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ABSTRACT: This study provides the first description of the reproductive features of a red coral *Corallium rubrum* population. This circum-Mediterranean octocoral has been over-harvested and commercial stocks are depleted. The population we studied was gonochoric at both the colony and polyp levels, and its sex ratio was significantly biased toward females. The minimum age at first reproduction was 2 yr. The percentage of fertile colonies increased with age, reaching 100% fertility for those over 5 yr. Due to the low frequency of older colonies, $^2/_3$ of the population was unreproductive. The seasonal cycle of oocyte maturation resulted in a rapid increase in diameter after March, corresponding to a significant reduction in fecundity and fertility. Larval release occurred between late July and August, and settlement ended by mid-September. No significant difference was found in fecundity or fertility between colonies living at different depths (25 and 35 m). Both reproductive parameters depended on polyp position on the colony branches, being significantly lower in the tips of 1st order and proximal parts of 2nd order branches. Due to these opposing trends, no significant overall difference was found between branches of different orders. Female polyp fecundity (0.87 gonads per polyp) was considerably lower than fecundity measured in other octocorals, and the larval production depends on the size/age of the colony: while reproductive colonies in Class 2 (diameter 1.82 mm) produce on average 24 planulae, the larger, older colonies in Class 6 (diameter > 4.6 mm) produce 157 planulae on average. This clearly indicates large differences in larval production between populations with different size and/or age structures. A better understanding of red coral reproduction will help to match harvesting levels to recovery rates in overexploited populations.

KEY WORDS: Red coral · Octocorallia · Sexual structure · Reproduction · Mediterranean Sea

INTRODUCTION

Knowledge of reproductive biology, i.e. fecundity, sex ratio and timing of reproduction, is fundamental to our understanding of the population dynamics of marine organisms. The production of gametes is a key component of fitness (Beiring & Lasker 2000), and the age of sexual maturity and the sex ratio are crucial data for studying the demography of marine invertebrates (Harvell & Grosberg 1988). Sexual maturity is determined by a balance amongst growth, time-dependent risk of mortality and short generation-time advantages (Harvell & Grosberg 1988). Variations of age at first reproduction and the sex ratio affect population-intrinsic growth rates (Dobson 1998, Fujiwara & Caswell 2001).

Fecundity and reproductive rates of modular organisms are largely determined by the number of reproductive modules. In particular, in marine anthozoans the production of gametes is a function of both module (polyp) fertility and the number of fertile polyps per colony (Sakai 1998). Studies providing estimates of egg or larval production, by looking at clonal Anthozoa as a whole, indicate a large variability between colonies of different sizes (Sakai 1998, Beiring & Lasker 2000).

This paper focuses on the reproductive features of a red coral *Corallium rubrum* (L. 1758) population. This modular anthozoan (Octocorallia, Gorgonacea) is en-

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demic to the Mediterranean and neighboring Atlantic rocky shores, where it occurs between 20 and 200 m depth (Zibrowius et al. 1984). Red coral is one of the dominant components of Mediterranean 'coralligenous' species assemblages (Sarà 1973). These complex communities are composed of a wide variety of suspension feeders, exhibiting high species richness and functional diversity (Gili & Coma 1998).

Corallium rubrum is the red coral par excellence. This precious species has fascinated mankind since ancient times. Red coral pierced beads have been found in Mesolithic and Neolithic settlements and burial grounds at Concise (Switzerland), Württemberg (Germany), and Bolognano (Italy) (Ascione 1993). Its use as a jewel and talisman has remained constant through the centuries (Roth 2002). More recently, depletion of commercial stocks, which have long been heavily exploited (Santangelo et al. 1993a, Santangelo & Abbiati 2001), has led to renewed interest in this species (Cicogna & Cattaneo-Vietti 1993, Cicogna et al. 1999).

Several papers have addressed the reproductive ecology of octocorals (e.g. Grigg 1977, Sebens 1983, Brazeau & Lasker 1989, 1990, Babcock 1990, West et al. 1993, Coma et al. 1995a,b, Beiring & Lasker 2000), but reports on the reproductive ecology of red coral are still lacking. To date, except for the historical work of Lacaze-Duthier (1864), the only reports on red coral reproduction are those by Vighi (1972) and Weinberg (1979). According to these authors, red coral is iteroparous, undergoes internal fertilization and broods larvae internally ('planulator'). The embryonic period lasts about 30 d, and planulae, which are released during summer, survive only a few days and do not travel very far from the parent colonies. Colonies do not fuse together (in nature), and each adult colony therefore is likely to have originated from a single planula (Weinberg 1979, Stiller & Rivoire 1984).

Although fragmentation, which is common in modular marine invertebrates (Jackson 1986, Karlson 1986), was recently suggested as a possible reproductive pathway for red coral (Russo et al. 1999), no direct evidence of fragmentation has ever been found in the field (Santangelo & Abbiati 2001). Recruitment must therefore be considered to depend on larval settlement.

For several years our research efforts have been directed towards a coastal population of *Corallium rubrum*, composed of small, sparsely-branching colonies living in the eastern Ligurian Sea. The population occurs on the vaults of small crevices in dense patches. The population is a true self-seeding genetic unit (Abbiati et al. 1993, 1999), exhibiting closed population features and positive density-dependent recruitment (Santangelo & Abbiati 2001). We have focused on the demographic structure of this population by determining the relationship between size and age and the population size and age structure (Abbiati et al. 1992, Santangelo et al. 1999). The red coral population in question shows a maximum life span of 10 yr, but older colonies have frequently been encountered in deeper commercial banks (Garcia-Rodriguez & Massò 1986).

In this paper we address the population reproductive features, including the reproductive status of both polyps and colonies, as well as the sex ratio and timing of sexual maturity. Moreover, we have examined the colony reproductive cycle and inter- and intra-colonial variability in fecundity and fertility. Finally, we estimate the fecundity of female colonies of different size and/or age classes.

A better understanding of red coral reproductive biology will help us to develop improved demographic models, which in turn will help to protect and manage this precious species.

MATERIALS AND METHODS

Sampling. The population studied is located off the 'Calafuria' coast, near Leghorn, Italy (43° 30' N, 10° 20' E), in the eastern Ligurian Sea (Fig. 1). Colonies were collected by SCUBA from different crevices located along a vertical cliff at 2 different depths (25 ± 1 and 35 ± 1 m). From March to July, during which period most reproduction takes place (Vighi 1972), 30 colonies were sampled monthly during 1999 (15 at each depth). In November 1998 and January and September 1999, 20 colonies were collected, yet these were not subdivided by depth. An additional 72 small-sized colonies, falling into size/age classes 1 and 2, were collected in June of 1999. In total, 282 colonies, representing the entire size range of the population, were sampled and 3510 polyps were examined.

The temperature values throughout the entire year were recorded in the water column at 5 m intervals from the surface down to 35 m.

Size/age and female colony fecundity estimates. Size/age classes were determined by: colony diameter = $1.37 \times \text{age}^{0.75}$, where age was established by growth rings counts (Grigg 1974, Garcia-Rodriguez & Massò 1986, Santangelo et al. 1993b). This relationship allowed us to divide colonies into size/age classes on the basis of the range in which their diameter fell. Ten size/age classes were found in this population (Abbiati et al. 1992). Diameter was defined by averaging the minimum and maximum width measured by calipers at the base of colonies. Few colonies within this population fell into the largest classes (6 to 10), and therefore they were grouped together into a new class (6) that included all colonies having a diameter greater

than the upper limit for Class 5 (4.6 mm) (see Table 5).

The average number of polyps per colony was estimated on the basis of the functional relation between number of polyps (P) and colony size/age:

$$P_i = 15.07(\text{size/age})^{1.46}$$

where P_i is the number of polyps per colony in size/age class 1 (Abbiati et al. 1992, Santangelo et al. 1993b).

Finally, we estimated the number of gonads produced by each female colony in the different size/age classes by multiplying the average number of polyps in the colonies of each class by the average number of gonads each polyp produced (Santangelo & Abbiati 2001). The number of planulae produced by each colony was considered to correspond to the number of mature oocytes found in female polyps in June, before larval release.

Reproductive status and population sexual structure. Male and female polyps can be easily distinguished under a dissecting microscope (40, 60, 80×). According to Lacaze-Duthiers (1864) and Vighi (1972), oocytes are rounded and light yellow, while male gonads are milky, elongated and irregularly shaped.

The sexual status of both reproductive polyps and colonies, together with the population sex ratio, were determined on a subset of 232 colonies collected in the period of November to June, when oocytes and spermaries were easily distinguishable. The colonies collected in July and September lacked distinguishable gonads and were therefore not included in this analysis. The overall number of polyps examined was 2760; 11.9 per colony on average. The sample size varied proportionally with colony size, ranging from 3 polyps for class 1 colonies, up to 18 for colonies in classes 5 and 6. The proportion of colonies having reached reproductive maturity was then determined for each of the 6 different size/age classes.

Seasonal cycle of oocytes. Oocyte maturation was followed over the course of the year by determining the presence and diameter of oocytes. The maximum and minimum diameter of oocytes were measured with a calibrated micrometer mounted on the microscope eyepiece, and the geometric mean diameter was calculated. All the oocytes found in the 2850 polyps sampled from the 190 colonies collected between January and July were measured (15 polyps per colony, on average).

Two different reproductive parameters were examined: fecundity (number of oocytes per polyp) and fertility, i.e. number of fertile polyps/total number of polyps (%). The variations in polyp fecundity and fertility between different depths were analyzed during the March to July period.

Different multifactorial ANOVA models were followed for polyp fecundity and fertility. The model followed for fecundity had 2 orthogonal fixed factors: depth (2 levels) and time (5 levels), and a third factor nested in the interaction of the first 2, which was colony (3 levels). Ten polyps (replicates) were examined for each colony. The ANOVA model for fertility had only 2 orthogonal fixed factors: depth (2 levels) and time (5 levels); 3 colonies (replicates) were sampled for each time. Ten polyps from each colony were examined. Whenever the ANOVA revealed significant factors (thereby rejecting the null hypothesis), the Student-Newman-Keuls (SNK) test for *a posteriori* comparisons was applied to assess whether any pattern existed between levels of the same factor. The homogeneity of variance, an assumption for ANOVA, was tested by Cochran's test (Underwood 1997).

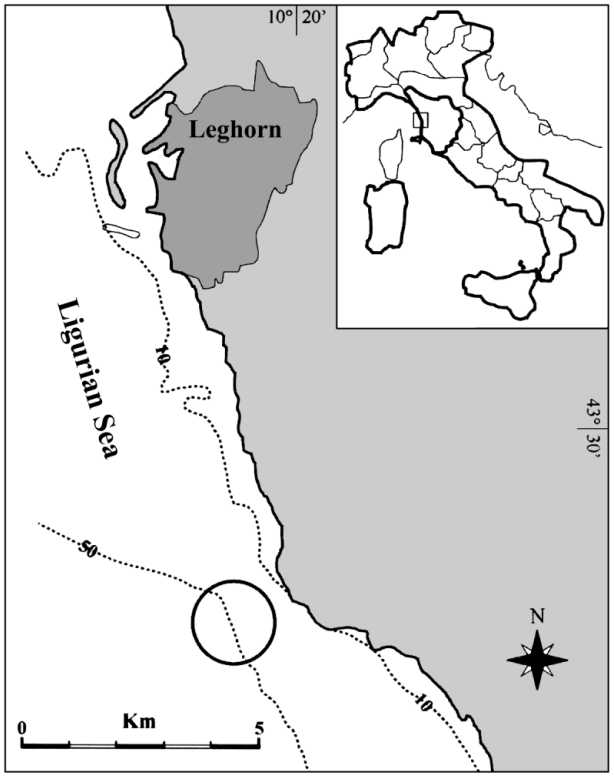

Fig. 1. Map of the sampling area, Calafuria coast, near Leghorn, Italy

Variability of reproductive parameters within colonies. As the majority of the reproductive colonies in this population had 2 orders of branches, the variability of reproductive parameters was examined within and between the 1st- and 2nd-order branches (sensu Brazeau & Lasker 1988; our Fig. 2). Branches were divided into 3 different segments corresponding to a different position: distal, central and apical (Fig. 2). The analyzed colonies came from 2 different depths (25 and 35 m). The polyps and colonies we utilized

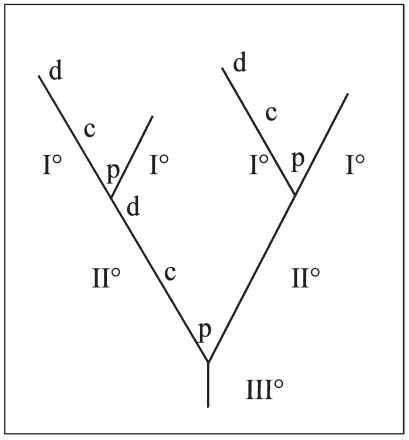

Fig. 2. *Corallium rubrum.* Scheme of colony division into 1st- (I°) and 2nd- (II°) order branches. Branches were further subdivided into 3 segments: proximal (p), central (c) distal (d)

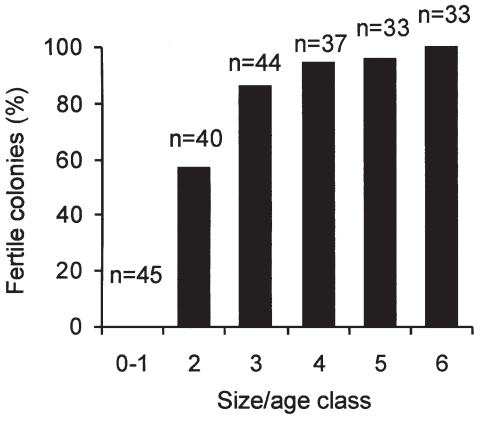

Fig. 3. *Corallium rubrum.* Percentage of fertile colonies in the different size/age classes

were selected from those examined for the seasonal cycle.

Variations within branches were examined by 2 different multifactorial ANOVA models. For 1st-order branches, whose data set was larger (colonies have 4 to 8 first-order branches), a more complex ANOVA model was followed, in which depth (2 levels) and position (3 levels) were orthogonal fixed factors, while colony (3 levels) was the third factor, nested in the interaction of the first 2. Two portions of different branches (which in this case were replicates) were examined for each colony. Overall, 18 colonies and 36 replicates were thus examined. Three polyps, selected from each branch portion, were examined to determine fecundity and fertility.

For 2nd-order branches, whose number was smaller, a simpler ANOVA model was followed, with 2 orthogonal fixed factors: depth (2 levels) and position (3 levels). In order to avoid data autocorrelation, 3 different colonies (replicates) were sampled for each position. Three polyps from each segment were examined.

Variations in fertility and fecundity between 1st- and 2nd-order branches (not subdivided into segments) were checked by the *t*-test for paired samples.

RESULTS

Sexual status and population sex ratio

The sexual structure of the population was clearly gonochoric at both the colony and polyp level. None of the 166 fertile colonies and 2136 polyps examined which was found to be sexually mature was hermaphroditic. Overall, 96 (57.8%) female and 70 (42.2%) male colonies were found, yielding a population sex ratio (1.37:1) significantly biased toward female colonies ($\chi^2 = 4.07$, $p < 0.05$).

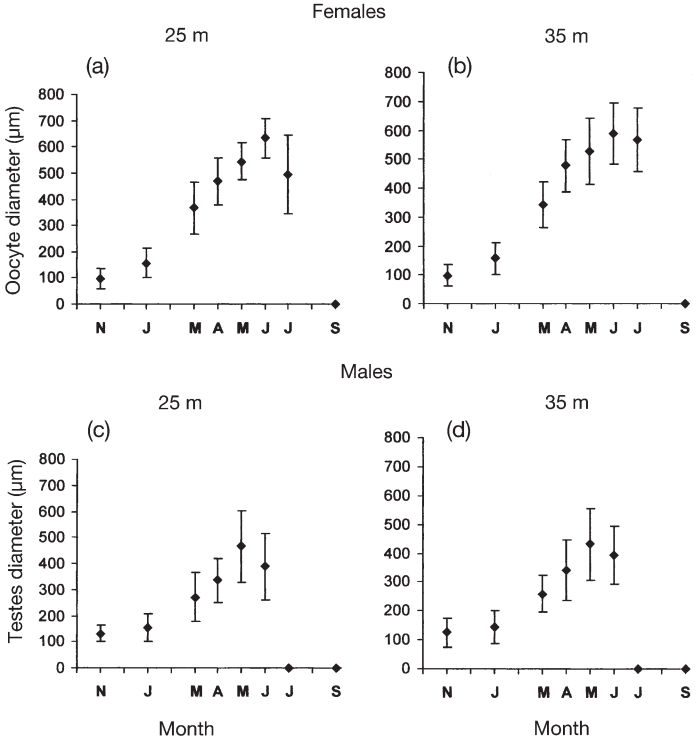

Fig. 4. *Corallium rubrum* gametogenic cycle. Colonies were collected at 2 different depths: (a) females 25 m; (b) females 35 m; (c) males 25 m; (d) males 35 m. Values given are means ± SD

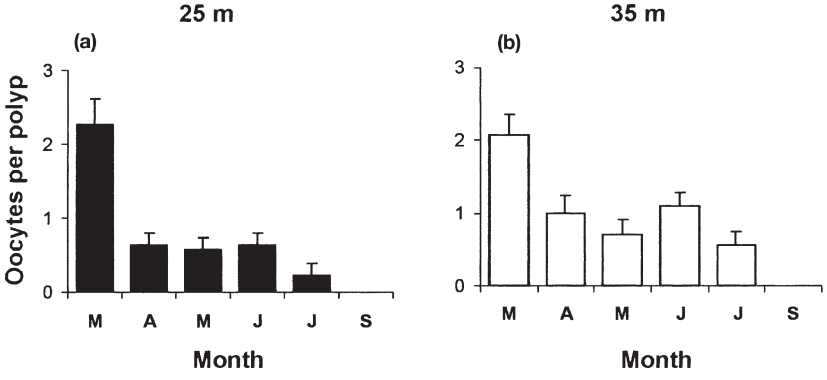

Fig. 5. *Corallium rubrum.* Polyp fecundity. Mean (±SD) number of oocyte per polyp over time in colonies collected at 2 different depths: (a) 25 m; (b) 35 m

Onset of colony fertility

Class 1 colonies were always sterile, but more than half the class 2 colonies (57%) were fertile. This percentage increased with age, following a sigmoid curve, and reached 100% for the colonies in size/age class 6 (Fig. 3). Since recruits (0 to 1 yr old colonies) dominated this population (over 50% of the individuals; Santangelo & Abbiati 2001), only 34.1% of the colonies in this population were fertile (1503/4407; n = 29).

Seasonal gonad cycle and reproduction timing in female colonies

An annual gametogenic cycle was observed during the period 1998 to 1999. Female gametes measured 98 ± 38 and 157 ± 54 µm (mean diameter ± SD) in November and January, respectively. In March the colonies collected at 25 and 35 m depth showed oocyte diameters of 366 ± 98 and 343 ± 78 µm, respectively, which in June reached 633 ± 60 and 590 ± 105.7 µm (Fig. 4a,b). Maturation thus seemed to be synchronous among colonies collected simultaneously at the different depths. A similar trend was also observed for male gonads (Fig. 4c,d).

The number of female gametes per polyp (i.e. fecundity), as well as the percentage of fertile polyps (i.e. fertility), decreased at the end of July (Figs. 5a,b & 6a,b). In the same period, several polyps were found to harbor 1 to 2 planulae. In early September neither female gametes nor planulae were encountered in polyps, while newly settled young individuals were observed in the proximity of the adult colonies. No settlement was observed after mid-September. Planulation (i.e. larval release) thus occurred in the period between July and the first half of September.

Temperatures varied yearly between 13°C in March and 21°C in October. During the gonad maturation period (March to July), the temperature ranged between 13 and 16.5°C, with only small differences between the 2 depths examined during the reproductive period (ΔT = 0.5°C). The maximum temperature difference between the 2 depths was measured in September (ΔT = 1.5°C).

Variability of reproductive parameters between female colonies

We examined the variability in both fecundity and fertility of female colonies at different depths (2 levels) and times (5 levels). As the results of the ANOVA showed (Tables 1 & 2), time was the only significant factor. The mean number of oocytes per polyp reduced significantly after March, as the SNK test showed. This trend was similar for both depths (Fig. 5a,b). Reabsorption of oocytes during maturation could explain this observation (Rinkevich & Loya 1979a, Kojis & Quinn 1984, Lam 2000). Maturation amongst the different colonies in the population is highly synchronized, since the number of eggs per polyp was constant in colonies collected at the same time (factor colony in Table 1, ANOVA not significant [ns]), and no significant difference was found between depths (Table 1, factor depth ns).

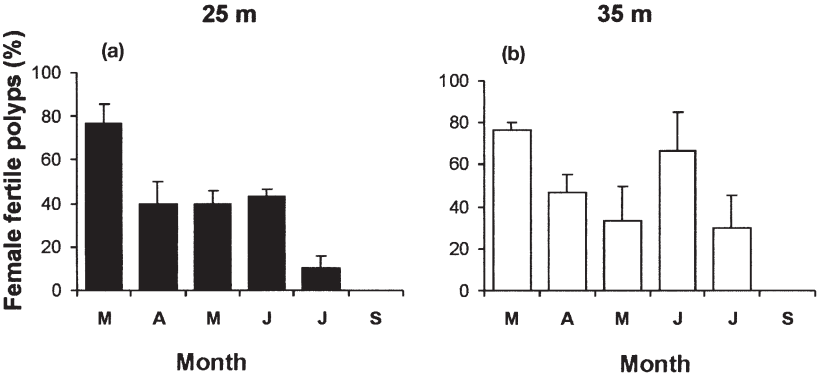

Fig. 6. *Corallium rubrum.* Polyp fertility. Mean (±SD) percentage of fertile polyps in female colonies collected at 2 different depths: (a) 25 m; (b) 35 m

Table 1. *Corallium rubrum.* Three-factor ANOVA showing the effect of time of collection on female polyp fecundity (***p < 0.001). Fecundity reduced significantly after March (T1) as Student-Newman-Keuls (SNK) test showed. Cochran test was not significant (no data transformation). T2 = April, T3 = May, T4 = June, T5 = July

Source of variation	df	Variance	*F*	p		*F* vs:
Depth = D	1	3.63	3.47	0.136	ns	D × T
Time = T	4	28.56	16.29	0	***	C (D × T)
Colony (D × T) = C	20	1.75	1.25	0.2158	ns	Residual
D × T	4	1.05	0.6	0.669	ns	C (D × T)
Residual	270	1.41				
SNK test	T1 > T2 = T3 = T4 = T5					

Table 2. *Corallium rubrum.* Two-factor ANOVA showing the effect of time of collection on female colony fertility (***p < 0.001). Cochran test: not significant (no data transformation). SNK: Student-Newman-Keuls test

Source of variation	df	Variance	*F*	p		*F* vs:
Depth = D	1	563.33	2.28	0	ns	D × T
Time = T	4	2686.6	7.46	0	***	Residual
D × T	4	246.67	0.69	1	ns	Residual
Residual	20	360				
SNK test	No alternative hypothesis					

In July, the average number of oocytes in each female polyp decreased slightly. This reduction was more evident in the 25 m depth colonies (Fig. 5a,b). At this time, 1 or 2 planulae were found in some polyps. In September, however, no polyp contained gametes (either male or female) at both depths examined.

The percentage of fertile polyps per colony decreased significantly with time (Table 2, Fig. 6a,b). In this case, however, there is no pattern (SNK test) in the decrease from one month to the next, but only a significant, overall reduction between March and July. No significant difference was found between the colonies collected at the 2 different depths (Table 2).

Variability of reproductive parameters within female colonies

Fecundity and fertility varied significantly with polyp position (Tables 3 & 4). The distal segments of 1st-order branches (as the SNK test showed) were significantly less fecund and fertile then other branch positions (Table 3, Fig. 7a). When sexually fertile, the smallest unbranched female colonies exhibited the same fertility distribution as 1st-order branches. The depth and colony factors, on the other hand, did not significantly influence fecundity or fertility, so both reproductive parameters were statistically constant across the different colonies and depths examined (Table 3).

Also for 2nd-order branches, position was the only significant factor for both reproductive parameters (Table 4). However, in this case, as the SNK test showed, the less fertile segment was the proximal one (Fig. 7b). This trend was independent of depth. Thus, the patterns of both reproductive parameters in the 2 branch orders were the opposite: in 1st-order branches, the distal segment showed significantly lower fecundity and fertility than the proximal and middle ones, while in 2nd-order branches it was the proximal segment that was less fecund and fertile.

As reported for other octocorals (Beiring & Lasker 2000), no significant difference in fecundity and fertility was found between the 2 branch orders (n = 19, $t = 1.78$, $0.01 > p > 0.05$). On the basis of this finding the following analyses were carried out without taking into account the significant variability between branch positions previously reported.

Table 3. *Corallium rubrum.* Three-factor ANOVA showing the effect of polyp position in 1st-order branches of female colonies (***p < 0.001). Fecundity (A) and fertility (B) are lower in distal (d) than in proximal (pr) and central (c) portions of branches, as Student-Newman-Keuls (SNK) test showed. Cochran test: not significant (no data transformation)

Source	A						B					
of variation	df	Variance	*F*	p		*F* vs:	df	Variance	*F*	p		*F* vs:
Depth = D	1	11.11	0.147222	0.78611	ns	C (D × P)	1	277.78	1.08	1.42083	ns	C (D × P)
Position = P	2	120.52.00	31.67	0	***	C (D × P)	2	29854.67	193.04.00	0	***	C (D × P)
Colony (D × P) = C	12	0.18125	1.01	3.33611	ns	Residual	12	154.32.00	0.45	6.36528	ns	Residual
D × P	2	3.53	0.064583	2.93264	ns	C (D × P)	2	277.78	1.08	1.43889	ns	C (D × P)
Residual	18	0.179167					18	339.51.00				
SNK test	pr = c > d						pr > c > d					

Table 4. *Corallium rubrum.* Two-factor ANOVA showing the effect of polyp position, in 2nd-order branches of female colonies (*p < 0.001, **p < 0.02). Fecundity (A) and fertility (B) are lower in proximal (pr) than in distal (d) and central (c) portions of branches as Student-Newman-Keuls (SNK) test showed. Cochran test: not significant (no data transformation)

Source of variation	A df	Variance	*F*	p		*F* vs:	B df	Variance	*F*	p		*F* vs:
Depth = D	1	0.22	0.11	5.147	ns	Residual	1	61.73	0.12	5.068056	ns	Residual
Position = P	2	22.39	0.834722	0.0016	**	Residual	2	9691.35.00	0.8347222	0.0002	*	Residual
D × P	2	1.06	0.54	4.13	ns	Residual	2	432.01.00	0.0604167	3.068056	ns	Residual
Residual	12	0.1069					12	493.83				
SNK test				d = c > pr						d = c > pr		

Female colony sexual production

Each fertile female polyp produced 1 to 4 mature oocytes per year. The average fecundity measured in the month of June (before the first planulae were found in polyps) was 0.87 oocytes per polyp and, as only 53.4% of female polyps were fertile, each fertile polyp produced, on average, 1.63 oocytes. No correlation was found between polyp fecundity or fertility and size/age of colonies. The number of polyps per colony (Table 5) was estimated on the basis of a functional relationship between polyp number and colony age (see 'Materials and methods'). All these data provide an estimate of the average number of planulae produced by a female colony in each size/age class (Fig. 8). The exponential curve we obtained indicates that the reproductive rate of colonies varied according to the age class by at least 1 order of magnitude. A class 2 colony, which has on average 27 polyps, will produce ca. 24 planulae per year, whereas a class 6 colony (including all colonies over 5 yr) has on average 180 polyps and will produce ca. 157 planulae per year (Table 5). We can now estimate the annual larval production per size/age class, and thus the overall larval production of the entire population.

Table 5. *Corallium rubrum.* Fecundity estimates of female colonies in different size/age classes. Number of planulae produced by each colony corresponds to the number of mature oocytes found before larval release

Diameter (mm)	Age	No. of polyps	Planulae yr^{-1}
0–1.4	1		0
1.4–2.3	2	27.2	23.7
2.3–3.1	3	57.4	50
3.1–3.9	4	93.9	81.7
3.9–4.6	5	135.5	118
>4.6	6	181.7	158

Male colonies reproductive features

Although our main focus was the female colony reproduction, data which are fundamental to the study of population dynamics, we also examined the reproduction of male colonies. Each polyp had 6 ± 3.5 spermaries, on average. An annual maturation cycle similar to that of females was observed; the diameter of spermaries increased greatly at both depths after March. No spermary was ever found in July and September (Fig. 4c,d). On the basis of a multifactorial ANOVA, no significant difference in fecundity or fertility was found between the different times (4 levels) or depths (2 levels) examined.

In 1st-order branches, multifactorial ANOVA revealed that the effects of the position factor (3 levels) on both reproductive parameters were highly significant at both depths examined. The SNK test revealed that apices have smaller reproductive values than the base and central branch portions. In contrast, in 2nd-order branches apices have the highest reproductive values. These findings were similar to those obtained for female colonies.

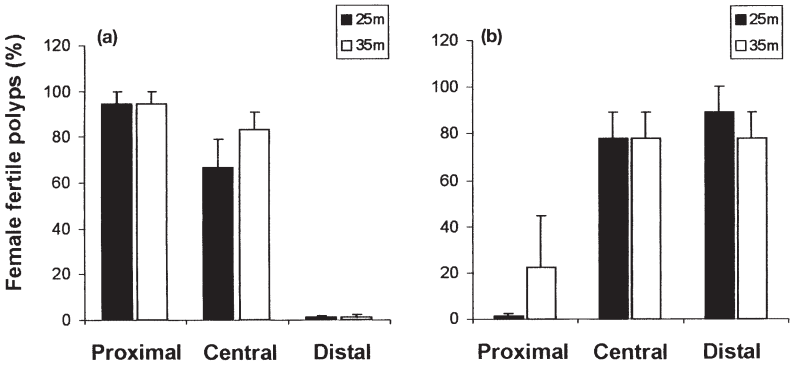

Fig. 7. *Corallium rubrum.* Within female colony fertility variation. Mean percentage (±SD) of fertile polyp in (a) 1st-order and (b) 2nd-order branches

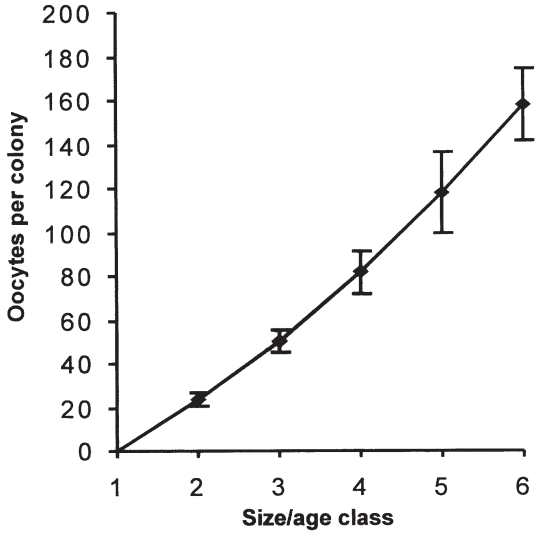

Fig. 8. *Corallium rubrum*. Female colony estimated reproductive output. Mature oocyte number (mean ± SE) in female colonies of the different size/age classes

DISCUSSION

Knowledge of population sexual structure and reproductive rates is crucial to the study of population dynamics (Ebert 1999, Fujiwara & Caswell 2001). A better understanding of the population reproductive features of the Mediterranean red coral *Corallium rubrum* helps to improve demographic models that can be used to effectively manage this overexploited species (Abbiati et al. 1992, Santangelo & Abbiati 2001).

The sexual status of the population was completely gonochoric at both the colony and polyp levels, confirming the dominance of gonochorism in octocorals (Vighi 1972, Benayahu et al. 1989, Brazeau & Lasker 1990, Coma et al. 1995a).

The population sex ratio was significantly biased toward female colonies (1.37:1). Such skewed sex ratios have been reported in some other octocorals: the gorgonian *Plexaura kuna* (Brazeau & Lasker 1989) and the blue octocoral *Heliopora coerulea* (Babcock 1990). An opposing pattern, with the sex ratio skewed towards males, is known for the gorgonian *Briareum asbestinum* (Brazeau & Lasker 1990).

More than 50% of the red coral colonies in the studied population reach sexual maturity in their second year, which is early compared to other octocorals (Gotelli 1991, Coma et al. 1995b); nearly 90% were mature by 3 yr and all colonies over 5 yr were fertile. This trend was similar for both males and females. The age at which sexual maturity is attained plays a fundamental role in determining fitness and population reproduction rates: size at maturation results from a trade-off between early maturation and offspring survival (Stearns 1997). All modules delay reproduction until the colony reaches a 'minimum size' (Karlson 1986, Harvell & Grosberg 1988, Bering & Lasker 2000). Moreover, if, according to Harwell & Grosberg (1988), a modular organism could postpone sexual reproduction until growth was limited by interspecific competition, then red coral colonies living in crowded monospecific patches, where interspecific competition is limited, should reach sexual maturity early.

In the red coral population studied, as well as in similar coastal populations harvested by recreational divers (Santangelo & Abbiati 2001), infestation by boring sponges (Corriero et al. 1997) and mass mortality (Garrabou et al. 2001) selectively affect the larger colonies. Under the effects of such mortality sources, early sexual maturity would lead to increased population survival.

No significant difference in either fecundity or fertility was found between colonies living at different depths (25 and 35 m). According to West & Coll (1993), gorgonian fecundity should vary widely with depth due to phenotypic plasticity. The lack of such a difference in our findings is likely due to the modest interval explored (25 to 35 m) within the much wider depth range specific to red coral (20 to 200 m). In fact, this 10 m depth difference corresponded to a very limited temperature range during the reproductive period ($\Delta T = 0.5$°C).

Fecundity and fertility differ significantly between the different segments of 1st- and 2nd-order branches, following 2 opposing trends: decreasing from the proximal portions to the tips in 1st-order branches, and increasing from the proximal to the distal portions in 2nd-order branches. These reproductive parameters did not differ significantly overall between 1st- and 2nd-order branches. This finding is likely the result of a balance between 2 opposing trends: the low fertility and fecundity of the tips of 1st-order branches (which have younger polyps), and the low fertility and fecundity of the bases of 2nd-order branches (which have older polyps). As both branches have 1 relatively infertile portion each, no significant difference in overall fertility resulted between them. A similar finding has been reported in the tropical octocoral *Briareum asbestinum* (West et al. 1993). On the other hand, a significant decrease in fertility with increasing branch order was found in the highly branching Mediterranean gorgonian *Paramuricea clavata* (Coma et al. 1995b).

Female fecundity and fertility were not statistically constant over time, but decreased after March, despite the fact that oocytes did not turn into planulae during this period. This trend, similar in colonies sampled at both depths, may be due to reabsorption of a portion of

oocytes during maturation, a process found in some other colonial anthozoans (Rinkevich & Loya 1979a, Kojis & Quinn 1984, Lam 2000). Such reabsorption of smaller oocytes could increase the nutritive material pool at the disposal of the larger, maturating oocytes that become planulae. In contrast, male colonies, in which no reabsorption occurs, did not show any significant variation of reproductive parameters over time.

Female gonad maturation, which was similar at different depths, showed an annual cycle with larval release occurring between July and August. In early September newly settled individuals were observed. No further planulae settled after mid-September. Thus, larval release and settlement are limited to a relatively short period of the year (Todd 1998). Male colonies show a similar trend, but sperm emission occurred about 1 mo before larval emission (July), thereby allowing oocyte fecundation.

Female polyp fecundity was considerably lower than that measured in the Mediterranean octocoral *Paramuricea clavata* (Coma et al. 1995b) and in several tropical hexacorals. Fecundity was comparable to the tropical free-spawing octocoral *Plexaura flexuosa* (Beiring & Lasker 2000) and the tropical octocoral *Briareum asbestinum* (West et al. 1993) which, like red coral, is an internal brooder.

According to our findings, and those on other octocorals (Coma et al. 1995b, Beiring & Lasker 2000), the reproductive output increases exponentially with colony size. Female colony fecundity varies among the different size/age classes by at least 1 full order of magnitude: while the smallest/youngest reproductive colonies (Classes 2 to 4) may produce some tens of planulae each (23.7 to 81.7), the older, larger colonies (Classes 5 to 6) may produce a hundred or more of them (118 to 157). Stiller & Rivoire (1984) estimated the production in red coral populations to be about 2000 larvae per colony. Based on our findings, such a value is an overestimation, at least for small-sized (10 cm maximum height), low-branched colonies like those in our study.

Despite the early sexual maturity, because of the population size/age structure, in which recruits were the dominant class (Santangelo & Abbiati 2001), only $^1/_3$ of the colonies were reproductive. All these factors lead to a small reproductive output for the population, increasing the risk of local extinction (Dobson 1998). It seems reasonable to assume that red coral populations showing such a size/age structure are above an optimal harvesting/recovery equilibrium threshold, which would be reached only if larger/older colonies survived.

Our study is the first to address the sexual structure and reproductive features of a Mediterranean red coral population. We produced the tools for estimating the overall population larval production and, through comparisons with data on local recruitment rates, the population reproductive success as well. Moreover, the results will enable us to improve life tables and develop population dynamic models (Hughes 1984, Hughes & Jackson 1985, Babcock 1994, Ebert 1999). Ultimately, this should lead to improved management of this threatened species by matching harvesting to reproduction rates.

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