matrices. These random draw simulations were also used to estimate the probabilities of quasi-extinction for each population for up to 150 years, using an extinction threshold of 10% of the initial population size, and starting with a population size of 300 at stable stage distribution. Second, we used annual estimates of each vital rate to calculate the temporal means, variances, and covariances of vital rates and used Tuljapurkar's small noise approximation to calculate stochastic sensitivity and elasticity values (Tuljapurkar 1990; programs from Morris and Doak 2002 and Doak et al 2005).

**Table 2**    Size-class transition matrices for *Paramuricea clavata* populations at Medes Islands and Cap de Creus.

| Size class t+1 | Medes Islands 2001-2002 | | | | | | | Medes Islands 2002-2003 | | | | | | | Medes Islands 2003-2004 | | | | | | | Cap de Creus 2002-2003 | | | | | | | Cap de Creus 2003-2004 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Size class at time t →* | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 | 0.000 | 0.000 | 0.000 | 0.003 | 0.089 | 0.378 | 0.810 | 0.000 | 0.000 | 0.000 | 0.003 | 0.089 | 0.378 | 0.810 | 0.000 | 0.000 | 0.000 | 0.003 | 0.089 | 0.378 | 0.810 | 0.000 | 0.000 | 0.000 | 0.003 | 0.089 | 0.378 | 0.814 | 0.000 | 0.000 | 0.000 | 0.003 | 0.089 | 0.378 | 0.814 |
| 2 | 0.667 | 0.380 | 0.033 | 0.000 | 0.000 | 0.000 | 0.000 | 0.636 | 0.500 | 0.020 | 0.000 | 0.000 | 0.000 | 0.000 | 0.750 | 0.570 | 0.020 | 0.000 | 0.000 | 0.000 | 0.000 | 0.769 | 0.460 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.667 | 0.250 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 3 | 0.000 | 0.292 | 0.730 | 0.043 | 0.000 | 0.000 | 0.000 | 0.000 | 0.136 | 0.860 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.179 | 0.850 | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 | 0.308 | 0.570 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.417 | 0.770 | 0.000 | 0.000 | 0.000 | 0.000 |
| 4 | 0.000 | 0.000 | 0.120 | 0.780 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | 0.850 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 | 0.040 | 0.870 | 0.007 | 0.000 | 0.000 | 0.000 | 0.000 | 0.260 | 0.820 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | 0.840 | 0.000 | 0.000 | 0.000 |
| 5 | 0.000 | 0.000 | 0.000 | 0.080 | 0.736 | 0.092 | 0.038 | 0.000 | 0.000 | 0.000 | 0.102 | 0.850 | 0.120 | 0.000 | 0.000 | 0.000 | 0.000 | 0.034 | 0.790 | 0.160 | 0.000 | 0.000 | 0.000 | 0.000 | 0.071 | 0.840 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.085 | 0.830 | 0.000 | 0.000 |
| 6 | 0.000 | 0.000 | 0.000 | 0.060 | 0.162 | 0.660 | 0.057 | 0.000 | 0.000 | 0.000 | 0.000 | 0.101 | 0.750 | 0.100 | 0.000 | 0.000 | 0.000 | 0.000 | 0.017 | 0.683 | 0.160 | 0.000 | 0.000 | 0.000 | 0.000 | 0.032 | 0.870 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.076 | 0.880 | 0.120 |
| 7 | 0.000 | 0.000 | 0.000 | 0.000 | 0.092 | 0.092 | 0.740 | 0.000 | 0.000 | 0.000 | 0.000 | 0.003 | 0.078 | 0.850 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.032 | 0.820 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.029 | 0.930 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.031 | 0.820 |

Finally, we employed the equations of Cochran and Ellner (1992) to calculate several different life history parameters for our mean matrices that are useful descriptors of longevity (below, C&E refers to equation numbers in their paper). Using their formulas we estimated: the survivorship function $l_x$, which gives the probability that a newborn will survive to age $x$ (C&E eq. 2); the conditional total lifespan for newborn colonies, which is the mean age at death for a colony, given that they survive long enough to enter size class $i$. (C&E eq. 6), and the mean age of residence in each size class, which provides a way to relate the size and age of a given colony (C&E eq. 29). To estimate these parameters we used the survival matrix P from the mean matrix from each site and the birth matrix B, which contains the reproductive values in the first rows and for which all other entries are zero (see Cochran and Ellner for details). These estimates were performed with the program STAGECOACH (Cochran and Ellner 1992).

We compared two life history patterns of red gorgonians obtained from our analyses with those of other sessile plants and animals. Following other studies (Silvertown et al 1993, Franco and Silvertown 1996) we plotted expected life span (after the first year) against the summed elasticities of early life stage events (see Forbis and Doak 2004 for methods). For this comparison we gleaned data from the literature from demographic studies of sessile marine invertebrates and algae, terrestrial herbs, and terrestrial shrubs and trees. We also contrasted the life span against the first age at sexual maturity with species for which we could glean the necessary data from the literature.

# ▌▌▌ Results ▌

## ▌ Life history and Sensitivity Analysis

As previous studies indicated (Weinberg 1991, Coma et al 1998), our results show that red gorgonian is a long-lived species. We found 63 to 97% survival, with lowest values for class 2 colonies and survival rising to 83 to 100% in the largest size class. In average, the studied populations showed a mean survival rate about 91% and a mean recruitment rate around 3% (see Table 3). In addition, growth rates are slow, with the medians of the probability of growing ranging from 0 to 41% across sizes and years. Just as strikingly, the probabilities of shrinking are larger than that of growing for many size classes in many years (see Table 2 and 3). Together, these characteristics suggest a life history that is at the "slow" end of the "fast-slow continuum" of life history traits (Partridge and Harvey 1988).

The red gorgonian follows a characteristic type III survivorship curve, with rapid declines in survivorship during the first years of life followed by slow and constant declines of large and old individuals and high longevity (Fig. 1a). Because survival of the smaller size classes is low, average total lifespan from settlement is relatively short, but if colonies survive to reach the largest size class, they expected to live more than 60 years (Fig. 1b). The high variance around each age-dependent life-span estimate indicates that the fates of individual colonies are highly variable, with some colonies living considerably longer than the average. The mean age of residence in

each class provides a direct way to examine the size-age relationship. The mean age of residence increases progressively with size class, with a predicted value of 54.9 years for colonies in size 7 (Fig 1c). As for total lifespan, the high variances in age of residence for larger sizes mean that some colonies will be far older than the mean, and some far younger.

The sensitivities to mean vital rates estimated by deterministic and stochastic models are quite similar (Fig. 2a, b), indicating that the degree of variability in demography observed over the study period was not particularly important for red gorgonian population dynamics. In addition, the sensitivities of $\lambda_s$ to variances and covariances of vital rates are extremely small (results not shown); consequently, we present only the deterministic elasticity results. Elasticities show a similar, but stronger, pattern to that of the sensitivities, indicating that gorgonian population growth is far more sensitive to changes in survival rates than to growth, shrink or reproductive rates (Fig. 3). The survivorship of the largest colonies (height >40 cm) does not have the highest elasticity values at either site, due to the relative rarity of these largest individuals. For the Medes Islands, the elasticity of survival rates for class 4 and 5 had the largest values, while in Cap de Creus, the highest elasticities were for survival of classes 5 and 6. The elasticity analyses also suggest that the reproductive parameters (such as reproductive values and survival of newborns and recruits) contribute little to the rate of population increase over the examined period.

| Site | Years | N | Survival | Growth | Shrink | Recruitment |
|---|---|---|---|---|---|---|
| Medes Islands | 2001-2002 | 578 | 89.79 | 8.43 | 8.26 | 5.36 |
| | 2002-2003 | 548 | 93.07 | 8.47 | 1.62 | 0.91 |
| | 2003-2004 | 516 | 90.12 | 3.62 | 5.52 | 3.29 |
| | Average | | 90.99 | 6.84 | 5.13 | 3.19 |
| Cap de Creus | 2002-2003 | 273 | 93.05 | 10.22 | 3.65 | 1.83 |
| | 2003-2004 | 259 | 91.51 | 6.92 | 4.23 | 5.4 |
| | Average | | 92.28 | 8.57 | 3.94 | 3.62 |

**Table 3**    Vital rates of *Paramuricea clavata* populations at Medes Islands and Cap de Creus over the studied period. Survival rates are represented as the % of survival colonies , Growth and Shrink rates as the % of colonies that changed of size class, and recruitment rates as the % of new colonies over the total population during each transition.

Figure 1    a) Survivorship curve for new established colonies from equation 2 of Cochran and Ellner, 1992. b) Total estimated remaining life span, conditional on reaching a size class. c) Mean age of residence, or the mean age of individuals expected to be found in a size class for a population at stable stage distribution. SDs calculated using formulae of Cochran and Ellner (1992) are show above each estimate.

**Figure 2** Deterministic and Stochastic sensitivities of population growth rate to mean vital rates for Medes Island (a) and Cap de Creus (b) populations.

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**Population growth and stage structure**

The annual multiplication rate associated with the different site and time matrices vary considerably (Table 4), but all matrices predict declines in gorgonian populations ($\lambda < 1$). Notably, $\lambda_1$ values for the two mean matrices are almost identical to $\lambda_s$ values for the populations, again indicating

the extremely small effects of environmental stochasticity. $\lambda_1$ values were generally lower for the Medes Islands population than for gorgonians at Cap de Creus. With $\lambda_s$ values less than one, long-term extinction is inevitable, and our simulations suggest high risk of extinction over moderate time horizons (Fig. 4). Quasi-extinction risks correspond to the differences in $\lambda_s$, with a median extinction time of 41 and 115 years at Medes Islands and Cap de Creus, respectively.

The damping ratios for all matrices were quite low, ranging from 1.02 to 1.19, and indicating slow convergence to a stable size structure (Table 4). The simulated evolution of size distributions from recently established populations showed that the proportion in each size class slowly converges to a mean value (see Fig. 5). In both sites an approximately stable stage distribution was obtained after 50 years. The observed size distribution was quite similar at Medes Islands and Cap de Creus, showing a dominance of small reproductive colonies ranged from 10 to 20 cm. The main difference between the sites was the greater proportion of large colonies (>20 cm) in Cap de Creus. The observed stage distributions were not significantly different from the predicted stable stage distributions for either population (Medes Islands: Kolmogorov-Smirnov test, D=0.167, p>0.1; Cap de Creus: K-S test D=0.333, p>0.10). Some differences can be observed, such as a small proportion in the smallest classes compared to that predicted for both populations, and larger proportion of colonies in class 5 in the observed distribution than in the predicted one for Cap de Creus site. Nonetheless, these size distributions indicate that the Medes Islands and Cap de Creus populations are likely to have existed at least 50 years.



**Figure 3** Elasticity values of deterministic population growth rate to vital rates.

| Site | Years | $\lambda_1$ | $\lambda_s$ | P |
|------|-------|-------------|-------------|---|
| Medes Islands | 2001-2002 | 0.929 | | 1.196 |
| | 2002-2003 | 0.988 | | 1.128 |
| | 2003-2004 | 0.935 | | 1.029 |
| | Mean | 0.937 | 0.936 | 1.124 |
| Cap de Creus | 2002-2003 | 0.996 | | 1.140 |
| | 2003-2004 | 0.933 | | 1.055 |
| | Mean | 0.974 | 0.974 | 1.149 |

**Table 4** Annual multiplication rates ($\lambda$) and damping ratios ($\rho$) of transition matrices constructed from different sites and years. $\lambda_1$=deterministic lambda, $\lambda_s$=stochastic lambda. Mean $\lambda_1$ values were estimated from the average matrix of the available transitions for each site.



**Figure 4** Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population. 50,000 simulations were run for each population.

## Comparative Life History

Across the species surveyed, there is a general decrease in reproductive elasticities with increasing the life span. Relative to its lifespan, the red gorgonian shows a lower importance of reproductive vital rates than do other marine invertebrates (Fig. 6a). However, it falls within the expected range of long-lived trees and shrubs - species that share its basic morphology, if differing in all other aspects of their biology. In our second comparison, of age at sexual maturity vs. life span (Fig. 6b), red gorgonian again conforms to the relationship seen for trees, but has a late age at sexual maturity compared with the other marine invertebrate species.

**Figure 5**  Observed size-frequency distributions of colonies and predicted size-distributions at two studied populations, Medes Islands and Cap de Creus. Observed distributions were estimated during the first year of study. Predicted distributions were calculated by iteratively multiplying a population vector consisting of one new established colony and other entries as zeros by population projection matrices for each site to obtain the stable stage distribution (SSD).

**Figure 6** a) Comparison of elasticity values of recruitment or seedling establishment and life span. b) Comparison of age at sexual maturity and life span of different marine species, herbs, shrubs and trees.

# ▌▌▌ Discussion

In most marine ecosystems, such as Mediterranean hard-bottom communities, too little is known about even the most important, structure-forming species to understand base-line eco-logic processes, and hence, the consequences of disturbances. Therefore, the first goal of this study was to quantify the life history and population viability of one of the most representative species of this community, and to identify the life-history traits to which population growth is most sensitive.

In the classification of life histories from fast to slow, the red gorgonian clearly shows a slow pattern, with high survival, low grow, and delayed reproduction. Our estimates of the conditional total life span demonstrate that if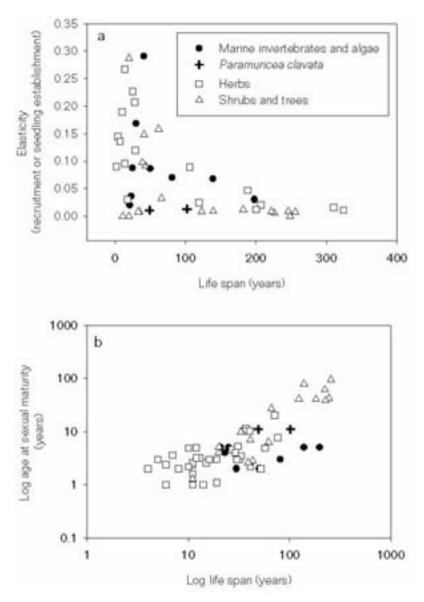 colonies can reach to largest class they may be between 60-100 years old, confirming the longevity of this species. Unlike most demographic analyses of marine organisms (e.g., Hughes 1984, Gotelli 1991, McFadden 1991, Lasker 1991), we focused our sensitivity and elasticity analyses on the vital rates that correspond to demographic processes, not on the matrix elements that are combinations of these rates. As noted by other authors (Zudeima and Franco 2001, Franco and Silvertown 2004), vital rate elasticities are more informative than those for matrix elements because they better correspond to fundamental demographic processes (fecundity, growth, shrinkage and survival). Our elasticity results suggest that population growth is overwhelmingly dependent on survival rates, principally of reproductive colonies (>10 cm). The differences observed between sites, with survival of larger colonies (>20 cm) in Cap de Creus showing higher elasticity values than those for the Medes Islands, are due to the different proportion of larger colonies (>20 cm) at the two sites (49% and 42% respectively) and the higher survival rates of these larger colonies in Cap de Creus (see Fig. 5). Red gorgonians thus conform to the generality that decreases in adult survival rate should more negatively effect population growth for long-lived species with low annual reproductive success than they will for short-lived and highly fecund species (Heppel et al 2000).

In contrast to survival rates, population growth for the red gorgonian is little affected by recruitment variation, as has been found for other gorgonian species (Gotelli 1991, Lasker 1991). Recruitment has widely been considered as an important factor structuring marine communities, with high fecundity of many marine invertebrates combining with spatial and temporal patchiness in larval supply to generate spectacular recruitment pulses and crashes in local populations (Caffey 1985, Caley et al 1996). In contrast to short-lived species, populations of some long-lived sessile species have been shown to be buffered against such fluctuations in recruitment, even when normally low yearly rates alternate with sporadic high peaks (Yoshioka 1996, Connell et al 1997, Hughes and Tanner 2000, Garrabou and Harmelin 2002). Our results suggest that this pattern is comparable for red gorgonian. For such taxa, recruitment variation has limited importance, at least for local populations and relatively short time scales. Instead, survival of large colonies is a key factor for the population persistence; in part because they determine how long a population can persist without recruitment. Still, recruitment patterns may be more important over longer time scales, governing the establishment of new populations, in particular. While the

patchy distribution of red gorgonian populations suggests that it may exist as a metapopulation, larger temporal and spatial scale surveys of the species are needed to investigate the role of recruitment in the dynamics of this long-lived organism.

One of the most striking result obtained in this study is the comparison with other sessile animals and plants, where the life history of the red gorgonian appears to fit in well with species that are similar in general form and lack of mobility, showing that the reproductive strategy of marine long-lived species can be more analogous to some terrestrial long-lived organisms than to other marine species, in spite of their completely different environment and evolutionary history. These comparisons may be extremely useful to achieve a better understanding of the dynamics and life history patterns of these difficult and under-studied marine species.

The values of recruitment elasticity for *Paramuricea clavata* are lower than those reported for other marine organisms but are similar to those reported for long-lived plants (Morris and Doak 1998, Forbis and Doak 2004, Silvertown et al 1993). Across species, fertility and recruitment elasticities are strongly correlated with age at maturation, mean fertility, generation time, and life expectancy. As described for other organisms (Heppell et al 2000, Forbis and Doak 2004), populations with high mean adult survival rates generally have low fertility elasticities and higher adult survival elasticities. In particular, our data are consistent with the relationship between recruitment-seedling establishment elasticities and longevity seen for other species with similar life-history traits such as herbs, shrubs and trees (Forbis and Doak 2004, Franco and Silvertown 2004) pointing to the existence of a clear fecundity/mortality trade-off (Fig. 6a). This trade-off is also evident if we relate the lifespan with the age at maturation and we compare red gorgonian with other similar organisms such as plants (Fig. 6b). This result, comparable to that reported for other gorgonian species (Lasker 1990, Gotelli 1991, Yoshioka 1998, Garrabou and Harmelin 2002), is in concordance with the bet-hedging theory, which predicts adults are selected for high survival when recruitment is highly variable because a long reproductive life is needed to counterbalance years of high juvenile mortality (Stearns 1992).

We also used our demographic models to investigate current population structures and likely future population health. Our simulations show that populations need around 50 years to approach stable stage distributions and that the observed population structures are quite similar from predicted stable stage distributions at both sites. The main difference is due to the very few colonies in the first observable class, possibly a consequence of recent recruitment failures. Because anthropogenic changes in mortality rates are likely to be relatively size-independent, any changes in demographic rates due to these impacts probably have had little effect on size distributions, also helping to explain the good match between our observed and predicted population stage structures.

Given the observed vital rates, both populations appear to be in decline, with both deterministic and stochastic growth rates less than one. The explanation for these declines is likely to be found in anthropogenic impacts. As noted above, while both study areas are located within marine protected areas, both are also heavily visited by divers. Other authors have described an increase in red gorgonian mortality rates in areas with a high numbers of divers, caused by mechanical disturbances (Coma et al 2004). The differences of the population growth rates in

the studied areas also suggest the importance of the diving impact on the population decline. While both areas have substantial diving activity, the Medes Islands have higher visitation, possibly explaining the higher mortality and lower population growth rates at this study site. However we have to be cautious about this explanation due to its correlative nature.

The fact that these populations were observed 30 years ago (M. Zabala, *personal communication*) with a similar distribution as observed now indicates a high persistence of these populations in a stable state. This results contrast with the decline and the extremely high extinction risk predicted by the model, but this apparent divergence may be explained by recent increases in mortality rates due to escalating anthropogenic disturbances. Better understanding of the general long-term patterns on gorgonian populations will require the study of other populations not affected by these kinds of perturbations.

The major limitation in our results comes from the relatively short time-period of data collection. Over our study period, temporal variability had little effect on population growth rates or sensitivity results. While recruitment variation is unlikely to substantially influence our results, infrequent mass mortality events have been observed in red gorgonian populations, and these pulses of mortality could substantially alter the population structure and dynamics we predict. Nonetheless, the model developed in this study allows us to better understand the demography of this species and the likely importance of different threats to population viability.

### Acknowledgements

[] **Immediate and delayed effects of a mass mortality event on a gorgonian population in the NW Mediterranean**

## Abstract

In summer 1999, many invertebrates of hard-bottom communities in the NW Mediterranean suffered mass mortality. Our study assessed the population of the temperate octocoral *Paramuricea clavata* before the event and monitored the population over the following four years. The effects of the mass mortality event exhibited several marked spatial and temporal patterns. Spatial patterns showed a clear depth effect (up to 30-35 m depth), but also a high local variability. The temporal pattern was characterized by a sharp decrease in biomass shortly after the event (58%) caused by the combined effect of colony death (9% of the population) and an increase in the extent of colony injury (from 9% before the event to 52% shortly after it). After 4 years of monitoring, our results indicated a large delayed effect of the event. Population density decreased continuously after November 1999. Over the 4 years after the event, the accumulated density decrease was 48% of the initial population. This decrease was mainly due to the death of colonies subjected to extensive injury and because recruitment could not balance this high mortality rate. After November 1999, biomass kept decreasing but at a slow rate, becoming almost constant after November 2001. Overall, the delayed effect of the event accounted for a 70% loss in *Paramuricea clavata* biomass. The observation of the stabilization of the density and biomass of the species during the last year of our study suggests that the delayed impact of the 1999 mass mortality event may be nearing its end. Nevertheless, given the low dynamics of the species and its role as a habitat former, the delayed effects of the mass mortality event indicates the relevant role that disturbance can play on the population dynamics of the species and as a community structuring force of the coralligenous community.

Keywords: Coralligenous community, injury, NW Mediterranean, *Paramuricea clavata*, partial mortality

# ▌▌▌ Introduction ▌

Diseases and mass mortalities of organisms have been increasingly reported in several marine ecosystems (e.g., Epstein et al 1998, Harvell et al 2002, 2004, Kim and Harvell 2004, Ward et al 2004). Most documented mass mortality events involve decline in ecosystem engineer species (Jones et al 1994), such as corals, sponges and gorgonians, whose structural complexity strongly contribute to the biodiversity of the ecosystem (e.g., Wendt et al 1985, Sebens 1991). In these cases, the main concern regarding the effects of mass mortality on the conservation of biodiversity are the losses at whole community level (Hughes 1994, Aronson and Precht 1997, Greenstein et al 1998, Loya et al 2001), more than the survival of a particular species, which, being mainly clonal organisms, have a great capacity to recover from partial mortality (Hughes and Cancino 1985, Hughes and Jackson 1985).

Many of these ecosystem engineer species are also long-lived and show parsimonious life-history traits. Among the commonest of these traits are poor dispersive attributes by sexual reproduction, delayed maturity, low and infrequent settlement, and high post-settlement mortality (Hughes and Cancino 1985, Jackson 1985, Garrabou and Harmelin 2002, Coma et al 2004). Because of their generally low recruitment success, the recovery of these populations depends mainly on the capacity of colonies to recover from damage, which may require a long time after the event (Hoegh-Guldberg 1999, Wilkinson et al 1999, Guzmán and Cortés 2001). In spite of this potential for long lasting effects, most assessments of the impact of mass mortality events, especially of bleaching events, have been conducted immediately after the event or over only short observation periods (McClanahan et al 2001, Baird and Marshall 2002). These studies allow detecting the immediate impact of such events, but do not assess the delayed impacts, which may be as or more important for the community health. Usually, major disturbances are considered such because of their immediate impacts, but, there is a increasing appreciation that long-term effects of these events also can be a significant risk to affected populations and ecosystems (Monson et al 2000).

In contrast to information on tropical mass mortality events, data on the impact of these events in temperate ecosystems is poor. In summer 1999 a mass mortality event affected many invertebrates of hard-bottom communities in the Ligurian Sea (NW Mediterranean, Cerrano et al 2000, Perez et al 2000). Mass mortality events in these communities have been reported in several NW Mediterranean locations (Rivoire 1991, Bavestrello et al 1994, Harmelin 1984, Mistri and Ceccherelli 1996). However, the summer 1999 event differed greatly from other reports in many ways. First, it affected a wide variety of species and taxa in contrast to previous events, which affected mainly a single species or taxa. Second, it affected communities at a regional scale (i.e., several hundreds of kilometers) in contrast to previous events that had a local (i.e., tens of meters or kilometers) effect.

Previous studies on the 1999 mass mortality were crucial to point out the occurrence of the event and to provide a first estimate of its impact (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001). However, the delayed impact of the event has not been documented because

previous studies were conducted shortly after the event, not accounting for the fate of partially injured colonies. A full evaluation of impact requires a temporal sequence of data from before the event, extending long enough afterwards to give data on a full sequence of recovery (Underwood 1994). The unpredictability of mass mortality events makes it very unlikely that researchers will have such data, but by chance we have survey data from before the mortality event of 1999 (see below).

This study is the first to examine the multi-year effects of the 1999 mass mortality event on the gorgonian species *Paramuricea clavata* (Risso, 1826), by tracking a population from before to 4 years after the event. This paper aims to improve our understanding of the role of both immediate and delayed impacts of low frequency disturbance events on the structure and dynamics of gorgonian populations, in particular, and on the coralligenous community in general.

## ▌▌▌ Material and methods

### ▌ Study system

The coralligenous community (Pérès and Picard 1964, Laubier 1966, True 1970, Ballesteros 2006) is one of the most emblematic of Mediterranean communities for recreational diving because of its high biological diversity and attractive landscapes. Sessile suspension feeders, such as sponges, cnidarians, bryozoans and tunicates, and encrusting coralline algae are the main contributors to the structure and biomass of Mediterranean hard-bottom circalittoral communities (True 1970, Ballesteros 2006). These communities, which have a low turnover (Coma et al 1998a, Ribes et al 1999, Garrabou et al 2002), are particularly vulnerable to accidental erosion by divers (Garrabou et al 1998, Coma et al 2004).

Concerned about the risks associated with diving activities, in late 1998, the Port-Cros National Park (NW Mediterranean, France) initiated a monitoring program of the coralligenous community. The long-lived gorgonian *P. clavata* was selected as a good indicator of this community because it is one of the main contributors to community structure and biomass (True 1970). The first survey of the population was conducted in June 1999. The first indication of mass mortality was detected in the Port-Cros area in late summer 1999 (Perez et al 2000). Owing to the virulence of the event, we surveyed the gorgonian population again in November 1999. Thereafter, we performed annual surveys until 2003.

The marine part of the Port-Cros National Park covers 1300 ha and encompasses two small islands of the Hyères Archipelago (France) in NW Mediterranean (Fig. 1). The distribution, bathymetric range and population structure of the *P. clavata* populations in the park were previously described by Harmelin and Marinopoulos (1994). The species is unevenly distributed, with dense populations found at four locations: La Gabinière, Pointe du Vaisseau et la Croix, Montrémian and La Galère (Fig. 1). The upper distributional limit in the park is approximately 15 m depth and it reaches the lower rocky foundations of the island at about

65 m where rocks are replaced by the sandy bottoms that surround the park (Harmelin and Marinopoulos 1994).



Figure 1   Distribution of the shallow *Paramuricea clavata* population at the Port-Cros National Park and location of the sampling sites. Permanent plots at Montrémian (M1, M2, M3), La Gabinière (G1, G2, G3) and depth transects (T1, T2, T3).

## Depth survey

The effect of depth on the occurrence of the mass mortality event was examined in November 1999 at the deepest population (La Gabinière). Three randomly selected transects were conducted. Each transect consisted of laying a line along the slope of the reef between 0 and 50 m

depth. Total height and the extent of injury of all the colonies within a 0.5 m width on both sides of the line were measured (N=284 colonies). The extent of injury was estimated as the proportion of each colony's total surface that showed no tissue (i.e. denuded axis) or overgrowth by other organisms (as in Nagelkerken et al 1997 and Harmelin et al 1999).

## Permanent surveys

Because of the patchy distribution of the species (Harmelin and Marinopoulos 1994) and the high local variability of the impact of the event (Perez et al 2000, Garrabou et al 2001), we used permanent plots to examine and monitor the population, and also to study the processes and mechanisms that determine the fate of damaged populations.

In June 1999, three permanent plots were setup at two locations, La Gabinière and Montrémian (Fig. 1). The plots were randomly selected within the same depth (approximately 25 m) and orientation (facing north) to reduce variance in population structure and density. Each plot was 4 m long and 0.8 m wide (3.2 $m^2$ in surface). To facilitate mapping accuracy, each plot was partitioned in 40x40 cm quadrats. The corners of each plot, as well as those of each quadrat, were marked with either steel climbing parabolts or PVC screws fixed to holes in rocky substratum with a two-component putty. In each survey, elastic bands were placed around the corners to facilitate the recognition of quadrat borders. Each plot was monitored six times. The first survey was performed in June 1999 (before the mass mortality event), the second shortly after the event (November 1999), and the rest in June 2000, November 2001, November 2002 and November 2003.

During the first survey, all gorgonian colonies in each 40x40 cm quadrat were mapped on a polyvinyl sheet by scuba divers. On subsequent dates, maps from former surveys were used to facilitate the re-identification of each colony. For each gorgonian, colony height, extent of colony injury and 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. The extent of colony injury was estimated as described (see above). The colonies at the depth studied develop mainly on a single plane, which facilitated the estimate of extent of injury. Epibionts were identified at the level of large taxonomic groups, and the most frequent were recorded considering their abundance (see below).

A number was assigned to each colony for purposes of recognition for the data-base and for use in following surveys. This procedure allowed us to monitor more than 100 colonies within each of the six permanent plots in the six surveys. Colonies were grouped for demographic analysis in size-classes in accordance with their height. Six classes were distinguished, each covering a range of 10 cm in height: 0-10, >10-20, >20-30, >30-40, >40-50, >50 cm.

In November 1999, we studied whether the partial colony mortality differed among the distinct parts of the colony. For each of 115 randomly selected damaged colonies, the following infor-

mation was recorded at about 25 m depth: colony height, extent of injury, type of injury and position of the injury within the colony (i.e., basal, central, apical, basal + central, basal + apical, central + apical, basal + central + apical). A Chi-square test was used to examine differences in the position of the injury within the colonies.

To address the inherent limitations of permanent plots (mainly that the results are representative of what occurs within the plot but may not be representative of what occurs over the whole population patch), we examined whether the results obtained within these differed from those of random plots within the same population patch. For this purpose, we used one of the two study locations (i.e., Montrémian, 25 m depth). At this location, the species exhibit three dense population patches of about 60 $m^2$ on separated rocky bars between 20 and 30 m deep. The comparison was performed on one of the three population patches. The extent of colony injury (partial colony mortality) from nine pairs of quadrats randomly selected (0.32 $m^2$ each pair) within a permanent plot was contrasted with that of nine pairs of quadrats randomly selected from the same population patch. We used ANOVA, with treatment and quadrat as the independent variables (quadrat nested in treatment) and partial mortality as the dependent variable.

## Analysis

The periodical surveys of the permanent plots allowed the monitoring of four parameters of the population at Port-Cros: total mortality, partial mortality, contribution of each of type of injury to total injury and colony size (height). Biomass monitoring over time came from the data on colony size and on the extent of injury.

Total mortality was estimated as the death of colonies within each plot over time. Death colonies included those exhibiting 100% injured surface and colonies that disappeared between surveys. To examine the effect of size on total mortality the population was pooled into 6 size-classes as described above. The population structure before the mass mortality event (June 1999) was compared with that of the colonies that died over the study period (June 1999-November 2003). A Chi-square test was used to examine differences in total mortality among size-classes. Partial mortality was estimated as the percentage of tissue loss (coenenchyme) of each colony including both, affected and unaffected ones. Partial mortality is described as the extent of injury (i.e., the proportion of the surface of each colony that showed no tissue or overgrowth by other organisms). At the beginning of the study we analyzed differences in observer estimates of the extent of injury. Several observers were asked to estimate injury levels on one hundred colonies that exhibited from 0 to 100% of colony surface injury. There were no significant differences in the estimates given by the different observers (one-way ANOVA $F_{2,297}=0.172$, p=0.841).

Differences in the extent of colony injury between the two locations (i.e., La Gabinière and Montrémian) were examined using a 2-way ANOVA, with location and plot (3 plots per each location) as independent variables (plot nested in location). To quantify the effects of size and

extent of injury on total mortality rate we distinguished between two size-classes (colonies <10 cm in height and colonies >10 cm in height) and four injury categories within each size class [unaffected colonies, colonies with less than 33% of surface injury (<33%), colonies with between 33 and 66% (>33-<66%), and colonies with more than 66% (>66%)]. The four surveys performed after the event (November 1999) provided four estimates of mortality rate as a function of size and extent of injury. The effect of size and extent of injury on mortality rate was examined by means of a 2-way repeated measures ANOVA, with size and injury extent as independent variables and the four times intervals as repeated estimates of mortality rate.

Recruitment was assessed as the number of new colonies that appeared in the permanent plots after each survey. Data on recruitment is essential as it contributes to our understanding of the population changes that occurred over the study period. However, the proper evaluation of recruitment rate of a long lived species such as *P. clavata* should be conducted within a long-term spatio-temporal evaluation of the parameter. Therefore, recruitment data is not analyzed in detail here.

The contribution of each type of injury (naked axis or epibiont taxa) to the total injury was estimated by examining the frequency and the rank of abundance of each type of injury. An index of abundance (I.A.) for each type of injury was calculated by weighting the frequency of each item with its abundance rank:

$$I.\,A. = \sum_{i=1}^{3} (4\text{-}i)\, f_i$$

where i was the ordinal rank (between 1 and 3) of abundance of each item among the epibiont taxa and naked axis of each injured colony; and, $f_i$ was the proportion of injured colonies (frequency of cases) in which this item was at the $i$ rank.

Size (height in cm) was measured for all colonies within the plots at each survey. Size was used to estimate biomass by using a relationship reported in a previous study (B=0.002 H $^{2.61}$, Coma et al 1998b), where B is biomass in grams of dry mass (DM) and H is colony height in centimeters. Corrections for biomass loss caused by injury were introduced to calculations by subtracting the percentage of biomass equivalent to the percentage of colony surface affected by injury.

# ▐▐▐ Results

## ▌ Effect of depth on the mass mortality event

The extent of colony injury with depth showed a similar pattern of decrease in the three examined transects. A clear depth threshold was observed around 30-35 m on the effect of the event

on the population (Fig. 2). The gorgonian colonies were severely affected above this threshold, whereas those below it were little affected (35-40 m) or unaffected (>40 m, Fig. 2).



Effect of depth on partial mortality (extent of injury, mean ± SE) of affected and unaffected *Paramuricea clavata* colonies along three depths transects at La Gabinière.

### Density, survival and recruitment

A total of 736 colonies were recorded at the beginning the study at the six permanent plots, which represents a mean density of 38 ± 11 colonies/m$^2$ (mean ± SD). The density of colonies differed among plots. Those at La Gabinière showed the lowest and highest densities (25-59 colonies/m$^2$) whereas those at Montrémian (33-38 colonies/m$^2$) were closer to the average density (Fig. 3). Nevertheless, all the plots showed the same pattern of decrease in density over time after the event (Fig. 3). Shortly after the mass mortality event, 9% of the colonies died exhibiting 100% injured surface. Whole colony mortality showed a progressively slower rate from November 1999 to November 2003. The mortality rate decreased from about 2.9 ± 0.4% per month (mean ± SE) from November 1999 to June 2000 to about 1.0 ± 0.2% per month (mean ± SE) from November 2002 to November 2003. In November 2003, the cumulative mortality of initial colonies amounted to a total of 48 ± 7% (mean ± SD) of the population (i.e. 358 colonies died, Fig. 3).

Patterns of density observed over the study period is the result of the integration of two processes: colony death (i.e. colony mortality) and the recruitment of new colonies. Recruitment over the 4 years accounted for a total of 116 colonies and was subjected to a mean annual mortality rate

of about 45%. Recruitment did not counterbalance mortality (i.e. 358 colonies) and, therefore, the population density decrease was driven mainly by the pattern of colony mortality (Fig. 3a, b).

By contrasting the size distribution of colonies at the beginning of the study (June 1999) with that of colonies that died over the study period (June 1999-November 2003), we observed that all size-classes exhibited similar proportions of dead colonies ($\chi_2$=5.449; d.f.=5; p=0.358, Fig. 4) and, thus, the overall mortality rate did not differ among size classes.



**Figure 3** Changes of density (N colonies/m$^2$) at the six permanent plots from June 1999 to November 2003: a) density includes new born recruits, b) only those colonies present at the beginning of the study were considered. Abbreviations for the permanent plots as in Fig. 1.

Figure 4    Contrast of the size structure of live colonies in June 1999 with the size structure of those that died over the study period (June 1999-November 2003). Data pooled from all plots (total live colonies: 736, total dead colonies: 358).

### Partial mortality

In June 1999, partial mortality affected 28.4 ± 6.0% (mean ± SD) of the colonies. Shortly after the event, this value increased to 76.1 ± 8.4% (mean ± SD). Furthermore, the average extent of colony injury, which, in June 1999, was about 9.2 ± 2.3% of the colony surface (mean ± SD), sharply increased to about 52.2 ± 13.1% of the colony surface (mean ± SD) after the event (Fig. 5a) at both locations.

The proportion of colonies exhibiting denuded parts (without fouling, naked category in figure 6) was low before the event (2.5% of the colonies in June 1999). The death of the coenenchyme left a large proportion of the axis of the colonies denuded shortly after the event (see Cerrano et al 2000 for a description of the process and Perez et al 2000 for documentation of the process at the study site), and allowed an extraordinary increase in injury and epibionts with respect to June 1999 (Fig. 6). The proportion of colonies exhibiting denuded parts increased to 35% in November 1999; however, this proportion decreased after November 1999 because a large proportion of the denuded axis was progressively covered by epibionts (5.5% in June 2000). Hydrozoans, bryozoans, polychaetes and algae were among the main epibionts that covered the denuded axis of the injured colonies (Fig. 6).

In November 1999, injury affected all parts of the colony (i.e. basal, central and apical parts) with equal probability ($\chi_2$=7.074; d.f.=5; p=0.215, Fig. 7) and the extent of injury did not differ among locations (2-way ANOVA, $F_{1,4}$=0.126, p<0.7407, Fig. 5a).

The extent of injury varied significantly with colony size (Table 1a), although it did not vary between the largest size classes (i.e., >10-20 cm, >20-30 cm, >30 cm, Table 1b). The average extent of injury of colonies >10 cm was over 2 fold (61.25 ± 1.45% of colony surface, mean ± SE) that of colonies <10 cm (24.14 ± 2.50% of colony surface, Table 1b).

From November 2001 to November 2002, although the overall extent of injury remained high (about 37%), the proportion of colonies with denuded axis was similar to the values observed before the event (2.5 and 2.8%, respectively). In November 2003, the proportion of denuded axes increased about two fold (6.0% of the colonies). Nevertheless, the overall extent of injury exhibited a slow but steady decrease from November 1999 to November 2003 (Fig. 5a).



Figure 5    Changes (mean ± SE): a) partial mortality (% of injured colony surface) including affected and unaffected colonies; b) biomass (g DM/m$^2$) over the study period (June 1999-November 2003) at the two locations (Montrémian and La Gabinière).

In November 2003, we examined whether estimates of extent of injury on the permanent plots were representative of the study area by contrasting these results with those obtained from the examination of randomly selected quadrats outside the plots. No significant difference in the average extent of colony injury between the two treatments was observed (permanent versus random, 2-way ANOVA, $F_{1,1}=100.907$, p=0.063); however, we found high small scale variability of the effects of the event.

At all levels of injury, the total mortality of colonies <10 cm in height was about 54% higher than that of large ones (>10 cm in height; 2-way repeated measures ANOVA, $F_{1,3}=12.285$, p=0.039, size effect; Fig. 8). Furthermore, the extent of injury increased total mortality of both size classes (2-way repeated measures ANOVA, $F_{3,9}=4.159$, p=0.042, injury effect) because the mortality rate of colonies affected by high levels of injury (i.e., >66% of the colony surface) increased between 1.5 and 2 fold (about 80%) for both size classes (Fig. 8). The interaction between size and injury was not significant.



**Figure 6**   Changes in the abundance index values of naked axis (Naked, arrow) and in groups of epibionts over time.

**Figure 7** Proportion (%) of affected colonies exhibiting injury in each of the positions within the colony (basal -B-, central -C-, apical -A-). Colonies with 100% injured surface were not considered.

| Source | df | MS | | F | P |
|---|---|---|---|---|---|
| Size Classes | 3 | 0,062 | | 114,890 | <0.001 |
| Error | 722 | 0,062 | | | |

**b) Scheffé's contrast test**

| Extent of injury | | 0,239 | 0,586 | 0,624 | 0,616 |
|---|---|---|---|---|---|
| Source | | (1) | (2) | (3) | (4) |
| 0-10 cm | (1) | | | | |
| 10-20 cm | (2) | < 0.001 | | | |
| 20-30 cm | (3) | < 0.001 | 0,615 | | |
| > 30 cm | (4) | < 0.001 | 0,743 | 0,994 | |

Extent of injury in Scheffé's contrast test are arctan transformed values

**Table 1** a) One-way ANOVA comparing extent of injury (%, arctan transformed) for *Paramuricea clavata* among size classes. Probability values of <0.05 were considered significant. Abbreviations: df, degrees of freedom; MS, mean square; SS, sum of squares; F, F ratio; P, probability.

Figure 8    Mortality rate (%dead colonies/month) for colonies <10 cm in height and colonies >10 cm subjected to different proportions of injury of the colony surface from November 1999 to November 2003.

## Biomass

At the beginning of the study, the mean biomass of the species was 431 ± 102 g DM m-2 (mean ± SD) at Montrémian and 338 ± 125 g DM m$^{-2}$ (mean ± SD) at La Gabinière (Fig. 5b). Shortly after the event, a decrease in colony density (total mortality) and in the extent of live colony tissue (partial mortality) resulted in a marked lost of biomass. The average decrease in biomass at the two locations was about 58 ± 3% (mean ± SD) of the June 1999 values. The pattern of decrease was similar at both locations (Fig. 5b). After November 1999, biomass values kept decreasing but at a slow rate. After November 2001, the mean biomass values remained about constant. In November 2003, the average cumulative drop in biomass at the two locations accounted for 70 ± 6% (mean ± SD) of the initial population (Fig. 5b).

# ‖‖ Discussion

The population of *P. clavata* at the Port-Cros National Park was strongly affected by the mass mortality event of the summer of 1999. The occurrence of this event at Port-Cros was first reported at the beginning of September (Perez et al 2000). Because of logistical reasons, our

first survey after the event was not possible until November 1999. This delay prevented us from observing the progressive death of coenenchyme and its detachment from the skeletal axis (see Cerrano et al 2000 for a detailed description of the process). However, the increase in extent of injury and mainly in denuded skeletal axis without macroscopic fouling observed in November 1999 is consistent with the relatively rapid occurrence of the event (in some cases it took a few days for healthy populations to show marked evidences of mortality, Perez et al 2000).

Previous studies on the 1999 mass mortality highlighted the occurrence of an unusual mortality for the population of several species from the coralligenous community (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001). These studies contributed to determining the geographic extent of the event, and the high diversity of taxa affected and, although data previous to the event was not available, these studies provided a first estimate of the impact on the population shortly after the event. The availability of data before the event has allowed us to provide a quantitative estimate of the immediate impact of the event in contrast to the status of the population before its occurrence. Furthermore, the 4-year monitoring after the event has allowed us to determine the delayed mid-term effects of the event on diverse parameters of the population.

In June 1999, the proportion of colonies with some amount of injury (28%) was similar to that previously reported for the *P. clavata* population at Port-Cros (33%, Harmelin and Marinopoulos 1994) and at Medes Islands (32%, Coma et al 2004). Furthermore, the average proportion of colony surface affected by injury (about 9 ± 2%) was also similar to the value documented at Medes Islands (8.6%) on the basis of a 6-year monitoring survey (Coma et al 2004). These results indicate that both the proportion of colonies with partial mortality and the extent of colony injury remain constant over time when not subjected to extraordinary events.

Despite the high site to site variability of the impact of the mass mortality event (proportion of affected gorgonians ranged from 60 to 100% of the population, Cerrano et al 2000, and up to 90% of the population, Perez et al 2000, in distinct localities), the increase in the number of colonies exhibiting partial mortality (from 28 to 76%) and in the average percentage of extent of injury (from 9 to about 52%) from June to November 1999 is consistent with the general values provided by previous reports. The estimates of colony injury previous to the event have provided a reference to quantify the impact of the 1999 event on the species. The mass mortality event at Port-Cros increased the number of colonies affected by partial mortality about three fold and the average extent of injury about six fold.

The death of the coenenchyme did not show a specific pattern, all parts of the colony from the base to the tips were affected similarly. This result is consistent with preliminary observations in *P. clavata* (Cerrano et al 2000) but also in *Corallium rubrum* (Garrabou et al 2001). However, *P. clavata* colonies >10 cm exhibited a greater extent of injury than those <10 cm. It is unclear why the former were more affected. The accumulation of commensals, parasites and borers in large colonies may make them more susceptible to partial mortality. A higher percentage of partial mortality in large colonies in contrast to small ones has also been documented in several coral species (Meesters et al 1996, Lewis 1997).

The amount and composition of epibionts showed a considerable variation over time. A succession of different types of epibionts was observed, from abundant naked tissue and pioneering species, such as hydrozoans, to older colonies of bryozoans, sponges and polychaeta. In spite of the increase and the variation of epibiosis after the mortality, epibionts covered the naked tissue but not increased the mortality of injured colonies as showed the pattern of the injured surface over time. Denuded parts in unaffected populations represent always a small proportion of partial mortality (usually <5%, Harmelin and Marinopoulos 1994, Coma et al 2004) because, as shown by the results, they are quickly overgrown by a succession of epibionts. Then, the extent and type of injury and epibionts can be considered as an indicator of whether a disturbance event has occurred recently or not.

Mortality rate of small colonies is much higher than that of large colonies when the population is not subjected to extraordinary events (Coma et al 2001, 2004). Then, the fact that the overall mortality rate did not differ among size classes (Fig. 4) indicates that the impact of the event on colonies >10 cm in height was higher than that on colonies <10 cm. This was due to the 2 fold higher extent of injury of colonies >10 cm in contrast to colonies <10 cm, and to the increase in mortality rate with to increase in injury level.

The immediate impact of the mass mortality event on the population indicated a high impact in terms of increase in the extent of colony injury, but showed a much smaller impact in terms of total colony mortality (5-14%, in average 9% of the population). These values are consistent with previous reports (10-18% of the population, Cerrano et al 2000). These values were highly relevant for *P. clavata* because natural mortality of this species when not subjected to extraordinary events has been estimated in the order of 3% of the population per year for colonies >10 cm (Coma et al 2004). However, after 4 years, total colony mortality amounted to almost half of the initial population. This appears to be due to a delayed stress response in the surviving colonies affected by extensive injury (>66% of the colony surface), because these exhibited a higher mortality rate than uninjured or less injured ones. The large increase (several fold) in mortality estimates shown by the contrast between the short-term versus the multi-year assessment of the event at the study site indicates a much greater impact on this species than that indicated by previous estimates (Cerrano et al 2000). The crucial role that low natural mortality rate of large colonies plays in attenuating the effects of long episodes of low recruitment on the population and against high mortality rates of small colonies (Coma et al 2001, 2004), makes uncertain the long-term consequences of this loss on shallow populations of the species. Modelling is required to address this issue. Population viability analysis (Morris and Doak 2002) can be conducted by simulating scenarios with distinct frequencies of catastrophic events. In this framework, our estimates on mortality and recruitment rates both during and after the mortality events together with previous data on mortality, recruitment, growth, density and size structure in non-catastrophic conditions may contribute to the development of these models.

The monitoring over the 4-years following the event has also shown that recruitment does not compensate for the losses caused by colony death (a total of 116 recruits subjected to a high mortality rate in contrast to the 358 colonies that died). Furthermore, a decrease in the extent of colony injury was more apparent during the first two years, diminishing thereafter. The obser-

vation that population biomass did not increase during the 4-years after the event, despite the decrease in extent of injury, indicates the breakage of the injured skeletal axis. This kind of breakage has been reported to be a healing mechanism in other Mediterranean gorgonians (i.e., *Eunicella cavolinii*, Bavestrello and Boero 1986). The stabilization of density and biomass during the last year indicates that the delayed impact of the 1999 mass mortality event may be nearing its end, and that from here on the population may start to show signs of recovery. However, recovery, understood as the restoration, following a disturbance, of a population to a degree comparable to its original state (Pearson 1981), is still far from being attained.

Several hypothesis have been proposed and discussed on the causes of the 1999 mass mortality event, including the presence of pathogens, chronic contamination (pollution), high temperature, and energetic constraints (Romano et al 2000, Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Martin et al 2002, Coma and Ribes 2003). Biological surveys done after the event indicate that the most probable cause is climatic. The persistence of water column stability and high temperatures were the most distinctive climatic anomalies during this time period caused by the scarcity of NW winds (Romano et al 2000).

The spatial distribution of the mass mortality event is complex at both large and small spatial scales (Perez et al 2000, Garrabou et al 2001, this study). However, the impact on the population exhibited a marked depth pattern in which the shallowest colonies were the most affected. The threshold between affected and unaffected populations (in our study between 35 and 40 m) was similar to that reported in eastern Ligurian Sea locations (i.e. 40 m, Cerrano et al 2000), but the event affected deeper populations at several other locations along the coast of Provence (45 m, Perez et al 2000). The mortality event at Port-Cros approximately coincided with the deepest thermocline that occurred at the end of summer 1999 (Harmelin 2004). This pattern supports the climatic hypothesis because of its relation with the thermal stratification present during that time period (Romano et al 2000, Harmelin 2004).

In this regard, the recent warming of the Mediterranean (Pascual et al 1995, Bethoux et al 1998) has been related to the 1999 summer event (Cerrano et al 2000, Coma et al 2000, Perez et al 2000, Garrabou et al 2001, Coma and Ribes 2003). In summer 2003, another mass mortality episode was observed across the NW Mediterranean coasts (Coma et al 2003, J.M. Culioli *personal communication* and J. Garrabou *personal communication*). Its occurrence indicates that the frequency of these events may be increasing as a result of the whole climate change. Therefore, a repetition of mass mortality events would be expected.

In this study, *P. clavata* was used as an indicator-species representative of the complex benthic communities along the circalittoral rocky bottoms of Mediterranean coasts. However, given the structural and biomass contribution of the species (True 1970) to one of the most diverse Mediterranean communities (more than 1600 species have been listed in the coralligenous communities, Ballesteros 2006), the survival of the community may be closely linked to that of the habitat-forming species. The absence or scarcity of this highly interactive species can leave a functional void that can cause linked changes to degraded or simplified ecosystems (Soulé et al 2003, Ribes and Coma 2005).

The importance of the delayed effects of mass mortality events together with the potential increase in the frequency of these events highlights the contribution of disturbance to the dynamics of *P. clavata* populations and its role as a community structuring force of the coralligenous community.

## Acknowledgements

This paper is dedicated to the memory of Lluís Dantart, who died on February 2005 from a car accident at the age of 42. He was a great naturalist, an excellent photographer and overall a good friend. We miss you.

[] Effects of a mass mortality event
on reproduction of the gorgonian
*Paramuricea clavata*

## Abstract

The impacts of disturbances are normally measured in terms of their effects on adult mortality, while less obvious impacts on reproductive biology are usually ignored. Although previous studies have contributed to the understanding of the impact of 1999 mass mortality on populations, none of them have focused on the effects of these events on the reproduction. The aim of this study was to determine the impact of the mass mortalities on reproduction of the gorgonian *Paramuricea clavata*. We studied the effect of the extent of injury one year (June 2000) and two years after the mortality event (June 2001). Females showed a greater decrease of the percentage of fertile polyps and loss of gonadal biomass than male colonies. Female colonies moderately affected exhibited about 22% decrease in the proportion of fertile polyps, while severely affected colonies showed about 35% decrease. In contrast, the highest affected male colonies showed only a slightly decrease of 12% of the fertile polyps. Female colonies displayed a progressive decrease in gonadal biomass with the increase of the extent of injury up to the >33%. In average, female colonies affected by extent of injury >33% exhibited a 73-77% reduction in oocyte production. In contrast, gonadal biomass in male colonies decreased rapidly from 5% of injured surface, showing stabilization of the biomass lost among the colonies exhibiting any extent of injury (>5%), in average these colonies showed a 48-61% reduction in spermary production. For male and female colonies, the mean diameter of gonads did not vary among colonies with different extent of injury, whereas the number gonads followed the same pattern exhibited by gonadal biomass with the increase of injury extent. The fact that the values of gonadal biomass obtained during 2001 were higher than those obtained during 2000 for female and male colonies seem indicate that the high temperature registered during the event had in some sense a direct effect over the reproduction. But furthermore, the effect of the extent of injuries over the reproduction output was maintained along at least two following years, meaning that the mortality impact over this biologic parameter was not only given during a specific time but during the impact. This study shows that as well as the 1999 mass mortality event directly affected the demographic parameters of the *P. clavata* populations, this event caused severe indirect effects on the reproduction of the species that may represent an additional difficulty to the recovery at long-term scales.

# ▌▌▌ Introduction

There is a general agreement that coastal marine ecosystems are being threatened by mass mortalities events and diseases linked to climate warming (Harvell et al 1999, Romano et al 2000, Harvell et al 2002). These events result in ecological responses concern to the performance of individuals, the dynamics of the populations and the processes determining the structure of the communities (Harley et al 2006).

Mediterranean hard-bottom communities dominated by long-lived species (Ballesteros 2006) have been recently affected by mass-mortality events associated to unusual increases of seawater temperature (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Linares et al 2005, Coma et al *in press*). In 1999 and 2003, mass mortality events affected hard-bottom communities at a regional scale in the NW Mediterranean. These events were the strongest ever recorded in the area and affected a wide variety of species and taxa along hundreds of kilometers (Cerrano et al 2000, Perez et al 2000, J. Garrabou, *unpublished data*). While several studies examined the impact of these mortalities in different gorgonian species short after the event (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001), others studies assessed their effects at a mid-term scale revealing that the delayed effect caused the death of about 50% of the population (Linares et al 2005, Coma et al *in press*). These mass mortality events are especially severe in long-lived organisms, such as the Mediterranean gorgonian *Paramuricea clavata*, because they exhibit a low resilience facing to disturbances (Linares et al 2005, Chapter IV).

The impacts of disturbances are normally measured in terms of their effects on adult mortality, while less obvious impacts on reproductive biology are usually ignored (Hughes and Connell 1999), even though the changes that affect reproduction may have significant effects on adult populations (Hughes et al 2000). Most of the studies about mass mortality events are related to coral bleaching (Glynn 1993, Brown 1997, Harvell et al 1999). However few studies have examined the bleaching impact on coral reproduction showing the negative effects of these events on different reproductive parameters (Szmant and Gassman 1990, Michalek-Wagner and Willis 2000, Baird and Marshall 2002, Mendes and Woodley 2002) in spite of the knowledge that damage to coral tissues and skeleton caused by different agents such as storms, sedimentation or predation affects important biological processes such as reproduction (Kojis and Quinn 1981, Van Veghel and Bak 1994, Kramarsky-Winter and Loya 2000, Oren et al 2001).

Even if it seems that the recruitment has limited importance on the persistence and viability of this gorgonian species, at least for local populations and relatively short time scales (Linares et al *in press*, Chapter III), studies of the mass mortality effects on sexual reproduction are clearly necessary given the importance of the sexual reproduction in the replenishment of gorgonian populations (Coma et al 1995a). Although previous studies have contributed to the understanding of the impact of 1999 mass mortality on populations, at our knowledge none of them have focused on the effects of these events on the reproduction (but see Cerrano et al (2005) for the examination of the population sex ratio).

The aim of this study was to determine the impact of the mass mortalities on reproduction of the gorgonian *P. clavata*. This impact was assessed in relation to the increase of colony injuries during 1999 mass mortality. To examine this impact on gonadal production, firstly, we studied the effect of the extent of injury one year after the mortality (June 2000) and secondly we evaluated the persistence of these effects over time (June 2001).

# ▌▌▌ Material and methods

## ▌ Reproduction biology of *Paramuricea clavata*

The red gorgonian *Paramuricea clavata* is a surface brooder species with a substantial investment in sexual reproduction each year. *P. clavata* is a dioecious species with a sex ratio generally not significantly different from 1:1. The spawning is synchronous and occurs twice each year during the month of June. Oocyte development lasts between 13 and 18 months contrasting to sperm development that takes place during 6 or 7 months. While all the male gonads are spawned each year, only female gonads greater than 200 $\mu$m are spawned during the year (Coma et al 1995a,b). Bearing in mind, that mass mortality occurred in late summer (1999), the potential effects on reproduction should be observed during the following reproductive cycle (2000).

## ▌ Gonadal production

The effect of the extent of injury on gonadal production was examined by means of samples from 120 different colonies divided in 4 categories of extent of injury of colony surface (<5%, >5-33%, >33-66%, >66%). During June 2000, samples from two populations affected by 1999 mass mortality (Gabiniere and Montremian) placed at Port-Cros National Park in France (see Linares et al 2005) were collected between 20 and 25 meters by Scuba divers. Samples were immediately fixed in 10% formalin in sea water. For each category, an apical fragment of 30 colonies ranging in height from 30 to 40 cm was randomly collected. In the laboratory, the sex of the colonies was determined in order to examine 10 males and 10 females, and 10 polyps of each colony were dissected under a binocular dissecting microscope (100 polyps for each category of injury at each locality), and the number and diameter of oocytes (greater than 200 $\mu$m in female colonies) and spermaries were recorded for each polyp (Coma et al 1995a).

To study the production of gonads, we estimated the percentage of fertile polyps, the number and diameter of oocytes and spermaries and the gonadal biomass per colony estimated from the number and diameter of gonads (Coma et al 1995b). Although gonadal biomass represents the illustrative parameter of the changes on reproduction, we also considered necessary show the

diameter and number of gonads to explain the possible changes on reproduction. Sex ratio was examined analyzing the proportion of both sexes of 120 colonies (30 for each degree of injury) sampled at both studied sites in 2000.

During June 2001, samples from colonies with <5 and >66% of injury surface were collected in one of the two sites sampled before (Montremian). The same methodology and the same number of samples were used to evaluate the gonadal production during this year and to examine the potential effects two years after the impact.

Finally, to test the effect of injury effect on the gonadal production of male and female colonies we used a two-way ANOVA test to determine differences between sites and extent of injury. To evaluate if the effect remained over time, we used a two-way ANOVA test to determine differences between years and extent of injury.

# Results

## Sex ratio

The red gorgonian population showed a sex ratio not different from 1:1 ($x_2$=0.7212; d.f.=1; p=0.395) in any of the two localities studied, Montremian (56 females and 61 males) and Gabiniere (59 females and 51 males). The number of indeterminate colonies was variable (3 and 9 respectively) and always corresponded to colonies with high degree of injuries (>33% affected tissue) (Table 1).

| Injury degree | Montremian | | | | Gabiniere | | | |
|---|---|---|---|---|---|---|---|---|
| | Female | Male | Indet. | N | Female | Male | Indet. | N |
| <5% | 14 | 16 | 0 | 30 | 18 | 12 | 0 | 30 |
| >5-<33% | 16 | 14 | 0 | 30 | 16 | 14 | 0 | 30 |
| >33-<66% | 13 | 16 | 1 | 30 | 15 | 12 | 3 | 30 |
| >66% | 13 | 15 | 2 | 30 | 10 | 14 | 6 | 30 |
| Total | 56 | 61 | 3 | 120 | 59 | 51 | 9 | 120 |

Table 1    Sex ratio of *P. clavata* colonies in relation to their injury degree at both studied localities of the Port-cros National Park. Indet.=colonies where sex was not possible to determine.

## Effects of injuries on gonadal production one year after the 1999 mass mortality

Unaffected colonies or with low injured surface showed 100% of fertile polyps. A decrease of the percentage of fertile polyps (containing oocytes or spermaries) with the increase of the extent of injury was more obvious in female colonies than in male colonies. Female colonies moderately affected (>33-<66% injury of colony surface) exhibited about 22% decrease in the proportion of fertile polyps (17% and 28% in Gabiniere and Montremian respectively), while severely affected colonies (>66% injury of colony surface) showed about 35% decrease in both sites. In contrast, the highest affected male colonies (with injuries >66%) showed only a decrease of 12% of the fertile polyps in both locations (Table 2).

| Sex | Year | Location | Injury degree | N colonies | N polyps examined | % fertile polyps |
|---|---|---|---|---|---|---|
| Female | 2000 | Gabiniere | <5% | 10 | 100 | 99 |
| | | | >5-<33% | 10 | 100 | 100 |
| | | | >33-<66% | 10 | 100 | 83 |
| | | | >66% | 10 | 100 | 66 |
| | 2000 | Montremian | <5% | 10 | 100 | 100 |
| | | | >5-<33% | 10 | 100 | 100 |
| | | | >33-<66% | 10 | 100 | 72 |
| | | | >66% | 10 | 100 | 64 |
| Male | 2000 | Gabiniere | <5% | 10 | 100 | 100 |
| | | | >5-<33% | 10 | 100 | 100 |
| | | | >33-<66% | 10 | 100 | 100 |
| | | | >66% | 10 | 100 | 88 |
| | 2000 | Montremian | <5% | 10 | 100 | 99 |
| | | | >5-<33% | 10 | 100 | 99 |
| | | | >33-<66% | 10 | 100 | 98 |
| | | | >66% | 10 | 100 | 88 |

**Table 2** Proportion of polyps with oocytes or spermaries observed in colonies pooled in 4 injury categories in June 2000 at two studied sites.

The gonadal biomass of female colonies differed between localities and among the extent of injury (Table 3a, Fig. 1a). Female colonies exhibited a higher biomass in Montremian, but despite the differences found between localities, colonies in both sites displayed a progressive decrease in gonadal biomass with the increase of the extent of injury up to the >33% .The biomass of oocytes did not vary between the two highest categories of injury extent (Table 3b). In average, female colonies affected by extent of injury >33% exhibited a 73-77% reduction in oocyte production.

While the mean diameter of oocytes was quite similar among the colonies exhibiting different extent of injury (Fig. 1b), the number of oocytes per polyp followed the same pattern exhibited by the decrease of female gonadal biomass with the increase of injuries (Fig. 1c).

In male colonies, gonadal biomass also varied significantly among sites and extent of injuries (Table 4a). In contrast to female colonies, gonadal biomass in male colonies was higher at Gabiniere and decreased rapidly from 5% of injured surface, showing a stabilization of the biomass lost among the colonies exhibiting any extent of injury (>5%), in average these colonies showed a 48-61% reduction in spermary production (Table 4b).

Like female colonies, the mean diameter of spermaries did not vary among colonies displayed different extent of injury (Fig. 2b), whereas the number of spermaries per polyp (Fig. 2c) followed the same pattern exhibited by the male gonadal biomass with the increase of injury extent.



**Figure 1**    Female colonies. Changes of the reproductive parameters with the extent of injury at two studied sites in 2000. a) Variation of gonadal biomass. b) Variation of the mean diameter of oocytes. c) Variation of the mean number of oocytes/polyp.

| a) | df | MS | F | p |
|---|---|---|---|---|
| Locality | 1 | 0.034 | 32.962 | <0.001 |
| Extent of injury | 3 | 0.205 | 196.202 | <0.001 |
| Interaction | 3 | 0.008 | 7.530 | <0.001 |
| Error | 772 | 0.001 | | |
| **b)** | | | | |
| Biomass of oocytes | 0.088 | 0.058 | 0.022 | 0.020 |
| Extent of injury | < 5% | > 5%-< 33% | > 33%- <66% | > 66% |
| < 5% | | | | |
| > 5%-< 33% | <0.001 | | | |
| > 33%- <66% | <0.001 | <0.001 | | |
| > 66% | <0.001 | <0.001 | 0.951 | |

**Table 3**     Female colonies. a) Two-way ANOVA comparing the effect of locality and extent of injury on gonadal biomass of *Paramuricea clavata*;Probability values of < 0.05 were considered significant. Abbreviations: df, degrees of freedom; MS, mean square; SS, sum of squares; F, F ratio; P, probability. b) Tukey posthoc test for the effect of extent of injury.

| a) | df | MS | F | p |
|---|---|---|---|---|
| Locality | 1 | 0.589 | 95.198 | <0.001 |
| Extent of injury | 3 | 0.393 | 63.547 | <0.001 |
| Interaction | 3 | 0.098 | 15.943 | <0.001 |
| Error | 792 | 0.006 | | |
| **b)** | | | | |
| Biomass of oocytes | 0.151 | 0.075 | 0.063 | 0.055 |
| Extent of injury | < 5% | > 5%-< 33% | > 33%- <66% | > 66% |
| < 5% | | | | |
| > 5%-< 33% | <0.001 | | | |
| > 33%- <66% | <0.001 | 0.415 | | |
| > 66% | <0.001 | 0.064 | 0.749 | |

**Table 4**     Male colonies. a) Two-way ANOVA estimating the effect of locality and extent of injury on gonadal biomass of *P. clavata*; Probability values of <0.05 were considered significant. Abbreviations: df, degrees of freedom; MS, mean square; SS, sum of squares; F, F ratio; P, probability. b) Tukey posthoc test for the effect of extent of injury.

Figure 2  Male colonies. Changes of the reproductive parameters with the extent of injury at two studied sites (Gabiniere and Montremian) in 2000. a) Variation of gonadal biomass. b) Variation of the mean diameter of oocytes . c) Variation of the mean number of oocytes/polyp.

## Comparison of the injury effect between 2000 and 2001

Although female and male colonies of *P. clavata* increased the gonadal biomass in 2001 (Fig. 3), the pattern of decrease of the gonadal biomass with the increase of the extent of injury was maintained in 2001 (Table 5). Gonadal biomass in non injured colonies was almost threefold higher than the most injured colonies for both sexes.

As we observed during the 2000, differences in gonadal biomass were due to differences in the number of oocytes o spermaries/polyp not to the mean diameter estimated for both injury categories in 2001 (Table 6).

| a) | df | MS | F | p |
|---|---|---|---|---|
| Year | 1 | 0.080 | 25.582 | <0.001 |
| Extent of injury | 1 | 0.421 | 133.835 | <0.001 |
| Year x Extent of injury | 1 | 0.002 | 0.573 | 0.449 |
| Error | 526 | 0.003 | | |
| b) | | | | |
| Year | 1 | 0.103 | 35.289 | <0.001 |
| Extent of injury | 1 | 0.402 | 137.295 | <0.001 |
| Year x Extent of injury | 1 | 0.006 | 2.190 | 0.139 |
| Error | 396 | 0.003 | | |

Table 5    Two-way ANOVA comparing the effect of year and extent of injury on gonadal biomass of *Paramuricea clavata* at Montremian Probability values of <0.05 were consideredsignificant. Abbreviations: df, degrees of freedom; MS, mean square; SS, sum of squares; F, F ratio; P, probability. a) Female colonies; b) Male colonies.
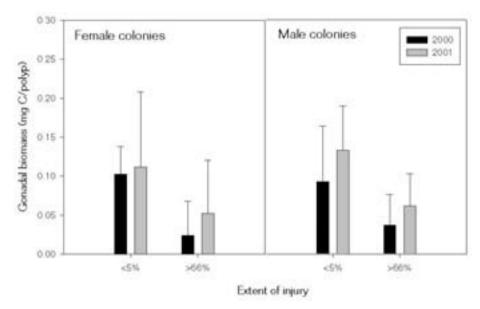


Figure 3    Female and male colonies. Comparision of the variation of the gonadal biomass with the extent of injury at Montremian between 2000 and 2001.

| Sexe | Injury degree | Gonadal diameter | | | Gonadal number/polyp | | N polyps examined | % fertile polyps |
|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | N | Mean | SD | | |
| Female | <5% | 379.01 | 43.91 | 578 | 14.46 | 12.49 | 100 | 100 |
| | >66% | 365.99 | 40.61 | 274 | 7.43 | 7.78 | 100 | 64 |
| Male | <5% | 397.66 | 92.47 | 589 | 14.71 | 6.67 | 100 | 100 |
| | >66% | 408.31 | 93.06 | 332 | 6.20 | 3.55 | 100 | 97 |

Table 6    Gonadal diameter and number of oocytes and spermaries/polyp and proportion of fertile polyps at Montremian in 2001.

# ||| Discussion

Understanding the consequences of the 1999 mass mortality event on the reproductive and population biology of gorgonian population may be essential to estimate the capability of gorgonian populations to recover from strong disturbances. This study shows that as well as the 1999 mass mortality event directly affected the demographic parameters of the *Paramuricea clavata* populations (Linares et al 2005, Chapter IV), this event caused severe indirect effects on the reproduction of the species that may represent an additional difficulty to the recovery at long-term scales.

Previous studies about the bleaching effect on coral reproduction suggested that the reproductive output was dependent on the severity of the impact and the species affected (Szmant and Gassman 1990, Michalek-Wagner and Willis 2000, Baird and Marshall 2002, Mendes and Woodley 2002). Stresses, such as increases of temperature or contamination, can produce alterations on gametogenic cycle, reducing only the gonad size (Guzmán and Holst 1993) or both parameters, size and number of gonads (Szmant and Gassman 1990, Michalek-Wagner and Willis 2000, Mendes and Woodley 2002). Contrasting with these results, the fact that the mean diameter of oocytes and spermaries did not vary among colonies with the extent of injury may denote that the mortality event did not affect directly the gametogenic cycles of this species, being the extent of injury surface the main parameter that determine the gonadal biomass by means of the number of gonads produced. The maintaining of the decrease pattern through time may support this hypothesis.

Our results showed a similar pattern at both studied localities, where colonies with higher injuries had a lower gonadal biomass than less affected colonies, in spite of the slight differences found between two studied localities which can be explained by the natural spatial variability displayed by the reproductive parameters of this species (Coma et al 1995a,b, R. Coma *unpublished data*).

Females showed the greatest loss of gonadal biomass (73-76% vs. 48-61% in females and males, respectively) as well as the highest decrease of fertile polyps (20% vs. 11% in female and male colonies). These results point out that female colonies suffered a greater impact on reproductive output than male colonies and may contribute to explain the results obtained for another *P. clavata* population located at Portofino promontory (Italy) that showed a higher resistance of male colonies than female colonies, due to a clear bias of the sex ratio in favor of males was observed as one of the effects of the 1999 mass mortality (Cerrano et al 2005). However, to document a clear bias in the sex ratio caused by this disturbance, further research is needed to study the current sex ratio in the Port Cros population and to examine other affected populations by the 1999 mass mortality to verify these results.

The decrease of gonadal production with the increase of injuries may imply a limitation of resources affecting energy allocation to reproduction, and this would be consistent with the energetic constraints observed on the energy budget of the species (Coma and Ribes 2003). As others authors have suggested, the decrease of the fecundity (considered as the number of gonads per polyp) is probably correlated to re-allocation of energy to maintain fewer eggs to ensure that they attained to mature size (Yamazato et al 1981, Michalek-Wagner and Willis 2000). For coral species, a trade-off between regeneration and reproduction had been previously reported (Kojis and Quinn 1981, Van Veghel and Bak 1994, Kramarsky-Winter and Loya 2000) by means of reducing coral fecundity only in the vicinity of the injury (Van Veghel and Bak 1994, Hall 1997) or extending the effects up to a far distance from the injured area (Oren et 2001). Like our results, the decrease on fecundity shown in these studies support the hypothesis that in long-living organisms, such as corals, there is a priority of energy allocation to recovery rather than to reproduction (Oren et al 2001) although a recovery from high extent of injury seem to be really improbably at least for *P. clavata* (Linares et al 2005).

Our data showed that the examined sex ratio in 2000 was 1:1 similar to those reported for the Italian population two years before the event in 1997 (Cerrano et al 2005) and for a red gorgonian population at the Spanish coast (Coma et al 1995). Although a male biased sex ratio had been previously described for other gorgonian species *Briareum asbestinum* (Brazeau and Lasker 1990), none correlation between this bias and the occurrence of previous mass mortality events was established.

The fact that the values of gonadal biomass obtained during 2001 were higher than those obtained during 2000 for female and male colonies seem indicate that the high temperature registered during the event had in some sense a direct effect over the reproduction. On the contrary, the effect of the extent of injuries over the reproduction output was maintained along at least two following years (2000 and 2001), meaning that the mortality impact over this biologic parameter was not only given during a specific time but during the impact. The two cohorts of oocytes observed in female colonies of *P.clavata* may explain the lasting effects on the reproduction until June 2000 if the 1999 event would affected the cohort of oocytes formed during this year that would spawned during the following year (2000), but could not explain the impact on the oocytes developed in 2000. On the other hand, the only cohort developed each year in male colonies and the impact observed in both studied years 2000 and 2001 also corroborate that the reproductive output is basically dependent of the extent of injury displaying by the colonies. Similar long-term

negative effects on reproductive output have been described for other stresses to coral species (Szmant and Gassman 1990, Guzman and Holst 1993, Mendes and Woodley 2002).
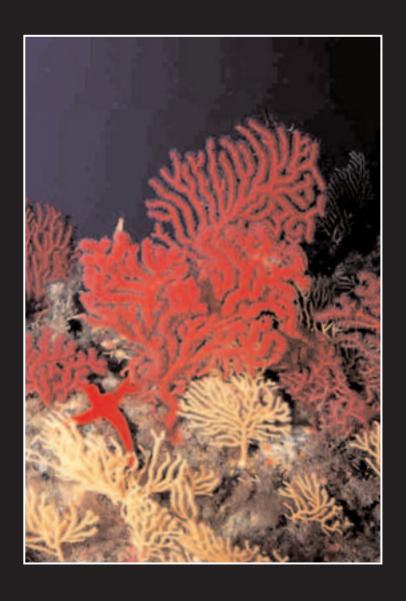
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A previous study of the same populations (Linares et al 2005) showed that although no differences of total mortality were found among the different size classes, colonies >10 cm exhibited a greater extent of injury than those <10 cm, involving more consequences in the reproductive output due to the loss of great part of the live tissue in reproductive colonies. In this species, the reproductive effort increases with size like most of the clonal organisms (Hughes and Cancino 1985). Thus in general, the reproductive output is dominated by a few large colonies (Hall and Hughes 1996). For instance, red gorgonian colonies higher than 40 cm have a contribution on gonadal production around 40% in female colonies and around 33% in male colonies (Coma et al 1995b). Therefore, disturbances affecting differentially larger colonies may have dramatic consequences on the population reproductive output due to the partial loss of their live tissue and the mortality of large colonies.

The great proportion of colonies with high extent of injury observed in the Port cros National Park (Linares et al 2005) indicates that the fecundity of most of the colonies was affected during this event. Both, the relationship between the extent of injuries and the reproductive output found in this study and the persistence of high percentage of injuries (showing a mean extent of injury about 35% of the whole surface) four years after the impact of 1999 mass mortality in the Mediterranean gorgonian *P. clavata* (Linares et al 2005, Chapter IV) point out the importance of delayed effects and the long-term consequences of this event, demonstrating that the recovery of populations can be likely measured in decades or even centuries. The replenishment from the same impacted populations may be strongly affected by the high percentages of reduction on reproductive output , as well as replenishment from other nearby non-affected populations is limited by the dispersal capability of the red gorgonian larvae (Chapter II) and the low recruitment rates (Coma et al 2003, Linares et al *in press*, Chapter III) displayed by this species.

### Acknowledgements

[] Modeling the effects of increasing disturbances on the local persistence of a Mediterranean long-lived marine octocoral

## ▯▯▯▯ Abstract

Populations of red gorgonian *Paramuricea clavata* are threatened by the increase of mortality sources. Additionally to the high diving activity that has been detected as an important threat in paradoxically some Marine Protected Areas (MPA), during the last decade two mass mortality events (1999 and 2003) related to climatic anomalies have heavily impacted these populations. Using demographic data obtained previously from three populations (two under contrasting levels of diving activity and one impacted by 1999 mass mortality event) located in three Mediterranean MPAs, we developed size-structured matrix models to investigate the long-term consequence of both disturbances under different scenarios of diver damage and different frequencies of mass mortality events separately and their interactive effects. Our results, showing that population stability can be achieved with an slight increase in survival of adult colonies (by 3% and 7% in Cap de Creus and Medes, respectively), demonstrate that a decrease in mortality of these by means of reducing divers impacts is an effective management measure. On the other hand, the low stochastic lambda (0.886) obtained from the impacted populations by the 1999 mass mortality event showed an extinction risk at extremely low time scale (30 years). The effects of mass mortality events aggravate the decline of gorgonian populations found in sites with high diving impact displaying times of quasi-extinction between 38 and 55 years under the actual frequency (5 years) of mass mortality events observed in the NW Mediterranean Sea. Moreover, low values of lambda ($\lambda$=0.936) had drastic effects on the population persistence independently of the simulated frequency of mass mortality events. Our simulations reveal the urgent need of management actions to ensure the gorgonian viability facing to the recurrent mass mortality events. This study shows that even with limited data available, size-structured matrix models can be useful tools to examine the consequences of disturbances and to identify the most crucial life history stages to implement effective management actions.

Keywords: Anthropogenic disturbances, diving impacts, climate change, matrix models, Population Viability Analysis, gorgonian, *P.clavata*

# ▐▐▐ Introduction

The increase of the magnitude and frequency of human-induced impacts such as overfishing, pollution, habitat destruction, and global warming on marine coastal ecosystems are causing the decline of 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 benthic species because they cannot avoid disturbances due to their sessile nature (Solan et al 2004).
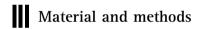
The coralligenous community is one of the most characteristic and high diverse of Mediterranean communities and is mainly dominated by sessile and long-lived species (see Ballesteros 2006 for a review). During the last ten years this sublittoral community has been heavily impacted by two mass mortality events (1999 and 2003) related to unusual climat anomalies in the NW Mediterranean Sea (Romano et al 2000, R. Coma and J. Garrabou, *personal communication*). The magnitude of these disturbances is provided by the fact that almost thirty species were reported to have been affected at a regional scale by the 1999 event. Gorgonian and sponges were the most impacted species because 60 to 100% of the colonies of several species exhibited a mean proportion of recent injuries about 50% of colony surface (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Linares et al 2005, Coma et al *in press*). The occurrence of two such events separated by only 4 years indicates that the frequency of these mass mortality episodes may be increasing as a result of the global warming and therefore that further repetitions of these die-offs are to be expected during the coming years (Coma and Ribes 2003).

The red gorgonian, *Paramuricea clavata*, is a dominant and characteristic species of Mediterranean coralligenous communities and is also one of the species most severely affected during mass mortality events (Linares et al 2005, Chapter IV). Although the immediate and mid-range impacts of mass mortality events on gorgonian populations has been widely documented (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001, Linares et al 2005, Coma et al *in press*), the longer-term consequences of an increase in the frequency of these events for the populations are unknown.

In addressing the impacts of global warming for population viability, it is important to also pay attention to other, less intractable threats. Global warming effects may be particularly dire for species already threatened by other local and global environmental changes (McCarty 2001, Maschinski et al 2006) due to the additive or multiplicative effects of multiple stressors for individual fitness and population viability (Philipart et al 2003, Vilchis et al 2005). In addition, while it seems to be unfeasible over the short-term to protect marine communities from stresses related to global warming, many interacting anthropogenic disturbances may be far more tractable. In the case of the red gorgonian, a major additional threat comes from the damage inadvertently inflicted by recreational diving activities. As with many similar effects on coastal communities due to passively inflicted damage from trampling or diving (Liddle and Kay 1987, Brosnan and Crumrine 1994, Garrabou et al 1998, Tratalos and Austin 2001, Coma et al 2004), effects of divers on gorgonians are strongest in a few areas with high levels of visitation. Howe-

ver, these areas are, ironically, also often those with the highest theoretical protection, such as marine parks and other Marine protected areas (MPAs). Therefore, understanding the risks these impacts and their interacting effects pose for the viability of disturbed populations may be essential to provide criteria for effective management of these species, especially when considered in the face of global change effects.

In this study, we used size-structured matrix models to investigate the long-term consequences of both diving disturbances and mass mortality events on *P. 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 and Jackson 1985, Dayton et al 1995, Garrabou and Harmelin 2002, Coma et al 2004). The actual and future expected increase of these mortality sources explains the urgent need to assess their threat to marine long-lived species, especially in MPAs (Rouphael and Inglis 2002). These threats emphasize the importance of obtaining demographic data from long-term monitoring to examine the response capacity of these species facing to rising disturbances. Alternatively, the use of matrix models (Caswell 2001) can be helpful to examine the future persistence of these species as well as to evaluate the effectiveness of possible management measures. Here, we use size-structure matrices parameterized with data from three Marine Protected areas to project *P. clavata*'s population growth rate under different scenarios of diver damage and different frequencies of mass mortality events.

# ▌▌▌ Material and methods ▌

## ▌ Study species

The red gorgonian *P. clavata* (Anthozoa, Octocorallia) is one of the key species of the Mediterranean coralligenous communities, playing an important role in increasing the biomass and the structural complexity of the sublittoral communities (True 1970, Ballesteros 2006). A demographic model we previously developed for *P. clavata* revealed the fragility of two distinct populations, with both declining and at high risk of extinction over moderate time horizons (Linares et al *in press*, Chapter III). These models also showed that annual population growth is far more sensitive to changes in survival rates than to growth, shrink or reproductive rates. The studied populations were located within marine protected areas heavily visited by divers, where there is a large and well-documented increase in red gorgonian mortality rates (Coma et al 2004). The differences of the population growth rates predicted by our models for these two populations also seems to correspond with differences in diver impacts, pointing out the importance of diving effects for population decline.

But the major threat to red gorgonian populations that we investigate here comes from a far less controllable disturbance. As we noted above, during the last several years, the coralligenous community of the Mediterranean has been affected by two mass mortality events. Monitoring of red gorgonian population affected by a 1999 massive mortality event showed a large delayed

effect on total mortality of 9% of the population estimated just after event to 48% four years after the mortality event. Moreover, red gorgonian populations displayed a high 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 the demographic parameters previously obtained from three red gorgonian populations located along the North-western Mediterranean coast and studied for 2 to 4 years (Medes Islands: 2001 to 2004, Cap de Creus: 2002 to 2004, Port-Cros: 1999 to 2003; Linares et al *in press,* Table 1). All three populations occur in areas where well-developed red gorgonians populations can be found and are located at the same depth range (15-25 meters) in Mediterranean Marine Protected areas with substantial levels of diving activity.

To examine the viability of red gorgonians population under different management and threat scenarios, we employed size-structured matrices. During a previous study on the life history of red gorgonians, we developed and parameterized size-structured demographic models for two plots monitored at Cap de Creus and four plots monitored at Medes Islands. To best evaluate the effects of different mortality sources on population growth and extinction risk, we constructed these models using separately-estimated, size-structured survival, growth, and shrinkage rates (see Linares et al *in press* for a thorough description of the construction of these matrix models and the procedures used to estimate the annual and average vital rates we used in them).

As baseline descriptions of gorgonian demography for the current study, we used these matrices and also followed the same methods to construct matrices for the monitored gorgonian at Port-Cros National Park. Because the Cap de Creus and Medes Islands populations were not impacted by the mass mortality event, this additional population is key to our investigation of how these events may influence the persistence of the gorgonians populations; during the 1999 mass mortality event, data were collected during a monitoring of six plots in Port-cros national Park and an additional four years of post-event data (1999-2003) were also collected (Linares et al 2005). As with other types of disturbances (e.g., fires: Gross et al 1998), the demographic rates for several years post-disturbance remain altered following a mass mortality event, with elevated total mortality rates and high shrinkage rates caused for the lasting high partial mortality displayed by the affected colonies for at least four years after the event.

| 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 |
| | | | | | | | |
| 2000-2001 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 |  | 0 | 0 | 0.003 | 0.089 | 0.378 | 0.814 |
| 2 | 0.698 | 0.372 | 0.041 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.326 | 0.633 | 0.097 | 0 | 0.012 | 0 |
| 4 | 0 | 0 | 0.065 | 0.694 | 0.228 | 0.071 | 0.043 |
| 5 | 0 | 0 | 0 | 0.075 | 0.496 | 0.188 | 0.021 |
| 6 | 0 | 0 | 0 | 0 | 0.063 | 0.518 | 0.234 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.094 | 0.532 |
| | | | | | | | |
| 2001-2002 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 |  | 0 | 0 | 0.003 | 0.089 | 0.378 | 0.814 |
| 2 | 0.692 | 0.449 | 0.007 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.244 | 0.711 | 0.070 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0.126 | 0.746 | 0.099 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0.106 | 0.747 | 0.172 | 0.061 |
| 6 | 0 | 0 | 0 | 0 | 0.077 | 0.719 | 0.091 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.758 |
| | | | | | | | |
| 2002-2003 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 | 0 | 0 | 0 | 0.003 | 0.089 | 0.378 | 0.814 |
| 2 | 0.686 | 0.490 | 0.000 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.196 | 0.816 | 0.038 | 0.0104 | 0 | 0 |
| 4 | 0 | 0 | 0.080 | 0.765 | 0.083 | 0.018 | 0.038 |
| 5 | 0 | 0 | 0 | 0.098 | 0.760 | 0.127 | 0.000 |
| 6 | 0 | 0 | 0 | 0 | 0.063 | 0.727 | 0.115 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.073 | 0.731 |

Table 1    Size-class transition matrices for *Paramuricea clavata* populations at Port-Cros National Park (France) from 1999 to 2003.

## Population viability under different scenarios

The main goal of this study was to explore the separate and interacting 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 will alter viability of gorgonian populations. To these end, we conducted sets of simulations to address three questions:

How effective must management of diving become in Marine Protected Areas
to substantially reduce the risk of gorgonian extirpation?

To simulate the reduction in diving effects, we used the two average matrices obtained for the Cap de Creus and Medes Islands populations (Linares et al *in press*, Chapter III). 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 and Kay 1987, Hawkins and Roberts 1997, Zakai and Chadwick-Furman 2002). However, a previous study showed that the principle impact of divers is mainly on the total mortality of largest colonies, because partial mortality was not significantly affected by high levels of visitation (Coma et al 2004). Population growth is also most sensitive to survival of these largest, otherwise long-lived, and most fecund colonies; therefore we focused our simulations on diver-driven effects on the survival of the four largest size classes (i.e. higher than 10 cm height) of colonies. Starting with the average matrix for each population, 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, increases went up to the point of the highest survival rates being 99% for some classes while other classes had some lower survival rate. We present the long-term population growth rates of the resulting matrices (lambda values) as functions of these increases in survival rates. Note that our previous analyses (Linares et al *in press*, Chapter III) show extremely little annual variation in vital rates, so use of deterministic analyses for this part of our question is warranted.

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

Simulations were performed for four different mean frequencies of mass mortality events: on average every 5 years (following the observations of the most recent episodes in 1999 and 2003), 10, 25 and 50 years. For these simulations we either used sets of annual vital rate estimates for the Medes Islands or the Cap de Creus population to simulate years when no mass mortality event was occurring or had occurred within four years. 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 years following an event, respectively. 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 four years, the appropriate Port-Cros matrix was used. A total of 5000 simulations of 100 years each were run for each frequency of mortality events 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 years, 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.

## Can reductions in diving impacts substantially change the threat posed by mass mortality events?

To address this question, we used the same general procedure as just outlined. Firstly, we used altered matrices from the Medes Islands and Cap de Creus populations that would reflect lowered diver-caused mortality. In particular, we used matrices for Medes Islands that had survival of the 4 largest classes raised to 0.98 and ones from Cap de Creus with these rates raised to 0.97; these increases corresponded to the increases needed for the average matrices for these populations (7% and 2%, respectively) to have lambda equal to 0.99. Results were obtained from 5000 replicate simulations modeling four different mass mortality frequencies (every 5, 10, 25 and 50 years). After that, we combined different frequencies of mass mortality events with different unaffected year matrices. Simulations were performed for 5 and 10 year average frequencies of mass mortality events. In particular, we used altered matrices for the Medes Islands, the population showing the highest diving impact, with survival rates for the four largest size classes increased from 0 to 7% over their estimated values. The simulations were performed following the same steps described above. 5000 replicate simulations were performed for each of the resulting 16 scenarios.

# ▌▌▌ Results ▐

## ▌ Diving control to reduce the decline of gorgonian populations

The increase in survival of reproductive colonies (>10 cm) that is needed to achieve a positive population growth rates was quite different between sites due to the different initial values displayed by both populations (Medes Islands, $\lambda$=0.936; Cap de Creus, $\lambda$=0.974; Linares et al *in press*, Chapter III). At Medes Islands, only the matrices with increases of survival of 7% or greater yielded $\lambda$ values greater than 1, while in Cap de Creus, population stability or growth was reached from an increase in survival rates of just 2% (Fig. 1). But the total survival rates of large colonies needed to achieve a lambda close to 1 was similar for both populations, between 97% and 98% for Cap de Creus and Medes Islands, respectively.

**Figure 1** Sensitivity of the population growth rate ($\lambda$) to changes in the survival of adult colonies (>10 cm) for two *Paramuricea clavata* populations: Medes Islands and Cap de Creus.

## The threat of increasing mass mortality events

The long-term estimated growth rates ($\lambda$ values) associated with the different annual matrices developed with demographic data obtained from the Port-Cros between 1999 and 2003 showed a strong declining trend ($\lambda<1$) (Table 2, Fig. 2). Furthermore, while there was some variation in survival rates and lambda values from year to year, the deterministic $\lambda$ value for the mean matrix was almost identical to $\lambda_s$ value (Table 2). Although all the matrices displayed $\lambda$ values under 1, the lowest value was obtained two years after the event. The survival rates for each classes obtained in the following years after the event also showed this trend as well. Although the smaller size classes suffered the highest mortality just after the event, at the end of the four years largest colonies displayed the lowest survival rate (Fig. 2). Despite the slightly positive trend of increasing $\lambda$ values after 2001, even at the end of the study lambda was less than one, and the $\lambda_s$ from all matrices predicted a high risk of extinction of approximately 30 years (Table 2). However, survival rates at Port Cros four years 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).

When simulating the extinction risk of gorgonian populations under a different frequency of mass mortality events, we obtained different results depending on the population used to obtain the unaffected year matrices. Modeling the mass mortality effects on Medes Islands populations (mean $\lambda=0.936$) showed drastic effects on persistence, with near-certainty of quasi-extinction predicted after 38 to 53 years with frequencies of events between 5 and 50 years (Fig. 3a). On the other hand, simulations for the Cap de Creus population (mean $\lambda=0.974$) showed near-certainty quasi-extinction at 55 and 84 years with frequencies of events of 5 and 10 years respectively, and substantially lower risks for under less frequent disturbance regimes (probability of extinction at 100 years of 88% and 59% for 25 and 50 year frequencies, respectively) (Fig. 3b).

| Sites | Years | $\lambda_1$ | $\lambda s$ | Time quasi-extinction |
|---|---|---|---|---|
| Port-cros | 1999-2000 | 0.873 | | |
| | 2000-2001 | 0.823 | | |
| | 2001-2002 | 0.931 | | |
| | 2002-2003 | 0.933 | | |
| | Mean | 0.889 | 0.886 | 30 years |

**Table 2**  Annual multiplication rates ($\lambda$) of transition matrices for *Paramuricea clavata* populations affected by a mass mortality event from different years at the Port-Cros National Park. $\lambda_1$=deterministic lambda, $\lambda_s$=stochastic lambda.



**Figure 2**  Comparison of the survival rates of different size classes and annual population growth rates at Port-Cros National park from 1999 to 2003 and the mean survival rates obtained from Medes Islands populations (2001-2004) and from Cap de Creus populations (2002-2004).

**Figure 3** Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population under four frequencies of mass mortality events (5, 10, 25, 50 years). 3a) Simulations developed for Medes Islands population ($\lambda=0.936$). 3b) Simulations developed for Cap de Creus population ($\lambda=0.974$).

| Management measures to reduce the threat of mass mortality events

Theoretical gorgonian populations with lowered diver-caused mortality (such that $\lambda$ was close to 1 for unaffected-year matrices) had significantly lower quasi-extinction risks. The results obtained for both populations were very similar. With mass mortality events occurring at 5 year fre-

quencies, quasi-extinction approached 100% after 75 years; with 10 year frequencies, 100% probability was approached only after 100 years; and, with lower mass mortality frequencies, much lower risks were seen (Fig. 4a,b). While these risks of quasi-extinction are substantial, they are markedly lower than those seen in simulations using currently estimated (and presumably diver-impacted) survival rates (Fig. 3).



**Figure 4**  Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population under four frequencies of mass mortality events (5, 10, 25, 50 years). 4a) Simulations developed for theoretical Medes Islands population with an increase of the survival of large size classes of 7% (λ=0.996). 4b) Simulations developed for Cap de Creus population with an increase of the survival of large size classes of 2% (λ=0.998).

Figure 5 shows the differential effect of mass mortality events (using frequencies of 5 and 10 years) in relation to the degree of diving control, represented as increments of survival rates from 1% to 7%. Under mass mortality events occurring at 5 year frequencies, the times for approximately 100% quasi-extinction were increasing from 37 years (for non control-original Medes matrix) to 60 years (for a complete diving control with survival increases of 7%; Fig 5a). The effects of diving control in reducing the threats from mass mortality events were even more obvious under a low frequency of these events (Fig. 5b).
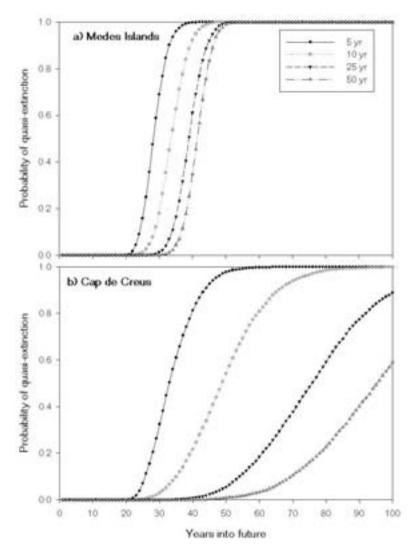


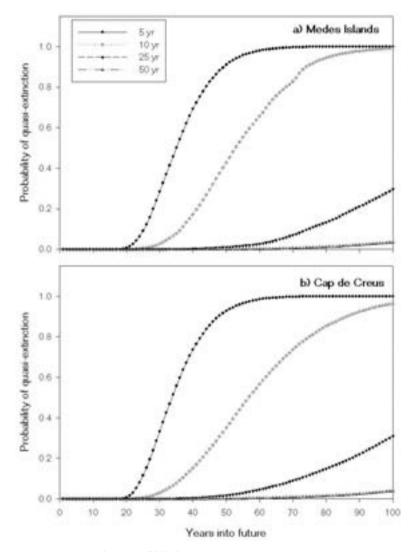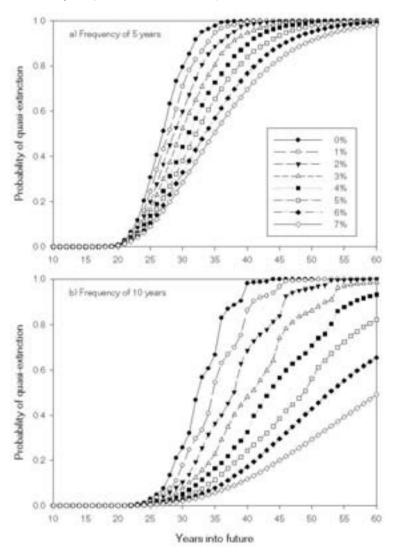Figure 5   Cumulative distribution function (CDF) for the time to reach a quasi-extinction threshold of 10% of initial population under frequencies of mass mortality events each 5 years (a) and 10 years (b). Simulations developed for Medes Islands population under different increases survival (from 1 to 7%) of large (>10cm) size classes (with λ values associated to the matrices of 0.939, 0.946, 0.954, 0.962, 0.970, 0.987, 0.996).

# ▌▌▌ Discussion

▌ **How effective must management of diving become in Marine Protected Areas to substantially reduce the risk of gorgonian decline?**

One of the main concerns of managers of some Marine Protected Areas 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. Although the examination of diver "carrying capacity" has been an important issue among several studies, the discrepancies found (ranging from 500 to 15000 dives per year) depending on the site and species studied (Hawkins and Roberts 1992, Dixon et al 1993, Zakai and Chadwick-Furman 2002) point out 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 to detect impacts on threatened populations as well as to examine the effectiveness of potential management actions has been demonstrated in many systems (Crowder et al 1994, Doak et al 1994, Pfister and Bradbury 1996, Holmes and York 2003, Morris and Doak 2002). Our modeling of increased survival of reproductive colonies shows clear effects on the studied populations, and most importantly shows that the local persistence ($\lambda$=1) of gorgonian populations can be achieved with only modest increases in colonies (>10 cm) survival (3% and 7% in Cap de Creus and Medes populations, respectively). These goals for increased survival should only be considered approximations and thereby long-term monitoring is needed, especially in Cap Creus, to verify the results obtained for three years (note that Coma et al (2004) examined the mortality rates in Medes Islands over a 9 years monitoring). Still, the differences in mortality reduction needed at the two sites may reasonably be attributed to different levels of diving activity because while in Medes Islands the estimated number of divers is about 70,000 divers/year, in Cap de Creus the estimated number of diver is about 30,000 divers/years (Zabala et al 2003).

The elevation of mortality rates of adult colonies by high diving activity over natural rates were previously estimated as from 2.7% to 7.4%/year (Coma et al 2004). However, in the absence of a modeling effort to translate these changes into effects on population persistence, the relevance of these values for management was difficult to comprehend. Our results, quantifying the increases of survival needed to reduce short and medium-term extinction risk are thus valuable in adjusting management criteria to address clear biological goals. Most importantly, our work show that modest, and thus achievable, decreases of the mortality of adult colonies through the reduction of divers within the Marine Protected areas by means of an active management can have large and important effects on population viability of a long-lived and slow-growing species.

These results, together with the sensitivity and elasticity values displayed by this species (Linares et al *in press*, Chapter III), verify the applicability of demographic sensitivity analysis approach as a helpful management tool to examine a suite of hypothesized threats and potential management strategies (Heppel et al 2000, Gerber and Heppel 2004). In this study, the use of

simple demographic models confirms that for some species, a small reduction in mortality of adults will substantially improve the population's viability.

The persistent low $\lambda$ values obtained from the size-structured matrices of Port-Cros populations confirmed the delayed and long-lasting effects of mass mortality events described in a previous study about this event (Linares et al 2005, Chapter III). The lowest value of $\lambda$ was obtained one year after the occurrence of the mortality (2000-2001; $\lambda$=0.823) not just after the event (1999-2000). The simulation carried out (displaying a $\lambda_s$ value of 0.886) showed rapid extinction (30 years). The increase of $\lambda$ 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 recovery are, however, not yet clear and will require longer-term monitoring after more events.

The effects of mass mortality events aggravate the decline of gorgonian populations found in sites with high diving activity. The simulations clearly showed that if the impacted populations are those with low $\lambda$ values, as for the Medes Islands population, even low frequencies of sea-water temperature anomalies will substantially compromise population viability over the short and medium term. In contrast, lambda values close to 1 reduce the short-term (though not the longer-term) risk of gorgonian populations to these global warming effects. This difference is demonstrated by the results obtained for Cap de Creus populations, with a mean $\lambda$ of 0.974 and the times of quasi-extinction are between 55 and 84 years in comparison with the 38 and 45 years obtained for the Medes Islands populations for frequencies of event repetition of 5 and 10 years.

## Management and climate change on gorgonian populations

Modeling the possible effects of mass mortality events on populations under high diving activity has shown the urgent need to develop management actions that ensure population viability in the face of recurrent mass mortality events. Even during the less optimistic scenario of 5 years frequencies of events, the time of quasi-extinction was considerably higher than those estimated for our studied populations when the non-mass mortality lambda values were close to 1. The effects of diving control are much more pronounced at lower mass mortality frequencies, further indicating their feasibility as an indirect, 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 and James 2005, Vilchis et al 2005). Our findings confirm that human impacts such as high diving activity together with the global warming trend can combine to have dramatic effects on the viability of marine long-lived and slow-growing species. Faced to these risks, managers of MPA may nonetheless have some effective ways to forestall population collapse. We also show that the use of PVA can help managers to determine guide-lines of efficient conservation. Finally, effective responses to the important threats that

are 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.

### Acknowledgements

[] Restoration of threatened gorgonian populations:
an experimental and modeling approach

## Abstract

The increasing disturbances currently affecting marine communities highlight the need to examine restoration measures to add to other conservation efforts on threatened populations. The main goal of this study was to examine the usefulness of ecological restoration in the management of gorgonian populations damaged by diving activity in intensively visited Marine Protected Areas (MPA). We used field experiments as well as simulations from size-structured matrices to assess the utility of transplantation of living fragments from damaged colonies to increase the viability of threatened gorgonian populations. Despite results showing that method failure caused the loss of 40% of transplants, well-attached transplants achieved similar survival rates (80%) to natural colonies. Surprisingly, environmental conditions did not have a significant effect on the natural death of transplants but on the methodological failure (37% of transplants were lost in the photophilous treatments in contrast to the 25% lost registered in sciaphilous treatment). The simulations showed substantial improvement in the annual population growth rate ($\lambda$) only when the transplantation was performed every 2 years and under the most exigent conditions (recovering 75% of the dead colonies and obtaining 3 fragments from each one). The predictions obtained from the size-structured matrix model suggest severe limitations of this technique at larger spatial and temporal scales. However, our study confirms the feasibility of this restoration measure to contribute to the recovery of populations in MPAs affected by local disturbances. The experimental and modeling approaches developed here represent a first step towards the restoration of gorgonian populations and may provide useful guidelines for future studies.

Keywords: *Paramuricea clavata*, Transplants, Matrix models, Conservation, Marine Protected Areas

# ▌▌▌ Introduction

The current decline of high diversity marine communities, such as coral reefs and kelp forests, due to the increasing frequency and severity of anthropogenic impacts have highlighted the need to implement efficient restoration strategies as a complement to the management and conservation of existing populations (Rinkevich 1995, Lirman and Miller 2003, Carney et al 2005).

The red gorgonian *Paramuricea clavata* is an important structural species of the Mediterranean coralligenous assemblages (Ballesteros 2006). This long-lived and slow-growing species exhibits demographic parameters in concordance with the dynamics of the community it inhabits (Coma et al1998, Coma et al 2004). Among its life-history traits, red gorgonian species display a delayed sexual maturity and a great annual investment on sexual reproduction that contrasts with the low recruitment rates observed (Coma et al 1995, Coma et al 2001). According to the results obtained from size-structured models developed for this species (Linares et al *in press*, Chapter III), these values would be sufficient to ensure the persistence of red gorgonian populations under the low mortality rates observed in natural conditions (Coma et al 2004). This identifies the survival of reproductive colonies as the main vital rate (with the highest elasticity values) to guarantee population viability.

However, Mediterranean gorgonian species are presently adversely impacted by a wide variety of disturbances that substantially increase their natural mortality rates. Some of these disturbances are directly of anthropogenic origin such as anchors, fishing nets, divers and contamination (Harmelin and Marinopoulus 1994, Coma et al 2004, Arnoux et al 1992) and others, such as recent mass mortality events (Garrabou et al 2001, Linares et al 2005), appear to be indirectly related to humans through the increase in seawater temperature (Romano et al 2000).

Managers of Marine protected Areas (MPA) must be seriously concerned with these threats, especially because of an unsolved paradox: although the creation of marine protected areas is a fundamental tool for the conservation of marine habitats (Kelleher and Kenchington 1992), they tend to attract more tourism and associated recreation activities such as diving that can have a considerable impact on several benthic communities (Garrabou et al 1998, Wielgus et al 2002, Coma et al 2004). The problem may be of special importance in small protected areas because they are often exposed directly to various anthropogenic activities without being adequately sheltered by buffer zones (Schwartz 1999). The impact of diving has been demonstrated to increase mortality rates of *P. clavata* by a factor of three at the Medes Islands MPA (Coma et al 2004), an increase that is threatening the long-term persistence of the population (Chapter VI).However, intense diving activity is present not only at the Medes Islands MPA but at many Mediterranean MPAs (Harmelin and Marinopoulus 1994, Francour et al 2001).

Although the practice of ecological restoration has long been applied towards erosion control, reforestation, and habitat and range improvement (Young et al 2005), it has only been approximately in the last decade that the science of restoration ecology has started to be applied to marine communities (Ambrose 1994, Rinkevich 1995, Edwards and Clark 1998, Fonseca et al

2000, Hernandez-Carmona et al 2000, Epstein et al 2001). The clonal nature of gorgonian species allows the recovery from partial and total mortality (Hughes and Cancino 1985). While several restoration techniques have been explored to restore damaged coral reefs, most of them are expensive and labor intensive and can result in high mortality of coral transplants (Edwards and Clark 1998). However, there have been a few examples of successful restoration on a relatively large-scale (Guzman 1991).

Detachments from the substratum together with injuries are the main causes of gorgonian mortality (Yoshioka and Yoshioka 1991, Whale 1985, Weinberg 1979, Coma et al 2004). Although the recovery of detached colonies might be possible if they succeed in reattaching, a common process in some tropical gorgonians (Lasker 1990, Coffroth and Lasker 1998), the ability of *P. clavata* for natural reattachment has proven to be extremely poor (Coma et al 1995). Therefore, detached colonies accumulated on the bottom of the walls and boulders can survive for several months but finally die from sedimentation and abrasion with the substratum. The low recruitment rates (Coma et al 2001) and the high post-settlement mortality observed in the red gorgonian *P. clavata* (Chapter II) lead to an examination of whether transplantation of living colonies may be a suitable tool for the restoration of damaged populations. Furthermore, the great availability of detached colonies overcomes the main drawback of restoration which relies on the acquisition of colonies from a donor area (Edwards and Clark 1998).

Whether restoration is a feasible tool towards contributing to the survival of these populations is an important issue for managers involved with the conservation of *P. clavata* populations in most MPAs. Transplant failures can be due to two different causes: a failure of attachment (technique) or post-attachment survival (environmental factors). The search for techniques to attach the colonies to the natural substratum with high survival rates is a preliminary step to examine the effectiveness of the transplantation as a management tool. The selection of the appropriate technique as well as the examination of the survival of transplanted colonies together with previous knowledge about the population dynamics of the species allow the utilization of structured matrix models (Caswell 2001) to simulate and predict the usefulness of transplantation techniques on the enhancement of damaged populations. In particular, the size-structured matrices can be used to estimate the magnitude of transplantation that would be necessary in each case to reach an objective of demographic stability (i.e. to accomplish an annual population growth rate ($\lambda=1$; Doak et al 1994).

Furthermore, the transplantation of colonies in different environmental conditions may allow us to assess the role that biotic and abiotic conditions play on their survival. In this sense, the lack of gorgonian populations in shallow areas with high irradiance suggest that light either directly or indirectly enhances the competitive success of overgrowing algae and hinders the development of red gorgonian colonies (Weinberg 1979).

Our study was conducted at the Medes Islands, a NW Mediterranean Marine Protected Area that experiences some of the heaviest pressure from recreational diving in the Mediterranean (about 70 000 annual dives in only 32 ha) (Coma et al 2004). The main goals of this study were: first, to examine different transplanting techniques involving low labor effort and low economic cost; second, to estimate the survival of transplanted colonies in relation to the selected tech-

nique and to abiotic and biotic factors such as irradiance and competition with filamentous algae; and finally, to predict using a matrix model the survival of the transplanted colonies as well as the transplanting effort necessary to obtain values of annual population growth rates ($\lambda$) close to 1, ensuring the long-term persistence of these populations. The results obtained in this study may allow us to discuss the ability of transplantation as a useful management technique at least for small protected areas where both valuable marine biodiversity and intense diving activity interact as in our study site.

# ||| Material and methods

The experimental work was carried out at the Medes Islands Marine Protected Area (NW Mediterranean Sea, 42° 02' N, 3° 13' E) where well-developed populations of *Paramuricea clavata* cover the more exposed and vertical sides of the rocky walls (Gili and Ros 1985).

## Attachment

The first step was to find a useful technique to transplant fragments of surviving colonies found on the bottom of the walls. We searched two basic prerequisites for the selected technique: low labor cost and low economic cost since the final objective was to develop a technique easy to perform not only by scientists, but also by volunteers and managers of MPAs working together.

Using two-component epoxy putty as glue, we first tested the success of attachment of three different methods to install the colonies: *raw*, gluing them directly to the bottom; *tube*, putting the base of the fragment in a plastic tube (as a sheath) 2 cm long to avoid the direct contact of live tissues with the putty; and *stick*, adding a PVC stick 5 cm long at the side and fixing the fragment to it by means of a plastic bridle (Fig. 1).

We also planned to test the effect of size on the survival of transplants, by comparing two different sizes of transplants: small (3-10 cm) and large (10-20 cm). However, preliminary assays indicated that large transplants always displayed high losses of attachment independently of the method chosen. This was due to the higher resistance of large transplants to water flow which easily opened a hole at the base of the transplant before the putty solidifies. Subsequently, we exclusively used small transplants, since they showed a better attachment success.

The transplantation experiment was carried out within a well-developed red gorgonian population at 20-25 m depth and 60 fragments between 3 and 10 cm from damaged colonies larger than 30 cm were employed for each method. The experiment began in June 2001 and the survival of

transplanted colonies was monitored monthly during the first four months; then the survivorship was noted approximately each four months until October 2002.



Figure 1    Scheme of the different methods of gorgonian transplantation used in this study. (a) *raw* technique, fragment transplanted directly to the substrate with epoxy. (b) *tube* technique, fragment transplanted using a plastic tube in the base of the colony to avoid the direct contact with the epoxy. (c) *stick* technique, fragment transplanted using a PVC stick to hold up the colony in contact directly with the epoxy.

## Environmental factors

Once the best transplant method was selected, we initiated a second experiment to distinguish the role of the main factors that may contribute to setting the upper limit of the distribution of *P. clavata* such as light and competition with algae (Weinberg 1979, Ballesteros 2006). Following the characteristic vertical zonation pattern (i.e. belt-like distribution) of rocky benthic Mediterranean communities (Pèrés and Picard 1964, Gili and Ros 1985), the upper limit of red gorgonian populations inhabiting steep rocky walls used to be a clear-cut border parallel to the sea border (following definite isobaths). But in large walls experiencing changes in orientation and irradiance, this pattern is substituted by a diagonal line (upper to the north and lower to the east and south) strongly suggesting a dependence of the distribution of red gorgonian colonies on light and shallow depth. Taking advantage of this observed pattern, in April 2002 we started an experiment transplanting colonies with the following experimental design: 20 transplants were installed on the same rocky wall and at the same depth (15-20 m) at each of three environmental conditions: 1) in sciaphilous ambient with low levels of irradiance, within well-developed gorgonian populations (at the lower side of the diagonal), 2) in photophilous ambient with high levels of irradiance without gorgonians and with algae (at the upper side of the diagonal), and 3) in a

photophilous area with high levels of irradiance without gorgonians but also without algae (because they were removed during the first four months of the experiment, when the peak of algal growth occurs). This design was repeated at three different localities (Pedra de Deu, Pota del Llop and Tascons) where well-developed red gorgonian populations can be found (Fig. 2).



Figure 2    Experimental design of transplantation. Note that the oblique border between algal dominated and gorgonian dominated communities allows to transplant at the same depth. a) Transplants within photophilous ambient with algae. b) Transplants within photophilous ambient without algae. c) Transplants within sciaphilous ambient.

To characterize the different irradiance at the study sites, light was recorded where the transplants were installed by 2 synchronized HOBO® LI data loggers (Onset Computer) for the two different light treatments (sciaphilous and photophilous). Measurements were recorded in lumens feet-2. Figure 3 shows the differences in light conditions between the photophilous and the sciaphilous treatments at two of the three experimental sites. Despite the fact that the three environmental conditions were located at the same depth, differences in orientation produced several fold differences in the irradiance reaching transplants at the two photophilous treatment sites in contrast to the sciaphilous site. This difference was tested at the beginning of the experiment, showing a tenfold different in irradiance values (Fig. 3)



**Figure 3** Light quantities recorded in two sites of the Medes Islands where the transplantation was performed (Tascons and Pota del Llop). 20 transplants were installed in the two communities where the survival was studied (sciaphilous and photophilous communities) at the same depth (15-20 m) for each sites.

The survival of transplants was monitored monthly for six months after the beginning of the experiment (October 2002), and from then, once a year during the following three years (2003, 2004 and 2005). The loss of transplants as well as the death of transplanted colonies was noted during each census as separate items in order to distinguish between a failure of the methodology (attachment) and the mortality of the transplants due to natural causes (survival). A Kruskall-Wallis test was applied to test the effect of the three treatments on the percentage of colonies found for the three possible situations (alive, dead and lost transplants).

## Modeling approach

In addition to the experimental work, we used a size-structured matrix model (see Linares et al *in press*, Chapter III) to evaluate the transplanting effort that would be necessary to reach the conventional objective of enhancing the annual population growth rate ($\lambda$) at values equal or close to one.

To run all simulations we used the average matrix of three annual matrices obtained for Medes Islands populations from 2001 to 2004 (Table 1). Matrices were constructed using a set of seven age- and size-defined stage classes following the steps detailed in a previous study (Linares et al *in press*, Chapter III). A large contribution to the low lambda value obtained for this matrix (0.937, reference lambda) is the estimation of a threefold increase in natural mortality caused by the high diving activity in this MPA (Coma et al 2004).

| Size class | Size class at time t | | | | | | |
|---|---|---|---|---|---|---|---|
| t+1 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 | 0 | 0 | 0 | 0.003 | 0.089 | 0.378 | 0.810 |
| 2 | 0.684 | 0.483 | 0.018 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.202 | 0.813 | 0.034 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0.087 | 0.833 | 0.057 | 0.020 | 0 |
| 5 | 0 | 0 | 0 | 0.072 | 0.759 | 0.124 | 0.019 |
| 6 | 0 | 0 | 0 | 0 | 0.052 | 0.731 | 0.059 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.063 | 0.850 |

**Table 1**    Average population projection matrix for the red gorgonian populations at the Medes Island Marine protected area (see Chapter III).

The transplantation of a colony represents a change from an absolute loss to a new incorporation through a loop in the dynamics of the matrix model. In this loop, the otherwise lost colonies from the size classes 4 to 7 (10-20 cm, 20-30cm, 30-40 cm, and >40 cm) would be new incorporations to the chosen transplanted class; i.e. fragments of 3-10 cm (class 3) and fragments of 10-20 cm (class 4) (Fig. 4).Although large transplants exhibited a higher proportion of technique failure (see above) than small transplants, simulations were run using both sizes in order to assess whether a higher investment in improving the technique for installing large colonies for future management applications.



**Figure 4** Life cycle graph of the gorgonian *Paramuricea clavata* showing the natural demographic processes (lines in black) as well as the transplantation processes (lines in grey). G=growth, F=fecundity, Shr=shrinkage. First class is an age-based class, Class 2 colonies are at least two-year olds between 0.3 and 3 cm in height, 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.

A large damaged colony found lost on the bottom can be split into small healthy fragments, and from each lost gorgonian more than one transplant can be obtained. Obviously, the number of resulting fragments is positively related with the size of the damaged gorgonian and negatively related to the size of the transplant. On the other side, the percent of the whole number of lost gorgonians found and recovered depend on the magnitude of the surveillance effort. Thus, the efficacy of this methodology could be improved by means of both recovering more colonies and splitting those colonies into more fragments. Finally, the effort also can be improved by repeating the transplantation at increasing frequencies (annual rather than one-time transplantation).

During a first step and beginning with the minimum effort, we simulated the effect of a sole transplantation under less exigent conditions (one fragment from each recovered colony and 10% colonies recovered). We estimated the increase in survival obtained from this simulation and then we added this increase to the right elements of the matrix that have been benefited from this transplantation, class 3 ($a_{34}$, $a_{35}$, $a_{36}$, $a_{37}$) or class 4 ($a_{45}$, $a_{46}$, $a_{47}$). To run the model we used the transplanted matrix and then the original matrix for the other iterations, and we used the stochastic log growth rate by Tuljapurkar's approximation (Morris and Doak 2002) to choose some matrices more often than others.

In a second step, still using a sole transplantation we simulated the effects of increasing the efficiency of transplantation by means of different combinations of the two parameters mentioned before. The % of dead colonies recovered by the transplantation was simulate at 10%, 25%, 50% and 75%, and the number of fragments recovered from these colonies was tested at 1, 3 and 5 fragments for transplants of 3-10 cm and 1, 2 and 3 fragments for transplants of 10-20 cm. The simulations were performed following the same steps that have been previously explained.

Finally, to test the effect of repeated transplants we used the matrices obtained during the previous interactions to iterate the transplant matrix with the original matrix with increasing frequency over time, testing a unique transplantation every 100 years (1/100), 1/10 yrs, 1/5 yrs, 1/3 yrs, 1/2 yrs, 1/1yr.

# ⫼ Results

## ▌ Technique: attachment success

The use of a PVC stick to attach the transplanted gorgonian to the rocky substrata provided the highest survival among the examined techniques (Fig. 5) With this technique, 70% of transplanted colonies survived beyond one year, while the survival using the *tube* technique was only 50%. With the *raw* technique, direct attachment of the colonies to the substrata, only 30% of colonies lived until October 2002.



Figure 5    Transplant survival of the three methods developed, during the first year of the study (from June 2001 to June 2002) surveyed each month during the first four months and then each four months. Data are shown as a percentage of the 20 original transplants for each method.

## Environmental factors

The survival of transplants under the three different experimental conditions assayed (sciaphilous, photophilous with algae, and photophilous without algae) is shown in Figure 6 against the survival expected for natural (non-transplanted) colonies. The decrease of survival includes both causes of mortality: failure of attachment and death. In general, the survival under the three environmental conditions displayed a similar temporal pattern in which two phases can be distinguished: a strong decrease around the first year of the study (between April 2002 and October 2003) much higher than the expected natural mortality and a second phase where survival was similar to natural values (80% excluding the lost transplants vs. over 85%, see Table 1). As a result, after three years (October 2005) the survival of transplants was only 16% compared with 52% under natural conditions. When comparing among treatments, the colonies transplanted within their typical sciaphilous community had the highest survivorship (58%) one year after the beginning the experiment (April 2003); and maintained a significant difference of survival of 14% with the photophilous conditions at the end of the study (Kruskal-Wallis, p=0.042).

The colonies transplanted to high levels of irradiance (photophilous community) showed similar survival rates independently of the exposure to the competition with algae. Only a small difference between these treatments was noted during the first period (between April and October 2002) when the maximum growth peak of these algae takes place. In this period, the survival of the transplanted colonies where the filamentous algae were removed was 73% in contrast to 63% with algae. Three years after the beginning of the experiment, only about 2% of the transplants survived in both photophilous treatments (Fig. 6).



Figure 6  Transplant survival under the three experimental treatments from April 2002 to October 2005). Data are shown as a percentage of the 20 original transplants located in three different replicates, mean ± SD was estimated averaging the three replicates for each treatment (N total=60 for each treatment).

Figure 7 shows the fate of transplants, separating alive, dead and lost transplants to look for the causes of mortality (technique or environmental). Unexpectedly, the differences in survival between treatments were not a consequence of differential death of the transplants after being transplanted either to sciaphilous or photophilous conditions (ranging between 58% and 61%), but to differences in the success of attachment despite the use of the same transplant procedure. Although no significant differences were found among treatments (Kruskal-Wallis, p=0.062), both photophilous treatments displayed a higher percentage of loss (37% and 36%) than the sciaphilous treatment (25%). These losses were basically encountered during the first year of the transplantation (Fig. 6).



**Figure 7**    Fate of the transplanted colonies (%) separated among "surviving" transplants, "dead" transplants due to a natural mortality and "lost" transplants due to a method failure). The SD was estimated averaging the three localities where we performed each treatment. P values are from a Kruskal-Wallis test comparing the effect of treatment on the percentage of colonies surviving, dead and lost.

### Modeling approach

Simulations were conducted on the basis of survival rates of well-attached transplants which do not differ from natural values (see above). The simulations of a unique transplantation with increasing efficiencies did not substantially modify the lambda values (Fig. 8, see results for a unique transplantation every 100 years). Therefore, the first simulation with a sole transplantation did not modify the low value of the reference lambda (Fig. 8). In contrast, if the transplantation is periodically repeated, significant increases in lambda were observed. However, lambda values close to 1 were achieved only under a high transplantation efficiency (i.e. transplanting on the order of 75% of the dead colonies) and high transplantation frequency (at least 1/2 yr).

**Figure 8**   Effect of transplantion frequency over the annual population growth rates. Five frequencies are represented using the higher efficiencies on both: number of fragments and percent of recovered colonies for the two transplants sizes. Black line represents the reference lambda value. Dashed line represents the long-term population persistence of the population ($\lambda$=1).

Figure 9 shows the positive effect on the lambda values of increasing the efficiency through the proportion of recovered colonies and the number of transplants obtained from them at the maximum frequency of transplantation (every year). Both transplant sizes exhibited a similar pattern of lambda increase with an increasing proportion of recovered colonies (Fig. 9a,b). Although all the simulations showed an improvement with respect to the reference lambda, the lambda values were close to or higher than 1 only when over 50% of the dead colonies were recovered and more than one transplant was obtained (Fig. 9).

**Figure 9** Annual population growth rates (λ) obtained under transplantation repeated each year. Simulations were performed changing simultaneously the percentage of recovered dead colonies and the number of fragments obtained from recovered colonies through the transplantation of fragments of two size-classes. a) Transplants of 3-10 cm. b) Transplants of 10-20 cm. Black line represents the reference lambda value. Dashed line represents the long-term population persistence of the population (λ=1).

# ▍▍▍ Discussion

## ▮ Technique

During the technique-related experiment performed within the gorgonian community, the rather high survival (almost 70%) displayed by the *stick* method confirmed that this technique might allow a successful transplantation. However, low survival and a high loss percentage were observed during the second experiment aimed to test the effect of environmental conditions. In this second experiment, method failure was an important cause of mortality, basically due to either a break in the epoxy hold on the substrata or loss of the stick. Over 40% of transplanted colonies were lost due to a bad installation, especially under strong hydrodynamic conditions.

On the contrary, it is worth noting that once the attachment failure was passed, well-attached transplants achieved similar survival rates to those of natural colonies. The contrast between the losses due to attachment and the survival of well-attached transplants appears clear in the two patterns that can be observed in Figure 6. In the first phase, the attachment failure caused mortality much higher than natural conditions, but in the second phase the slopes displayed by all treatments were similar to that exhibited by natural colonies. Although this may be considered enough to recognize the restoration method as a feasible management tool, our study has revealed some of the uncertainties of marine restoration and demonstrates that planting techniques are difficult and some degree of failure should be expected as other authors have indicated in previous works (Edwards and Clark 1998, Yap 2000, Carney et al 2005). In this sense, an improvement of the technique regarding the initial installation of transplants on the substratum must be the primary goal of future studies on transplantation of gorgonians.

## ▮ Effects of environmental conditions on colony survival

Surprisingly, the environmental conditions did not have a significant effect on the natural death of the transplants but on the methodological failure. The differences between the sciaphilous and photophilous communities were due more to the higher number of technical losses for the photophilous treatment than to the process of competition or to differences in irradiance that we expected to affect the survival of the transplanted colonies. One possible explanation for these unexpected results could be the difference in intensity of water flow that the transplants experienced under different treatments. As the water movement depends strongly on depth (Ballesteros and Zabala 1993), we would expect the same water flow in both treatments. Nevertheless, at a finer scale, the cover provided by the gorgonian forest (sciaphilous treatments) to the small transplants decrease water movement between 20-40% (M. Ribes, *unpublished data*) which may have contributed to the improved success of transplants.

## Modeling

Three main facts lead us to consider small transplants as the best size for transplantation. First, preliminary experiments pointed out that the use of large transplants exhibited a higher technique failure because of their higher resistance to water flow. Second, simulations did not exhibit a substantial difference in lambda values between both transplant sizes. This would be in accordance with previous experimental studies, which did not observe large differences between transplant sizes (Lewis 1991, Yap et al 1998). Third, the use of large transplants would require a higher investment in the installation technique.

Under the actual high rates of mortality due to the influence of diving, the simulation showed that a sole transplantation followed by the same management measures had no effect on the viability of this population. The annual population growth rate improved substantially only after increasing the frequency of transplantation. *P. clavata* populations continued to decline ($\lambda<1$) unless the transplantation was performed every 2 years under the most exigent conditions, recovering 75% of the dead colonies and obtaining 3 fragments of each. For an annual transplantation, it was still necessary to recover more than 50% of the colonies and to obtain more than one fragment from them to reach our objective of "population persistence" ($\lambda=1$).

## Transplantation and conservation of threatened populations

Managers of Marine Protected Areas (MPAs) are concerned about the different sources of disturbances that are currently affecting the coralligenous community (see introduction). The predictions obtained from the matrix models suggest severe limitations of this technique at larger spatial and temporal scales. Therefore, the transplantation method appears to be unable to counteract the high mortalities displayed by recent mass mortality events (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001), where on the order of 50% population losses have been estimated (Linares et al 2005, Chapter IV, Coma et al *in press*). However, the results indicate that transplantation could be a viable method to contribute to the recovery of populations in MPAs locally affected by disturbances (i.e. diving activity, anchors, fishing nets, contamination and mass mortality events).

Nevertheless, it should be considered that our study case is probably not representative of the common conditions experienced by red gorgonians along the Mediterranean coast. The high diving activity at the Medes Islands MPA causes extremely high mortality rates (Coma et al 2004) that probably require a disproportionately high transplantation effort and repetition to guarantee population persistence. In our opinion, restoration actions at this MPA should be considered together with other conservation efforts designed to attenuate the impact of diving (Chapter VI).

The use of models to assess the effectiveness of transplantation techniques in improving the viability of red gorgonian populations has provided some clear-cut results that can help managers and scientists to estimate the convenience and utility of this restoration technique.

The experimental and modeling approaches developed in this study represent a first step towards the restoration of gorgonian populations and may provide practical guidelines for future studies. Modeling has shown that the current frequency of disturbances may affect recruitment to the point of endangering population viability (Linares et al *in press*, Chapter III). Restoration may contribute to the re-establishment of the lost link in the recruitment chain and therefore ensure population persistence in long-lived species such as gorgonians with rare and episodic successful recruitments.

## Acknowledgements

[] **General discussion and conclusions**

This thesis was developed at a time when anthropogenic impacts were growing exponentially on land and at sea, including the Mediterranean waters where we were diving and studying (Vitousek et al 1997, Roberts and Hawkins 1999, Bianchi and Morri 2001, Sala 2004). Social awarness about these human threats also grew, alongside our conviction to work towards the conservation of Mediterranean marine ecosystems.

Conservation biology has made great theoretical and methodological breakthroughs (e.g. Simberloff 1988, Boyce 1992, Alvarez-Buylla 1994, Caswell 2001, Morris and Doak 2002 Reed et al 2002), although mostly in terrestrial systems. In marine ecosystems, advances in conservation science have been less numerous because of the intrinsic difficulty to work underwater and the consequent scarcity of data on the biology of threatened species and ecosystems.

To evaluate the level of threat of a species we need a solid knowledge of its natural history (including distribution range, abundance, feeding behavior, physiology, reproductive biology, and interactions with other species), and an accurate description of the dynamics of its populations based on demographic data. In particular, demographic studies of marine species are the most demanding because of the need for temporal replication over large population samples.

This thesis was intended to fill a gap concerning the conservation status of a Mediterranean benthic habitat. Throughout this thesis we have demonstrated that *P. clavata* is a threatened species because of its life history, partly because of its slow dynamics. All of the unknown aspects of the life story of *P. clavata* that we studied indicate its fragility. The same conclusion arises from the demographic models under different scenarios across a gradient of human disturbance. Assuming the plausible fact that *P. clavata* can be selected as indicator (representative) species of the coralligenous because of its quantitative contribution to the structure and functioning of the community (True 1970, Gili and Coma 1998, Ribes and Coma 2006; but see Ballesteros 2006), our results also suggest that the coralligenous is a threatened community.

# Exploring life history and demographic traits to examine the fragility of the species

## Spatial Distribution

*Paramuricea clavata* shows a contagious and asymmetric distribution in our study area that is clearly related to its early life history traits and the sensitivity to abiotic factors. Moreover, the study at large spatial scales showed that the upper limit of distribution has become deeper across a North-South gradient. This indicates a relationship between the distribution limits of the species and the variability of abiotic factors, probably irradiance and temperature (Chapter I).

The relatively low number of populations (ca. 50), the small size of these populations (ca. 500m maximum length), and the distance between them (ca. 80 km in average) are relevant characteristics for the long-term persistence of the species (see Introduction and Chapter I). From a metapopulation perspective, these distribution patterns together with the low capacity of dispersal of *P. clavata* larvae (ca. 10 days) make rescue processes very unlikely and local populations especially vulnerable to disturbances. The distribution pattern of this species is in accordance with the isolated distribution required to be considered a vulnerable species following the UICN criteria (UICN 2001).

## Size structure distributions

The application of demographic approaches widely used in plant ecology, such as the study of size distributions shapes and the exploration of self-thinning on gorgonian populations has allowed identifying two contrasting population dynamics displayed by the two commonest gorgonian species: the red gorgonian *Paramuricea clavata* and the white gorgonian *Eunicella singularis* (Chapter I).

Red gorgonian populations were close to carrying capacity, as demonstrated by the fact that most populations were placed close to the self-thinning line (Yoda et al 1963). This is typical of long-lived and slow-growing species. The movement away from this line displayed by damaged populations confirmed the relationship between the populations placed under the self-thinning line and disturbance events. This approach would be really useful for identifying the existence of biological or physical disturbances, especially for species displaying a high vulnerability according to their demographic characteristics (Chapter III).

*P. clavata* showed stable bell-shaped distributions, where the low proportion of small colonies suggests they suffer short supply of recruits and/or higher mortality rates during early life stages. None of the *P. clavata* populations in the large-scale study corresponded to a young or expanding population, which indicates a scarcity of the initial stages of this population species and a general recruitment failure.

In contrast, *E. singularis* showed a greater variability on population structure that suggests a higher dynamism and also high recruitment rates.

## Early life history stages

The results of the study of the early life history of the species showed that the larvae of *P. clavata* seemed capable to swim and crawl in an apparent exploratory behavior. In our laboratory experiments the time required for the metamorphosis into primary polyps (minimum of 10 days) could suggest rather high dispersal potential. However, *P. clavata* exhibits several mechanisms oriented to favor the retention of the eggs close to the parental colonies. First, the

eggs are kept together within a mucus that may favor both sinking and adhering to the nearby substrates. Second, the larvae are rather efficient crawlers and tend to keep contact with the substrate in artificial containers during laboratory experiments. Third, the negative phototaxis recorded in the laboratory allows the larvae to seek crevices and other dark habitats. This negative phototaxis may also represent a strategy of larvae for avoiding the competition with fast-growing algae, especially in photophilic habitats (Chapter II). The retention mechanisms displayed by the early life history stages appear to contribute to the contagious and asymmetric distribution of the species (Chapter I). Future studies using molecular approaches may elucidate the spatial range of dispersal in this species and the connectivity between populations.

Our results showed that only 60% of the eggs transformed into planulae, 40% of the larvae survived and survival was extremely low (5% in the laboratory) during the metamorphosis. After settlement, none of the polyps survived in the field for more than seven months and none of them developed into more than one polyp during the study period (Chapter II). These results contribute to explain the low recruitment rates observed in the field (Chapter III) and also demonstrate the ecological fragility of this emblematic species.

The slow dynamics of the settlers (Chapter II) has revealed that the small recruits that we observed during the monitoring of permanent transects are at least two years old, pointing out that there is a "black box" during the first year that we can not observe in the field. This might be a general feature of benthic organisms that inhabit in coralligenous assemblages. This early life stage would be equivalent to a seed bank that may lie dormant for years (Morris and Doak 2002). The quantification of these aspects of their life histories is essential to develop accurate size-structured matrices to be used in demographic models (Chapter III).

# ▌▌▌ Gorgonian mortality from human–induced disturbances

Divers, anchors, fishing lines and the development of filamentous algae have been considered the main human-induced sources of red gorgonian mortality (Harmelin and Marinopoulus 1994, Bavestrello et al 1997, Coma et al 2004, Giuliani et al 2005). But this consideration has changed since the occurrence of mass mortality events during the last years in the NW Mediterranean Sea.

During the 1999 mass mortality event, about 30 invertebrate species dwelling mainly in coralligenous communities were affected along the French and Italian coasts (Cerrano et al 2000, Perez et al 2000). This event did not have any effect on populations along the Spanish coast, except the *E. singularis* populations located in the Menorca Island (Balearic Islands) showed the impact of this event (Coma et al *in press*).

In order to obtain baseline data on injury rate in "healthy" gorgonian populations a large scale survey was carried out along the Spanish coast. These data were necessary to accurately quantify the impact of future mortality events. The results obtained from "healthy" populations showed

that the mean percentage of injured tissue and the proportion of totally injured colonies was lower in *E. singularis* (5% and 1%, respectively) than *P. clavata* (10% and 3%, respectively). Moreover, a larger proportion of healthy colonies was observed in *E. singularis* (90% vs. 78%) (Chapter I). These values were similar to those reported previously for unaffected populations (Harmelin and Marinopoulus 1994, Coma et al 2004).

In contrast, the population of *P. clavata* at the Port-Cros National Park, France, was strongly affected by the mass mortality event in the summer of 1999. Shortly after the event, the mortality prompted a sharp decrease in biomass (58%) caused by the combined effect of colony death (9% of the population) and an increase in the extent of colony injury (from 9% before the event to 52% shortly after it). The partial mortality affected more than 76% of the colonies down to 35-40 m of depth. The comparison of these results and those obtained for "healthy" populations (Chapter I) points out the magnitude of this event. After 4 years, our results indicated a large delayed effect of the event accounting for a 70% loss in biomass and about 50% of total mortality of the initial population.

The population decline was due to a delayed stress response in the surviving colonies affected by extensive injury (>66%) because they exhibited a higher mortality rate than uninjured or less injured ones. In addition, the low recruitment rates estimated could not balance this high mortality rate (Chapter V).The contrast between the short-term versus the multi-year assessment of the 1999 mass mortality event at the study site indicated a much greater impact on this species than that indicated by previous estimates (Cerrano et al 2000, Perez et al 2000, Garrabou et al 2001) (Chapter IV).

Furthermore, the 1999 event also caused severe effects on the reproduction of the species that may represent an additional difficulty for the recovery at long-term scales. Females showed the greatest lost of gonadal biomass (73-76% vs. 48-61% in females and males, respectively) and the highest decrease of fertile polyps (20% vs. 11% in female and male colonies). The reproductive output was mainly dependent on the extent of injury affecting the colonies (Chapter V), as indicated by the persistence of the effect of injury over the reproduction output along at least two following years (2000 and 2001). The decrease of gonadal production with the increase of injury may imply a limitation of resources affecting energy allocation to reproduction, and this would be consistent with the energetic constraints observed on the energy budget of the species (Coma and Ribes 2003).

Both the relationship between the extent of injury and the reproductive output found in this study and the persistence of high levels of injuries (mean extent of injury about 35% of the whole surface) four years after the impact (Chapter IV) indicate the importance of the delayed effects and the long-term consequences of the 1999 event, demonstrating that the recovery of populations can be likely measured on the order of decades.

This thesis has focused especially on the impacts of mass mortality events related to rising seawater temperature as well as on the negative effects of the high diving activity detected (paradoxically) in some Marine Protected Areas (MPA). But other disturbance sources can play an important role in the population viability and they must be considered for conservation purposes.

Currently, the strongest impact is the invasion of alien species, especially algae, that has been detected in several Mediterranean localities during the last years. Some introduced algae (*Womersleyella setacea, Acrothamnion preissii, Caulerpa taxifolia, Caulerpa racemosa* var. *cylindracea, Asparagopsis taxiformis, Lophocladia lallemandii*) threaten to overgrow the coralligenous community because, although they usually prefer well illuminated bottoms, they can also thrive on deeper, low-lighted environments where the coralligenous dwells (Ballesteros 2006, Ballesteros *unpublished data*). Although the impact of these invasions on gorgonian populations has not been detected during this thesis, it is worth to note that that the permanent plots at Port-Cros National Park (France) have been invaded by the green alga Caulerpa racemosa var. cylindracea during in 2006.The response of gorgonian populations face to this disturbance will have to be examined during the next years.

In summary, the detection of several sources of mortality and the high sensitivity displayed by *Paramuricea clavata* to these impacts suggests again the fragility of the species. However, we need to develop demographic models for understanding the real consequences of these impacts over the long-term viability.

# ‖‖‖ Modeling the population dynamics of *Paramuricea clavata*

One of the most important parts of this thesis was the development of matrix models. The use of these models has allowed us to evaluate the long-term viability of the red gorgonian *P. clavata* (Chapter III), to examine what factors that determine the viability of its populations (Chapter VI), and to assess the best management actions for facilitating their survival (Chapter VII).

The first important step for developing these models is to define the matrix structure, the number of classes and the vital rates that belong to each size class. We analyzed the demography of red gorgonians by a set of seven age- and size-defined stage classes. Using results obtained from the study of the early life history, matrix models were developed with the first class as age-based class, representing the "newborn" colonies (primary polyps) that we were unable to directly observe in the field. Class 2 colonies were at least two-year olds between 0.3 and 3 cm in height (we assumed that all newly observed colonies in the field fall into this class). The remaining colonies were all size-based classes.

The development of both deterministic and stochastic size-based matrix models has allowed us to estimate basic life history traits for this species and to evaluate the sensitivity of population growth to different vital rates.

Red gorgonian individuals followed a characteristic type III survivorship curve, with rapid declines in survivorship during the first years of life (Chapter II) followed by slow and constant declines of large individuals which displayed a greater longevity. Our estimates of the conditional total life span suggest that if colonies can attain the largest class they may be 60-100 years old (Chapter III). The

use of these models also confirmed the high longevity of the gorgonian populations in our study areas. Our simulations (Chapter III) showed that populations need approximately 50 years for approaching stable stage distributions and that the observed population structures (Chapter I) are quite similar from predicted stable stage distributions at Medes Islands and Cap de Creus.

Before the modeling of population dynamics of the *P. clavata* had not been performed, we were convinced that the low recruitment was the key factor determining the fragility of the species. However, sensitivity and elasticity analysis demonstrate that gorgonian population growth is far more sensitive to changes in survival rates than to growth, shrinkage, or reproductive rates (Chapter III). Recruitment patterns may be crucial over longer time scales, governing the establishment of new populations. Thus, red gorgonians conform to the generality that decreases in adult survival rate should more negatively affect population growth for long-lived species with low annual reproductive success more than for short-lived and highly fecund species (Heppel et al 2000).

These results have important consequences for the conservation of this species. Survival of large colonies is a key factor for the persistence of populations because it determines how long a population can persist without recruitment. This demographic trait, comparable to that reported for other gorgonian species (Lasker 1990, Gotelli 1991, Yoshioka 1998, Garrabou and Harmelin 2002), is in agreement with the bet-hedging theory, that predicts adults are selected for high survival when recruitment is highly variable because a long reproductive life is needed to counterbalance years of high juvenile mortality (Stearns 1992).

Using the elasticity analysis, we have compared the life history patterns of the red gorgonian to those of other sessile species of invertebrates and terrestrial plants. One of the most striking results from this comparison was the similarity in life history traits between red gorgonians and terrestrial plants despite having very different environments and evolutionary histories (Chapter III).

The values of recruitment elasticity for *P. clavata* are lower than those reported for other marine organisms but they are similar to those reported for some long-lived plants (Morris and Doak 1998, Forbis and Doak 2004, Silvertown et al 1993). These values and the delayed age of sexual maturity, in combination with the longevity of the species, show a clear fecundity/mortality trade-off seen for other species with similar life-history traits such as herbs, shrubs and trees (Forbis and Doak 2004, Franco and Silvertown 2004).

Together, all these demographic characteristics suggest a life history that is at the "slow" end of the "fast-slow continuum" of life history traits (Partridge and Harvey 1988) and evidence the "demographic fragility" of this species as well as the need for conservation efforts on red gorgonian populations.

This study has focused on the shallowest gorgonian populations because they are more exposed to the effects of human-induced disturbances. These populations probably represent only a small proportion of gorgonian populations because they can also be found in deeper areas than 50 meters. Thus, distances between populations can be much shorter and rescue processes much more likely. Moreover, we do not know to what extent the studied populations are repre-

sentative of the population dynamics displayed by deeper populations. Considering this lack of knowledge, further research must be focused on the examination of the abundance and functioning of these deeper populations as well as understanding the connectivity between shallow and deep populations. This knowledge would be essential for understanding the long-term persistence of red gorgonian species.

Furthermore, the role of asexual reproduction has not been considered into the demographic models. Although it has been considered of low relevance for this species (Coma et al 1995), to achieve a full understanding of the population dynamics of the species it is necessary to examine the importance of the "regrowth" of new branches from the base of the colony after the injury of the main stem as happens for several tree species. This strategy could be an important advantage facing to strong disturbances where the mortality is really high (Chapter IV).

## III Modeling the effects of anthropogenic disturbances

The negative growth of red gorgonians populations (all matrices showed annual population growth rates <1) indicates the fragility of this species, showing the studied populations in decline and a high risk of extinction over moderate time horizons. Quasi-extinction risks correspond to the differences in $\lambda_s$, with a median extinction time of 41 and 115 years at Medes Islands and Cap de Creus, respectively. These declines appear to be related to a recent increase in anthropogenic disturbances (Chapter III).

### The effects of diving activity

Effects of divers on gorgonians are strongest in a few areas with high levels of visitation, as occurs in other areas and communities affected by damage from trampling or diving (Liddle and Kay 1987, Brosnan and Crumrine 1994, Garrabou et al 1998, Tratalos and Austin 2001). In sites such as the Medes Islands, natural mortality rates can increase from 3%/yr to 7%/yr due to high diving activity (Coma et al 2004). However, in the absence of a modeling effort to translate these changes into effects on population persistence, the relevance of these values for management was difficult to comprehend.

Our modeling of increased survival of reproductive colonies showed clear effects on the studied populations, and most importantly showed that the local persistence ($\lambda=1$) of gorgonian populations can be achieved with only modest increases in adult survival (3% and 7% in Cap de Creus and Medes populations, respectively).

The contrasting population growth rates in the studied areas also suggest the importance of the impact of diving on population decline. The differences in mortality reduction needed at the two sites may reasonably be attributed to different levels of diving activity; while in Medes Islands the estimated number of divers is about 70,000 divers/year, in Cap de Creus the estimated number of diver is about 30,000 divers/years (Zabala et al 2003) (Chapter VI).

## The effects of strong disturbances: mass mortality events and climate change

The effect of mass mortality events was also assessed using PVA analysis with regard to the probable increase in the frequency of the events (see above). The 1999 mass mortality event has been related to the recent warming of the Mediterranean (Pascual et al 1995, Bethoux et al 1998). The occurrence of a new event in summer 2003 (some signals of mortality have been detected in some localities in the NW Mediterranean Sea during the summer of 2006) indicates that the frequency of these events may be increasing as a result of the whole climate change. Therefore, new repetitions of mass mortality events could be expected.

By simulating the extinction risk of gorgonian populations under different frequency of mass mortality events, we obtained different results depending on the population used to obtain the non-affected year matrices. Modeling the mass mortality effects on Medes Islands populations ($\lambda$=0.94) showed marked effects on persistence, with near-certainty of quasi-extinction predicted after 38 to 53 years under different mass mortality frequencies. On the other hand, simulations for the Cap de Creus population ($\lambda$=0.97) showed near-certainty of quasi-extinction at 55 and 84 years with frequencies of mass mortality events (displaying the same impact observed at Port-Cros) each 5 and 10 years, respectively, and substantially lower risks under less frequent disturbance regimes (Chapter VI).

Our findings confirm that human impacts such as high diving activity together with the global warming trend can combine to have dramatic effects on the viability of marine long-lived and slow-growing species.

# ▌▌▌ Restoration by gorgonian transplantation: a feasible management tool? ▌

An experimental approach was used to test the viability of gorgonian transplantation as a management tool. Regardless of initial method failure that needs to be improved, well-attached transplants achieved survival rates (80%) similar to natural colonies.

The application of population viability analysis to examine the effectiveness of potential management actions has been demonstrated in many systems (Crowder et al 1994, Doak et al 1994, Pfister and Bradbury 1996, York and Holmes 2003, Morris and Doak 2002). In this study, matrix models have been used to assess the effectiveness of transplantation techniques in improving the viability of red gorgonian populations. The simulations showed substantial improvement in the annual population growth rate ($\lambda$) only when the transplantation was performed every 2 years under the most exigent conditions (recovering 75% of the dead colonies and obtaining 3 fragments from each one) (Chapter VII).

The experimental and modeling approaches have provided some clear-cut results that can help managers and scientists to determine the convenience and utility of this restoration technique. Both approaches suggest severe limitations of this technique at larger spatial and temporal scales. However, our study confirms the feasibility of this restoration measure that can contribute to the recovery of populations in MPAs affected by local disturbances. This study opens a door to further research on the restoration of marine populations.

> In summary, the results obtained during this thesis have revealed the fragility of the red gorgonian *Paramuricea clavata* facing to the increasing disturbances. The demographic approaches developed here, especially the use of population viability analysis (PVA), have demonstrated to be essential for understanding the long-term persistence of populations. Moreover, this thesis may offer managers of Marine Protected areas useful guidelines on efficient conservation of long-lived marine species.

# ▌▌▌ Conservation of long–lived marine species: learning from terrestrial ecosystems ▌

When trying to synthesize the results of this study in a more general framework, we have two major, partly contradicting thoughts.

On one hand, we have a feeling of surprise and novelty. It is still difficult to find in the discipline of marine benthic ecology, at least in the Mediterranean, references to populations with characteris-

tics similar to those of the red gorgonian: communities persisting for hundreds of years; 'individuals' (colonies) decades to hundreds of years old; and characteristic life history traits. These traits include extremely low recruitment despite an enormous annual reproductive effort, very low natural mortality, and great importance of the survival of the oldest colonies for population dynamics.

On the other hand, we have a feeling of deja vu because, despite the difference in size, the red gorgonian populations are very similar to terrestrial forests. Probably, not only red gorgonians, but also other benthic organisms with low turnover (such as perennial brown algae, sponges, red coral and other suspension feeders) also show similarities with large terrestrial plants and forests.

These similarities can provide a great source of inspiration for understanding benthic ecosystems and guiding future research. In particular, it would be worth trying to import theory and methodologies from disciplines such as dendrochronology, management of exploited forests, or conservation of old growth forests.

After the outstanding knowledge of the biology of several marine species attained during the last decades, a more generalized ecological approach may be achieved to carry out the future research of marine benthic communities. Although this is convincing for gorgonian populations as we have demonstrated in this study, almost certainly it could be applied for other persistent species such as corals, sponges...

The development of the demographic and modeling methods to the study of the red gorgonian *Paramuricea clavata* has opened the way to the application of these methods to the conservation of several species of marine hard-bottom communities. However we have to warn about the difficulties of the application of these studies to other benthic species in an indiscriminate way. A supplementary effort would be necessary to select an appropriate pool of model species, and to understand the particular demography of each species.

# Further directions for future research

In addition to the application of demographic approaches developed basically from terrestrial ecology to the future research on other marine long-lived species, there are other interesting questions that presently remain unsolved; their development can be essential for understanding the dynamics of the red gorgonian populations and the coralligenous in general.

## The study of the synergistic effects of disturbances

According to our results, global warming effects may be particularly negative for species already threatened by other local and environmental changes, due to the additive or multiplicative effects

of multiple stressors on individual fitness and population viability. While it seems to be unfeasible over the short-term to protect marine populations from stresses related to global warming, many interacting anthropogenic disturbances may be far more tractable. Future research on conservation of marine long-lived species should consider the synergistic effects of disturbances. Threats such as climate change, abrasion from diving activity, proliferation of filamentous and invasive algae should be studied together if effective conservation plans are to be made for their preservation.

## The role of asexual reproduction on *Paramuricea clavata* dynamics

As mentioned before, the growth of new branches from the base of the colony could be an important strategy for the red gorgonian *Paramuricea clavata* to recover from strong disturbances such as mass mortality events. A good knowledge of the dynamics of these new branches originated from the base of red gorgonian colonies (from a descriptive and experimental approach) may allow us to elucidate the significance of this strategy for the resilience of red gorgonian populations.

## Genetic studies in *Paramuricea clavata*

To achieve a complete knowledge of the biology of the red gorgonian *Paramuricea clavata*, the dispersal of larvae and the connectivity of red gorgonian populations must be studied using molecular approaches. Population genetic studies of *P. clavata* will allow us to assess the genetic structure of this species associated with dispersal features, and the relative importance of sexual versus asexual reproduction at a fine spatial scale. Understanding the genetic structure of *P. clavata* will be essential for elucidating the resilience of these populations and the ability of the species to recover from the threat of local extinction.

## The biodiversity in the red gorgonian forests

Previous studies have described the species composition and abundance of *P. clavata* assemblages in some Mediterranean localities (True 1970, Gili and Ballesteros 1991). However owing to the great difficulty to perform taxonomic studies, the importance of red gorgonian populations for the biodiversity of the coralligenous community remains unknown at a large spatial scale. A quantification of the biodiversity on *P. clavata* assemblages along a gradient of human disturbance (analogous to a gradient of density) will provide us useful baselines to determine the role of the presence of red gorgonian colonies on the biodiversity of the coralligenous community.

Moreover, despite the selection of *P. clavata* as an indicator species of the community due to its contribution of to the structure and functioning of the coralligenous community (True 1970, Gili and Coma 1998, Ribes and Coma 2006; but see Ballesteros 2006), we are unaware of the effects of perturbations on the species composition and abundance in gorgonian forests. The detection of changes on the biodiversity along a gradient of human disturbances will also elucidate the magnitude of the disturbance effects over the whole community.

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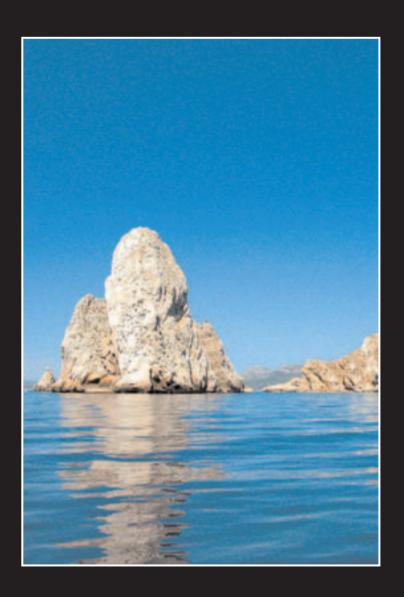Soong K (1993) Colony size as a species character in massive reef corals. Coral Reefs 12: 77-83

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[] Resum

# ▌▌▌ Introducció

▌ **La Biologia de la conservació davant l'augment de les pertorbacions**

Les activitats humanes estan canviant dràsticament els sistemes naturals, causant una progressiva degradació i pèrdua dels hàbitats, i per tant una conseqüent pèrdua d'espècies i de variabilitat genètica (Vitousek et al 1997). Davant d'aquest context, la biologia de la conservació sorgeix com una resposta de la comunitat científica davant dels canvis ambientals que estant fent perillar una important part de la diversitat biològica (Soulé i Kohm 1989). Actualment, un dels reptes més importants pels ecòlegs és conèixer les conseqüències d'aquest augment de les pertorbacions així com oferir possibles estratègies de gestió per tal almenys de minimitzar els danys humans sobre els ecosistemes naturals (Peterson i Estes 2001).

Sempre s'ha pensat que les activitats antropogèniques tenien major impacte en l'estructura i funcionament dels ecosistemes terrestres que en els marins (Ehrich 1995, Vitousek et al 1997, Fahrig 2001). Però aquesta apreciació està canviant a mesura que les pertorbacions humanes modifiquen els hàbitats marins a una escala espacial més gran (Roberts i Hawkins 1999). Actualment, tot i que els canvis en els ecosistemes marins són més difícils de detectar, nombrosos estudis han confirmat grans pèrdues de diversitat així com important canvis en els funcionament d'aquests ecosistemes (Botsford et al 1997, Vitousek et al 1997, Gray 1997, Roberts i Hawkins 1999).

A diferència dels ecosistemes terrestres, on la pèrdua d'hàbitat és la principal causa del declivi i fins i tot de l'extinció d'espècies, en els ecosistemes marins la principal amenaça és la sobreexplotació que afecta directament moltes espècies claus i modifica l'estructura de les xarxes tròfiques (Dayton et al 1995, Jennings i Kaiser 1998, Pauly et al 1998, Jackson et al 2001). Però d'altra banda, també cal destacar-ne altres que tenen efectes significatius sobre les comunitat marines, com la contaminació, la introducció d'espècies, malalties, degradació del habitat i canvi climàtic (Harvell et al 1999, Steneck i Carlton 2001, Hughes et al 2003, Kappel 2005, Harley et al 2006).

Concretament, una font important d'estrès per les espècies i comunitats tant marines com terrestres, són els efectes del canvi climàtic que es donen tant a escala global com local sobre tots els nivells d'organització: des de les poblacions, canviant el trets vitals de moltes espècies, fins a les comunitats, alterant la composició específica, estructura i funcionament de molts sistemes naturals (McCarty 2001, Walther et al 2002, Harley et al 2006).

Totes aquestes pertorbacions antropogèniques, tenen un efecte més dramàtic en espècies i comunitats, tant marines com terrestres, amb una lenta dinàmica poblacional. La majoria de les espècies que mostren una gran vulnerabilitat davant d'aquests impactes són espècies longeves amb un lent creixement, una tardana maduresa sexual i una baixa fecunditat, o sigui espècies de tipus K (Mac Arthur i Wilson 1967, Pianka 1972). Això ens fa pensar que un coneixement acu-

rat dels trets vitals de les espècies pot ser clau alhora d'entendre millor els efectes dels impactes antropogènics i per tant poder predir les futures trajectòries poblacionals sota diferents escenaris de degradació humana (Halpern 1989, Musick 1999).

També, és important considerar el fet que moltes d'aquestes espècies longeves estiguin considerades com "espècies enginyeres", pel seu paper clau en l'estructura i funcionament de molts ecosistemes, incrementant la diversitat biològica de les comunitats on es troben (Jones et al 1994). La conservació d'aquestes espècies és vital per mantenir l'organització i la diversitat de les comunitats (Mills et al 1993).

Aquests trets demogràfics a priori tan desfavorables han estat seleccionats pel fet que han evolucionat com ecosistemes madurs sota poques fluctuacions ambientals, mostrant per tant una alta complexitat estructural i una baixa dinàmica (Margalef 1963). Però l'augment de les activitats humanes ha posat de manifest la fragilitat d'aquests ecosistemes madurs (Margalef 1997).

No és sorprenent que davant aquesta relació entre fragilitat i dinàmica poblacional, la majoria dels esforços realitzats en el camp de la biologia de la conservació hagin estat focalitzats en l'estudi de la dinàmica poblacional i en l'estimació dels paràmetres demogràfics així com en el desenvolupament de models quantitatius que puguin ajudar als gestors a prendre decisions davant del declivi de moltes poblacions (Simberloff 1988, Beissinger i Westphal 1998). Algunes preguntes claus ens poden ajudar durant l'aproximació a la conservació d'espècies amenaçades: Està la població en declivi? Quins són els factors que determinen la viabilitat de la població? Quins són els estadis vitals més crítics per la viabilitat de la població? Quines estratègies de gestió ofereixen més probabilitats per la supervivència de la població? (Heywood i Iriondo 2003).

Davant d'aquestes qüestions, els anàlisis de viabilitat de poblacions (PVA) són una de les eines més potents en el camp de la Biologia de la conservació (Boyce 1992). Aquests anàlisis estan basats en models demogràfics que utilitzen el càlcul matricial i són utilitzats principalment per estimar la taxa anual de creixement poblacional ($\lambda$), la distribució estable i la sensitivitat i elasticitat del diferents trets vitals més sensibles al creixement poblacional (Caswell 2001, Morris i Doak 2002). L'augment de les pertorbacions evidencia la importància d'aquests models per examinar la futura persistència de les espècies amenaçades així com avaluar l'efectivitat de possibles mesures de gestió (Beissinger i Westphal 1998, Reed et al 2002).

Mentre que aquests models han estat àmpliament utilitzats per estimar la viabilitat de moltes espècies terrestres tant animals com vegetals (Doak et al 1994, Silvertown et al 1996, Menges 2000, Caswell 2001, Beissinger i McCullough 2002), aquests han estat poc utilitzats en l'àmbit de la conservació marina (Gerber i Heppell 2004). Sobretot han estat aplicats en l'estudi d'espècies emblemàtiques com mamífers marins, tortugues i altres vertebrats (Crowder et al 1994, York 1994, Thompson et al 2000, Holmes i York 2003) i en canvi han estat poc desenvolupats en l'estudi d'altres espècies més representatives com els invertebrats marins.

Precisament, molts grups d'invertebrats marins (esponges, briozous, antozous...) mostren una organització clonal que els proveeix d'una gran plasticitat i habilitat de recuperació en front d'esdeveniments de mortalitat parcial (Hughes i Cancino 1985, Hughes i Jackson 1985). Són parti-

cularment aquestes característiques, unides a una inherent dificultat per portar a terme estudis científics sota l'aigua a escales temporals i espacials rellevants (Hughes i Connell 1999), que dificulten l'aplicació de models demogràfics clàssics (Hughes i Cancino 1985).

## El coral·ligen Mediterrani: el nostre marc de referència

La Mediterrània ha estat identificada com un important focus de diversitat (Bianchi i Morri 2000). Gran part d'aquesta biodiversitat prové dels ecosistemes bentònics costaners principalment fons rocosos i praderes de Posidonia (Boudouresque 2004). Entre les comunitats de fons durs, destaca el coral·ligen per la seva riquesa biològica (aproximadament unes 1666 espècies han estat identificades) i per la seva extraordinària complexitat estructural (Ballesteros 2006).

El coral·ligen té origen biogènic i es desenvolupa principalment per l'acumulació d'algues calcàries incrustants que creixen en condicions de baixa irradiància. Encara que es desenvolupa bàsicament a la zona circalitoral també es troba a la zona infralitoral en parets verticals, canals o extraploms, ocupant petites superfícies (Ballesteros 2006).

La majoria dels estudis d'aquestes comunitats s'han centrat més en aspectes descriptius i qualitatius (Pérès i Picard 1964, Laubier 1966, Gili i Ros 1984) que en els funcionals i dinàmics (True 1970, Coma 1994, Garrabou 1997, Ribes 1999). El baix nombre d'estudis basats en la dinàmica del coral·ligen podria ser explicat per alguns característiques d'aquest hàbitat. Primer, com és impossible estudiar la dinàmica de totes les espècies que habiten en una comunitat tan rica, la selecció d'una espècie representativa de tota la comunitat sempre és difícil. A més la natura clonal de la majoria d'espècies amb una important contribució a la biomassa i cobertura de la comunitat implica problemes metodològics importants: la recuperació de mortalitats parcials, el creixement negatiu mitjançant la pèrdua de fragments apicals, la fusió i fissió dels individus i la seva capacitat asexual, dificulten l'obtenció d'una correlació significativa entre talla i edat. El teòric creixement il·limitat tampoc facilita la relació entre la talla i les característiques demogràfiques com poden ser la fertilitat i la supervivència.

L'estabilitat dels factors ambientals a les fondàries on es desenvolupa (principalment sota els 20 metres), la falta de grans pertorbacions naturals i l'absència d'excessives pressions antropogèniques en el passat ajuden també a explicar la falta d'estudis més aplicats a la conservació (veure Garrabou i Harmelin 2002, Coma et al 2004).

Actualment, aquest hàbitat es troba sota l'impacte de pertorbacions antropogèniques importants com són la contaminació, la pesca especialment de ròssec, activitats recreatives com el busseig, la invasió d'espècies i el canvi climàtic (veure Ballesteros 2006 per una revisió). Probablement és aquest últim impacte amb el conseqüent escalfament de la Mediterrània, l'amenaça més preocupant per aquest hàbitat (Bethoux i Gentilli 1996, J. Pascual *dades no publicades*). Recentment, dos esdeveniments de mortalitat massiva (1999 i 2003) han afectat a moltes espècies d'invertebrats marins, principalment suspensívors (Cerrano et al 1999, Perez et al 2000, Garrabou et al

2001, Linares et al 2005, Coma et al *en premsa*). Aquests esdeveniments, que han afectat a les poblacions més someres (per sobre dels 35 m), han estat relacionats amb inusuals anomalies tèrmiques amb una clara connexió amb el canvi climàtic (Romano et al 2000, Coma i Ribes 2006).

El primer esdeveniment de mortalitat massiva va tenir lloc a finals de l'estiu de 1999, quan aproximadament unes 30 espècies d'invertebrats marins de 5 phyllums diferents van resultar greument afectades a una escala espacial sense precedents, des de les costes italianes a les costes balears (Cerrano et al 1999, Perez et al 2000, Garrabou et al 2001, Coma et al *en premsa*). Un altre esdeveniment de mortalitat massiva va tenir lloc durant l'estiu del 2003 provocat per les altes temperatures assolides durant una forta onada de calor que va afectar a tota Europa (Harmelin 2004, N. Benssoussan *dades no publicades*). Aquest episodi va afectar a les mateixes espècies però a una escala espacial encara major, incloent poblacions del Mediterrani espanyol, del centre d'Itàlia i de les illes de Còrsega i Sardenya (R. Coma et al *dades no publicades*, J. Garrabou et al *dades no publicades*).

## ■ Les gorgònies com a cas d'estudi

En aquesta tesis, la gorgònia vermella *Paramuricea clavata* (Risso 1826) va ser seleccionada com a espècie representativa del coral·ligen per tal d'avaluar la viabilitat d'aquesta comunitat davant l'actual increment de les pertorbacions. En altres paraules, la idea va ser testar en aquesta espècie "fàcil" la utilitat de les diferents eines emprades en l'àmbit de la biologia de la conservació per examinar la resiliència d'aquesta espècie dins l'actual escenari de pertorbacions i així poder en un futur ser aplicades a altres espècies longeves més difícils de estudiar.

Entre els organismes clonals més representatius del coral·ligen (algues calcàries, esponges, cnidaris, briozous i tunicats), les gorgònies presenten moltes avantatges per dur a terme estudis demogràfics. La seva forma arborescent facilita la identificació com individus separats. Aquest fet i la relativa "gran" talla facilita la seva localització, identificació i mesurament durant els mostrejos subaquàtics. També, malgrat la seva clonalitat, les gorgònies mostren un clar patró morfològic i continu creixement, que permet una bona relació entre la talla (màxima alçada) i edat (Coma et al 1998a). Per últim, les poblacions d'algunes espècies de gorgònies presenten, una marcada distribució a taques dins les quals les colònies es troben en alta densitat (Gili et al 1989, Gili i Ballesteros 1991) i una gran similitud amb els boscos terrestres que permeten que moltes tècniques desenvolupades pels ecòlegs forestals puguin ser emprades durant el seu estudi.

A simple vista, la selecció de *P. clavata* com espècie indicadora de tota la comunitat pot semblar abusiu, però diferents arguments fan raonable aquesta assumpció. Primer de tot, tenint en compte que l'absència de les espècies estructurals claus pot deixar un important buit funcional fins arribar a provocar la simplificació o degradació de les comunitats on es troben (Soulé et al 2003), la supervivència de la comunitat hauria d'estar estretament relacionada amb la persistència d'aquesta espècie donat el seu paper clau en la comunitat (Gili i Coma 1998). La lenta taxa

de creixement anual (0.8 cm en alçada/any) obtinguda per *P. clavata* (Coma et al 1998a, R. Coma *dades no publicades*) està en concordança amb la lenta dinàmica mostrada per altres espècies del coral·ligen (Turon i Becerro 1992, Garrabou 1999, Garrabou i Zabala 2001, Garrabou i Harmelin 2002) confirmant la hipòtesis que les principals espècies representatives mostren una dinàmica molt semblant a la de la comunitat en general.

Cal afegir que la gorgònia *P. clavata* pot ser considerada una bona indicadora dels canvis en la magnitud i la intensitat de les pertorbacions que afecten en general al coral·ligen. Per una banda, aquesta espècie ha mostrat una gran sensitivitat a l'efecte erosiu del busseig (Coma et al 2004), dels fils de pesca (Bavestrello et al 1997) i a la proliferació de mucílags que poden recobrir totalment les colònies (Mistri i Cecherelli 1996, Guliani et al 2005). D'altra banda, aquesta espècie va ser una de les més afectades durant els dos esdeveniments de mortalitats massives esmentats anteriorment (Cerrano et al 1999, Perez et al 2000). Finalment, hi ha dos raons més que varen influir en aquesta selecció: el coneixement de molts dels aspectes biològics més importants d'aquesta espècie (Coma et al 1994, 1995a,b, 1998a,b, Ribes 1999) i el fet que la seva distribució isolada restringida a petites àrees emblemàtiques suggereix una gran vulnerabilitat de l'espècie enfront factors externs.

# ▌▌▌ Objectius i resultats principals

El principal objectiu d'aquesta tesis ha estat estudiar la demografia de la gorgònia vermella *Paramuricea clavata* per tal d'examinar la resiliència de les seves poblacions enfront l'augment de les pertorbacions que estan amenaçant la seva persistència a llarg termini. Per tal d'assolir aquest objectiu, es van realitzar diferents treballs descriptius, experimentals i de modelització.

**Capítol I. Estructura de talles, densitat i pertorbació en dues gorgònies Mediterrànies: *Paramuricea clavata* i *Eunicella singularis***

El Capítol I està centrat en l'avaluació de l'actual estat de les poblacions de gorgònies a la costa Mediterrània espanyola des de Cap de Creus fins Cabo de Gata, amb especial atenció a les dues espècies més representatives d'aquesta àrea: *Paramuricea clavata* i *Eunicella singularis*. Aquest estudi es va iniciar després del primer esdeveniment de mortalitat massiva detectat durant l'estiu de 1999 al llarg de les costes franceses e italianes. Els objectius van ser dos: examinar l'impacte d'aquesta mortalitat en les "nostres" poblacions i establir una línea de referència en relació a la distribució i salut de les poblacions de gorgònies ibèriques davant l'eventual ocurrència d'altres pertorbacions. Però aquest treball ens va permetre assolir altres objectius. Tenint en compte la falta d'estudis demogràfics sobre aquest tipus d'espècies a escales espacials rellevants en l'àmbit de la conservació ($10^3$ Km), les dades quantitatives obtingudes en aquest tre-

ball ens permeten detectar possibles diferències regionals en la distribució i demografia d'aquestes espècies. Paral·lelament, la comparació de l'estructura demogràfica de les dues espècies així com la seva resposta a les pertorbacions ens ha permès detectar quina espècie necessita un major esforç de conservació.

Les dues espècies estudiades han mostrat uns patrons de distribució clarament contrastats. Mentre que *E. singularis* està distribuïda regularment al llarg de la costa mediterrània ibèrica, *P. clavata* mostra una distribució clarament de contagi I asimètrica, essent les seves poblacions molt més comuns en el Nord que en el Sud. Respecte al límit superior de distribució, en *P. clavata* aquest va disminuir clarament al llarg del gradient Nord-Sud.

L'exploració extensiva al llarg del litoral ibèric mediterrani dels efectes de la mortalitat massiva de l'estiu de 1999 va mostrar que cap de les poblacions va resultar afectada per aquesta pertorbació. Els nostres resultats van ser molt similars als obtinguts en poblacions sanes (Harmelin i Marinopoulus 1994, Coma et al 2004). El percentatge mig de teixit mort i la proporció de colònies totalment mortes va ser menor en *E. singularis* (5% i 1%, respectivament) que *P. clavata* (10% i 3%, respectivament), a més una major proporció de colònies "sanes" (sense teixit afectat) va ser observada en *E. singularis* (90% vs. 78%).

Els resultats obtinguts explorant les estructures de talles també suggereixen una dinàmica poblacional molt diferent per les dues espècies. Moltes poblacions de *E. singularis* mostren la primera classe de talla com la més abundant, mostrant una gran dinamisme de les colònies joves. En canvi, en les poblacions de *P. clavata* domina una falta general de reclutament, essent les classes intermèdies sempre les més abundants.

La relació entre biomassa i densitat estimada per ambdues espècies, mostra una correlació significativa i negativa en les poblacions de *P. clavata* amb una pendent molt propera a -3/2, com la que s'obté per poblacions dominades per mecanismes de "self-thinning" (auto-tala). Aquest resultat demostra l'existència d'una certa capacitat de càrrega per les poblacions de *P. clavata*. Les trajectòries obtingudes per poblacions afectades per fortes pertorbacions mostren com aquests impactes allunyen les poblacions de la línia de saturació, al perdre densitat i biomassa, i que amb el temps hi ha una certa tendència a apropar-se de nou a aquesta "línia de saturació". En contrast, les poblacions de *E. singularis* no mostren cap pauta clara.

> **Capítol II. Estudi de les primeres fases de vida de *Paramuricea clavata*:**
> **algunes implicacions per la dinàmica poblacional**

El Capítol II focalitza en l'estudi de les primeres fases de vida d'aquesta espècie. Aquestes primeres etapes són probablement les més critiques per la supervivència dels organismes bentònics, en els quals la capacitat de dispersió, de colonització de noves àrees i el manteniment de les poblacions locals depenen en gran mesura de l'èxit en els estadis larvaris. Per això, és sorprenent que amb tot el coneixement que es té de la reproducció de *P. clavata* (Coma et al

1995a, Coma et al 1995b), hi hagi una gran desconeixença dels primers estadis de vida d'aquesta espècie, sobretot quan es compara la gran inversió en reproducció sexual amb la baixa taxa de reclutament observada en el camp.

L'estudi d'aquestes primeres fases ha estat abordat des de diferents aproximacions tant descriptives com quantitatives: descrivint per primera vegada aquests primers estadis des dels ous fins als pòlips primaris, quantificant la supervivència d'aquestes fases i mostrant les implicacions per la dinàmica poblacional d'aquesta espècie. Cal afegir, que els resultats obtinguts durant aquest estudi són essencials alhora de construir les matrius estructurades pel model demogràfic desenvolupat en el següent capítol (Capítol III) per tal d'estudiar la viabilitat a llarg termini d'aquesta espècie.

Durant els tres anys d'estudi (2001, 2002, 2003), l'alliberament de gònades va ser observat durant dos episodis en el mes de Juny molt propers als dies de lluna plena i lluna nova. Les gònades al ser alliberades es mantenen a la superfície de les colònies mitjançant una substància mucilaginosa). La fertilització és externa, com havia estat suggerit prèviament (Coma et al 1995a), tal com suggereixen els següents resultats. Primer, el fet que la majoria dels ous no estaven fertilitzats quan van ser recol·lectats després de l'alliberament. Segon, que la taxa de fertilització va augmentar en funció del temps que es mantenen els ous sobre la superfície de les colònies parentals (la taxa de fertilització va augmentar del 62% al 96% al llarg de dos dies). I tercer, l'alta variabilitat de les taxes de fertilització obtingudes durant els diferents episodis d'alliberament (mentre que es van obtenir taxes molt altes durant els primers episodis (68% i 62%), aquestes taxes van ser molt menors (22%) i més variables (de 0 a 75%) durant el segon episodi d'alliberament.

Pel que fa al desenvolupament, mentre que la blàstula i la plànula van ser observades 48 hores i entre 48-72 hores respectivament, després de l'alliberament de les gònades, la metamorfosi dels pòlips no es va completar fins 10-18 dies després.

Les plànules van mostrar un comportament clarament fotòfob, coherent amb la distribució dels adults. El 60% dels ous es va transformar en plànules i el 40% d'aquestes larves va sobreviure fins el inici de la metamorfosi. Únicament el 5% de les plànules es va convertir en pòlips primaris en el laboratori. Després de l'assentament en el camp, cap dels pòlips assentats va viure més de 7 mesos i cap d'ells es va dividir en més d'un pòlip.

## Capítol III. Demografia i viabilitat d'una espècie marina longeva: la gòrgonia vermella

En el Capítol III, la demografia de dues poblacions de *Paramuricea clavata* va ser estudiada mitjançant models demogràfics a partir de matrius estructurades (Caswell 2001). Tot i que les dues poblacions estaven situades dins dues Àrees Marines protegides al Mediterrani Nord-Occidental (Illes Medes i Cap de Creus), ambdues estaven subjectes a una considerable freqüentació per busseig (Zabala et al 2003, Coma et al 2004).

Models deterministes i estocàstics van ser utilitzats per assolir tres objectius. En primer lloc, estimar els trets de vida bàsics d'aquesta espècie així com utilitzar els models resultants per avaluar la sensitivitat de la taxa de creixement poblacional a les diferents taxes vitals. En segon lloc, examinar el desenvolupament de l'estructura poblacional al llarg del temps i analitzar la viabilitat de les poblacions estudiades. I per últim, comparar els patrons demogràfics mostrats per aquesta espècie amb altres espècies d'invertebrats marins i plantes terrestres.

La gorgònia vermella va mostrar una corba de supervivència tipus III, amb una gran mortalitat durant els primers anys de vida seguit d'una baixa i constant mortalitat de les colònies més grans i longeves. Les nostres estimes mostren que les colònies que arriben a la classe de talla més gran poden arribar a tenir entre 60 i 100 anys de vida.

El lent creixement i la baixa mortalitat d'aquesta espècie tenen com a resultat una lenta convergència cap a la distribució estable de la població (obtinguda després de 50 anys d'evolució). La distribució estable obtinguda en les simulacions va resultar ser molt semblant a les obtingudes en les poblacions estudiades. Tot i que les nostres poblacions semblen estar en un estat d'estabilització, les baixes taxes anuals de creixement poblacional ($\lambda$) mostren a les poblacions en declivi i prediuen un alt risc d'extinció a mig termini.

Tal i com es dóna en moltes espècies longeves amb una dinàmica poblacional lenta, els anàlisis de sensitivitat i elasticitat demostren que el creixement poblacional és molt més sensible als canvis en les taxes de supervivència que als canvis en el creixement, decreixement o taxes reproductives. Els valors d'elasticitat del reclutament obtinguts per aquesta espècie són els mes baixos en comparació amb altres espècies d'invertebrats marins així com amb plantes terrestres.

Tot i que aquesta modelització mostra alguns resultats molt clars, la variabilitat en alguna de les estimes suggereix la importància de l'obtenció de dades a escales temporals més grans per entendre millor l'efecte de l'increment de les pertorbacions sobre aquestes poblacions.

**Capítol IV. Efectes a curt i a mig termini d'un esdeveniment de mortalitat massiva sobre la dinàmica poblacional de _Paramuricea clavata_**

Com s'ha comentat abans, algunes poblacions del coral·ligen han estat afectades per episodis de mortalitat massiva relacionades amb l'escalfament global. Els Capítols IV i V estimen els efectes de la mortalitat massiva de l'estiu de 1999 sobre les poblacions de gorgònia vermella al Parc Nacional de Port-Cros (França). Per entendre la resiliència d'aquesta espècie davant aquestes fortes pertorbacions, les poblacions varen ser estudiades just abans i després del impacte i durant els quatre anys després de la mortalitat (1999-2003).

Els efectes de la mortalitat massiva de 1999 varen mostrar alguns patrons característics tant espacials com temporals. Respecte als patrons espacials, l'impacte de la mortalitat va mostrar

un clar efecte en fondària, afectant a les poblacions més somes per sobre dels 30-35 metres, però també va mostrar una alta variabilitat a escala local.

Pel que fa als patrons temporals, aquest esdeveniment es va caracteritzar per una important disminució de la biomassa (al voltant del 58%) estimada uns mesos (Novembre 1999) després del impacte. Aquesta disminució va ser causada per un increment de la mortalitat total (9%) però sobretot per un extraordinari increment del percentatge de teixit afectat (d'un 9% a un 52%). Els nostres resultats varen mostrar que aquest esdeveniment va tenir importants efectes decalats en el temps, mostrant que la densitat va disminuir un 48% durant els quatre anys després de la mortalitat. Aquesta pèrdua de densitat va ser deguda principalment a la mort de les colònies afectades per grans proporcions de teixit afectat i al fet que el reclutament no va ser suficient per balancejar les importants pèrdues. Quatre anys després d'aquest esdeveniment es va estimar que un 70% de la biomassa inicial es va perdre com a conseqüència d'aquesta mortalitat.

## Capítol V. Efectes d'un esdeveniment de mortalitat massiva sobre la reproducció de la gorgònia *Paramuricea clavata*

Per arribar a tenir un bon coneixement de les conseqüències d'aquests tipus d'impacte, s'estudiaren els efectes en l'esforç reproductor.

Els impactes de la mortalitat massiva del 1999 sobre la reproducció de *P. clavata* van ser més importants en les colònies femelles que en les masculines. Les colònies femenines van mostrar una major disminució del percentatge de pòlips fèrtils així com de la biomassa gonadal en funció del grau de afectació. Mentre que les colònies moderadament afectades van exhibir una disminució del 22% en la proporció de pòlips fèrtils, les colònies més afectades van mostrar una disminució del 35%. En contrast, les colònies mascles més afectades van presentar una lleugera disminució del 12%.

Mentre que la pèrdua de biomassa gonadal en les colònies femelles amb proporcions de teixit afectat >33% va ser estimada al voltant del 73-77%, les colònies mascles van mostrar una disminució menor (48-61%) però aquesta disminució va ser significativa a partir de les colònies lleugerament impactades (>5% del teixit afectat). Tant per les colònies mascles com femelles la caiguda en la biomassa gonadal va ser deguda a una disminució del número de gònades produïdes i no a una disminució del diàmetre mig de les gònades.

El fet que els valors de biomassa gonadal varen ser més alts durant el 2001 que els obtinguts un any abans sembla indicar que les altes temperatures registrades durant l'estiu de 1999 va tenir algun tipus d'efecte directe sobre la reproducció. Però s'ha de tenir en compte, que l'efecte de la proporció de teixit afectat sobre l'esforç reproductor es va mantenir dos anys després de l'impacte (2000 i 2001). Aquest resultat suggeriria que els efectes de la mortalitat sobre la reproducció es van prolongar al llarg del temps probablement pel manteniment de l'alta proporció de teixit afectat.

## Capítol VI. Modelització dels efectes del increment de les pertorbacions sobre la persistència local de la gorgònia vermella

La gran vulnerabilitat de les poblacions de gorgònia vermella enfront dels impactes antròpics emfatitza la importància d'obtenir estimes demogràfiques per examinar la resiliència d'aquesta espècie. Per això, tenint en compte la longevitat de l'espècie, són necessàries dades obtingudes de seguiments a llarg termini. Davant la dificultat d'esperar a tenir intervals de temps prou rellevants per aquesta espècie, els models poden ser útils per examinar les futures trajectòries poblacionals així com avaluar l'efectivitat de possibles mesures de gestió.

En aquest capítol, els models matricials desenvolupats al Capítol III són utilitzats per investigar les conseqüències a llarg termini de dos de les principals pertorbacions que estan afectant a les poblacions de *P. clavata*: l'escalfament global i l'activitat intensiva del busseig. Les simulacions varen ser desenvolupades per tal de poder oferir alguns criteris als gestors de les dues Àrees Marines Protegides que varen ser estudiades en el Capítol III. En primer lloc, es va explorar l'evolució de la taxa anual de creixement poblacional sota diferents increments de la taxa de supervivència (assumint que aquests increments provenen de reduccions en el nombre d'escafandristes dins les reserves, una mesura factible que pot ser aplicada pels gestors d'aquestes Àrees Protegides). En segon lloc, es varen utilitzar les matrius obtingudes de les poblacions afectades per la mortalitat de 1999 (Capítol IV), per avaluar la resposta de les poblacions de *P. clavata* a diferents freqüències de repetició d'aquestes pertorbacions.

Les simulacions desenvolupades durant aquest estudi mostren com l'increment en la supervivència de les colònies reproductives té un efecte positiu millorant la viabilitat de les poblacions. Si la supervivència de les colònies s'incrementa un 3% en les poblacions de Cap de creus i un 7% en les poblacions de les Illes Medes, es podria garantir la persistència d'aquestes poblacions.

Paral·lelament, les baixes taxes de creixement poblacional ($\lambda$=0.88) de les poblacions afectades per la mortalitat massiva del 1999 indiquen un alt risc d'extinció d'aquestes poblacions a mig termini (30 anys). Els efectes d'aquestes pertorbacions agreugen el declivi de les poblacions que es troben en llocs amb una intensa activitat de busseig. En aquests indrets, els temps de quasi-extinció s'estima entre 38 i 55 anys si la freqüència d'aquestes mortalitats massives és similar a l'actual, és a dir cada 5 anys. Però cal afegir, que les baixes taxes de creixement poblacional obtingudes per la població de Medes ($\lambda$=0.94) té efectes molt greus en la viabilitat de les poblacions independentment de la freqüència simulada (cada 5, 10, 25 i 50 anys).

## Capítol VII. Restauració de poblacions amenaçades: una aproximació experimental i de modelització

Per últim, per tal d'evitar que aquesta tesi estigui centrada únicament a descriure els impactes negatius sobre aquestes poblacions, s'ha intentat examinar alguna mesura eficaç de restauració per contrarestar la baixa resiliència a priori mostrada per aquesta espècie. En el Capítol VII, el

transplantament de gorgònies es proposa com una eina útil de gestió per tal de millorar la conservació d'aquestes poblacions. Els principals objectius d'aquest estudi varen estar primer, proposar mètodes de transplantament que necessitin poc esforç de treball i un baix cost econòmic, i segon, estimar la supervivència de les colònies trasplantades en relació a diferents factors biòtics i abiòtics com poden ser la irradiància i la competència amb algues filamentoses. Per últim, es varen utilitzar els models demogràfics per examinar l'esforç de trasplantament necessari per obtenir taxes de creixement poblacional (λ) properes a 1 que assegurin la persistència d'aquestes poblacions a llarg termini.

Durant l'experiment de transplantament, un 40% de les colònies trasplantades es van perdre per causes metodològiques (fixació al substrat). Malgrat això, la supervivència dels trasplantaments ben instal·lats va ser molt similar a la de les colònies naturals (80%). Sorprenentment, les condicions ambientals no van tenir un efecte significatiu en la supervivència de les colònies trasplantades però sí en les pèrdues degudes a la fixació (37% dels trasplantaments varen ser perduts en els tractaments fotòfils en contrast amb el 25% perdut en el tractament esciòfil).

Les simulacions suggereixen que per arribar a una substancial millora de la viabilitat de les poblacions és necessari fer un transplantament cada dos anys amb un gran esforç de trasplantament (recuperant el 75% de les colònies perdudes i 3 fragments per cada colònia recuperada). Aquests resultats suggereixen que aquest esforç es pot plantejar únicament en petites zones protegides de gran valor ecològic i patrimonial.

Tot i que aquesta tesi ha estat concebuda com un tot, cada capítol ha estat o serà sotmès com un article independent (de fet els Capítols III i IV han estat ja publicats), i per tant contenen suficient informació per ser considerats independentment en revistes científiques. Aquest fet fa que alguns dels principals arguments d'aquesta tesi estiguin repetits en alguns capítols, i pot provocar una molesta sensació de redundància. Per tant, demanem a tots els lectors d'aquesta tesis sinceres disculpes davant d'aquestes repeticions.

# ▌▌▌ Discussió i conclusions

Aquesta tesi ha estat desenvolupada en un temps on els impactes antròpics creixen de manera exponencial. La Mediterrània, on les nostres observacions i estudis tenen lloc, està patint també un fort augment d'aquestes pertorbacions (Vitousek et al 1997, Roberts and Hawkins 1999, Bianchi and Morri 2001, Sala 2004). Davant d'aquest preocupant escenari, considerem que és necessari focalitzar els nostres esforços cap a la conservació dels ecosistemes marins mediterranis.

En el camp de la biologia de la conservació s'han realitzat importants avenços tant tecnològics com teòrics (e.g. Simberloff 1988, Boyce 1992, Alvarez-Buylla 1994, Caswell 2001, Morris i Doak 2002, Reed et al 2002), però aquests han estat desevolupats bàsicament en els ecosistemes terrestres. En els ecosistemes marins, els treballs sobre conservació encara són poc

abundants, degut a la dificultat inherent dels treballs subaquàtics i per tant a la falta de dades sobre la biologia de les espècies i comunitats amenaçades. Però per avaluar el grau d'amenaça d'una espècie, és necessari un coneixement sòlid de la biologia d'aquesta espècie i una acurada descripció de la dinàmica poblacional.

Aquesta tesi ha intentat omplir alguns dels buits existents sobre l'estat de conservació de les comunitats bentòniques Mediterrànies. Amb aquest treball hem demostrat que la gorgònia vermella *Paramuricea clavata* és una espècie vulnerable degut als seus trets vitals, principalment la seva lenta dinàmica poblacional. Tots els aspectes desconeguts fins ara de l'historia natural d'aquesta espècie indiquen la seva fragilitat. A la mateixa conclusió s'arriba des dels models demogràfics desenvolupats en diferents gradients de pertorbació humana. Assumint com factible el fet que *P. clavata* pugui ser una espècie indicadora dels canvis en tot el coral·ligen degut a la seva contribució en l'estructura i funcionament de la comunitat (True 1970, Gili and Coma 1998, Ribes and Coma 2006, veure també Ballesteros 2006), podem afirmar que els nostres resultats també mostren al coral·ligen com una comunitat amenaçada.

## Explorant la història natural i els trets demogràfics per examinar la fragilitat de l'espècie

### Distribució

Tal i com es dóna a escala de tot el Mediterrani occidental (veure Introducció), la gorgònia vermella *Paramuricea clavata* segueix una distribució de contagi i asimètrica clarament relacionada amb els trets de vida dels primers estadis d'aquesta espècie i amb la seva sensibilitat als factors ambientals. L'exploració de la demografia d'aquesta espècie a escales rellevants ens ha permès confirmar l'increment de la fondària del límit superior d'aquesta espècie al llarg d'un gradient Nord-Sud. Aquest resultat evidencia la relació entre els límits de distribució i la variabilitat dels factors abiòtics al llarg de l'escala explorada, sobretot amb la irradiància i la temperatura (Capítol I).

El baix nombre de poblacions de *P. clavata*, la petita superfície que ocupen i la distància entre elles són característiques determinants per la persistència a llarg termini d'aquestes poblacions (veure Introducció i Capítol I). Com metapoblacions, els patrons de distribució units a les característiques biològiques d'aquesta espècie (concretament la baixa capacitat de dispersió de les larves) fan especialment vulnerables les seves poblacions. Els patrons de distribució d'aquesta espècie estan en concordança amb la distribució isolada que mostren les espècies vulnerables (UICN 2001).

### Estructura de talles

L'aplicació de diferents aproximacions demogràfiques àmpliament emprades en l'ecologia terrestre, tals com l'anàlisi de les estructures de talles i l'exploració de possibles mecanismes de autoregulació com el "self-thinning", ens ha permès identificar dues dinàmiques poblacionals molt contrastades en dues espècies de les gorgònies més representatives de la Mediterrània: la gorgònia vermella *Paramuricea clavata* i la gorgònia blanca *Eunicella singularis*.

La robustesa dels resultats respecte a la relació biomassa/densitat (-3/2) trobada per la gorgònia *P. clavata* demostra que les seves poblacions presenten una capacitat de càrrega, com s'observa típicament en espècies longeves de lenta dinàmica poblacional (Yoda et al 1963). En espècies amb una gran fragilitat d'acord als seus trets demogràfics, aquesta aproximació pot contribuir a la detecció de les pertorbacions així com a estimar la magnitud dels impactes (Capítol I).

La baixa proporció de colònies joves així com la falta de poblacions en estadis inicials de desenvolupament observada per *P. clavata* (Capítol I) demostra el baix èxit del reclutament en aquesta espècie.

En contrast, els trets demogràfics obtinguts per les poblacions de *E. singularis* demostren un l'important paper del reclutament en la dinàmica d'aquesta espècie.

### Les primeres fases vitals de *Paramuricea clavata*

Tot i que en els nostres experiments al laboratori, el temps necessari per la metamorfosi a pòlips primaris (mínim 10 dies) suggereix una alta capacitat de dispersió, és evident que *P. clavata* mostra diferents mecanismes per tal d'afavorir la retenció dels ous prop de les colònies parentals que semblen contribuir a la particular distribució d'aquesta espècie. Tot i aquestes observacions, seran necessaris estudis genètics per determinar el rang de dispersió d'aquesta espècie (Capítol II).

La baixa supervivència de les primeres fases de *P. clavata* contribueixen a explicar el baix reclutament observat en el camp (Capítol III) i alhora demostren la fragilitat d'aquesta espècie.

La lenta dinàmica dels assentats (Capítol II) ens ha mostrat que els petits reclutes (a partir de 0.3 cm) que observem en el seguiment de les poblacions mitjançant transsectes fixes tenen almenys 2 anys de vida, indicant l'existència d'una "caixa negra" durant el primer any on no podem observar els reclutes in situ. Molt probablement, aquest patró és general en molts organismes bentònics que es troben al coral·ligen, essent aquest estadi equivalent a les llavors que es mantenen dorments en moltes espècies de plantes (Morris i Doak 2002). La quantificació d'aquests tipus d'aspectes és essencial alhora de desenvolupar acurades matrius estructurades.

███ **Mortalitat i pertorbacions antròpiques**

El efectes erosius dels bussejadors, ancores i fils de pesca així com la proliferació de mucílags d'origen algal han estat considerats com els factors més importants per la mortalitat de les gorgònies (Harmelin i Marinopoulus 1994, Bavestrello et al 1997, Coma et al 2004, Giuliani et al 2005). Però aquesta consideració ha canviat durant els últims anys després dels esdeveniments de mortalitat massiva descrits a la Mediterrània Nord-Occidental.

La mortalitat massiva detectada durant l'estiu de 1999 no va afectar a les nostres poblacions estudiades al llarg de la costa Mediterrània. Únicament, en les poblacions de *E. singularis* a la costa nord de la Illa de Menorca (Illes Balears) es va detectar l'impacte d'aquest esdeveniment (Coma et al *en premsa*). Els valors obtinguts en l'exploració d'aquest impacte al llarg de la costa ibèrica mediterrània van ser similars als descrits prèviament per poblacions sense signes de pertorbacions (Harmelin i Marinopoulus 1994, Coma et al 2004).

En canvi, les poblacions de *P. clavata* al Parc Nacional de Port-Cros es van veure totalment afectades per aquest esdeveniment. Els contrastats efectes a curt i a mig termini (4 anys després de la mortalitat) indiquen un major impacte d'aquesta pertorbació que el descrit en estudis previs (Cerrano et al 2000, Pérez et al 2000, Garrabou et al 2001). La mortalitat del 1999 també va provocar efectes greus en la reproducció, representant una dificultat addicional per la recuperació d'aquesta espècie. La disminució de la producció de gònades en funció del grau d'afectació suggereix una limitació dels recursos cap a la reproducció, fet que seria consistent amb les restriccions energètiques mostrades durant el balanç d'aquesta espècie (Coma i Ribes 2003).

Tant la relació entre el grau de afectació i l'esforç reproductor (Capítol V) com la persistència d'altes proporcions de teixit afectat en les poblacions de Port-Cros (amb aproximadament el 35% del teixit afectat) després de 4 anys del impacte (Capítol IV) mostra la importància dels efectes i les conseqüències d'aquesta pertorbació almenys a mig termini, i suggereix que la recuperació d'aquestes poblacions pot ser estimada en ordre de dècades.

Tot i que, aquesta tesi ha estat focalitzada especialment en l'estudi de dos tipus d'impactes: la intensa activitat de busseig detectada paradoxalment en algunes reserves Marines i els esdeveniments de mortalitat massiva, hi ha altres causes de mortalitat que poden tenir un paper clau en la viabilitat de les poblacions i per tant haurien de ser considerades dins la conservació d'espècies marines bentòniques.

Actualment, un dels impactes mes importants és la invasió d'espècies introduïdes, bàsicament algues, que han estat detectades en moltes localitats mediterrànies durant els últims anys. Algunes espècies d'algues (*Womersleyella setacea, Acrothamnion preissii, Caulerpa taxifolia, Caulerpa racemosa* var. *cylindracea, Asparagopsis taxiformis, Lophocladia lallemandiï*) estan amenaçant la comunitat del coral·ligen, perquè tot i que prefereixen habitualment fons amb més irradiàncies, també poden trobar-se en ambients més esciòfils on es desenvolupen les comunitats del coral·ligen (Ballesteros 2006, E. Ballesteros *dades no publicades*). Encara que fins ara, en cap de les poblacions estudiades s'havien detectat aquestes invasions, és important destacar que durant aquest any 2006, en els transsectes permanents situats dins el Parc

Nacional de Port-Cros s'ha pogut detectar la presència de l'alga *Caulerpa racemosa* var. *cylindracea*. L'efecte d'aquesta invasió en les poblacions de gorgònies haurà de ser avaluada durant els propers anys.

La detecció de factors de mortalitat importants per les poblacions de gorgònies així com la sensibilitat mostrada per aquesta espècie enfront d'aquestes pertorbacions demostra la gran fragilitat de l'espècie. Però per entendre les conseqüències d'aquests impactes sobre la viabilitat a llarg termini de les poblacions de *P. clavata* és necessari desenvolupar models demogràfics.

## Modelització de la dinàmica poblacional de *Paramuricea clavata*

Una de les parts més importants d'aquesta tesis ha estat el desenvolupament de models demogràfics per la gorgònia vermella *P. clavata*, que ens ha permès estimar la viabilitat a llarg termini de les poblacions de *P. clavata* (Capítol III), examinar quins factors són més determinants per la viabilitat d'aquestes poblacions (Capítol VI), i avaluar les possibles mesures per millorar la viabilitat de les poblacions (Capítol VII).

La modelització ens ha permès estimar la longevitat de l'espècie i de les poblacions, demostrant que les colònies més grans poden arribar a tenir entre 60 i 100 anys. Amb aquests models també hem pogut calcular que la població estable s'assoleix cap als 50 anys i que les poblacions estudiades mostren unes estructures molt semblants a la població estable i que per tant han de tenir almenys 50 anys.

Mitjançant anàlisis d'elasticitat hem pogut comparar alguns patrons demogràfics de la gorgònia vermella amb altres espècies d'invertebrats bentònics i fins i tot amb altres espècies terrestres de plantes i arbres. Aquesta comparació ens ha permès demostrar que la gorgònia vermella comparteix el patró general mostrat per la majoria d'espècies longeves on la disminució de la supervivència dels adults té efectes molts més negatius en comparació amb espècies de creixement ràpid i alta fecunditat (Heppel et al 2000).

Aquests resultats són essencials per la conservació de l'espècie. El fet que la supervivència sigui el factor clau per la persistència de les poblacions és de gran importància perquè determina quant de temps poden persistir sense reclutament. De fet, el reclutament és important a escales temporals més grans al determinar l'establiment de noves poblacions. Aquest fet, és comparable al que succeeix en altres espècies de gorgònies (Lasker 1990, Gotelli 1991, Yoshioka 1998, Garrabou i Harmelin 2002), i està en concordança amb la teoria del "bet-hedging" que prediu que els adults són seleccionats amb una alta supervivència quan el reclutament és fortament variable degut a que un llarga vida reproductiva és necessària per contrarestar l'alta mortalitat juvenil (Stearns 1992). En aquest sentit, els valors d'elasticitat del reclutament de *P. clavata* van ser molt més baixos que els descrits per altres organismes marins però similars als descrits per algunes plantes i arbres longeus (Morris i Doak 1998, Forbis i Doak 2004, Silvertown et al 1993). Aquests valors juntament amb l'avançada edat de maduresa sexual, i en

combinació amb la longevitat d'aquesta espècie, mostra un clar balanç entre fecunditat i mortalitat descrit per altres espècies de plantes i arbres amb una demografia similar (Forbis i Doak 2004, Franco i Silvertown 2004).

Totes aquestes característiques demogràfiques situen clarament a la gorgònia *P. clavata* amb els organismes de lenta dinàmica poblacional (Partridge i Harvey 1988) i evidencien una "fragilitat demogràfica" i per tant la necessitat de majors esforços per la conservació de les seves poblacions.

Sobre els "dramàtics" resultats referents a la viabilitat i la persistència de les poblacions de gorgònia vermella, és necessari tenir en compte que aquest estudi ha estat focalitzat en les poblacions més someres degut a que probablement són les que estan més sotmeses a les pertorbacions antròpiques. Actualment es desconeix si aquestes poblacions representen una petita proporció de les poblacions de la gorgònia vermella ja que aquesta espècie es pot trobar a fondàries per sota dels 50 metres, i si la dinàmica poblacional d'aquestes poblacions someres és representativa de les poblacions més fondes. Tenint en compte aquest desconeixement, futurs estudis haurien de focalitzar els seus esforços en l'examinació de l'abundància i funcionament d'aquestes poblacions més fondes per així conèixer la connectivitat entre les poblacions somes i fondes. Aquest coneixement serà essencial per entendre la persistència d'aquestes poblacions a llarg termini.

Una altra consideració que s'ha de fer en aquest estudi és el fet que el paper de la reproducció asexual no ha estat tingut en compte. Tot i que aquest tipus de reproducció ha estat considerat poc rellevant per *P. clavata* (Coma et al 1995), per tal d'assolir un coneixement complet de la dinàmica poblacional d'aquesta espècie s'hauria d'examinar la importància del creixement de noves branques a partir de la base de les colònies, com succeeix en moltes espècies d'arbres i com probablement es dóna també en el corall vermell. Aquesta estratègia de "rebroll" podria ser molt avantatjosa enfront l'impacte de fortes pertorbacions on la mortalitat total és molt elevada, sobretot davant el baix reclutament observat per aquesta espècie (Capítol V).

### Modelització dels efectes de les pertorbacions

La utilitat dels anàlisis de viabilitat poblacional per examinar l'efectivitat de diferents mesures de gestió ha estat confirmada prèviament en molts sistemes (Crowder et al 1994, Doak et al 1994, Pfister i Bradbury 1996, York i Holmes 2003, Morris i Doak 2002).

En les Illes Medes, l'efecte del busseig pot provocar un increment de la mortalitat natural de la gorgònia *P. clavata* d'un 3% a un 7% anual (Coma et al 2004). Els models demogràfics ens permeten estimar les conseqüències d'aquest increment per la viabilitat de les poblacions. La modelització, simulant un augment en la supervivència de les colònies reproductores, mostra uns efectes positius en les poblacions estudiades. Les simulacions han demostrat que la persistència de les poblacions ($\lambda=1$) es pot aconseguir amb modests i factibles increments de la supervivència (al voltant d'un 3% i un 7% en les poblacions de Cap de Creus i Medes, respec-

tivament). Les diferencies observades entre les dues poblacions poden ser atribuïdes a diferents nivells d'intensitat de busseig. Mentre que a les Illes Medes s'estimen 70,000 bussejadors per any, al Cap de Creus s'estimen uns 30,000 bussejadors per any (Zabala et al 2003) (Capítol VI).

La mortalitat del 1999 ha estat relacionada amb l'escalfament de la Mediterrània (Pascual et al 1995, Bethoux et al 1998). L'ocurrència d'una nova mortalitat durant l'estiu del 2003 (i tenint en compte que durant aquest estiu 2006 s'han observat alguns indicis de mortalitat) suggereix que la freqüència d'aquests esdeveniments està incrementant com a resultat del canvi climàtic, i per tant, s'esperen en un futur proper noves repeticions d'episodis de mortalitat massiva.

Els efectes de les mortalitats massives també han estat examinats utilitzant els Anàlisis de Viabilitat de Poblacions (PVA) amb l'objectiu d'estudiar els efectes de l'increment de la freqüència d'aquestes pertorbacions. Els resultats obtinguts mostren com la combinació dels impactes antròpics com la intensa activitat del busseig junt amb els efectes de l'inevitable canvi climàtic poden tenir conseqüències dramàtiques per la viabilitat de les espècies marines amb una lenta dinàmica poblacional. Aquest estudi també confirma la utilitat dels PVA per estimar quines mesures de gestió s'han de promoure per una millor conservació de les poblacions.

## El transplantament de gorgònies: una eina de gestió viable?

L'estudi de les tècniques de trasplantament alhora de garantir la viabilitat de les poblacions de *P. clavata* s'ha examinat experimentalment i mitjançant els models demogràfics. Aquest estudi ha aportat alguns resultats clars que poden ajudar als gestors i científics alhora d'estimar la conveniència de la utilitat d'aquestes tècniques (Capítol VII). Tot i que, tant l'aproximació experimental com la modelització mostren greus limitacions per desenvolupar els transplantament a gran escala, els resultats mostren la viabilitat d'aquesta tècnica per contribuir a la restauració de poblacions afectades per pertorbacions locals dins petites Àrees Marines protegides. Aquesta primera aproximació al transplantament de gorgònies deixa una porta oberta per la futura recerca en l'àmbit de la restauració marina.

En resum, els resultats obtinguts en aquesta tesis han mostrat la fragilitat de la gorgònia *Paramuricea clavata* enfront l'augment de les pertorbacions que afecten les seves poblacions. Les aproximacions demogràfiques utilitzades en aquest estudi, especialment el desenvolupament dels Anàlisis de Viabilitat de Poblacions (PVA) han demostrat ser essencials alhora de desenvolupar estudis en relació a la conservació d'espècies marines longeves. Finalment, els resultats obtinguts poden ser de gran interès pels gestors de les Àrees Marines protegides per tal de garantir la viabilitat de les seves poblacions.

### La conservació d'espècies marines longeves: Aprenent dels ecosistemes terrestres

Al final d'aquest estudi, els resultats obtinguts suggereixen dos tipus de pensaments aparentment contradictoris. Per un costat, sorprèn la dificultat de trobar estudis científics sobre l'ecologia marina bentònica (almenys a escala mediterrània) on es mostrin poblacions amb les característiques demogràfiques de la gorgònia vermella, és a dir poblacions amb colònies centenàries i amb uns trets de vida que porten a la permanent persistència de les seves poblacions. Per altra banda, quan es busquen referències en els ecosistemes terrestres, és inevitable no adonar-se que aquest és un patró general mostrat per moltes espècies de plantes i arbres, indicant que els nostres resultats estan dins la "normalitat" dels patrons ecològics a escala global.

La semblança amb espècies terrestres ens pot servir com una font de inspiració per entendre millor els ecosistemes marins bentònics i per guiar la futura recerca en aquest àmbit. Seria raonable pensar que la nostra recerca podria obtenir grans beneficis si s'incorporen molts dels avenços teòrics i metodològics assolits en altres àmbits de recerca com són l'esclerocronologia, la restauració i gestió de ecosistemes explotats, i la conservació d'espècies longeves entre d'altres exemples.

Desprès de l'ampli coneixement de la biologia de moltes espècies marines adquirit durant les ultimes dècades, la recerca futura de les comunitats bentòniques marines hauria de considerar una aproximació ecològica més àmplia, oblidant (sempre que sigui possible) les fronteres entre els sistemes marins i terrestres. El desenvolupament d'aquests models demogràfics ha obert una porta a l'aplicació d'aquests mètodes per la conservació de moltes espècies marines. Malgrat això, hem d'alertar de les dificultats de l'aplicació d'aquestes metodologies a altres espècies marines bentòniques d'una manera indiscriminada. Hem de destacar que es necessitarà un esforç addicional per la selecció de l'espècie objecte d'estudi així com per entendre la demografia particular de cadascuna de les espècies.

### Recerca futura

A part de l'aplicació dels mètodes demogràfics desenvolupats principalment des de l'ecologia terrestre a altres espècies semblants, encara queden moltes qüestions no resoltes referents a la dinàmica de la gorgònia *Paramuricea clavata* i al coral·ligen en general.

### El estudi dels efectes sinèrgics entre pertorbacions

En aquesta tesi, hem vist com els efectes del canvi climàtic poden ser particularment negatius per espècies afectades per altres pertorbacions locals degut als efectes sinèrgics de diferents fonts d'estrès. Tot i que sembla difícil donar respostes per fer front als efectes climàtics, hi ha altres impactes de més fàcil solució. Els futurs estudis haurien de considerar totes les pertorba-

cions que estan afectant a les poblacions així com els seus efectes sinèrgics. Impactes com el canvi climàtic, el busseig, la proliferació d'algues filamentoses i la invasió d'espècies introduïdes hauran de ser estudiades conjuntament per tal d'oferir efectius plans de conservació per les espècies amenaçades.

## El paper de la reproducció asexual en la dinàmica de *Paramuricea clavata*

Com hem esmentat abans, el creixement de noves branques des de la base de les colònies de *P. clavata* tal com es dóna en moltes espècies d'arbres podria ser una important estratègia per fer front a les fortes pertorbacions que causen una gran mortalitat en les poblacions de la gorgònia *P. clavata*. Un bon coneixement de la dinàmica d'aquestes noves branques (des d'un punt de vista descriptiu i experimental) podria ajudar-nos a entendre la importància d'aquesta estratègia per la resiliència de les poblacions de *P. clavata*.

## Estudis genètics

Per assolir un coneixement més complet de la biologia de la gorgònia *P. clavata*, la dispersió de les larves i la connectivitat de les poblacions haurien de ser estudiades mitjançant eines moleculars. Els estudis genètics ens poden permetre avaluar l'estructura genètica de l'espècie en relació a la seva capacitat de dispersió i estimar la relativa importància de la reproducció sexual i asexual de l'espècie.

Així també, conèixer l'estructura genètica de *P. clavata* serà essencial per entendre la resiliència de les poblacions i la capacitat d'aquesta espècie per fer front a l'amenaça de possibles extincions locals davant l'augment de les pertorbacions.

## La biodiversitat dels boscos de gorgònies

Estudis previs han examinat la composició i l'abundància d'espècies de les poblacions de la gorgònia *Paramuricea clavata* en algunes localitats mediterrànies (True 1970, Gili and Ballesteros 1991). Però degut a la dificultat de dur a terme estudis taxonòmics, la importància de les poblacions de la gorgònia vermella per la diversitat del coral·ligen no ha estat estudiada a una escala més important. La quantificació de la diversitat dins dels boscos de *P. clavata* al llarg d'un gradient de pertorbació humana (que podria ser equivalent a un gradient de densitat) podria aportar dades de referència necessàries per determinar el paper de la presencia de les colònies de *P. clavata* en la diversitat de les comunitats.

Tot i que nosaltres hem seleccionat aquesta espècie com indicadora del coral·ligen per la seva important contribució a l'estructura i funcionament de la comunitat (True 1970, Gili i Coma 1998,

Ribes i Coma 2006, Ballesteros 2006), desconeixem l'efecte de les pertorbacions (que han afectat a *P. clavata*) sobre la composició i abundància de les espècies acompanyants que es troben en els boscos de gorgònies. La detecció de possibles canvis de la diversitat al llarg del gradient proposat abans podria evidenciar la magnitud d'aquestes pertorbacions sobre tota la comunitat.