



Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*

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ABSTRACT

This research seeks to quantify recruitment, early survival and early colony growth in different populations of the precious Mediterranean red coral. Although basic to our understanding of red coral ecology and population dynamics, these early life-history descriptors are still poorly understood. To fill this lack of knowledge, marble settlement tiles were placed at 35 ± 1 m depth within 3 populations of *Corallium rubrum* dwelling in the coralligenous habitat of different geographic areas of the north-western Mediterranean: Calafuria and Elba Island (Italy), and Medes Islands MPA (Spain), following a multifactorial ANOVA model and sampled photographically for four years (2003–2006). Overall, 517 red coral recruits settled on the tiles during the experiment, 189 of which (126 at Calafuria and 63 at Elba) were still surviving, in 2007, when the tiles were removed. The recruitment density at Medes was only one tenth of that at Calafuria and Elba (0.56 ± 0.21 vs. 6.06 ± 1.75 and 4.66 ± 1.01 recruits dm^{-2} , mean \pm SE). No colony survived after four years at Medes, where the lowest recruitment rate was also found. As the age of each new settled colony was known, it was possible to measure the early growth rates of individual colonies. The growth rates thus obtained were two to three times higher than that measured in older colonies and differed significantly between the geographic areas (the growth of colony basal diameter was 0.68 ± 0.02 and 0.59 ± 0.19 mm/year at Calafuria and Elba), while no significant difference was found between the actual colony growth and that previously measured in the former area. A test for secondary substrate selectivity, carried out in one area, showed that red coral preferentially settles on tubes of Serpulida than on other encrusting organisms. However, since recruitment density at Medes was lower despite the four-fold higher cover of Serpulida found there, other factors, intrinsic to the populations, such as different size–age structures or densities, leading to different larval output, may likely have determined red coral recruitment rates in the studied areas.

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1. Introduction

According to Margalef (1992) “the demography of single populations has to be integrated in the dynamics of multiple populations, and thus becomes a part of the study of succession and of the development of spatial organization”. Different populations may have different life histories and may be characterised by different demographic features, thus they must be considered as true conservation units. Demographic models, as well as conservation plans, have to be based on the peculiar features of different populations living in different geographic areas (Beissinger and McCullough, 2002; Santangelo and Bramanti, 2006).

Gorgonian corals are long-lived, slow-growing, habitat forming species which population features may differ greatly throughout the Mediterranean Sea (Cupido et al., 2009; Gili and Coma, 1998; Gori et al., 2011; Rossi and Gili, 2007). A prime example of such variability is the red coral, *Corallium rubrum*, a precious, long-lived temperate gorgonian inhabiting Mediterranean rocky bottoms and neighbouring Atlantic areas. Red coral is an internal brooder (*planulator*), which releases planulae during a limited time period in summer (Santangelo et al., 2003). The species tends to be genetically structured at a small spatial scale (Abbiati et al., 1993; Costantini et al., 2007, 2011; Ledoux et al., 2010). Most of the larger colonies of this species have been harvested at shallow depths, and the population structure has consequently shifted towards smaller sizes (Bramanti et al., 2009; Linares et al., 2010; Tsounis et al., 2010).

Previous studies on gorgonians have suggested that population growth is far more sensitive to changes in adult survival than in reproductive and recruitment rates (Gotelli, 1988, 1991; Lasker, 1991;

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Lasker et al., 1998; Linares et al., 2007). However, important factors in early gorgonian population dynamics, and hence in the persistence and re-colonisation of local populations, may also be larval supply and larval mortality, which affects 90–97% of larval output (e.g. Grigg, 1988; Lasker et al., 1998; Santangelo et al., 2007), as well as post-settlement processes, which may profoundly influence recruitment rates (Caley et al., 1996; Perkol-Finkel and Benayahu, 2008; Todd, 1998). This study focuses on the early life-history traits of red coral populations living within the sublittoral *coralligenous* habitat (Ballesteros, 2006; Boudouresque, 2004). Red coral develops crowded patches within the coralligenous resulting in the *C. rubrum* facies (Pérès and Picard, 1964).

Although our knowledge of the demographic features of shallow red coral populations has increased considerably in recent years, (e.g. Tsounis et al., 2010 and references therein), their early life-history traits are still largely obscure. This research seeks to quantify recruitment, early survival and growth of red coral in different *shallow* populations (those living between 10 and 50 m depth in the shallowest belt of the species' bathymetric distribution range). Even if such knowledge is basic to our understanding of red coral population dynamics, these early life-history descriptors are difficult to examine directly in the field in long-lived circa-littoral, benthic species. They can however be successfully estimated on long-lasting settlement plates (Garrabou and Harmelin, 2002; Gotelli, 1988; Lasker et al., 1998; Mundy and Babcock, 2000). In particular, studies on red coral colonisation on marble plates, whose carbonate composition is similar to that of the coralligenous substrate, may be particularly useful in obtaining recruitment and post-recruitment mortality estimates, which are otherwise quite difficult to gather (red coral recruits are only 0.6 mm in diameter; Bramanti et al., 2005). Moreover, as new settlers may be favoured or constrained by other encrusting organisms (Nandakumar, 2000), tiles should allow also detecting whether red coral settlement exhibits any selectivity towards certain substrates of biological origin.

A previous single-population study on red coral recruitment and early survival on seasoned marble tiles have highlighted the tendency of red coral to permanently colonise them (Bramanti et al., 2005). Moreover, no colony settled on tiles was affected by boring sponges, which spread over 50% of the colonies in the studied population, thereby increasing their mortality and reducing their economic value (Corriero et al., 1997). These findings suggest that red coral re-colonisation of depleted areas could be fostered by transferring and re-fixing colonised marble tiles, rather than individual colonies (Benedetti et al., 2011; Oren and Benayahu, 1997). Following up on these findings, tiles were inserted within different geographic red coral populations. Some preliminary results obtained during the first 2 years of this *in situ* experiment (*sensu* Underwood, 1997), revealed that settlement tiles were in fact colonised by red coral in the different areas (Bramanti et al., 2007), but it was unknown whether the method could be applied effectively over longer periods. Moreover, as the method previously set out by Marschal et al. (2004) to assess the age of red coral colonies failed during the first period of colony life (1–4 years), it was thought that direct measurement of growth over such a period could furnish important data on the early life-history of this precious gorgonian. At least, lasting settlement tiles for an extended time period enabled us to follow the life history of individual settlers of different age classes (*cohorts*) and thus to set out *cohort-based life-history tables* (Stearns, 1997) representing the trends of the newly settled colonies over time in different geographic areas, thus adding new, additional information to previous studies.

This paper presents the final findings of the full four-year study on recruitment, early mortality, average annual colony growth rate and settlement. The ultimate aim of this research was to broaden the geographic and time scale of the early life-history parameters of shallow-water red coral populations in order to provide a better understanding of their complex dynamics.

2. Materials and methods

2.1. Sampling

This study compared the early life-history traits of three red coral shallow-water populations living in the *coralligenous* habitats of different geographic areas: Calafuria (Livorno, Italy 43° 30' N, 10° 20' E); Cap Fonza (Elba Island, Italy, 42° 44' N, 10° 17' E) and Medes Islands (Gerona, Spain, 42° 03' N, 3° 13' E). While this last population dwells in a MPA, the first 2 are located in unprotected areas. The original substrates on which coralligenous communities settle are composed of sandstone at Calafuria, marl-limestone and sandstone at Elba and limestone at Medes.

At the end of June 2003, 54 white marble tiles (1 dm² wide) were fixed via a central Fischer screw (Bramanti et al., 2007) to the *coralligenous* substrate encrusting the vaults of crevices in which red coral colonies dwell at 35 ± 1 m depth, below the summer thermocline (Fig. 1). In all studied areas the tiles were put in place about 4 weeks before red coral larval release (late July; Santangelo et al., 2003; Tsounis et al., 2006), to allow biofilm to cover their surfaces (Bramanti et al., 2005).

The tiles were monitored yearly by photographic sampling over the period 2003–2006 using a Nikonos V underwater camera with 35-mm lens, TTL strobe and macro 1:3 extension tube. To easily identify and count recruits, macro-photographs were always taken at the end of October, a time at which red coral recruits can be easily identified (Bramanti et al., 2005). Four recruitment cycles over 3 areas (6 sites) have been thus analysed. Because red coral recruits were identified on photographs, this procedure provided a survival data series of 4 cohorts of newly settled colonies without having to remove the tiles.

In order to test for geographic variability in red coral recruitment, the tiles were placed following a multifactorial ANOVA design with two factors: 1) *area*, fixed with 3 levels: Calafuria, and Elba (Italy) and Medes MPA (Spain); 2) *site* (nested in area), with 2 levels (two sites randomly chosen in each area a few hundred metres apart from one other). Nine tiles (replicates) were placed in each site. The number of tiles was limited by technical aspects: it would be difficult to fix and monitor more by SCUBA diving at 35 m depth due to bottom-time constraints.

The tiles were removed at the beginning of September 2007 in order to analyse colony growth rates, biological concretions and the frequency of red coral settlers on the different encrusting organisms.

All ANOVAs were processed using the GMAV software programme. The trends for the first cohort of recruits (settled in 2003) over the

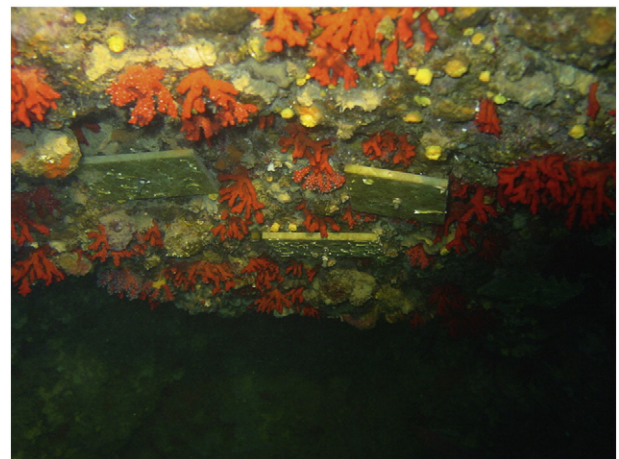


Fig. 1. Marble tiles fixed to the vault of a crevice colonised by red coral at the Medes Islands MPA.

following four years have been represented as a *Life table per cohort* (Stearns, 1997). The life table reports the survival of the first cohort and the mortality during the transition from one year to the next. Log-mortality rates ($k = \log n_t/n_{t+1}$) are also reported. The net recruitment (i.e. the number of settlers minus the number of dead colonies found on tiles each year at the end of October), and the final number of colonies that survived on tiles after four years have also been examined.

2.2. Early colony growth rate

The averaged basal diameter was measured on all colonies still settled on tiles upon their removal after 4 years, and the mean annual early colony growth rate then calculated. As no colony survived at Medes, colony growth could not be measured there.

The age of all salvaged colonies was determined on the basis of the first time they were identified as recruits and mapped on photos, and the average annual growth of each colony was calculated by simply dividing its basal diameter of by its age. Each colony contributed a number of values equal to its age to the calculation of the overall average annual growth rate. For example, a four-year-old colony contributed 4 average annual growth values to the calculation; a three year-old colony 3 values, and so on. This procedure was followed in order to enable calculation of the average early growth rate over a larger number of values. It should be noted that such procedure is made possible by the nearly constant growth rates found during the first 4 years of colony life (Bramanti et al., 2005). In this way, 186 annual growth rate values were obtained from the 126 colonies salvaged on tiles at Calafuria, and 83 from the 63 colonies salvaged at Elba. The sum of the average annual colony growth rates was then divided by the total number of values obtained to calculate the overall average annual growth rates of the two populations, which could then be compared. The early annual growth rates (weighted averages) thus obtained were also compared with that calculated on the 403 values previously recorded on 163 colonies at Calafuria over the period 1998–2001 (data in Bramanti et al., 2005). The *t*-test was applied to analyse the differences in the 2003–2007 colony growth rates between Elba and Calafuria, and between the resulting growth rates for the latter area from 2003 to 2007 and 1998–2001.

2.3. Colonisation of tiles and red coral settlement

Some general features of the four-year-long colonisation process by various organisms encrusting the tiles were also examined. The encrusting organisms have been identified and classified according to broad taxonomic categories by observing them on macro-photographs, and their percentage cover areas measured on digitised photographs using Adobe Photoshop CS5.

After four years, the tiles were salvaged and the dry weight of encrusting organisms settled on them examined. Encrusted tiles were oven-dried overnight at 90 °C and the biological concretions accumulated on them were completely scraped and weighed. Differences in the final overall percentage cover and dry weight between different geographic areas and sites were examined using PERMANOVA (Anderson, 2005). A pairwise test was also conducted (because of the unbalanced number of replicates) using the PRIMER software.

The selectivity of red coral settlement on the three most common taxonomic categories of encrusting organisms was also examined. To this end, the frequency of red coral settlers on the most common organisms covering the tiles salvaged at Calafuria (the population exhibiting the highest coral settlement density) was examined. These tiles were carefully examined just after collection via dissection microscope (40–80×) in order to identify living red coral settlers that, made up of 1–2 polyps, measured only 0.2 ± 1 mm in diameter, as well as the taxonomic category of the organisms on which they settled. Given these logistic constrains, this analysis was performed

only at Calafuria. Divergence from randomness (i.e. frequency of red coral settlers on organisms of a specific taxonomic category in proportion to their percentage cover) was checked using a chi-square test.

3. Results

3.1. Red coral recruitment and early mortality

Overall, 517 recruits settled on tiles during the 4 years of the experiment. All three populations studied recruited each year, though recruitment showed high variability over time (Fig. 2) and between both geographic areas and sites; sites were colonised by recruits in 21 out of 24 occasions and the average density was 3.88 ± 0.68 recruits dm^{-2} (mean \pm SE), varying between 23 and 0 recruits per 100 cm^{-2} . The recruitment density found was ten fold lower at Medes Islands than at Calafuria and Elba (0.56 ± 0.21 vs. 6.06 ± 1.75 and 4.66 ± 1.01 recruits dm^{-2} , mean \pm SE), a finding consistent with the lower percentage of tiles colonised by red coral in this area (50% at Medes, vs. 80% and 93% at Calafuria and at Elba Island). In 2006 an exceptionally high recruitment density, 3 times higher than the average, and an increased variance (due to 3 tiles only) were found at both Calafuria and Elba Island. These findings led to a significant variance heterogeneity (Cochran Test), which persisted despite all attempts at data transformation, thus ruling out including the 2006 data in an ANOVA (Underwood, 1997). For this reason and due to the limited number of replicates available, different Nested ANOVAs were carried out for each single year (2003, 2004, 2005; Table 1). The percentage of the total variance due to the factor *site*, was significantly higher in the first year and then decreased over time ($2003 > 2004 > 2005$). Contrariwise, the percentage of variance due to the factor *geographic area* increased over time and became significant over the last two years, thus exhibiting an opposite trend ($2005 > 2004 > 2003$; Table 1). No significant correlation was found between recruitment density and the percentage of tile area covered by the encrusting organisms ($r = 0.02$, $n = 128$, $p > 0.1$).

In order to describe the life history of newly settled colonies, a “life table per cohort” (Stearns, 1997) was compiled for the oldest (2003) cohort in each geographic area (Table 2). The four-year survival (L_2) of this cohort was 0.37 (i.e. 63% of the original 2003 cohort died in 2006) at Calafuria and 0 (mortality = 100%) at Elba and Medes. The *age specific mortality rate* (m_x), reported also on a natural-log scale (k_x), was highest for the transition from the first year (the year of settlement) to the second at Medes, and lower at Elba and Calafuria ($m_0 = 0.86$, 0.29 and 0.49 and $k_0 = 1.9$, 0.34 and 0.66, respectively). Between the second and the third years, no mortality occurred at Calafuria, while high mortality occurred at Elba ($m_1 = 0.75$

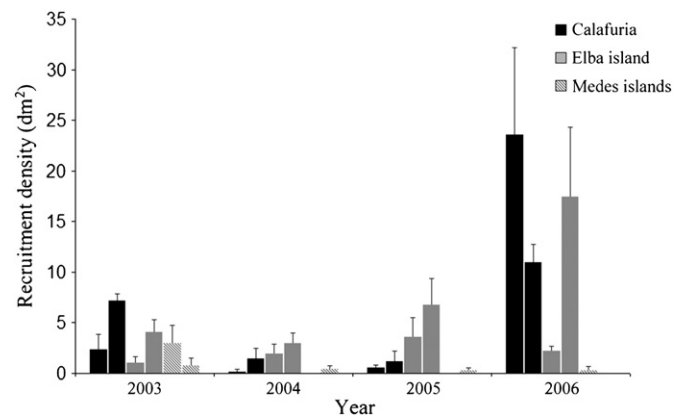


Fig. 2. Recruitment density (mean \pm SE) in different sites over the period 2003–2006.

Table 1

Recruitment variability in consequent years examined by nested ANOVAs. The variance % due to factor *site* decreases while that due to factor *area* increases with time, indicating an increased variability at a larger spatial scale (between different geographic areas).

Source of variability	SS	DF	MS	F	P	F versus	Variance %	
Area	2003	22.75	2	11.37	0.42	0.69	Si (Ar)	14.91
Site (Area)		82.12	3	27.37	4.49	0.016	Res	39.65
Residual		109.75	18	6.09				45.45
Tot		214.62	23					
Area	2004	37.75	2	18.87	11.9	0.037	Si (Ar)	27.40
Site (Area)		4.75	3	1.58	0.42	0.739	Res	9.16
Residual		67.5	18	3.75				63.44
Tot		110	23					
Area	2005	10.20	2	5.10	8.65	0.06	Si (Ar)	61.10
Site (Area)		1.77	3	0.59	2.09	0.14	Res	8.35
Residual		5.07	18	0.2				30.55
Tot		17.04	23					

and $k_1 = 0.60$) and no colony survived at Medes ($m_1 = 1$; $k_1 = \infty$). The yearly net recruitment rate (recruitment minus mortality) during the entire study period (2003–2006) shows a clear-cut positive trend at Calafuria, a slightly positive one at Elba and a negative one at Medes Island (Fig. 3).

3.2. Early colony growth rate

In order to determine the average early growth rate of red coral in the different geographic areas, the age of all the colonies surviving on the tiles salvaged in September 2007 was determined based on the year of their settlement, and their mean basal diameter measured. This was possible only for Calafuria and Elba, as none of the colonies that settled on the Medes tiles survived until 2007.

Overall, 189 colonies (126 at Calafuria and 63 at Elba) were found and, as their age was known, they were divided into different cohorts (2003, 2004, 2005, 2006). The distribution of newly settled colonies in the different age classes is reported in Table 3. The average annual colony growth rate during the first years of life was 0.68 ± 0.02 mm/year (mean \pm SE) at Calafuria and 0.59 ± 0.02 mm/year at Elba. These growth rates were also compared with the annual growth rate measurements recorded on 163 colonies at Calafuria over the period 1998–2001 (0.67 ± 0.01 mm/year; data in Bramanti et al., 2005). According to the *T* test, a significant difference in early growth rates exists between Calafuria and Elba ($p < 0.01$), while no significant difference was found between the current colony growth rate found at Calafuria and that previously measured in the same area in 2001. These findings suggest that early colony growth rate is nearly

Table 2

Life table of the first (2003) cohorts in different geographic areas. a_x = new settled colonies survival (%) in different years. l_x = first cohort survival; s_x and m_x = colonies survived or died in the passage from one year to the following; k_x log mortality.

	Age (x)	a_x	l_x	s_x	m_x	k_x
Calafuria	0	41	1.00	0.51	0.49	0.66
	1	21	0.51	1.00	0.00	0.00
	2	21	0.51	0.71	0.29	0.33
	3	15	0.37			
Elba Island	0	34	1.00	0.71	0.29	0.34
	1	24	0.71	0.25	0.75	1.38
	2	6	0.18	0.00	1.00	
	3	0	0.00			
Medes Islands	0	14	1.00	0.14	0.86	1.9
	1	2	0.14	0.00	1.00	
	2	0	0.00			
	3	0	0.00			

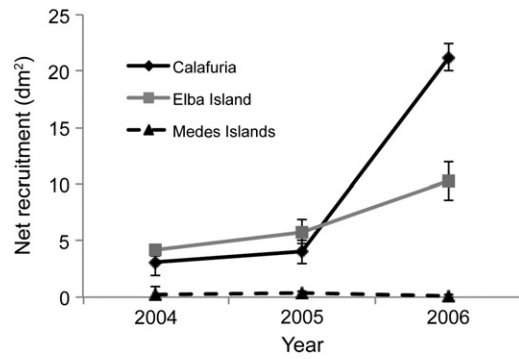


Fig. 3. Net recruitment rate (recruitment minus mortality; mean \pm SE).

constant over time throughout a single geographic area, but different in different areas.

3.3. Biological cover and red coral settlement

During the 4 years of submersion, the tiles have been covered by a highly diverse fouling community made up of Cyanobacteria, Rhodophyta, Porifera, Cnidaria, (Octocorallia and Hexacorallia), Annelida (Serpulida), Mollusca (Bivalvia and Gastropoda) and Bryozoa. Cirripedia and Tunicata were found on only a few tiles at Medes. Rhodophyta, showing 12 and 14 cover % at Calafuria and Elba, were not found on the tiles fixed at Medes.

The progress of the colonisation process through the four years of the experiment is illustrated in Fig. 4. Overall, after four years the colonised area attained a coverage of 80.28%, 66.33%, and 70.55% of the tile surfaces at Calafuria, Elba and Medes, respectively (Fig. 4d). According to PERMANOVA, geographic areas differed significantly ($p < 0.01$), the overall relative cover being significantly higher at Calafuria and similarly lower at Elba and Medes (Pairwise test NS). No significant difference was found between sites in the same area, suggesting some homogeneity of the colonisation process in each area.

Bryozoa, dominant in all geographic areas, were always the taxon showing the maximum relative cover. After four years, these organisms covered 60.13%, 42.8% and 42.17% of the tile surfaces at Calafuria, Elba and Medes, respectively. Serpulida, found on all tiles, represented respectively 7.1%, 3.5%, and 25.2% of the overall cover at Calafuria, Elba and Medes (Fig. 4a, b, c, d).

The dry weight of bio-concretions (Fig. 5) was significantly higher at Medes Islands than in the other two areas (9.9 g/dm² and 4.7 g/dm² and 4.6 g/dm² respectively at Medes, Calafuria and Elba; PERMANOVA $p = 0.01$). No significant difference was found between the latter two areas (Pairwise test NS).

The frequency of red coral settlement on the most common taxonomic categories of encrusting organisms, Serpulida, Bryozoa and Rhodophyta, was also examined on the tiles salvaged from Calafuria, where, after 4 years of submersion, they represent 98.4% of the total cover. Overall, 77 red coral settlers were found on the encrusting

Table 3

Number of colonies of the different cohorts (Age) found on tiles after 4 years and annual colony growth rate at Calafuria and Elba Island in 2003–2006 and at Calafuria in 1998–2001.

	Age					Annual growth	
	1	2	3	4	Tot	Mean	St. dev.
Calafuria 03–06	98	9	6	13	126	0.68	0.26
Elba 03–06	45	16	2	0	63	0.59	0.19
Calafuria 98–01	50	33	33	47	163	0.67	0.14

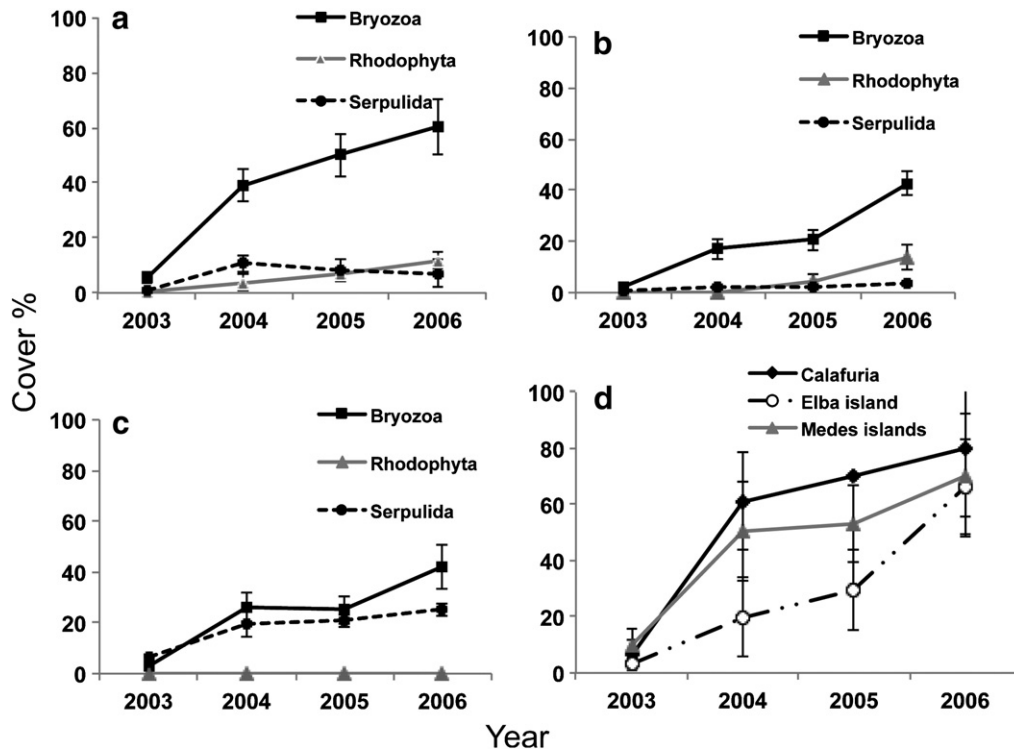


Fig. 4. Colonisation on tiles. Cover % of the most common taxonomic categories in the three geographic areas examined (a, b, c) and overall cover % (d) over the period 2003–2006.

organisms of the above-mentioned taxa (Fig. 4), 42 (54%) of which had settled on the tubes of Serpulida, 27 (36%) on Bryozoa and 8 (10%) on Rhodophyta. We tested whether the settlement frequency on the main encrusting taxa was proportional or not to the relative percentage cover area (18%, 68% and 14% respectively for Serpulida, Bryozoa and Rhodophyta). In the case of the last, settlement can be considered non-random (i.e. selective). Our results showed a significant divergence from randomness in the frequency of red coral settlement on Serpulida ($\chi^2 = 17.3$; $n = 9$; $p < 0.03$) and Bryozoa ($\chi^2 = 18.96$; $n = 9$; $p < 0.03$), while no significant divergence from randomness was found for Rhodophyta. As shown in Fig. 6, the observed frequency of *C. rubrum* recruits is significantly higher than expected for Serpulida, and significantly lower for Bryozoa. These findings suggest selectivity of red coral larval settlement that is positive towards Serpulida tubes and negative towards Bryozoa. No selectivity was found for Rhodophyta.

4. Discussion

The research described herein has managed to shed light on some of the main demographic early life-history traits in three different

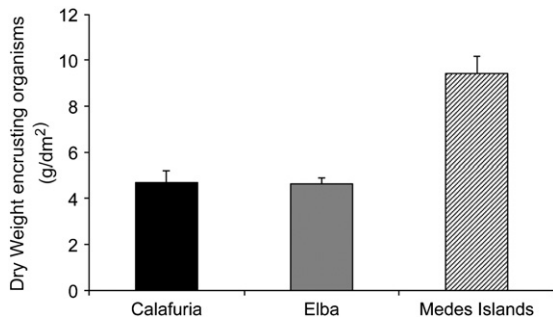


Fig. 5. Dry weight (mean ± SE) of biological concretions found on tiles in the different geographic areas.

geographic populations of the precious Mediterranean red coral by means of suitable settlement plates. As many *C. rubrum* populations have been overexploited, studies on the capacity of this species to permanently colonise settlement plates of a natural substrate (marble) could be particularly meaningful for both demographic and restoration studies. Moreover, the age of young (1–4-year-old) red coral colonies cannot be determined even by the latest, most dependable methods, which rely on thin-section annual growth ring staining (Marschal et al., 2004; Torrents, 2007). Therefore, direct measures on early colony growth rate, carried out on different geographic populations, could fill an important gap in our knowledge.

The collection of 189 colonies of known age on the salvaged tiles from two geographic areas enabled us to assess the average annual colony growth rate over the first years of their life. The resulting growth of colony basal diameter (0.68 and 0.59 mm year⁻¹) was two to three times higher than those measured in adult colonies in different areas and habitats (ranging from 0.35 to 0.15 mm year⁻¹;

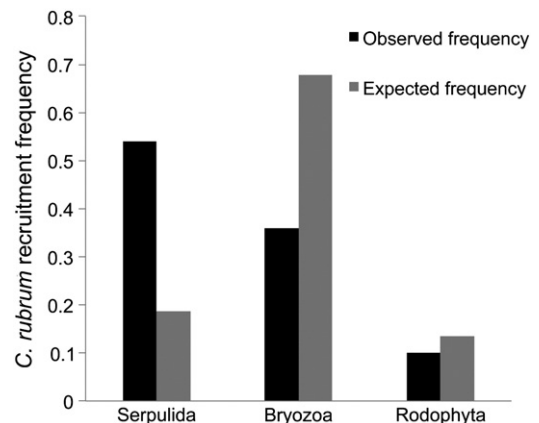


Fig. 6. Frequency of settlers on the most common encrusting organisms found on marble tiles.

Gallmetzer et al., 2010; Garrabou and Harmelin, 2002; Marschal et al., 2004; Torrents, 2007), thereby evidencing a higher growth during the first years of colony life. These findings fill an important gap in our knowledge of the early growth of the Mediterranean red coral. They moreover suggest that early colony growth rates are different in geographically distinct populations and constant over time in the same area. Such variability may be due to differences in the availability of food; it has been shown that seston quantity and quality may be very different even at micro and meso spatial scales because of different environmental features, which would have a direct impact on the growth rate of suspension feeders (Gili and Coma, 1998; Rossi and Gili, 2007). On the other hand, such differences could be limited to early colony life, as some authors have suggested a more constant growth rate for older colonies (Gallmetzer et al., 2010; Linares et al., 2010).

All three populations recruited regularly each year, showing an average recruitment density ($3.88 \text{ recruits dm}^{-2} \text{ year}^{-1}$) unusually high among Gorgonian corals (Cupido et al., 2009; Gotelli, 1988; Grigg, 1988; Lasker et al., 1998; Linares et al., 2008), however such values varied considerably. For example, in 2006 recruitment at Calafuria and Elba was three times higher (and also exhibited greater variability) than in the previous years. This finding was due to a few tiles, which showed an anomaly high recruitment only that year. Irregular annual oscillations and stochastic peaks are frequently found in recruitment of benthic invertebrates (e.g. Caley et al., 1996; Gotelli, 1988; Todd, 1998). One of the few studies on red coral recruitment, carried out on limestone settlement plates installed in a 25 m long horizontal cave (Garrabou and Harmelin, 2002) showed a high variable, sporadic recruitment which was only a one twentieth of that found in this study ($0.18 \text{ vs. } 3.88 \text{ recruits dm}^{-2}$). Moreover, the mortality of new settled colonies was remarkably lower (14%) than our present (63–100%) and previous findings (66–69%); (Bramanti et al., 2005). Local hydrodynamic features and irregular reproductive pulses may be key factors in understanding recruitment variations in this sheltered environment.

Overall, despite the great variability in recruitment rates we found, some general trends can be discerned among the three geographic areas. A higher percentage of colonised tiles and ten-fold higher recruit densities were found at Calafuria and Elba than at Medes Islands, where the highest mortality was also encountered. Synergy between these two factors evidently led to a negative net recruitment rate and eventual extinction of all the cohorts previously settled on the tiles in the Spanish MPA. This last finding suggests lower population growth rates and recovery capacities for this area. A clear-cut positive net recruitment rate was found only at Calafuria, confirming our previous findings in this area (Bramanti et al., 2005). These last findings indicate that fixing and transplanting marble tiles with recently settled red coral into new areas (Benedetti et al., 2011; Bramanti et al., 2007; Oren and Benayahu, 1997; Perkol-Finkel and Benayahu, 2008) could be a suitable tool to foster population recovery mainly at Calafuria and in populations with similarly high recruitment and survival rates.

Recruitment variability between neighbouring sites in the same geographic area decreased over the period 2003–2005, while the variability between areas increased, thereby exhibiting opposite trends. As the tile surface covered by encrusting organisms was comparable in the two sites of the same area, it is clear that the fouling colonisation occurred in a similar manner in neighbouring sites, which would likely affect red coral recruitment in the same manner, thus reducing its local variability with time.

According to Boudouresque (2004) and Ballesteros (2006), the species assemblages of coralligenous habitats differ greatly across the Mediterranean. While some trends common to the different areas examined were found (e.g. the dominance of Bryozoa in all sites and areas), the proportions of the various colonising organisms differ considerably. Moreover some taxa (Cirripedia and Tunicata) were

found only at Medes. On the contrary Rhodophyta were not found on the tiles fixed there despite of being very common in that area (Garrabou et al., 2002), and in the coralligenous assemblage in general (Ballesteros, 2006). The lack of this highly representative taxon in this location underlines some limits in the correspondence between the colonisation process occurring on tiles and on the natural primary substrate. Although marble and coralligenous are chemically similar they do exhibit some important differences in surface texture and structure leading to different epibiosys (Vermeij, 2005).

Although Serpulida seems to be a more suitable substrate for red coral settlement than other common encrusting organisms, the higher cover of this taxon at Medes did not result in higher red coral recruitment in this area. The ten-fold lower recruitment, as well as the likely high early mortality found at Medes MPA, could depend on other local factors, such as interspecific competition (Giannini et al., 2003) or predation (Rius and Zabala, 2008). We suggest that the high density of carnivorous and herbivorous fishes in this small protected area (Sala, 1997), may have a direct impact on coral settlers. The low recruitment found at Medes MPA is also consistent with previous findings in this area of a lower colony density (about 1/2) and a lower reproductive output (about 1/3) compared to that reported for the Calafuria population (data in Tsounis et al., 2006; Santangelo et al., 2007). The recruitment density found at Calafuria, consistent with previous findings (Bramanti et al., 2005), confirms that a higher recruitment usually occurs in this area.

Our findings suggest different dynamics at work in the different populations examined. Furthermore, the negative net recruitment rate found at the Medes Islands MPA (whatever the reasons) could severely limit population recovery in the event that mass mortalities (like those that affected shallow-water red coral populations in some NW Mediterranean areas only a few years ago) increase in frequency (Santangelo et al., 2007). On the other hand, the crowded, highly reproductive Calafuria population, in which some recruitment density-dependence was found (Santangelo and Bramanti, 2010), would more likely recover after anomalous mortality or negative net recruitment events. Because of the low dispersal capacity of red coral planulae (Costantini et al., 2007, 2011; Ledoux et al., 2010), the recovery of extinct patches may be a very long-term process. Future red coral management programmes must carefully take such indications into account to preserve shallow-water *C. rubrum* local populations.

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References

- Abbiati, M., Santangelo, G., Novelli, S., 1993. Genetic variation within and between two populations of the coral *Corallium rubrum*. Mar. Ecol. Prog. Ser. 95, 245–250.
- Anderson, M.J., 2005. Permanova: A Fortran Computer Program for Permutational Multivariate Analysis of Variance. Dep. Statistics-University of Auckland, Auckland.
- Ballesteros, E., 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanogr. Mar. Biol. Annu. Rev. 44, 123–195.
- Beissinger, S.R., McCullough, D.R., 2002. Population viability analysis. The University of Chicago Press, Chicago.
- Benedetti, A., Bramanti, L., Tsounis, G., Faimali, M., Pavanello, G., Rossi, S., Gili, J.M., Santangelo, G., 2011. Applying cathodically polarized substrata to the restoration of a high value coral. Biofouling 27, 799–809.
- Boudouresque, C.F., 2004. Marine biodiversity and the status of species, populations and communities. Sci. Rep Port-Cross National Park 20, 97–146.
- Bramanti, L., Magagnoli, G., De Maio, L., Santangelo, G., 2005. Recruitment, early survival and growth of the Mediterranean Red Coral *Corallium rubrum* 1758, a four-year study. J. Exp. Mar. Biol. Ecol. 314, 69–78.

- Bramanti, L., Rossi, S., Tsounis, G., Gili, J.M., Santangelo, G., 2007. Settlement and early survival of red coral on settlement plates: some clues for demography and restoration. *Hydrobiologia* 580, 219–224.
- Bramanti, L., Iannelli, M., Santangelo, G., 2009. Mathematical modelling for conservation and management of gorgonian corals: young and olds, could they coexist? *Ecol. Model.* 220, 2851–2856.
- Caley, M.J., Carr, M.H., Hixon, M.A., Huges, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27, 477–500.
- Corriero, G., Abbiati, M., Santangelo, G., 1997. The sponge complex inhabiting a Mediterranean red coral population. *PSZN Mar. Ecol.* 18, 147–155.
- Costantini, F., Fauvelot, C., Abbiati, M., 2007. Fine-scale genetic structuring in *Corallium rubrum*: evidence of inbreeding and limited effects of larval dispersal. *Mar. Ecol. Prog. Ser.* 340, 100–119.
- Costantini, F., Rossi, S., Pintus, E., Cerrano, C., Gili, J.M., Abbiati, M., 2011. Low connectivity and declining genetic variability along depth gradients in *Corallium rubrum* populations. *Coral reefs* 30, 911–1003.
- Cupido, R., Cocito, S., Barsanti, M., Sgorbini, S., Peirano, A., Santangelo, G., 2009. Unexpected long-term population dynamics in a canopy-forming gorgonian following mass mortality. *Mar. Ecol. Prog. Ser.* 394, 195–200.
- Gallmetzer, I., Haselmair, A., Velimirov, B., 2010. Slow growth and early sexual maturity: bane and boon for the red coral *Corallium rubrum*. *Estuarine Coastal Shelf Sci.* 90, 1–10.
- Garrabou, J., Harmelin, J.G., 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. An. Ecol.* 71, 966–978.
- Garrabou, J., Ballesteros, E., Zabala, M., 2002. Structure and dynamics of north-western Mediterranean benthic communities along a depth gradient. *Estuarine Coastal Shelf Sci.* 55, 493–508.
- Giannini, F., Gili, J.M., 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, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends Ecol. Evol.* 13, 316–321.
- Gori, A., Rossi, S., Berganzo, E., Pretus, J.L., Dale, M.R.T., Gili, J.M., 2011. Spatial distribution patterns of the gorgonians *Eunicella singularis*, *Paramuricea clavata* and *Leptogorgia sarmentosa* (Cape of Creus, Northwestern Mediterranean Sea). *Mar. Biol.* 158, 143–158.
- Gotelli, N.J., 1988. Determinants of recruitment, juvenile growth and spatial distribution of a shallow water gorgonian. *Ecology* 69, 157–166.
- Gotelli, N.J., 1991. Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology* 72, 457–467.
- Grigg, R.W., 1988. Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. *Mar. Ecol. Prog. Ser.* 48, 121–126.
- Lasker, H.R., 1991. Population growth of a gorgonian coral: equilibrium and non-equilibrium sensitivity to changes in life history variables. *Oecologia* 86, 503–509.
- Lasker, H.R., Kim, K., Cofforth, M.A., 1998. Production, settlement and survival of plexaurid gorgonian recruits. *Mar. Ecol. Prog. Ser.* 162, 111–123.
- Ledoux, J.B., Garrabou, J., Bianchimani, O., Drap, P., Féral, J.P., Aurelle, D., 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., Doak, D., Coma, R., Diaz, D., Zabala, M., 2007. Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology* 88, 918–928.
- Linares, C., Coma, R., Mariani, S., Diaz, D., Hereu, B., Zabala, M., 2008. Early life history of the Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics. *Invertebr. Biol.* 127, 1–11.
- 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.
- Margalef, R., 1992. Marine eutrophication and population dynamics. In: Colonbo, G., et al. (Ed.), *Proceedings of 25 EMBS*. Olsen & Olsen Fredenborg, Dk.
- Marschal, C., Garrabou, J., Harmelin, J.G., 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.
- Mundy, C., Babcock, R., 2000. Are vertical distribution patterns of Scleractinian corals maintained by pre or post-settlement processes? A case study of three contrasting species. *Mar. Ecol. Prog. Ser.* 198, 109–119.
- Nandakumar, K., 2000. Overgrowth competition in encrusting bryozoans assemblages of the intertidal and infralittoral zones of Alaska. *Mar. Biol.* 136, 813–822.
- Oren, U., Benayahu, Y., 1997. Transplantation of juveniles corals: a new approach for enhancing colonization of artificial reefs. *Mar. Biol.* 127, 499–505.
- Pérès, J., Picard, J.M., 1964. *Nouveau manuel de bionomie benthique de la Mer Méditerranée*. Recl. Trav. Staz. Mar. D'Endoume 47, 5–137.
- Perkol-Finkel, S., Benayahu, Y., 2008. The role of differential survival patterns in shaping coral communities on neighbouring artificial and natural reefs. *J. Exp. Mar. Biol. Ecol.* 369, 1–7.
- Rius, M., Zabala, M., 2008. Are marine protected areas useful for the recovery of the Mediterranean mussel populations? *Aquat. Cons. Mar. Freshw. Ecosyst.* 18, 527–540.
- Rossi, S., Gili, J.M., 2007. Short-time-scale variability of near bottom seston composition during spring in a warm temperate sea. *Hydrobiologia* 557, 373–388.
- Sala, E., 1997. The role of fishes in the organization of Mediterranean sublittoral communities. II: Epifaunal communities. *J. Exp. Mar. Biol. Ecol.* 212, 45–60.
- Santangelo, G., Bramanti, L., 2006. Ecology through time: an overview. *Biol. Forum* 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., Bramanti, L., Iannelli, M., 2007. Population dynamics and conservation biology of the over-exploited Mediterranean Red coral. *J. Theor. Biol.* 244, 416–423.
- Stearns, S.C., 1997. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Todd, C.D., 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia* 375–376, 1–21.
- Torrents, O., 2007. *Biologie des populations du corail rouge de Méditerranée*. Ph.D. thesis, Université de la Méditerranée, Marseille, p 221.
- Tsounis, G., Rossi, S., Aranguren, M., Gili, J.M., Arntz, W., 2006. 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., Grigg, R., Santangelo, G., Bramanti, L., Gili, J.M., 2010. The exploitation and conservation of precious corals. *Oceanogr. Mar. Biol. Annu. Rev.* 48, 161–212.
- Underwood, J.A., 1997. *Experiments in Ecology: Their Logical Interpretation and Design*. Cambridge University Press, Cambridge.
- Vermeij, M.J.A., 2005. Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. *Mar. Ecol. Prog. Ser.* 295, 123–133.