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Demographic parameters of two populations of red coral (*Corallium rubrum L.* 1758) in the North Western Mediterranean

**L. Bramanti · I. Vielmini · S. Rossi · G. Tsounis ·
M. Iannelli · R. Cattaneo-Vietti · C. Priori ·
G. Santangelo**

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Abstract The demographic and reproductive structure of populations represents the main data set needed for conservation and management plans. Mediterranean red coral *Corallium rubrum* has been exploited for 2,000 years, but only recently management plans have been solicited by the international community. We examined and compared the demographic features of two red coral shallow populations located in distinct geographic locations: Portofino (Italy) and Cap de Creus (Spain). Adults and juveniles density, growth rates, population size and age structure, fecundity and fertility were examined. Juveniles were the dominant class (33 %) in both populations. The analysis of the gamete content of 653 colonies revealed that the populations have balanced sex ratios and similar fertility and polyp fecundity. The average annual growth rate, determined on 119 colonies by annual growth rings count, was similar in both populations (0.24 mm year^{-1}), decreasing with colony age. Maximum life span of 99 % of the colonies was 60 and 40 years at Portofino and Cap de Creus, respectively. Minimum harvestable size (7 mm basal diameter) was reached in 30–35 years, and the percentage of colonies above it was 6.7 % at Portofino and 2.1 % at Cap de Creus, where juvenile and adult colony densities were significantly lower and the percentage of commercial-sized colonies reduced by 25 % in just a few years. Notwithstanding similar growth and fecundity, the two populations showed different densities and size/age structures suggesting local factors, together with different fishing pressures, have to be taken into account in the management plans for this species.

Introduction

Population dynamics depend largely on demographic histories (Dobson 1998; Ebert 1999, particularly for slow-growing, long-lived species, which have been subjected to dramatic reductions in survival, reproduction and/or recruitment rates (e.g., Fujiwara and Caswell 2001;

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Present Address:
L. Bramanti (✉)
CNRS, UMR8222, LECOB, Observatoire Océanologique,
Université Pierre et Marie Curie, 18 Avenue du Fontaulé,
66650 Banyuls-sur-Mer, France
e-mail: philebo@gmail.com

L. Bramanti
Instituto de Ciencias del Mar, Barcelona (ICM-CSIC), Passeig
Maritim de la Barceloneta 37-49, 08003 Barcelona, Spain

L. Bramanti · C. Priori · G. Santangelo
Department of Biology, Università di Pisa, Via Volta 6,
56126 Pisa, Italy

I. Vielmini
AquaTT, P. O. Box 8989, Dublin 2, Ireland

S. Rossi
Environmental Science and Technology Institute, Autonomous
University of Barcelona, Campus UAB s/n, 08193 Barcelona, Spain

G. Tsounis
Leibniz Center for Tropical Marine Ecology GmbH (ZMT),
Fahrenheitstrasse 6, 28359 Bremen, Germany

M. Iannelli
Department of Mathematics, Università di Trento, Via Sommarive
14, 38123 Povo, Trento, Italy

R. Cattaneo-Vietti
Dipartimento per lo Studio del Territorio e delle sue Risorse
(Dip.Te.Ris), Università di Genova, C.so Europa 26,
16132 Genoa, Italy

Santangelo and Bramanti 2006; Arrigoni et al. 2011). Demographic studies can supply clues to improving conservation and management plans, providing information on past dynamics and future trends of populations. In particular, population size frequency distribution, demographic traits (e.g., sex ratio and population density) and life history variables (e.g., growth rates, age and fecundity) can be used to assess population performances, evaluate the current status of a population and to investigate spatial differences between population (Table 1; Ebert 1999; Beissinger and McCullough 2002).

Demographic population models, based on life history tables and transition matrixes, combine the informations from population structure, demography and life history traits and have been applied to conservation of several marine species: e.g., the loggerhead sea turtle *Caretta caretta* (Crouse et al. 1987) and the Right whale *Eubalena glacialis* (Fujiwara and Caswell 2001). Matrix population models account for recruitment, reproduction and demographic parameters and represent an advanced tool for conservation with respect to classical fishery models based on yield per recruit (Beverton and Hollt 1957). The demographic features and life history variables used to parameterize these models are gathered in life history tables describing the demographic structure of the population by means of size/age structure, fecundity, fertility, survival and recruitment rate.

Gorgonians are long-lived, engineering and habitat-forming species (Gili and Coma 1998) frequently affected by anthropogenic pressure of different origins (e.g., Cupido el al. 2009; Tsounis et al. 2012, and references herein). Moreover, due to their high economic value, some species have suffered intensive exploitation (Tsounis et al. 2010, 2013). Conservation of harvested, long-lived, slow-growing species is one of the most difficult challenges faced by ecologists. Determining the best approach for the sustainable exploitation of precious octocorals is still a controversial matter (Bruckner 2009; Santangelo and Bramanti 2010; Tsounis et al. 2010, 2013; Iwasaki et al. 2012). Ad hoc studies must therefore be addressed at understanding the complex dynamics of the populations in order to evaluate their conservation and management status (Edmunds and Elahi 2007; Santangelo et al. 2007; Bramanti et al. 2009).

The Mediterranean red coral *Corallium rubrum* is a long-lived, slow-growing precious gorgonian endemic to the Mediterranean and neighboring Atlantic areas (Zibrowius et al. 1984), frequently forming dense monospecific patches within the Mediterranean coralligenous assemblages. Harvested for over two thousand years due to its highly valued axial skeleton used as raw material for jewelry, this species has played and still plays an important economic and cultural role in European and Eastern Asian countries (Cicogna and Cattaneo-Vietti 1993; Tsounis et al. 2010). The long history of red coral harvesting is a paramount example of longtime, highly specialized exploitation, selectively addressed toward a single species.

Following management needs, an operational distinction has been made between shallow and deep *C. rubrum* populations (Santangelo and Abbiati 2001; Costantini et al. 2010). The shallow populations live between 10 and 50 m depth and have been long overharvested due to the ease of accessibility. They are mainly characterized by dense patches of small-sized colonies (Garrabou and Harmelin 2002; Tsounis et al. 2006a) with low economic value but high naturalistic and touristic value (Bramanti et al. 2011). The deep populations (50−200 m) are composed of sparse large colonies (Rossi et al. 2008; Priori et al. 2013) with differing genetic structure (Costantini et al. 2011) and are nowadays the main target of fishery (Santangelo and Bramanti 2010; Priori et al. 2013; Tsounis et al. 2013). There is some evidence that the long-term harvesting pressure on shallow red coral populations may have caused a shift in their structure toward higher colony densities and smaller size (Garrabou and Harmelin 2002; Tsounis et al. 2006a; Bramanti et al. 2009; Linares et al. 2010, 2012). However, the lack of demographic data on pristine populations limits our knowledge of the past population structure (Knowlton and Jackson 2008).

The last 20 years of scientific research on *C. rubrum* showed that the exploitation of shallow populations must be avoided due to the risks represented by climate change (Santangelo et al. 2007; Bramanti et al. 2013). The exploitation of deep dwelling populations needs a careful management based on sound population and fishing data and reliable analysis of demographic trends (Santangelo and Abbiati 2001). Moreover, different populations can show different demographic characteristics linked to the different environment in which they live and/or to different histories (Table 1). Basing on this assumption, the management of *C. rubrum* has to be thought taking into account the differences between populations.

Due to the international concern for conservation, recent attempts have been made to regulate the trade of the species of the genus *Corallium*, including all species of this genus in the annex II of CITES (Convention for International Trade of Endangered Species; Bruckner 2009; Tsounis et al. 2010). Due to the lack of data necessary to determine whether or not the population decline meets CITES criteria, all such attempts have failed (Tsounis et al. 2013). According to the queries raised in the course of international meetings (Bruckner 2009; IFPC 2009, 2012; GFCM 2010, 2011), comparative demographic data are urgently needed in order to set management and conservation plans suitable for sustainable harvesting of the Mediterranean red coral. On the basis of the works of Santangelo et al. (2004, 2007) and Bramanti et al. (2009), the demographic approach to the study of the population dynamics has been

Table 1 Summary table showing how information on population structure (skewness), demography (density and sex ratio) and life history variables (growth rate, age and fecundity) have been used so far in other marine species to define population performance, current status of the populations and spatial differences. In the fourth column some studies in which these applications have been used are reported

Data used	Objective			
	Population performance	Population status	Spatial differences	Bibliography
Size structure	Skewness can be used as an indicator of young/olds ratio (positive = more youngs; negative = more olds)	Missing age/size classes in the population structure could be indication of a past disturbance	Population dwelling in different locations can have different size structures	Rossi et al. (2012) Goffredo and Chadwick-Furman (2003) Linares et al. (2010)
Demography (density, sex ratio)	Unbalanced sex ratio could determine low reproductive output Low density could determine poor performance	Unbalanced sex ratio could be indicator of disturbance Low densities are associated to poor population status	Population in different locations can have different sex ratio and/or densities	Bramanti et al. (2009) Tsounies et al. (2006b) Priori et al. (2013)
Life history (growth rate, age, fecundity)	Low growth and fecundity rates and short life span (low maximum age) could determine poor performances	A population in good status display long life span (high maximum age) and high fecundity and growth rates	Population in different locations can show different growth rates, fecundity and maximum age	Bramanti et al. (2005) Torrents and Garrabou (2011) Santangelo et al. (2007)

pinpointed as a key instrument in the management of *C. rubrum* (Bramanti et al. 2010).

Since the seminal work of Huges (1984), the demographic approach has been widely applied to corals (e.g., Hughes and Jackson 1985; Babcock 1991; Fong and Glynn 1998; Goffredo and Chadwick-Furman 2003). These authors used a combination of demographic data such as fecundity, growth and survival rate in order to estimate population growth and describe the dynamics of different species of scleractinian corals. However, only in few cases the projection capacity of demographic models has been used to propose conservation and management measures (Santangelo et al. 2007; Bramanti et al. 2009, 2010).

The estimation of colony age and growth rates is required to assess the population age structure (Tsounis et al. 2006a) and to make inferences of future population trends. While size is a basic descriptor of coral population structure and demographic models can be based on size rather than age (e.g., Huges 1984), age determination allows for a temporal resolution of the model, by estimating the most probable age for each size class. The calculated growth rate gives then a time step for the reiteration of size-structured population models (Caswell 2001). To this end, a method for age determination of *C. rubrum* colonies was applied to the populations object of this study. Species displaying skeletal calcareous structures such as mollusks, cnidarian and bryozoans can be analyzed by sclero chronological techniques in order to have information on the age (e.g., Knutson et al. 1972; Millstein and O'Clair 2001). Coral reef species, in particular, are the most widely studied due to the presence of annual alternance of low- and high-density bands (Knutson et al. 1972; Barnes and Lough 1993). We applied a method developed and validated by Marschal et al. (2004) for the aging of *C. rubrum* colonies. The method have been previously applied to other *C. rubrum* populations (Torrents et al. 2005; Gallmetzer et al. 2010; Priori et al. 2013).

The study of population size frequency distribution can give insights to estimate the response of coral populations to the environment (Bak and Meesters 1998) and to climate change (Bak and Meesters 1999). Rossi et al. (2012) used the analysis of the size structure of a population of *Eudendrium racemosum* in order to estimate the trophic impact of this species, while Linares et al. (2010) compared the skewness values of the size frequency distribution of *C. rubrum* in different marine protected areas. The size frequency distribution can also give information on the disturbances that affected a population in the past, as showed by Linares et al. (2008a) for *Paramuricea clavata* and *Eunicella singularis*.

Recruitment, a crucial basic demographic parameter determining population growth rate (Benayahu and Loya 1985; Grigg 1988), is an operational term defining the initial sighting of a recently settled juvenile (Caley et al. 1996). In the present paper, the term juveniles refers to the first age class in the population and includes settlement and survival of newly settled individuals. Due to the difficulty in identifying very small individuals (Bramanti et al. 2003), this class has been examined only in a few *C. rubrum* populations (Garrabou and Harmelin 2002; Bramanti et al. 2005; Bramanti et al. 2007; Santangelo et al. 2012).

The present research aims at analyzing the demographic and reproductive features of two shallow red coral populations living in two different locations in the NW Mediterranean, separated by 550 km: Portofino (Italy) and Cap de Creus (Spain). Demographic and reproductive features will be analyzed in terms of: (1) juveniles and adult colonies density; (2) colony growth rate; (3) size and age structure; (4) sex ratio, fertility and fecundity. A comparison between the reproductive and demographic features of the two population will be performed. The data obtained are the first step for the parameterization of robust demographic models based on sound information on the demographic parameters (Santangelo et al. 2007). The ultimate aim is to shed light on the current status of the populations of this precious species by means of comparative demographic evidence.

Materials and methods

The study areas

This study was carried out in two locations in the NW Mediterranean Sea, located 550 km from each other (Fig. 1a): Portofino Promontory marine reserve (Eastern Ligurian Sea 44°18.18′N; 09°12.83′E, Italy; Fig. 1b) and Cap de Creus marine reserve (Costa Brava; 42°29.21′N; 3°30.18′E, Spain; Fig. 1c).

Extending along a 13-km coastline, the 3.46 km^2 Portofino marine reserve was established in 1999. In 2002, it was included in the SPAMI list (Special Protected Area of Mediterranean Interest) due to the species richness of its coralligenous species assemblage. The southern slope of the promontory is characterized by a heterogeneous habitat with patches of different species of gorgonians, among which *C. rubrum* is the most common. Red coral harvesting, as well as many other fishing activities, has been banned inside the marine reserve since 1999.

The marine reserve of Cap de Creus, established in 1998, extends for 30.5 km^2 along 40 km of coastline and was included in the SPAMI list in 2001. National and regional laws regulate harvesting and fishing activities inside the marine reserve; in particular, *C. rubrum* can be collected, only manually and in some locations, by licensed fishermen. The yearly quota of raw *C. rubrum* that each of 10–12 licensed fishermen can harvest is 400 kg. The harvesting season lasts from May to October and the size limit is 7 mm in basal diameter (recently proposed by FAO; GFCM 2011), although illegal red coral harvesting is frequently conducted throughout the reserve (Tsounis et al. 2013).

Values of chlorophyll a, water transparency and total organic matter (TOM) in the two locations are summarized in Table 2. According to Durrieu de Madron et al. (2011), these values place both populations in the same eco-region.

Sampling

Sampling was carried out by SCUBA diving between 30 and 35 meters depth in both marine reserves (Locations) in

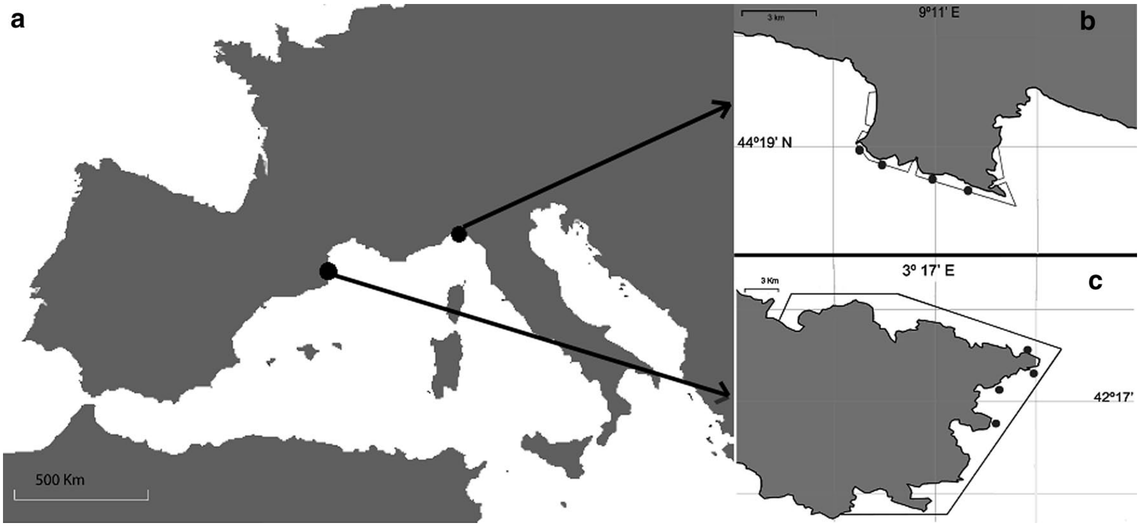

Fig. 1 **a** Western Mediterranean Sea. **b** Portofino marine reserve. **c** Cap de Creus marine reserve. *Black dots* indicate sampling Sites

Table 2 Average annual values of environmental characteristics recorded in Portofino (Bavestrello et al. 1995) and in Cap de Creus (Rossi and Gili 2005)

	Portofino	Cap de Creus
Water transparency (m)	14.8	15.25
Chlorophyll a (μg l^{-1})	0.6	0.7
TOM (mg l^{-1})	3.3	3.9

June–July 2009. Adult colony and juveniles densities were examined according to a nested ANOVA sampling design; in each Location (fixed factor, 2 levels: Portofino and Cap de Creus), four Sites (random factor, 4 levels, nested in area) were randomly selected. In each Site, three 20 × 20 cm quadrats (replicates) were selected randomly. Overall, 24 replicates were sampled, and the percentage of variance explained by each factor of the nested ANOVA was calculated (R software, package 'stats,' command 'aov'). Before performing the test, all the assumptions of ANOVA were verified.

All adult colonies in each quadrat were individually detached by a chisel, collected by hand and placed in plastic jars. As the sampling was carried out in marine reserves, both the extent and number of samplings were limited. Once adult colonies had been collected (thus revealing the underlying smaller colonies they concealed), the quadrats were photographed with a digital camera (Canon G10 with IKELITE housing and TTL strobe) and juveniles were identified through image analysis of pictures. As red coral juveniles, measuring on average 0.6 mm (basal diameter; Bramanti et al. 2005, 2007), are difficult to be identified, the pictures were taken in macro mode (resolution 40 megapixels) and examined at higher magnification in the laboratory. This method is extremely accurate; however, it could be biased due to the difficulty of handling smaller colonies (2–3 mm), some of which may have been lost during sampling (Santangelo and Bramanti 2010). Part of the smaller colonies (1–2 mm) and juveniles do not detach from the substrate due to their small dimensions, and they are counted on photographs.

Removed adult colonies ($n = 620$; 477 from Portofino and 143 from Cap de Creus) were fixed immediately after collection in 4 % formaldehyde–seawater-buffered solution to be subsequently processed for laboratory analyses to determine size, age, sex, fertility and fecundity of female colonies. Due to the lower density of colonies at Cap de Creus, an additional sample of 33 colonies was taken from that Location at the end of June 2009 and used only for the sex ratio analysis.

Population size structure

Colony basal maximum and minimum diameters were measured with a caliper (precision ±0.05 mm) at the inflection point (1 ± 0.2 mm from colony bases) and averaged. The size structure of the population was obtained by dividing all the colonies into 1 mm diameter classes. Skewness, a measure of the asymmetry of a distribution (Linares et al. 2008a; Gori et al. 2011; Rossi et al. 2012), was then calculated, and the hypothesis of symmetry (skewness = 0) was tested by Agostino's test (R software, package 'moments,' command 'agostino.test'),

Colony age and growth rate

Colony age was determined according to the thin section—organic matrix staining method (Marschal et al. 2004). After decalcification and staining, thin sections were photographed under a stereomicroscope. Each image was calibrated according to the proper magnification and processed by the graphic software ImageJ (Rasband 1997). Age was estimated as the average number of growth rings recorded on three linear transects, each drawn in a different sector of a thin section (Fig. 2). The first visible growth ring usually appears after 4 years at a distance from the medullar region (Marschal et al. 2004; Vielzeuf et al. 2008); hence, the age of colonies was calculated by adding 4 to the number of growth rings counted. Only a subsample of the collected colonies ($n = 119$) was suitable for this method due to holes made by boring sponges as well as to the irregular morphology of some colonies that hindered annual growth rings count (Priori et al. 2013). The surface of the circular crown area (CCA) delimited by two subsequent growth rings was also measured on a subsample of the colonies ($n = 33$). Each CCA is the annual increase in surface of the colony base section; thus, each colony yielded a number of CCA measurements proportional to its age. Finally,

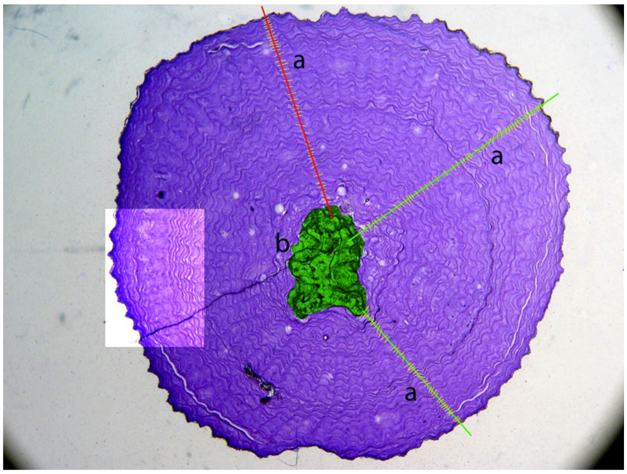

Fig. 2 Thin section of a *C. rubrum* colony after decalcification and staining (Marschal et al. 2004) where growth rings are visible. **a** Transect lines along which rings count have been performed (see 'Materials and methods' section). **b** Medullar region

the annual increment of the overall CCA of the 33 colonies (i.e., the sum of the CCAs) was plotted against age. As age determination by growth rings count can have some uncertainties due to the first years of growth, CCAs were grouped into 3-year intervals. The annual growth rate was calculated by dividing the averaged basal diameter by colony age. The relationship between colony diameter and age was fitted to the subsample of colonies whose age was determined by the annual growth ring count ($n = 119$ colonies). This relationship was then applied to divide all the sampled colonies into size/age classes according to their average annual growth rate (Santangelo et al. 2007). The relationship between the age and the mean annual growth rate of colonies was examined via Pearson's linear correlation coefficient r (CurveExpert Pro software).

Reproductive features

Overall, 653 colonies (620 from the replicated quadrats and 33 additional from Cap de Creus) were examined, and the sexual status of all the colonies sampled in the quadrats was determined. The number of polyps examined in each colony varied proportionally according to colony size, ranging from five polyps in the smaller colonies (<3 mm of basal diameter) up to 18 in larger ones (>5 mm basal diameter; Santangelo et al. 2003). Male and female colonies were distinguished via microscope analysis of gonads (Santangelo et al. 2003; Tsounis et al. 2006b; Torrents and Garrabou 2011; Priori et al. 2013). Polyps were dissected and observed under a stereomicroscope, at 10−80× and then examined by an optical microscope at 250–1,000× to identify oocytes and sperm sacs. Colonies in which no gametes were found were considered sterile. Sex ratios were tested using a chi-square test (R software, package 'stats'; command 'chisq.test'). After sex identification, the number of oocytes in each polyp was counted along with the average polyp fecundity calculated as the ratio between the overall number of oocytes found and the number of polyps analyzed.

Results

Population density

Overall, out of the 24 replicated quadrats, 620 adult colonies were found ($n = 477$ for Portofino and $n = 143$ for Cap de Creus), corresponding to a density of 39.7 ± 17.8 and 11.9 ± 6.9 (mean ± SD) colonies 400 cm^{-2} for Portofino and Cap de Creus, respectively (Fig. 3a). The observed differences in adult colonies density between the two populations, were confirmed by the nested ANOVA (Table 3a) which revealed that the main variance component is due to the factor Location (60.47 %), while the factor Site (nested in Location) accounts for 1.54 % of the variance.

Overall, 278 juveniles were found: 210 at Portofino and 68 at Cap de Creus, corresponding to 17.5 ± 4.7 and 5.6 ± 2.8 (mean ± SD) recruits 400 cm^{-2} (Fig. 3b), respectively. Similarly to the adult density analysis, a significant difference between the two Locations was revealed by the nested ANOVA, showing Location accounted for 97.39 % and Site for only 1.61 % of the variance (Table 3b). Moreover, the variance component associated with residual was remarkably higher for adult colonies than for juveniles (37.99 vs. 1.0 %; Table 3b), indicating a larger variability occurred in the density of adult colonies. Both adult and juveniles densities were about threefold higher in Portofino than in Cap de Creus, and thus, the ratio adult/juveniles was similar in both populations (~2.15/1).

Colony size, growth rate and age

The average basal diameter of colonies was 4.42 ± 1.69 mm at Portofino and 4.08 ± 1.24 (mean ± SD) mm at Cap de Creus, with a maximum of 14.48 mm in the former and 11.5 mm in the latter population. The size distribution at Portofino (Fig. 4, black bars) is characterized by a significantly positive skewness (skewness = 0.61,

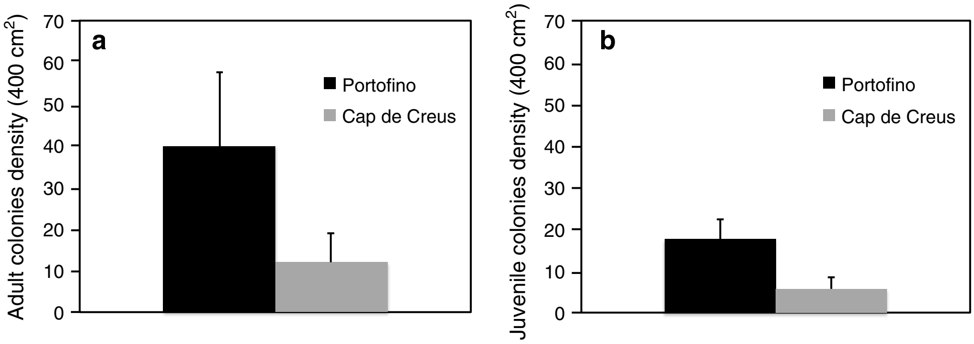

Fig. 3 Adults (**a**) and recruits (**b**) average density (colonies 400 cm^{-2}) in Portofino (*black columns*) and Cap de Creus (*gray columns*). *Error bars* represent SD

Table 3 Nested ANOVA for *C. rubrum* adult colonies (a) and juveniles (b) densities

Source	SS	DF	MS	*F*	*p*	*F* versus	Variance %
a: Adult colonies							
Location	3,626.04	1	3,626.04	16.58	0.01	Site (area)	60.47
Site (location)	1,313.58	6	218.76	0.84	0.56	RES	1.54
RES	4,175.33	16	260.96				37.99
TOT	9,113.96	23					
b: Juveniles							
Location	847.87	1	847.87	41.1	0.0007	Site (location)	97.39
Site (location)	123.77	6	20.62	1.59	0.215	RES	1.61
RES	208.16	16	13.01				1.00
TOT	1,179.80	23					

Factors are Location (Portofino and Cap de Creus) and Site (four randomly chosen Sites inside each Location. In both cases, the main variance percentage was explained by the factor Location

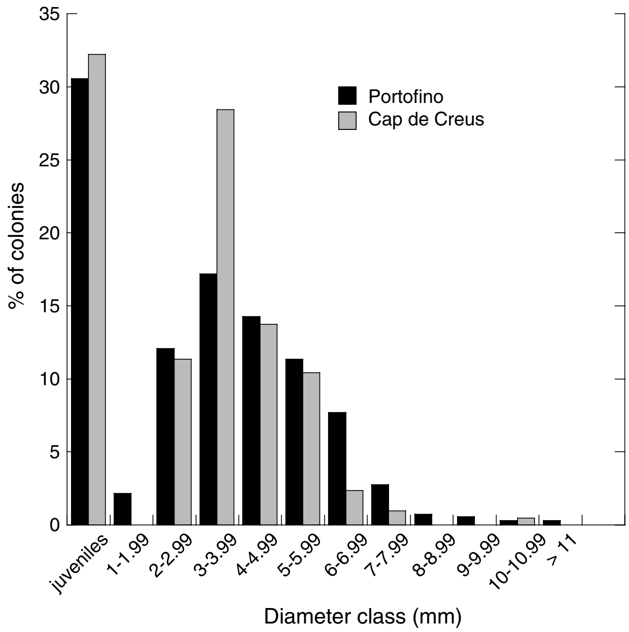

Fig. 4 Size (basal diameter) distribution in the Portofino (*black bars*) and Cap de Creus (*gray bars*) populations of *C. rubrum*

$z = 3.01$, $p = 0.003$), due to the larger colonies there, while Cap de Creus distribution (Fig. 4, gray bars) was not significantly skewed (skewness = 0.129, $z = 0.426$, $p = 0.67$). The frequency of adult colonies larger than 7 mm in diameter (the minimum legally harvestable size) was 6.7 and 2.1 % at Portofino and at Cap de Creus, respectively. Juveniles are the dominant class in both populations in 79 % of the sampled quadrats, representing 30.6 and 32.2 % of the overall colonies at Portofino and Cap de Creus, respectively.

Overall, 119 colonies ($n = 75$ for Portofino and $n = 44$ for Cap de Creus), encompassing all diameter classes (1 mm each), were sectioned and stained (Marschal et al. 2004; Priori et al. 2013), and the annual growth rings were counted (Fig. 2). Colonies bored by endobiont sponges (unsuitable for age determination) were 50.3 % at Portofino and 41.5 % at Cap de Creus. The average colony growth rate was 0.241 ± 0.061 and 0.237 ± 0.062 mm year^{-1} (mean ± SD) at Portofino and at Cap de Creus, respectively. As these values did not differ significantly (t test, $t = 0.9$; $df = 43$, $p = 0.27$), they were pooled and the average colony growth rate of both populations was 0.24 ± 0.06 mm year^{-1} (mean ± SD). A significant negative, linear correlation was found between the mean annual growth rate of a colony and its age (r Pearson = −0.43; $n = 119$; $p < 0.001$). This finding indicates a decrease in the growth rate of colony basal diameter with age. The yearly increase in the circular crown area was constant during the life of the colonies (Fig. 5a). The yearly average colony growth in diameter is well fitted by the power curve

$$y = 0.552x^{0.689}\left(R^2 = 0.57; N = 119; p = 0.01;\ \text{Fig. 4b}\right) \quad (1)$$

where x is the age (years) of the colony and y the diameter (mm). When data on the initial 4 years of colony growth (Bramanti et al. 2005; Santangelo et al. 2012) are included in the fit, the significance of the power curve representing colony growth remarkably increases ($y = 0.646x^{0.652}$; $R^2 = 0.88$; $N = 180$; $p = 0.003$; Fig. 4c).

Based on the relationship between age and size reported above [Eq. (1); Fig. 5b], all the colonies sampled in the two Locations ($n = 620$) were divided into annual size classes determined on the basis of their average annual growth in diameter (i.e., thereby assigning the colonies to the most probable age group, based on their size; Santangelo et al. 2007). Juveniles, the dominant class in both populations, were also included in the size/age structures. Both size/age structures were well represented by monotonic decreasing curves with negative exponents ($y = 210\ \mathrm{e}^{-0.109x}$ and $y = 68\ \mathrm{e}^{-0.115x}$ for Portofino and Cap de Creus, respectively, Fig. 6a, b). The size/age distributions revealed a 33 % longer life span at Portofino, where 99 % of the colonies have a maximum estimated age of 60 years, while at

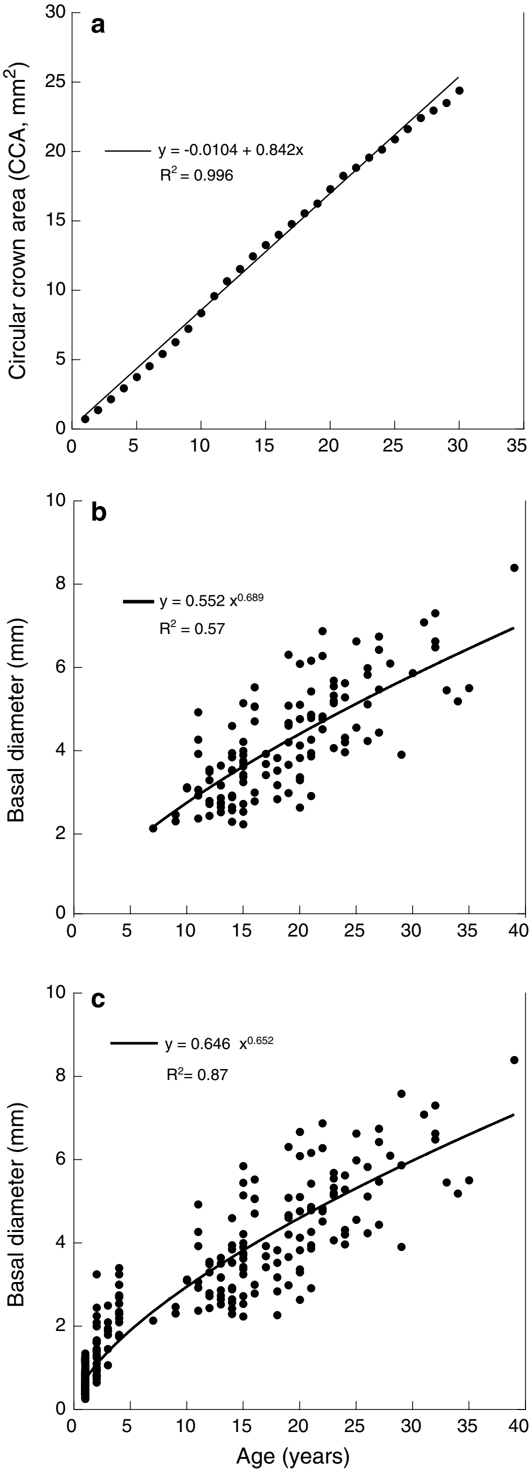

Fig. 5 **a** The growth of the circular crown area (CCA) of colony base is fitted by a linear equation ($R^2 = 0.99$), indicating an increase in CCA constant along colony life span. **b** Relationship between colony age (determined by annual growth rings count) and basal diameter. **c** Relationship between colony age (determined by annual growth rings count) and basal diameter including data of the first 4 years of colony growth (Bramanti et al. 2005; Santangelo et al. 2012)

Cap de Creus 99 % of the colonies have a maximum estimated age of 40 years. The size distribution of the Portofino population also showed significant skewness due to the presence of larger colonies (Fig. 4). The maximum estimated age was 110 and 79 years at Portofino and Cap de Creus, respectively.

Reproductive features

Overall, 7,294 female polyps ($n = 6{,}318$ for Portofino and $n = 976$ for Cap de Creus) were dissected and examined. The mean fecundity of female polyps was 0.64 ± 0.33 at Portofino and 0.42 ± 0.30 at Cap de Creus (oocyte polyp^{-1}; mean ± SD) with no significant difference between the two Locations (t test; $t = 1.9$; $df = 39$; $p = 0.067$). No significant relationship between polyp fecundity and colony size/age was found (r Pearson = 0.18; $n = 146$; $p = 0.39$).

About 74 % (353/477) of the adult colonies examined at Portofino and 78.6 % (143/181) of those examined at Cap de Creus were found fertile with no significant difference between the two Locations (chi-square test: chi-square = 0.15; $p = 0.69$). Overall, 24 % of colonies are sterile (162/658) representing 26.3 % of the 1−3 mm diameter classes and 9 % of the 4−6 mm classes. No sterile colonies were found in larger classes (>6 mm). The sex ratio of both populations did not diverged from randomness, being the male/female ratio 0.95/1 (172/181) and 0.74/1 (61/82) at Portofino and at Cap de Creus, respectively (chi-square = 0.39; $p = 0.53$ for Portofino, and 0.1, $p = 0.75$ for Cap de Creus).

Discussion

In this paper, we analyzed the demographic and reproductive features of two populations of the precious gorgonian *C. rubrum* in two different geographic locations: Portofino (Italy) and Cap de Creus (Spain). Results showed a significant higher density of adult and juveniles in Portofino.

Juveniles density found at Portofino was similar to that found in other shallow populations of the Eastern Ligurian Sea, similarly characterized by high colony density (Bramanti et al. 2005; Santangelo et al. 2012). Low juvenile colony densities, similar to the values we found in Cap de Creus, have been also found in the red coral population of Medes marine reserve, located at about 20 km from Cap de Creus and similarly composed by low density patches (Tsounis et al. 2006a; Santangelo et al. 2012).

Notwithstanding the large differences in juveniles and adults densities, a similar ratio between these two life stages was found in both populations, suggesting

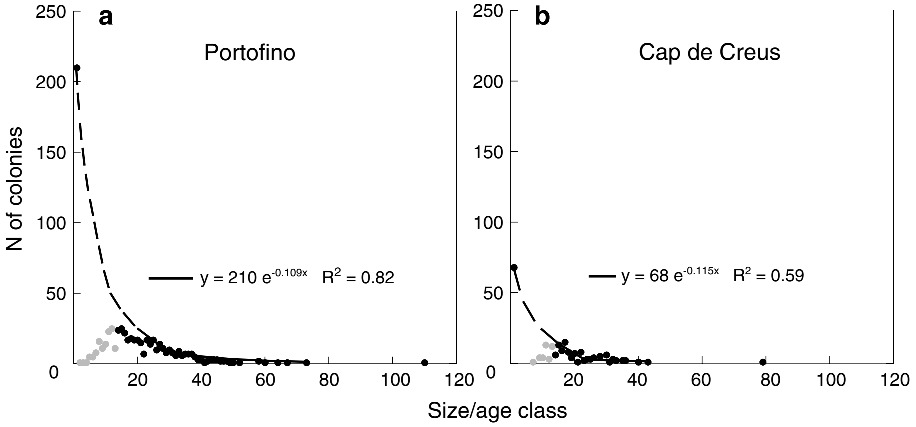

Fig. 6 Size/age structure in the two locations. **a** Portofino. **b** Cap de Creus. *Black dots* represent colonies >3 mm (average basal diameter). *Gray dots* represent colonies <3 mm that may be underestimated due to the sampling method

density-dependent correlation between these two life stages could occur (Garrabou and Harmelin 2002; Santangelo et al. 2007). The colony size distributions of the two populations revealed that the percentage of colonies above the minimum legal harvestable size (7 mm in diameter) at Cap de Creus is threefold lower than in Portofino (2.1 vs. 6.7 %) and fourfold lower than in year 2003 (Tsounis et al. 2007). Notwithstanding the sampling method was different from the one used in our study (in Tsounis et al. 2007, a photographic sampling of adult colonies was carried out), the comparison with our results suggested a 20 % reduction in the average diameter of colonies has occurred in the Spanish reserve over the course of only a few years.

Due to the presence of large colonies at Portofino, the size distribution was significantly skewed. This pattern was not found at Cap de Creus, where large colonies were much more scarce and the maximum size was lower by 1/3. An even more evident shift toward large colonies has been observed by Tsounis et al. (2006a; Linares et al. 2012) at Medes islands (Costa Brava, Spain) and by Linares et al. (2010) at Scandola (Corsica, France), Carry-le Ruet (Marseille, France) and Banyuls-sur-Mer (Languedoc-Roussillon, France), where harvesting is strictly forbidden and controlled. These findings underline that in some marine reserves, the enforcement has an effect on the size of red coral colonies.

The average colony growth rate found in this study (0.24 ± 0.06 mm year^{-1}) was consistent with the values reported for other shallow populations (Garrabou and Harmelin 2002; Marschal et al. 2004; Torrents et al. 2005; Gallmetzer et al. 2010) and slightly lower than the one found by Priori et al. (2013) for deep dwelling populations (0.26 mm year^{-1}). All these findings suggest some constancy in the average colony growth rate of shallow populations.

The significant negative correlation found between the mean annual growth rate of the colonies and their age indicates a decrease in the growth of colony basal diameter with age. Moreover, it has been found that during the first 4 years, colony diameter grows 2–3 times faster than in subsequent years (Cattaneo-Vietti et al. 1993; Bramanti et al. 2005, 2007). Thus, a decreasing curve should better describe the trends of colony growth with age. A reduction in basal diameter growth with time is furthermore confirmed by the constant growth of the circular crown area (CCA) we found.

The not significantly skewed size/age distributions in Cap de Creus, where 99 % of colonies have a maximum age of 40 years, confirmed a shorter (66 %) life span than those in Portofino, where the maximum age of 99 % of the colonies was 60 years. In both populations, the minimal legal harvestable size (7 mm) corresponds to an estimated age of 30–35 years.

The dominant age group in both populations is represented by juveniles. Although occasional pulse peaks of recruitment have been described in red coral populations (Garrabou and Harmelin 2002; Santangelo et al. 2012), our results indicate that the dominance of juveniles over the older classes is a pattern common to both the populations studied. The monotonic decreasing pattern of the size/age structure is another common feature of the two populations examined and is also similar to that found in other red coral populations living in shallow waters (Santangelo et al. 2007). The low recruitment rate found in the Cap de Creus population could likely be determined by a low larval production due to low density and small sizes of local colonies. This could be amplified by low larval retention rates and low larval supply from neighbor populations (Ledoux et al. 2010; Costantini et al. 2011; Guizien et al. 2012). Despite main life history parameters (colony growth rate, sex ratio and colony fertility and fecundity) were similar in both populations, adults and juveniles densities as well as population life span were remarkably lower for the population at Cap de Creus. The environmental characteristics reported in Table 2, in particular chlorophyll a, are good proxies for phytoplankton and zooplankton (Estrada 1996). As phytoplankton and zooplankton represent between 22 % and 57 % of the diet of *C. rubrum* colonies (Tsounis et al. 2006c), the similar values of these characteristics in the two locations could explain the similar values of growth rates and fecundity found in the two populations. The observed differences in the demographic structures could then be due to the different mortality rates at which the larger/older colonies have been and are still subjected, probably due to harvesting that selectively affects large colonies. Red coral harvesting at Cap de Creus is a historic local tradition, resulting in intense longstanding harvesting continuing until today (Rossi et al. 2008; Tsounis et al. 2010, 2013). In contrast to Cap de Creus, red coral harvesting at Portofino has always been less intense, decreasing some years before the establishment of the marine reserve in 1999. Moreover, due to the smaller extension of Portofino reserve, enforcement may be easier and more effective. Lastly, Cap de Creus population is subject to lower infestation by boring sponges (Corriero et al. 1997), producing colonies with axial skeletons more suitable for jewelry, thus increasing the commercial value of colonies, which could have encouraged a more intense harvesting at Cap de Creus. According to Tsounis et al. (2007), overharvesting may have caused a threefold reduction in the colony life span in Cap de Creus population, a difference similar to that found between the two populations object of the present study. The low genetic diversity found at Cap de Creus represents a further evidence of a recent bottleneck likely due to overharvesting (Costantini et al. 2011).

Based on the present data, we are unable to assess whether harvesting is the only cause of the density and size decline recorded in Cap de Creus population. However, our findings suggest that the legislation and the enforcement in this location are likely insufficient to sustainably manage the local overharvested red coral population. If actual harvesting rates (to which an unquantified effect of poaching must be added) will be allowed to continue, it may lead the population to local extinction, with related economic loss (Bramanti et al. 2011).

As several shallow red coral populations dwell in non-protected areas (Bramanti et al. 2011), a unique Mediterranean legislation banning red coral harvesting in the Mediterranean Sea above 50 m bathymetry (as proposed by GFCM in 2011) together with an increased local enforcement could supply the best tool to ensure the proper protection to this species. Our findings provide additional field evidence in support of the recent GFCM proposal.

Other additive factors have to be considered to understand why a potential local extinction of red coral shallow patches in Cap de Creus could be forecasted (Tsounis et al. 2007). First, mass mortality events strongly affecting octocorals in the Mediterranean Sea (Cerrano et al. 2000; Garrabou et al. 2001, 2009; Bramanti et al. 2005) could be an important factor of mortality, especially for populations living at the edge of the summer thermocline (Linares et al. 2008b; Cupido et al. 2009). Moreover, it has been shown that the synergistic effects of overharvesting and heat wave-induced mass mortalities could reduce the resilience of shallow red coral populations if these two stressors will increase in frequency (Santangelo et al. 2007; Garrabou et al. 2009). Second, once red coral patches have been depleted, competition for space could arise: The low recruitment of red coral, together with a reduction in density, may lead to successional stages in which *Leptopsammia pruvoti* could occupy the space previously occupied by red coral colonies (Cattaneo-Vietti et al. 1993; Giannini et al. 2003).

Population dynamic models based on demographic traits such as fecundity, fertility, growth and recruitment rates can be used to project the population structure overtime. These models are widely applied in marine, freshwater and terrestrial ecosystems (Tuljapurkar and Caswell 1997). Finally, our data underline the role of local factors in the population dynamics of *C. rubrum* and represent a sound basis in the development of demographic models for populations dynamics of this species.

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References

Arrigoni M, Manfredi P, Panigada S, Bramanti L, Santangelo G (2011) Life-history tables of the Mediterranean fin whale from stranding data. Mar Ecol 32(1):1–9

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol Monogr 61:225–244

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. Mar Ecol Prog Ser 162:301–306

Bak RPM, Meesters EH (1999) Population structure as a response of coral communities to global change. Am Zool 39:56–65

Barnes DJ, Lough JM (1993) On the nature and causes of density banding in massive coral skeletons. J Exp Mar Biol Ecol 167:91–108

Bavestrello G, Cattaneo-Vietti R, Cerrano C, Danovaro R, Fabiano M (1995) Annual sedimentation rates and role of resuspension processes along a vertical cliff (Ligurian sea, Italy). J Coastal Res 11(3):690–696

Beissinger SR, McCullough DR (2002) Population viability analysis. The University of Chicago Press, Chicago

Benayahu Y, Loya Y (1985) Settlement and recruitment of a soft coral: why is Xenia macrospiculata a successful colonizer? Bull Mar Sci 36(1):177–188

Beverton RJH, Hollt SJ (1957) On the dynamics of exploited fish populations. Fish Invest Minist Agric Fish Food GB Ser N 19:533

Bramanti L, Magagnini G, Santangelo G (2003) Settlement and recruitment: the first stages in the life cycle of two epibenthic suspension feeders (*Corallium rubrum* and *Anomia ephippium*). Ital J Zool 70:175–178

Bramanti L, Magagnini G, De Maio L, Santangelo G (2005) Recruitment, early survival and growth of the Mediterranean red coral *Corallium rubrum* (L. 1758), a 4-year study. J Exp Mar Biol Ecol 314:69–78

Bramanti L, Rossi S, Tsounis G, Gili JM, Santangelo G (2007) Recruitment and early survival of red coral on settlement plates: some clues for demography and restoration. Hydrobiologia 580:219–224

Bramanti L, Santangelo G, Iannelli M (2009) Mathematical modelling for conservation and management of gorgonians corals: young and olds, could they coexist? Ecol Model 20(21):2851–2856

Bramanti L, Iannelli M, Santangelo G (2010) The importance of demographic approach to conservation and management of Mediterranean red coral (*Corallium rubrum*). GFCM-General Fisheries Commission for the Mediterranean SAC-SCESS-SCMEE-SCSA. In: Proceedings on the transversal workshop on red coral

Bramanti L, Vielmini I, Rossi S, Stolfa S, Santangelo G (2011) Involvement of recreational scuba divers in emblematic species monitoring: the case of Mediterranean red coral (*Corallium rubrum*). J Nat Conserv 19(5):312–318

Bramanti L, Movilla J, Guron M, Calvo E, Gori A, Dominguez-Carriò C, Martinez-Quintana A, Pelejero C, Lopez-Sanz A, Ziveri P, Rossi S (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Glob Change Biol 19:1897–1908

Bruckner AW (2009) Rate and extent of decline in Corallium (pink and red coral) populations: existing data meet the requirements for a CITES Appendix II listing. Mar Ecol Prog Ser 397:319–332

Caley MJ, Carr MH, Hixon MA, Hugher TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477–500

Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates, Sunderland, MA

Cattaneo-Vietti R, Bavestrello G, Senes L (1993) La facies a *Corallium rubrum* lungo il Promontorio di Portofino (Mar Ligure). Biol Mar 1(Supp l):281–284

Cerrano C, Bavestrello G, Bianchi CN, Cattaneo-Vietti R et al (2000) A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. Ecol Lett 3:284–293

Cicogna F, Cattaneo-Vietti R (1993) Red coral in the Mediterranean Sea, art, history and science. Ministero Risorse Agricole, Alimentari e Forestali, 263 pp

Corriero G, Abbiati M, Santangelo G (1997) The sponge complex inhabiting a Mediterranean red coral population. PSZN Mar Ecol 18:147–155

Costantini F, Taviani M, Remia A, Pintus E, Shembri PJ, Abbiati M (2010) Live colonies of *Corallium rubrum* from the Mediterranean deep-sea: a preliminary genetic characterisation. Mar Ecol 31:261–269

Costantini F, Rossi S, Pintus E, Cerrano C, Gili JM, Abbiati M (2011) Low connectivity and declining genetic variability along depth gradients in *Corallium rubrum* populations. Coral Reefs 30(4):991–1003

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conversation. Ecology 68:1412–1423

Cupido R, Cocito S, Barsanti M, Sgorbini S, Peirano A, Santangelo G (2009) Unexpected long-term population dynamics in a canopy-forming gorgonian coral following mass mortality. Mar Ecol Prog Ser 394:195–200

Dobson A (1998) Conservation and biodiversity. Scientific American Library, New York

Durrieu de Madron X et al (2011) Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean. Prog Oceanogr 91:97–166

Ebert TA (1999) Plant and animal populations: methods in demography, vol 639. Academic Press, San Diego, CA

Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the caribbean reef coral *Montastraea annularis*. Ecol Monogr 77:3–18

Estrada M (1996) Primary production in the northwestern Mediterranean. Sci Mar 60(2):55–64

Fong P, Glynn PW (1998) A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the Eastern Pacific? Mar Biol 130:663–674

Fujiwara M, Caswell H (2001) Demography of the endangered North Atlantic right whale. Nature 414:537–541

Gallmetzer I, Haselmair A, Velimirov B (2010) Slow growth and early sexual maturity: bane and boon for the red coral *Corallium rubrum*. Estuar Coast Shelf Sci 90:1–10

Garrabou J, Harmelin JG (2002) A 20-year study on life-history traits of a harvested long-lived temperate coral in NW Mediterranean: insights into conservation and management needs. J Anim Ecol 71:966–978

Garrabou J, Perez T, Santoretto S, Harmelin JG (2001) Mass mortality event in red coral *Corallium rubrum* populations in the provence region (France, NW Mediterranean). Mar Ecol Prog Ser 217:263–272

Garrabou J, Coma R, Bensoussan N, Chevaldonné P et al (2009) Mass mortality in NW Mediterranean rocky benthic communities: effects of the 2003 heat wave. Glob Change Biol 15:1090–1110

GFCM (General Fisheries Commission for the Mediterranean Scientific Advisory Committee SAC) (2010) Report of the transversal workshop on red coral Alghero (Sardinia), Italy, 16–17 September 2010. SAC 13/2011/if. http://151.1.154.86/GfcmWebSite/SAC/2010/Red_Coral/Report.pdf

GFCM (General Fisheries Commission for the Mediterranean Scientific Advisory Committee SAC) (2011) Report of the transversal workshop on red coral Ajaccio (Corsica), France, 5–7 October 2011

Giannini F, Gili JM, Santangelo G (2003) Relationships between the spatial distribution of red coral *Corallium rubrum* and coexisting suspension feeders at Medes Islets Marine Protected Area (Spain). Ital J Zool 70:233–239

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine substrates. Trends Ecol Evol 13(8):316–321

Goffredo S, Chadwick-Furman NE (2003) Comparative demography of mushroom corals (Scleractinia: Fungiidae) at Eilat, northern Red Sea. Mar Biol 142:411–418

Gori A, Rossi S, Linares C, Berganzo E, Orejas C, Dale MRT, Gili JM (2011) Size and spatial structure in deep vs shallow populations of the Mediterranean gorgonian *Eunicella singularis* (Cap de Creus, northwestern Mediterranean Sea). Mar Biol 158:1721–1732

Grigg RW (1988) Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. Mar Ecol Prog Ser 45:121–126

Guizien K, Belharet M, Marsaleix P, Guarini JM (2012) Using larval dispersal simulations for marine protected area design: application to the Gulf of Lions (northwest Mediterranean). Limnol Oceanogr 57(4):1099–1112

Huges TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Am Nat 123(6):778–795

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

IFPC International Forum on Precious Coral (2009) Report of the first meeting in Hong Kong. International Association on Promoting of Precious Coral Study, 48 pp

IFPC International precious coral forum (2012) Report of the meeting in Kochi, Japan. Precious Coral Protection and Development Association, 137 pp

Iwasaki N, Fujita T, Bavestrello G, Cattaneo-Vietti R (2012) Morphometry and population structure of non-harvested and harvested populations of the Japanese red coral (*Paracorallium japonicum*) off Amami Island, southern Japan. Mar Freshw Res 263:468–474

Knowlton N, Jackson J (2008) Shifting baselines, local impacts, and global change on coral reefs. PLoS Biol 6(2):215–220

Knutson DW, Buddemeier RW, Smith SV (1972) Coral chronometers: seasonal growth bands in reef corals. Science 177:270–272

Ledoux J, Garrabou J, Bianchimani O et al (2010) Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. Mol Ecol 19:4204–4216

Linares C, Coma R, Garrabou J, Diaz D, Zabala M (2008a) Size distribution, density and disturbance of two Mediterranean gorgonians: *Paramuricea clavata* and *Eunicella singularis*. J Appl Ecol 45:688–699

Linares C, Coma R, Zabala M (2008b) Restoration of threatened red gorgonian populations: an experimental and modelling approach. Biol Conserv 141:427–437

Linares C, Bianchimani O, Torrents O, Marschal C, Drap P, Garrabou J (2010) Marine protected areas and the conservation of long-lived invertebrates: the Mediterranean red coral. Mar Ecol Prog Ser 402:69–79

Linares C, Garrabou J, Hereu B, Diaz D, Marschal C, Sala E, Zabala M (2012) Assessing the effectiveness of marine reserves on unsustainably harvested long-lived sessile invertebrates. Conserv Biol 26:88–96

Marschal C, Garrabou J, Harmelin JG, Pichon M (2004) A new method for measuring growth and age in the precious Mediterranean red coral *Corallium rubrum* (L.). Coral Reefs 23:423–432

Millstein J, O'Clair CE (2001) Comparison of age-length and growth-increment general growth models of the Schnute type in the Pacific blue mussel, *Mytilus trossulus* Gould. J Exp Mar Biol Ecol 262:155–176

Priori C, Mastascusa V, Erra F, Angiolillo M, Canese S, Santangelo G (2013) Demography of deep-dwelling red coral populations. Age and reproductive structure assessment. Estuar Coast Shelf Sci 116:1–7

Rasband WS (1997) ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA. http://imagej.nih.gov/ij/, 1997–2011

Rossi S, Gili JM (2005) Composition and temporal variation of the near-bottom seston in a Mediterranean coastal area. Estuar Coast Shelf Sci 65:385–395

Rossi S, Tsounis G, Orejas C, Padrón T, Gili JM, Bramanti L, Teixidó N, Gutt J (2008) Survey of deep-dwelling red coral (Corallium *rubrum*) populations at Cap de Creus (NW Mediterranean). Mar Biol 154(3):533–545

Rossi S, Bramanti L, Broglio E, Gili JM (2012) Population dynamics of short lived species can validate the models of long lived species: the hydrozoan case study. Mar Ecol Prog Ser 467:97–111

Santangelo G, Abbiati M (2001) Red coral: conservation and management of an overexploited Mediterranean species. Aquat Conserv Mar Freshw Ecosyst 11:253–259

Santangelo G, Bramanti L (2006) Ecology through time: an overview. Biol For 99:395–424

Santangelo G, Bramanti L (2010) Quantifying the decline in *Corallium rubrum* populations. Mar Ecol Prog Ser 418:295–297

Santangelo G, Carletti E, Maggi E, Bramanti L (2003) Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Mar Ecol Prog Ser 248:99–108

Santangelo G, Maggi E, Bramanti L, Bongiorni L (2004) Demography of the overexploited Mediterranean red coral (*Corallium rubrum* L. 1758). Sci Mar 67(3):199–204

Santangelo G, Bramanti L, Iannelli M (2007) Population dynamics and conservation biology of the over-exploited Mediterranean red coral. J Theor Biol 244:416–423

Santangelo G, Bramanti L, Rossi S, Tsounis G, Vielmini I, Lott C, Gili JM (2012) Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. J Exp Mar Biol Ecol 411:7–13

Torrents O, Garrabou J (2011) Fecundity of red coral *Corallium rubrum* (L.) populations inhabiting in contrasting environmental conditions in the NW Mediterranean. Mar Biol 158:1019–1028

Torrents O, Garrabou J, Marschal C, Harmelin JG (2005) Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean). Biol Conserv 121:391–397

Tsounis G, Rossi S, Gili JM, Arntz W (2006a) Population structure of an exploited benthic cnidarian: the case study of red coral (*Corallium rubrum* L.). Mar Biol 149:1059–1070

Tsounis G, Rossi S, Aranguren M, Gili JM, Arntz W (2006b) Effects of spatial variability and colony size on the reproductive output and gonadal development cycle of the Mediterranean red coral (*Corallium rubrum* L.). Mar Biol 148:513–527

Tsounis G, Rossi S, Laudien J, Bramanti L, Fernández N, Gili JM, Arntz W (2006c) Diet and seasonal prey capture rate in the Mediterranean red coral (*Corallium rubrum* L.). Mar Biol 149:313–325

Tsounis G, Rossi S, Gili JM, Arntz W (2007) Red coral fishery at the Costa Brava (NW Mediterranean): case study for an over harvested precious coral. Ecosystems 10:975–986

Tsounis G, Rossi S, Grigg RW, Santangelo G, Bramanti L, Gili JM (2010) The exploitation and conservation of precious corals. Oceanogr Mar Biol Annu Rev 48:161–212

Tsounis G, Martínez L, Viladrich N, Bramanti L, Martínez A, Gili JM, Rossi S (2012) Effects of human impact on the reproductive effort and allocation of energy reserves in the Mediterranean octocoral *Paramuricea clavata*. Mar Ecol Prog Ser 449:161–172

Tsounis G, Rossi S, Bramanti L, Santangelo G (2013) Management hurdles for sustainable harvesting of *Corallium rubrum*. Mar Policy 39:361–364

Tuljapurkar S, Caswell H (1997) Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, NY

Vielzeuf D, Garrabou J, Baronnet A, Grauby O, Marschal C (2008) Nano to macroscale biomineral architecture of red coral (*Corallium rubrum*). Am Mineral 93(11–12):1799–1815

Zibrowius H, Montero M, Grasshoff M (1984) La repartition du *Corallium rubrum* dans l'Atlantique. Thetis 11:163–170