

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

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## Summary

1. Gorgonians are long-lived engineering species and their conservation is crucial to maintaining the biodiversity of marine communities. The slow dynamics displayed by these species make them especially vulnerable when faced with increasing disturbances.

2. The sessile nature and structural role of gorgonians provide several ecological similarities with trees, allowing the application of different approaches developed by forest ecology studies to overcome the constraint of long time-scales to collect valuable dynamic data. Using these approaches, we examined the distribution and demography of two representative Mediterranean gorgonian species, *Paramuricea clavata* and *Eunicella singularis*, along a regional spatial scale as well as their response to disturbances.

3. The regular spatial distribution and the upper distribution limit of *E. singularis* suggest that this species is more tolerant to a wide range of environmental conditions than *P. clavata*, which exhibited a more asymmetrical spatial distribution and variation in the upper distribution limit on the latitudinal scale.

4. Size distributions of both species showed contrasting population dynamics. The size distribution of *E. singularis* was characterized by initial stages of populations (0–10 cm) in contrast to the scarcity of this stage displayed by *P. clavata*. This suggests differences in recruitment between species. Furthermore, only *P. clavata* populations displayed a strong negative correlation between density and biomass with a slope close to  $-3/2$ , indicating a self-thinning mechanism and therefore the existence of a carrying capacity. This result and the trajectories of disturbed populations below the self-thinning line revealed this approach as a useful method to identify the effects of biological or physical disturbance.

5. *Synthesis and applications.* The approaches used in this study provide insights into management needs in face of the difficulty of having to deal with the population dynamics of very slow-growing threatened species. In particular, gorgonian populations can be used as an indicator of the effects of climatic anomalies on the coralligenous community.

**Key-words:** conservation, demography, NW Mediterranean Sea, octocoral, partial mortality, self-thinning, spatial distribution

## Introduction

The increase in frequency and impact of anthropogenic disturbances has led to diversity losses and changes in ecosystem functioning of a wide range of marine ecosystems

(Botsford, Castilla & Peterson 1997; Gray 1997; Vitousek *et al.* 1997; Roberts & Hawkins 1999). Long-lived species displaying slow growth, late maturity and low fecundity are among those most affected by strong disturbances (Musick 1999) and, generally, their presence is crucial to maintaining the organization and diversity of the communities in which they dwell (Mills, Soule & Doak 1993; Jones, Lawton & Schachak 1994).

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In temperate marine habitats, most gorgonians are long-lived engineering species displaying slow population dynamics that make them especially vulnerable to anthropogenic disturbances (Garrabou & Harmelin 2002; Coma *et al.* 2004; Linares *et al.* 2007). Thus, knowledge of their demographic characteristics is the first step to developing a reliable conservation plan. Obtaining demographic data on large temporal and spatial scales could allow us to establish a baseline to determine the magnitude and intensity of disturbances and to anticipate the future trajectories of disturbed populations. Unfortunately, data regarding the life-history traits of most long-lived marine species are difficult to acquire, especially over the large temporal scales that are most appropriate given their long life spans (Hughes & Connell 1999).

The sessile nature and structural role of gorgonians make them ecologically similar to trees. The application of several theoretical and methodological advancements developed through forest ecology studies may therefore prove useful for the study of disturbances that are affecting these marine species.

Forest ecologists have overcome the constraint of requiring long time-scales to collect valuable data on population dynamics by using static size distributions to provide useful insights into many important macro-ecological phenomena (Niklas, Midgley & Hand 2003). Although they cannot be used to predict future growth or health accurately (Condit *et al.* 1998), size distributions coupled with measurements of plant density have been used to explore specific demographic dynamics in response to past disturbances (Niklas, Midgley & Hand 2003). Furthermore, by assuming a substitution of space for time (Pickett 1989), this method can be used to reconstruct the expected population dynamics.

Another approach used extensively in forest ecology has been the assessment of density-dependence on population dynamics by means of examining the relationship between size/biomass and density. Ecologists have long recognized the effects of intra- and interspecies competition and how it can alter the shape of populations in saturated landscapes as they approach the carrying capacity of the ecosystem (Shinozaki & Kira 1956). Competition emerges in the form of a negative density-dependent effect when populations become sufficiently dense. The exploration of self-thinning mechanisms in gorgonian populations and their size distribution curves can allow us to predict population responses to environmental changes when long-term monitoring cannot be conducted.

Two mass mortality events during the summers of 1999 and 2003 affected Mediterranean gorgonians severely at a regional scale (about 1000 km; Cerrano *et al.* 2000; Perez *et al.* 2000; Garrabou *et al.* 2001; Linares *et al.* 2005; Coma *et al.* 2006). Furthermore, a relationship between the occurrence of these episodes and climatic anomalies has been suggested which would imply an increase of these events as a result of global climate change (Cerrano *et al.* 2000; Coma *et al.* 2000; Perez *et al.* 2000; Garrabou *et al.* 2001; Coma & Ribes 2003). Therefore, an extensive survey was launched between 2002 and early 2003 in order to evaluate the health of the shallowest

gorgonian populations along the Mediterranean Spanish coast after the 1999 mass mortality event and to collect qualitative and quantitative demographic data about Mediterranean gorgonian populations along a regional spatial scale.

There were a number of goals of this study. First, to obtain reference data of density, size and injuries from the shallowest populations (which are more vulnerable to climatic anomalies) of two of the more abundant gorgonian species in the NW Mediterranean, the red gorgonian *Paramuricea clavata* (Risso, 1826) and the white gorgonian *Eunicella singularis* (Esper, 1791), at a regional spatial scale; and secondly, to characterize the gorgonian populations in an attempt to explain the current distribution patterns, emphasizing upper depth distribution limit. Finally, to explore the applicability of classic forest ecology approaches to these marine species by examining size distribution and self-thinning mechanisms to obtain an insight into the occurrence of recent or past disturbances to predict future population trajectories.

## Materials and methods

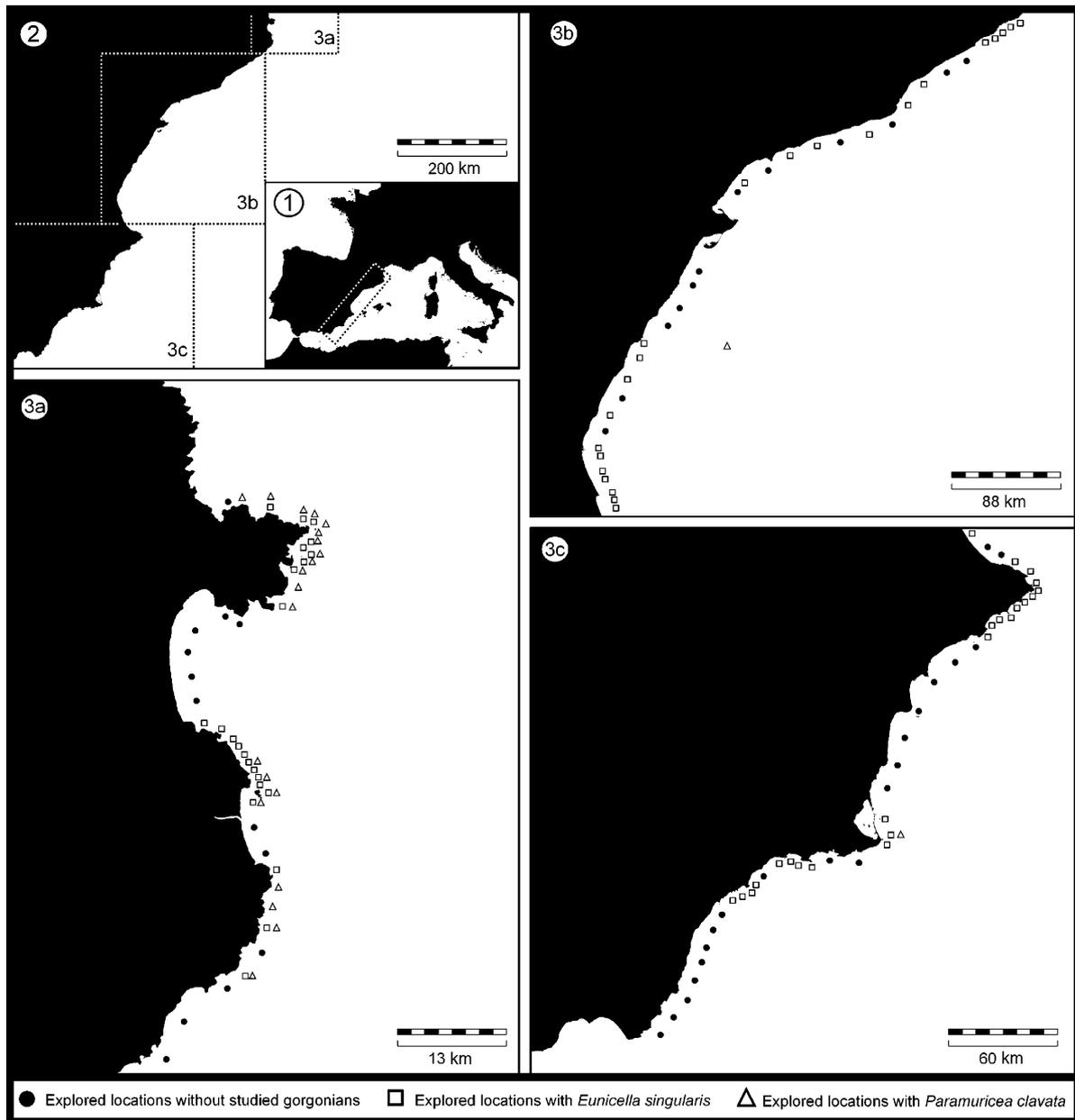
### DISTRIBUTION SURVEYS

In NW Mediterranean Sea, gorgonians are usually present in sites exposed to currents (Weinberg 1975, 1980). In order to obtain representative information about the distribution of both species, we compiled information from technical reports, field diving guides and diving centres. The presence of gorgonian populations of both species was determined in a total of 120 locations. Surveys, distributed along the Spanish coast (more than 600 km) from Cabo de Gata (36°51' N, 2°6' O) to Port-Bou (42°25' N, 3°10' E, Fig. 1) were conducted by scuba divers between 2002 and early 2003. The depth distribution at each site was studied by noting the presence of gorgonians at 5-m intervals to the depth limit. The depth limit corresponded to the end of the rocky wall and/or a change of substrate, and thus it coincided with the lower limit of populations at the base of the cliff. The maximum depth was 45 m, although most populations were shallower. In each depth range where gorgonians were present, a minimum of five 50 × 50 cm quadrats were examined randomly in order to obtain a qualitative estimate of population abundance. Abundance was classified as one of five categories: 0, 1 (> 0–1 gorgonians per m<sup>2</sup>), 2 (> 1–5 gorgonians per m<sup>2</sup>), 3 (> 5–10 gorgonians per m<sup>2</sup>) and 4 (> 10 gorgonians per m<sup>2</sup>). To explore the existence of a latitudinal pattern on the upper limit of distribution of the gorgonian stand we considered representative populations with a density category equal to or larger than 2 (> 1–5 gorgonians per m<sup>2</sup>).

### QUANTITATIVE SURVEYS

After this extensive survey, 19 populations of *P. clavata* and 21 populations of *E. singularis* were selected to carry out a quantitative demographic study (see Figs S1 and S2 in Supplementary material). The depth survey conducted previously showed that the highest population abundance was between 15 and 35 m. Therefore, we selected populations with a cover extension of at least 50 m of horizontal length within this depth range.

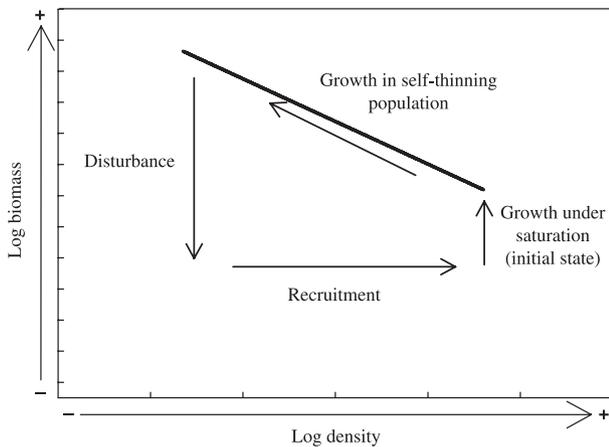
The standard error (SE) sample size function was used to determine the minimum sample size needed to examine the density and extent



**Fig. 1.** Map of the study area. Explored sites without gorgonian (solid circles;  $n = 45$ ), *Paramuricea clavata* populations (open triangles;  $n = 23$ ), *Eunicella singularis* populations (open squares;  $n = 67$ )

of injury of the colonies at each site. In a previous study the minimum sample size for *E. singularis* was estimated to be of 1.75 m<sup>2</sup> and 50 colonies, when the variance of the density and extent of injury stabilized at approximately 5–10% of the mean (Coma *et al.* 2006). For *P. clavata*, preliminary sampling was conducted at one of the sites by examining 17 m<sup>2</sup> using 50 × 50 cm quadrats placed randomly on the substrate between 17 and 22 m depth. The SE as a proportion of the mean of density decreased quickly with increasing sample size and their stabilization was obtained at a sample size of 1.5 m<sup>2</sup>, where the variance became approximately 10% of the mean. 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 (R. Coma, unpublished data).

Density was estimated by means of examining all colonies within 50 × 50 cm quadrats or in a belt transect plotted randomly through the site on scuba diving. The method used was selected in order to accommodate the extreme variability of density (mainly in *E. singularis*), with the objective of measuring at least the minimum sample size in terms of colony number. For each colony, we measured maximum height and the extent of injury of colony surface (i.e. denuded axis or overgrowth by other organisms, Harmelin *et al.* 1999). For *P. clavata*, 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), which was corrected for the proportion of injured surface (Linares *et al.* 2005). Data on the variation of the extent of injury of the colonies among localities and with depth were arc-tan transformed and analysed using one-way



**Fig. 2.** Pattern of growth and mortality under self-thinning process 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.

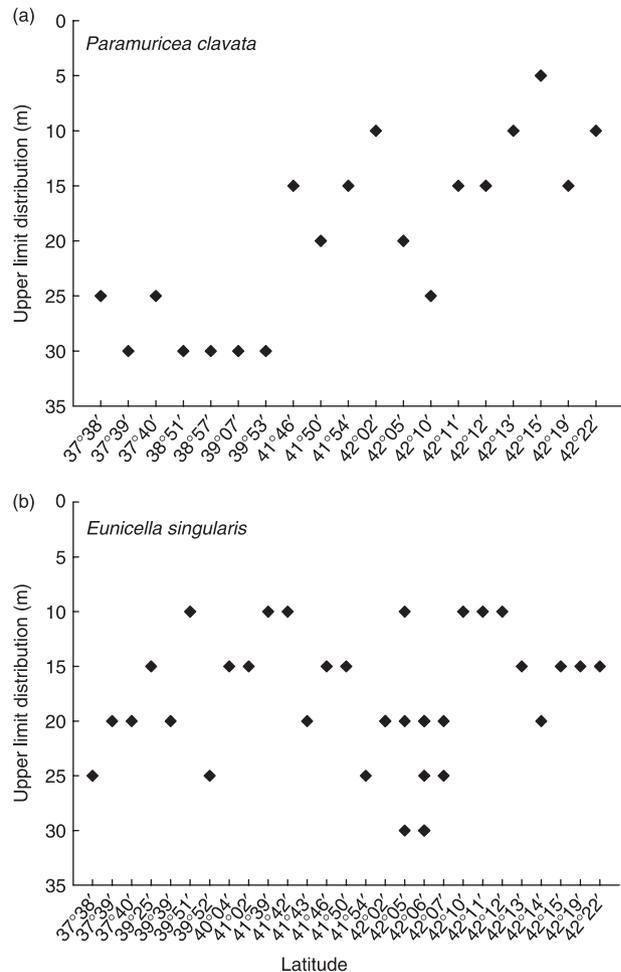
analysis of variance (ANOVA) tests. Pearson's product-moment correlation (Sokal & Rohlf 1995) was used to examine the relationship of the different demographic parameters estimated with depth.

#### SIZE DISTRIBUTION AND SELF-THINNING ANALYSIS

The size distribution curve was analysed in terms of descriptive statistics using skewness and kurtosis. Skewness ( $g_1$ ) is a measure of the symmetry of a distribution using its mean. If skewness is significant, the distribution is asymmetric. Positive skewness indicates the prevalence of small size classes in the population, while negative skewness points to the dominance of large size classes. Kurtosis ( $g_2$ ) is a measure of the peakedness of a distribution near its central model. A significant value of kurtosis indicates that the variable has longer tails than those for a normal distribution and therefore the prevalence of a particular size class in the population. Skewness and kurtosis coefficients are significant if  $g_1$  per SES (standard error of skewness) or  $g_2$  per SEK (standard error of kurtosis) is greater than 2 (Sokal & Rohlf 1995).

To determine occurrence of self-thinning, we plotted the log mean biomass (in the case of *E. singularis* we used the log mean height because currently we do not have a height-biomass relationship) vs. the log of density. These plots also allowed us to explore the existence of past or current disturbances on populations. In non-disturbed populations subjected to self-thinning by intraspecific competition, an ideal trajectory (Fig. 2) may be traced from 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 vertically (growing without loss of density) to reach the biomass saturation point, next moving to the upper-left corner along the expected line (slope of  $-3/2$  for density-biomass relationship and slope of  $-1/2$  for density-height relationship, Yoda *et al.* 1963; White 1981) under a self-thinning process by means of colony growth and density decline (Adler 1996). However, if populations are affected by disturbance, we expect both their position to be displaced far below the self-thinning line due to a loss in both density and biomass (Fig. 2).

The validity of these assumptions was tested on data from a previous monitoring of two *P. clavata* populations affected by the 1999 mass mortality event at Port-Cros National Park (France) conducted before, just after and again 4 years after the event (Linares *et al.* 2005).



**Fig. 3.** Variation of upper depth limit distribution along the explored latitudinal range.

## Results

#### LATITUDINAL DISTRIBUTION

Among the 120 locations explored along the 600 km coastline of the studied area, we found *E. singularis* populations in 67 locations and *P. clavata* populations in 23 locations. The two species were found together in 18 locations and neither species was observed in 45 locations (Fig. 1).

The species differed in the patterns of distribution along the latitudinal gradient. *E. singularis* was distributed more or less regularly, whereas *P. clavata* showed more contagious and asymmetric distribution with populations more common in northern than in the southern areas (Fig. 1).

#### UPPER DEPTH DISTRIBUTION LIMIT

The upper limit of *P. clavata* varied substantially along the latitudinal gradient. The shallowest populations (10–15 m) were found in the Northern part of the Spanish Mediterranean coast, including a location where *P. clavata* colonies were found at only 5 m depth. In the southern part, the upper limit of distribution was situated between 25 and 30 m (Fig. 3a).

**Table 1.** Mean percentage of extent of injury (% injury) per colony and proportion of healthy colonies (with < 10% of extent of injury), affected colonies (between ≥ 10 and ≤ 99% of extent of injury) and totally dead colonies (with 100% of extent of injury). *Paramuricea clavata* (a) and *Eunicella singularis* (b)

	Depth	N	% Injury		% Colonies		
			mean	SD	< 10%	≥ 10 – ≥ 99%	100%
<b>(a) <i>Paramuricea clavata</i></b>							
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	21.32	77.88	19.08	3.04
<b>(b) <i>Eunicella singularis</i></b>							
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	13.46	89.27	9.39	1.34

The upper limit of distribution of *E. singularis* also ranged between 10 and 30 m but did not show any clear pattern along the latitudinal range (Fig. 3b).

#### PARTIAL AND TOTAL MORTALITY

The extent of injury of *P. clavata* colonies tissue varied significantly among populations between 0.6 and 19% (one-way ANOVA  $F_{18,1938} = 7.20$ ,  $P < 0.001$  on arc-tan transformed data). On average for all populations, the extent of injury of *P. clavata* colonies was  $10.1 \pm 6.2\%$  [mean  $\pm$  standard deviation (SD)]

(Table 1a). The extent of injury of *E. singularis* colonies was  $4.7 \pm 5.4\%$  (mean  $\pm$  SD), ranging significantly from 0 to 24% (one-way ANOVA  $F_{20,2164} = 8.75$ ,  $P < 0.001$ , Table 1b). The mean extent of injury of the colonies did not correlate with the depth of either species (*E. singularis*,  $r^2 = 0.136$ ,  $P = 0.099$ ; *P. clavata*,  $r^2 = 0.1605$ ,  $P = 0.089$ ).

On average, *P. clavata* populations had a lower proportion of uninjured colonies (about 78% of colonies exhibited < 10% of extent of injury) than *E. singularis* populations (about 89% of colonies exhibited < 10% of extent of injury). Moreover, *P. clavata* populations had a higher proportion of affected

**Table 2.** Characteristics of studied populations of *Paramuricea clavata* [depth, number of gorgonians (N), area (m<sup>2</sup>), density (N gorgonians per m<sup>2</sup>) and biomass (g per m<sup>2</sup>)] and distribution parameters [height (H), skewness (g<sub>1</sub>) and kurtosis (g<sub>2</sub>)]. Sig. (> 2): skewness and kurtosis are considered significant if the absolute value of coefficient/standard error (SE) is greater than 2

	Depth	N	m <sup>2</sup>	Density	Biomass	H-mean	H-SD	Min	Max	g <sub>1</sub>	SE g <sub>1</sub>	Sig. (> 2)	g <sub>2</sub>	SE g <sub>2</sub>	Sig. (> 2)
Els 3 frares	20–25	87	2.5	34.80	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 trençat	20–25	138	3.2	43.13	514.58	22.17	16.13	0.5	95	1.45	0.21	7.06	3.34	0.41	8.19
Els forcats	25–30	46	2.5	18.40	354.15	28.27	16.92	4	63	0.37	0.35	1.05	-1.10	0.69	-1.59
Massa d'Or	25–30	108	4.8	22.50	73.41	14.07	6.88	2.5	36	1.08	0.23	4.65	1.41	0.46	3.05
Pta falconera	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	303.88	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
Carall 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	5.05	0.41	12.44
Pota del Llop	30–35	154	3.2	48.13	289.83	17.34	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	0.98	-0.97	0.61	-1.59
Canons tamariu	25–30	131	4.3	30.82	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	0.05	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	34	-0.02	0.32	-0.07	-0.59	0.63	-0.94

**Table 3.** Characteristics of studied *Eunicella singularis* populations [depth, number of gorgonians (N), area (m<sup>2</sup>) and density (N gorgonians per m<sup>2</sup>)] and distribution parameters [height (H), skewness (g<sub>1</sub>) and kurtosis (g<sub>2</sub>)]. Sig. (> 2): skewness and kurtosis are considered significant if the absolute value of coefficient/standard error (SE) is greater than 2

<i>Eunicella singularis</i>	Depth	N	m <sup>2</sup>	Density	H-mean	H-SD	Min	Max	g <sub>1</sub>	SE g <sub>1</sub>	Sig. (> 2)	g <sub>2</sub>	SE g <sub>2</sub>	Sig. (> 2)
Tres frares	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 reparada	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	11.7	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	5.7	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
Pedra 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	2.2	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	6.2	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
Hormigón-1	27	63	3.2	19.68	22.86	10.06	2	41	-0.33	0.30	-1.10	-0.47	0.60	-0.79
Hormigón-2	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

(> 10% of extent of injury) or dead colonies (19% and 3% for *P. clavata* in contrast to 9% and 1% for *E. singularis*, respectively, Table 1a,b).

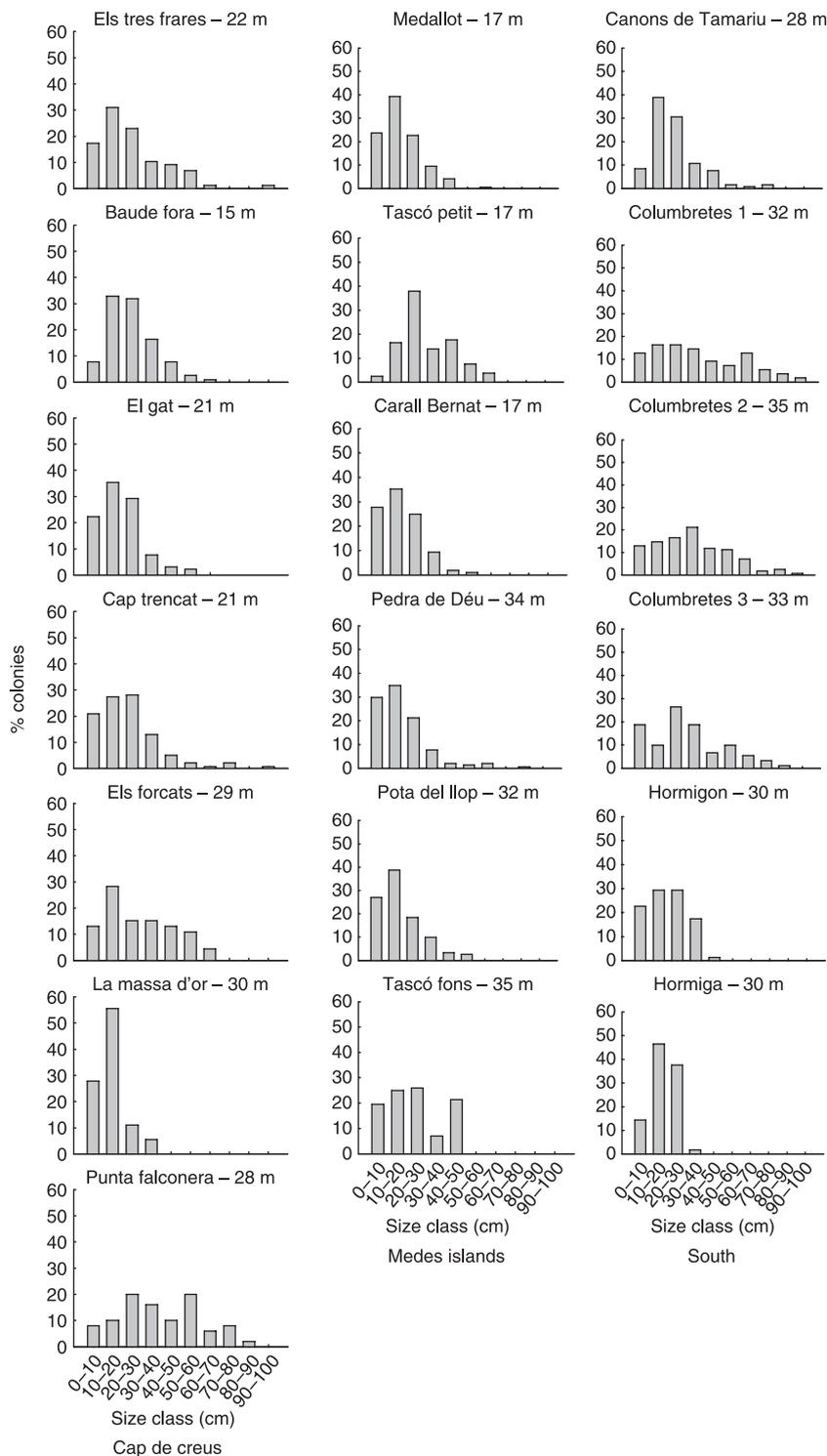
#### DENSITY AND MEAN COLONY HEIGHT

Density of *P. clavata* populations ranged between 11 and 53 gorgonians per m<sup>2</sup> (mean 33 ± 14 SD, Table 2). The density for *E. singularis* populations ranged from 1 to 56 gorgonians

per m<sup>2</sup> (mean 20 ± 18 SD, Table 3). Density of the colonies did not correlate with depth (*E. singularis*,  $r^2 = 0.173$ ,  $P = 0.060$ ; *P. clavata*,  $r^2 = 0.056$ ,  $P = 0.328$ ).

The mean and maximum colony height of *P. clavata* (24.2 ± 7.7; 98 cm) was greater than that of *E. singularis* (15.1 ± 6.1; 67 cm, Tables 2 and 3).

There was no significant correlation between mean colony height and depth for either species (*E. singularis*,  $r^2 = 0.116$ ,  $P = 0.132$ ; *P. clavata*,  $r^2 = 0.046$ ,  $P = 0.376$ ). In contrast,



**Fig. 4.** *Paramuricea clavata*. Size–frequency distribution of 19 populations along the explored spatial scale. Depth values next to population name refers to depth of each examined population.

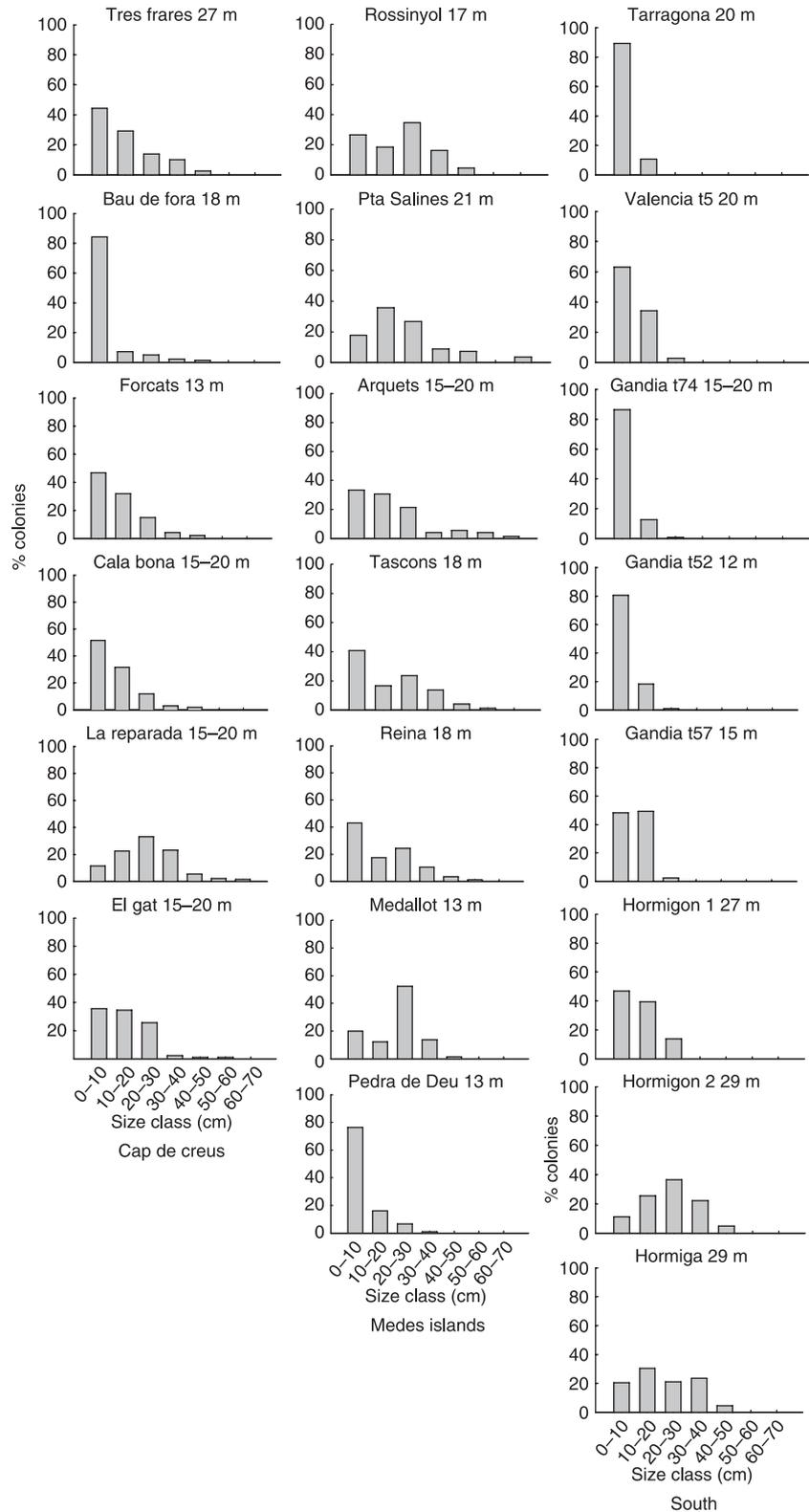
maximum height increased with depth for both species (*E. singularis*,  $r^2 = 0.926$ ,  $P < 0.05$ ; *P. clavata*,  $r^2 = 0.904$ ,  $P < 0.05$ ).

#### SIZE DISTRIBUTIONS

All size frequency distributions for *P. clavata* and *E. singularis* populations were unimodal, and more or less bell-shaped. However, there were differences between species and among

populations (Figs 4 and 5). In *P. clavata*, the proportion of smaller, non-reproductive colonies (< 10 cm, Coma *et al.* 1995b) was low, a peak always existed in the > 10–20 cm range and there was a low proportion of colonies larger than 30–40 cm (Fig. 4). In contrast, most *E. singularis* populations showed a high proportion of small colonies (< 10 cm) and a decrease in the proportion of larger size classes (Fig. 5).

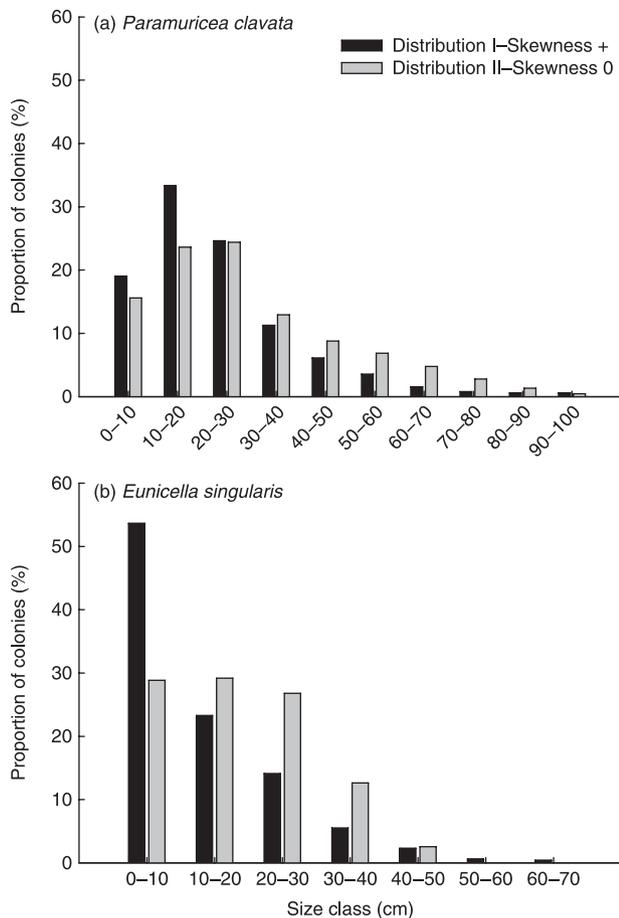
Skewness coefficients in *P. clavata* indicated that most of the size distributions were positively skewed ( $n = 12$ ) and the



**Fig. 5.** *Eunicella singularis*. Size–frequency distribution of 21 populations along the explored spatial scale. Depth values next to population name refer to depth of each examined population.

rest of distributions were symmetric ( $n = 7$ ) (Fig. 4, Table 2). All asymmetrical, positively skewed distributions were found among populations at  $< 25$  m depth. In contrast, most symmetrical distributions were found among the deeper populations ( $> 25$  m). Similarly, in *E. singularis*, although there were some symmetric distributions ( $n = 6$ ), most

distributions were positively skewed ( $n = 15$ ) (Fig. 5, Table 3). Grouping of populations by skewness allowed us to determine the main differences between symmetric and asymmetric size distribution of each species. These differences in *P. clavata* relied on the larger proportion of colonies between 10 and 20 cm, and the lower proportion of colonies  $> 40$  cm in



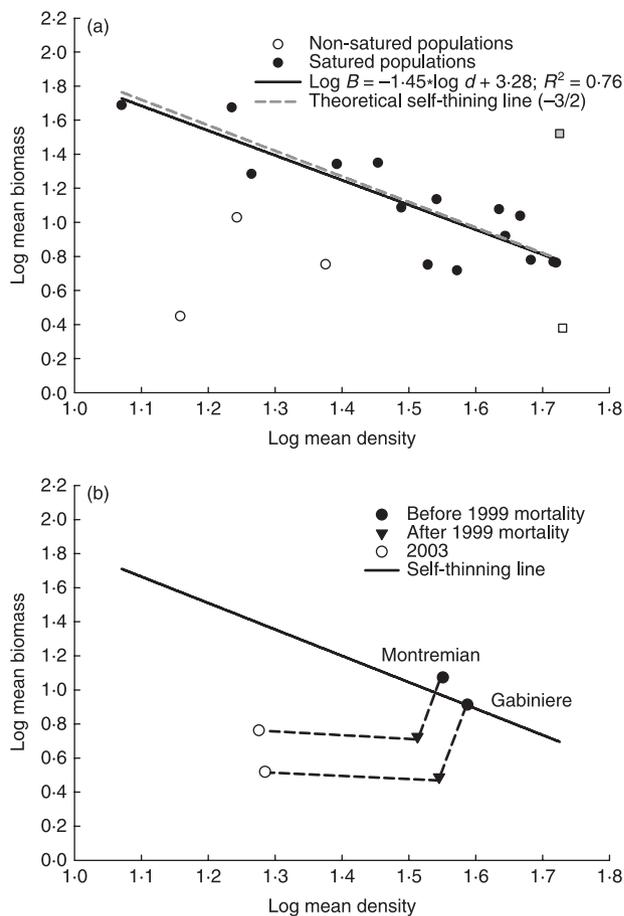
**Fig. 6.** Size–frequency distribution grouping the populations according their skewness coefficient.

positively skewed populations in contrast to symmetric populations (Fig. 6a). *E. singularis* populations with positive skewness displayed a distribution with most colonies in the initial size class (0–10 cm), while symmetric populations displayed a similar proportion of colonies in the first three size classes (0–10, 10–20 and 20–30 cm, Fig. 6b).

Kurtosis was variable between species and among populations. In *P. clavata*, 12 populations showed no significant kurtosis and seven populations displayed positive kurtosis. In *E. singularis*, 10 populations displayed positive kurtosis, eight populations showed no significant kurtosis and three populations displayed negative kurtosis. 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 overcentralized than normal distributions (Tables 2 and 3).

#### EVIDENCE OF SELF-THINNING MECHANISM IN GORGONIAN POPULATIONS

*E. singularis* populations did not show any pattern in a density–mean size relationship ( $r^2 = 0.021$ ,  $P = 0.531$ ). In contrast, the relationship between density and mean biomass of *P. clavata* populations showed a significant ( $P < 0.01$ ) negative slope in



**Fig. 7.** *Paramuricea clavata*. (a) Relationship among the density and biomass of the 19 studied populations, expressed in logarithmic terms (note that squares represent populations out of self-thinning line: Columbretes 2 (grey square) and a young population at Port-Cros National Park (white square); see Discussion). (b) Trajectory of two populations affected by 1999 mass mortality event, before (June 1999), just after (November 1999) and 4 years (November 2003) after the event (the slope represents the self-thinning line obtained for the studied populations).

which most populations were placed near a line with a  $-3/2$  slope (Fig. 7a). There were three populations (Massa d'Or, Tascons and Hormigon) separated from the self-thinning line that were not considered to perform the relationship between density and biomass. Moreover, the population Columbretes-2 (top-right corner in Fig. 7a) was not considered due to the extraordinary value of density in relation to its biomass, which appears to be related to an error in density assessment.

Under our hypothesis, populations placed under the line might be disturbed populations.

All points corresponding to *P. clavata* populations from Port-Cros National Park sampled before the 1999 mass mortality event placed near the self-thinning line. These populations exhibited a trajectory moving down and left shortly after the disturbance, indicating that these populations lost both density and biomass. Although biomass stabilized in the following years (1999–2003), both populations displayed a larger density loss during this period (Fig. 7b).

## Discussion

### DISTRIBUTION PATTERNS

It has been argued that species distributions can be used as an indicator of the capacity to survive and reproduce under particular conditions (MacArthur 1972). The extensive distribution of *E. singularis* on a regional scale may be related to its tolerance to a wide range of abiotic factors. In contrast, the restricted distribution of *P. clavata* appears to be a response to a narrow range of environmental conditions. This would be in accordance with previous studies that characterized the environmental framework in which both species dwell. *P. clavata* populations dwell in a narrow band of light conditions (irradiance values ranging between 0.12 and 27.6% of surface values, mean 7.6%) and typically in a vertical surface (although they can be found on other slope types with sediment-free bottoms; Weinberg 1975, 1979, 1980). In contrast, *E. singularis* is a species found commonly on horizontal or sloping sediment-covered bottoms subjected to irradiance conditions that range between 3 and 44% of surface values (mean 18.6%; Weinberg 1975, 1979, 1980).

Along the explored coast, the upper depth limit of distribution varied between the two species. While *E. singularis* did not show a clear pattern of the upper limit of distribution, a decrease in depth of this upper distribution along the latitudinal gradient was observed in *P. clavata* populations. This pattern appears to be related to the variability of the abiotic factors along this gradient. Changes in the limits of distribution of different NW Mediterranean benthic communities have been related previously to differences in factors such as light, temperature and hydrodynamism along a comparable spatial scale (Zabala & Ballesteros 1989). This spatial variation of abiotic factors and their relationship with the distribution of the species (Weinberg 1975, 1980) may determine the existence of areas where the depth range of distribution is compressed.

Variation of maximum height of the colonies of *P. clavata* along the latitudinal gradient was related to the decrease in the depth of the upper distribution limit. This is consistent with the increase of maximum height with depth observed previously (Harmelin & Marinopoulos 1994) and can be attributed to the decrease of strong hydrodynamic events with depth.

### BASELINE DATA FOR FUTURE DISTURBANCES

The mean extent of injury of colonies was lower in *E. singularis* than in *P. clavata* (Table 1). Moreover, a larger proportion of healthy colonies was observed in *E. singularis* than in *P. clavata*, suggesting that *E. singularis* has a higher tolerance to disturbance than *P. clavata*. The observed extent of injury exhibited by both species was much lower than previous assessments of the impact of mass mortality events on these species (about 50% extent of injury of colony surface, Cerrano *et al.* 2000; Perez *et al.* 2000; Linares *et al.* 2005; Coma *et al.* 2006). Therefore, the impact of the 1999 mass mortality events along the Mediterranean Spanish coast did not affect the examined gorgonian populations significantly.

### APPLICATION OF FOREST ECOLOGY APPROACHES TO GORGONIAN POPULATIONS

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

The overall results suggest that both the gorgonian species may have different recruitment dynamics. Size class 2 (10–20 cm, first reproductive colonies) was the predominant size class in *P. clavata* populations, similar to that observed in other locations (Harmelin & Garrabou 2005). This peak at the intermediate classes is in accordance with those observed in some previously studied gorgonian species (Jordán-Dahlgren 1989, 2002; Yoshioka 1994; Bastidas *et al.* 2004; Tsounis *et al.* 2006). In contrast, size class 1 (0–10 cm, the smallest and non-reproductive colonies; Ribes *et al.* 2007) was the predominant size class in *E. singularis* populations (14 of 21). This size distribution is similar to some coral species (Hughes & Jackson 1980, 1985; Babcock 1984; Soong 1993; Lewis 1997; Bak & Meesters 1998). Moreover, the fact that the largest colonies were abundant in more pristine conditions agrees with results found for other soft-coral species (Yoshioka 1994; Bastidas *et al.* 2004; Bianchimani 2005), but contrasts with the idea that under environmental deterioration coral populations display negative skewness coefficients (Bak & Meesters 1998; Meesters *et al.* 2001).

The skewness coefficient also revealed a more dynamic pattern for *E. singularis*. In this species two temporal stages could be distinguished, one with a large predominance of smallest colonies and a second stage with a higher presence of large colonies. For *P. clavata*, these two groups showed the same distribution shape, with the only difference being a higher increase of large colonies in symmetric populations located below 25 m.

The fact that along the large explored area none of the *P. clavata* stands corresponded to young stages of the population suggests that the species has a low recruitment. In contrast, the larger proportion of small colonies observed in *E. singularis* suggests high recruitment rates. The differences observed between species may be explained by different reproductive strategies. *P. clavata* is a surface brooder (Coma *et al.* 1995a), whereas *E. singularis* is an internal breeder (Weinberg & Weinberg 1979). This latter strategy may contribute to a reduction in mortality during the first stages of development of the colonies and increase local recruitment.

Examination of the size–density plot yielded a contrasting pattern for the two species. In *E. singularis* populations, the lack of pattern in the size–density plot points to other factors (such as predation, interspecific competition, disturbances, etc.) besides intraspecific competition governing the structure of their populations. *P. clavata* displayed a strong negative correlation between biomass and density of colonies. The closeness of the slope to the predicted value ( $-3/2$ ; Yoda *et al.* 1963) indicates a negative density-dependence that suggests intraspecific competition among *P. clavata* populations.

However, the mechanism remains unclear, because in these thinned populations more extant colonies should be expected.

The populations found below the self-thinning line may correspond to young populations or to disturbed populations. A young population of *P. clavata* was found during final surveys of other areas in the NW Mediterranean Sea, indicating the occurrence of young populations at very low frequency. Representation of the data for this young population (Fig. 7) provided additional evidence that self-thinning may be a relevant mechanism affecting population dynamics.

The effects of the 1999 mass mortality event at Port-Cros National Park agree with the expected placement of disturbed populations below the self-thinning line. In our study, the gorgonian populations that had distributions under the self-thinning line (e.g. Tascó population) were subjected most probably to high levels of mortality due to the high frequency of divers in a marine protected area (Coma *et al.* 2004) or populations where the environmental characteristics of the sites (e.g. high hydrodynamism) do not allow colonies reaching larger size classes (e.g. Massa d'Or and Hormigon populations).

In summary, wide-ranging studies combining measures of density and size are useful to obtain the state of the population of long-lived marine invertebrates in order to make preliminary assessments of their distribution and health status and also to infer which populations have been affected by disturbance. The demographic approaches used in this study have allowed us to obtain essential baseline data of two of the most common gorgonian species in the NW Mediterranean Sea along a regional spatial scale. The study has revealed different biological features of both species and different influence by environmental factors. The contrasting population dynamics may imply differences in vulnerability of both species. Consequently, although further studies are required to achieve a complete understanding of demographic characteristics of these species, our study suggests that shallow *P. clavata* populations require major conservation efforts to protect them from future disturbance events.

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## References

- Adler, F.R. (1996) A model of self-thinning through local competition. *Proceedings of the National Academy of Sciences USA*, **93**, 9980–9984.
- Babcock, R.C. (1984) Reproduction and distribution of two species of *Goniastrea* (Scleractinia) from the Great Barrier Reef province. *Coral Reefs*, **2**, 187–195.
- Bak, R.P.M. & Meesters, E.H. (1998) Coral population structure: the hidden information of colony size–frequency distributions. *Marine Ecology Progress Series*, **162**, 301–306.
- Bastidas, C., Fabricius, K.E. & Willis, B.L. (2004) Demographic processes in the soft coral *Simularia flexibilis* leading to local dominance on coral reefs. *Hydrobiologia*, **530**, 433–441.
- Bianchimani, O. (2005) *Évaluation Des Effets Des Aires Marines Protégées Sur les Populations de Corail Rouge (Corallium Rubrum): le Cas des Réserves Marines Françaises. DU d'Environnement Et Pollution*. Université de la Méditerranée, Centre d'Océanologie de Marseille, Marseille.
- Botsford, L.W., Castilla, J.C. & Peterson, C.H. (1997) The management of fisheries and marine ecosystems. *Science*, **277**, 509–515.
- Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P., Sara, G., Schiaparelli, S., Siccardi, A. & Sponga, F. (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (NW Mediterranean), summer 1999. *Ecology Letters*, **3**, 284–293.
- Coma, R., Linares, C., Ribes, M., Diaz, D., Garrabou, J. & Ballesteros, E. (2006) Consequences of a mass mortality event on the populations of the gorgonian *Eunicella singularis* (Cnidaria: Octocorallia) in Menorca (Balearic Islands, NW Mediterranean). *Marine Ecology Progress Series*, **327**, 51–60.
- Coma, R., Pola, E., Ribes, M. & Zabala, M. (2004) Long-term assessment of the patterns of mortality of a temperate octocoral in protected and unprotected areas: a contribution to conservation and management needs. *Ecological Applications*, **14**, 1466–1478.
- Coma, R. & Ribes, M. (2003) Seasonal energetic constraints in Mediterranean benthic suspension feeders: effects at different levels of ecological organization. *Oikos*, **101**, 205–215.
- Coma, R., Ribes, M., Zabala, M. & Gili, J.M. (1995a) Reproduction and cycle of gonadal development in the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series*, **117**, 173–183.
- Coma, R., Ribes, M., Zabala, M. & Gili, J.M. (1998) Growth in a modular colonial marine invertebrate. *Estuarine Coastal Shelf Science*, **47**, 459–470.
- Coma, R., Ribes, M., Zabala, M. & Gili, J.M. (2000) Seasonality in coastal benthic ecosystems. *Trends in Ecology and Evolution*, **15**, 448–453.
- Coma, R., Zabala, M. & Gili, J.M. (1995b) Sexual reproductive effort in the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series*, **117**, 185–192.
- Condit, R., Sukumar, R., Hubbell, S. & Foster, R.B. (1998) Predicting population trends from size distributions: a direct test in a tropical tree community. *American Naturalist*, **152**, 495–509.
- Garrabou, J. & Harmelin, J.G. (2002) A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. *Journal of Animal Ecology*, **71**, 966–978.
- Garrabou, J., Perez, T., Sartoretto, S. & Harmelin, J.G. (2001) Mass mortality event in red coral *Corallium rubrum* populations in Provence region (France, NW Mediterranean). *Marine Ecology Progress Series*, **217**, 263–272.
- Gray, J.S. (1997) Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, **6**, 153–157.
- Harmelin, J.G. & Garrabou, J. (2005) Suivi d'une population de *Paramuricea clavata* (Risso, 1826) (Cnidaria, Octocorallia, Gorgonacea) dans le parc national de Port-Cros (Méditerranée, France): comparaison des états 1992 et 2004 sur le site de la Galère. *Scientific Reports Port-Cros National Park, France*, **21**, 175–191.
- Harmelin, J.G. & Marinopoulos, J. (1994) Population structure and partial mortality of the gorgonian *Paramuricea clavata* (Risso) in the North-Western Mediterranean (France, Port-Cros Island). *Marine Life*, **4**, 5–13.
- Harmelin, J.G., Sartoretto, S. & Francour, P. (1999) *Mise en Place d'une Stratégie de Suivi de l'Ichtyofaune et des Peuplements de Gorgonaires de l'Archipel de Riou*. Contrat Ville de Marseille, Direction de L'environnement et Des Déchets and Centre d'Océanologie de Marseille, Centre d'Océanologie de Marseille, Publications Marseille, Marseille.
- Hughes, T.P. & Connell, J.H. (1999) Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography*, **44**, 932–940.
- Hughes, T.P. & Jackson, J.B.C. (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science*, **209**, 713–715.
- Hughes, T.P. & Jackson, J.B.C. (1985) Population dynamics and life histories of foliaceous corals. *Ecological Monographs*, **55**, 141–166.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Jordán-Dahlgren, E. (1989) Gorgonian community structure and reef zonation patterns on Yucatán coral reefs. *Bulletin of Marine Science*, **45**, 678–696.
- Jordán-Dahlgren, E. (2002) Gorgonian distribution patterns in coral reef environments of the Gulf of Mexico: evidence of sporadic ecological connectivity? *Coral Reefs*, **21**, 205–215.
- Lewis, J.B. (1997) Abundance, distribution and partial mortality of the massive coral *Siderastrea siderea* on degrading coral reefs at Barbados, West Indies. *Marine Pollution Bulletin*, **34**, 622–627.
- 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 Sea. *Marine Ecology Progress Series*, **305**, 127–137.
- Linares, C., Doak, D., Coma, R., Diaz, D. & Zabala, M. (2007) Life history and population viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology*, **88**, 918–928.
- MacArthur, R.H. (1972) *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- Meesters, E.H., Hilterman, M., Kardinaal, E., Keetman, M., de Vries, M. & Bak, R.P.M. (2001) Colony size–frequency distributions of scleractinian coral populations: spatial and interspecific variation. *Marine Ecology Progress Series*, **209**, 43–54.
- Mills, L.S., Soule, M.E. & Doak, D.F. (1993) The keystone-species concept in ecology and conservation. *Bioscience*, **43**, 219–224.
- Musick, J.A. (1999) Ecology and conservation of long-lived marine animals. *American Fisheries Society Symposium*, **23**, 1–10.
- Niklas, K.J., Midgley, J.J. & Hand, R.H. (2003) Tree size frequency distributions, plant density, age and community disturbance. *Ecology Letters*, **6**, 405–411.
- Perez, T., Garrabou, J., Sartoretto, S., Harmelin, J.G., Francour, P. & Vacelet, J. (2000) Mortalité massive d'invertébrés marins: un événement sans précédent en Méditerranée nord-occidentale. *Life Sciences*, **323**, 853–865.
- Pickett, S.T.A. (1989) Space for time substitution as an alternative for long-term studies. Preston's ergodic conjecture: the accumulation of species in space and time. *Long-Term Studies in Ecology* (ed. G.E. Likens), pp. 110–135. Springer-Verlag, New York.
- Ribes, M., Coma, R., Rossi, S. & Michelli, M. (2007) The cycle of gonadal development of *Eunicella singularis* (Cnidaria: Octocorallia): trends on sexual reproduction in Mediterranean gorgonians. *Invertebrate Biology*, in press.
- Roberts, C.M. & Hawkins, J.P. (1999) Extinction risk in the sea. *Trends in Ecology and Evolution*, **14**, 241–246.
- Shinozaki, K. & Kira, T. (1956) Intraspecific competition among higher plants. VII. Logistic theory of the C–D effect. *Journal of Institute Polytechnics, Osaka City University*, **12**, 69–82.
- Sokal, R. & Rohlf, F.J. (1995) *Biometry. The Principles and Practice of Statistics in Biological Research*, 3rd edn. Freeman, New York, New York.
- Soong, K. (1993) Colony size as a species character in massive reef corals. *Coral Reefs*, **12**, 77–83.
- Tsounis, G., Rossi, S., Gili, J.M. & Arntz, W. (2006) Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). *Marine Biology*, **149**, 1059–1070.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Weinberg, S. (1975) Écologie des octocoralliaires communs du substrat durs dans la région de Banyuls-sur-mer. *Bijdragen Tot de Dierkunde*, **45**, 50–70.
- Weinberg, S. (1979) Mediterranean Octocorallian communities and the abiotic environment. *Marine Biology*, **49**, 41–57.
- Weinberg, S. (1980) Autoecology of shallow-water octocorallia from Mediterranean rocky substrata. II. Marseille, Cote d'Azur and Corsica. *Bijdragen Tot de Dierkunde*, **50**, 73–86.
- Weinberg, S. & Weinberg, F. (1979) The life cycle of a gorgonian *Eunicella singularis* (Esper, 1794). *Bijdragen tot de dierkunde*, **48**, 127–140.
- White, J. (1981) The allometric interpretation of the self-thinning rule. *Journal of Theoretical Biology*, **89**, 475–800.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. Intra-specific competition among higher plants. *Journal of Biology, Osaka City University*, **14**, 107–129.
- Yoshioka, P.M. (1994) Size-specific life history pattern of a shallow water gorgonian. *Journal of Experimental Marine Biology and Ecology*, **184**, 111–122.
- Zabala, M. & Ballesteros, E. (1989) Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean. *Scientia Marina*, **53**, 3–17.

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## Supplementary material

The following supplementary material is available for this article.

**Fig. S1.** *Paramuricea clavata*. Map of the quantitatively examined populations

**Fig. S2.** *Eunicella singularis*. Map of the quantitatively examined populations

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01419.x>.

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