



HAL
open science

Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) (Octocorallia, Gorgonacea) in Marseille's area (France, NW Mediterranean)

O. Torrents, J. Garrabou, C. Marschal, J.G. Harmelin

► **To cite this version:**

O. Torrents, J. Garrabou, C. Marschal, J.G. Harmelin. Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) (Octocorallia, Gorgonacea) in Marseille's area (France, NW Mediterranean). *Biological Conservation*, 2005, 121 (3), pp.391-397. 10.1016/j.biocon.2004.05.010 . hal-00093827

HAL Id: hal-00093827

<https://hal.science/hal-00093827>

Submitted on 23 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Age and size at first reproduction in the commercially exploited red coral *Corallium rubrum* (L.) in the Marseilles area (France, NW Mediterranean)

O. Torrents^{*}, J. Garrabou, C. Marschal, J.G. Harmelin

Centre d'Océanologie de Marseille, UMR-CNRS 6540 DIMAR, Station Marine d'Endoume, rue Batterie des Lions, Marseille F-13007, France

Among species life-history traits, size and age at first reproduction are particularly relevant to design meaningful conservation plans. The main goal of this study was to define the size at first reproduction of colonies of the precious red coral *Corallium rubrum* (L.) and determine their age, thanks to a new reliable method. Sampled colonies come from two sites at 40 m depth on the French Mediterranean coast near Marseilles. Furthermore, we report trends in reproduction parameters in relation to colony size. The smallest fertile colonies (<30 mm height class) were on an average 24.0 mm in height and 3.6 mm in basal diameter: these colonies were on an average between 7 and 10 years. The reproductive effort, i.e., percentage of gravid polyps per colony, was higher in large (>50 mm in height) and medium size colonies (30–50 mm) than in small ones (<30 mm). Our results indicate that management strategies for the conservation of red coral should lead to increase the abundance of large colonies to guarantee a good reproduction output. Suggested measures are minimal harvesting sizes and no-take areas in shallow habitats (<50 m).

Keywords: NW Mediterranean; Octocorallia; Red coral; Maturity; Growth rings

1. Introduction

Ecologists have a great responsibility in providing key information to preserve biodiversity under the impact of global change effects (Lubchenco et al., 1991). Marine coastal ecosystems have been affected by an increasing number of human-induced disturbances over the last decades (Botsford et al., 1997; Harvell et al., 1999; Jackson et al., 2001). Among these disturbances, overfishing has reduced the maximum size and abundance of many targeted species (Dayton et al., 1995; Jennings and Kaiser, 1998). Overfishing especially affects long-lived species rather than species with a short life-span because long-lived species generally show slow growth rates, low fecundity and late maturity (Musick, 1999). These parameters determine that long-lived species tend to decline more rapidly and take much longer to recover after strong disturbances, as has been already

shown in several species such as sharks and rays, large teleosts, sea turtles, whales and sea birds species (Crouse, 1999; Musick, 1999). Meaningful conservation plans can only be built from knowledge of species life-history traits.

Among life-history traits, size and age at first reproduction are most relevant to characterize the population dynamics of marine invertebrates (Harvell and Grosberg, 1988). Age at first reproduction can affect population intrinsic-growth rates and determine the population's recovery potential after disturbances (Dobson, 1998; Fujiwara and Caswell, 2001). Data on age/size at first reproduction are scarce for long-lived anthozoans, even when they are exploited, such as antipatharian black corals (Grigg, 1977a,b, 2001; Parker et al., 1997) and the species studied here, the red coral (Caddy, 1993; Charbonnier and Garcia, 1984).

In the Mediterranean sea, red coral *Corallium rubrum* (L.) populations have been commercially exploited for use in jewellery since antiquity (Morel et al., 2000; Santangelo and Abbiati, 2001; Santangelo et al., 1993).

^{*}Corresponding author. Fax: +33-4-91-04-16-35.
E-mail address: torrents@com.univ-mrs.fr (O. Torrents).

Professional harvesting (Santangelo et al., 1993) and poaching (Hereu et al., 2001) are the main sources of mortality in this long-lived species (~100 years) (Garrabou and Harmelin, 2002; Marschal et al., in press). Harvesting has caused a marked decrease in mean and maximum colony size in present red coral populations (Garrabou and Harmelin, 2002). However, red coral is still abundant in the NW Mediterranean sublittoral habitats. Data available on larval biology (Weinberg, 1979) and genetic population structure (Abbiati et al., 1993) denote a low rate of exchange between local populations, indicating that persistence of populations is mainly supported by local recruitment. Therefore, the persistence of local populations may be mainly assured by the reproduction output of colonies smaller than the commercial size. Data available on size at first reproduction in red coral have confirmed this hypothesis (Abbiati et al., 1991; Santangelo et al., 2003). However, the age of these small fertile colonies has not been correctly evaluated (Marschal et al., in press).

The main goal of this study was to define the size and the age at first reproduction of colonies of red coral *Corallium rubrum* on the French Mediterranean coast near Marseilles. Furthermore, we reported trends in reproduction parameters in relation to colony size which are relevant to assessing the reproductive output of populations of this precious species.

2. Materials and methods

2.1. Study sites and sampling

The study area is the rocky coast around Marseilles (NW Mediterranean, France). This area is characterised by the occurrence of submarine caves and overhangs, which favor the development of the red coral (Laborel and Vacelet, 1960). Two sites at 35–40 m depth were studied: Riou Sud, on the south coast of Riou Island (43°10'40"N, 5°23'50"E) and Tiboulou du Frioul, an islet in the Frioul archipelago (43°16'6"N, 5°17'3"E).

Colonies of red coral were collected by SCUBA diving during annual gonad maturity period occurring around the beginning of summer (Santangelo et al., 2003; Vighi, 1970, 1972). A total of 89 at the Riou site (25th July 2001) and 83 at the Frioul site (2nd August 2001). Colonies were immediately fixed in 4% formalin in seawater after sampling.

2.2. Determination of size at first reproduction

In the laboratory, the following size measurements were determined for each colony: (1) Height (from the base to the top of the colony, ± 0.5 mm); (2) basal colony diameter (average of maximum and minimum diameter measured by callipers at the base of colony, ± 0.5

mm) and (3) wet weight (after epibiosis elimination, ± 0.01 g). For analysis and presentation purposes, colonies were classified in three height classes: small colonies (<30 mm), medium-sized colonies (30–50 mm) and large colonies (>50 mm).

Reproductive state and sex of colonies were determined by observing the presence of gonads (immature and mature) and larvae after dissecting 10 polyps in each colony under a binocular dissecting microscope, i.e., 1720 observed polyps. Sex of colonies is distinguishable even when only immature gonads (about 30–50 μ m in diameter) are present in the polyps (Torrents, 2002). In this study, a colony was considered fertile when at least one immature or mature gonad or larva was observed in at least one of the 10 examined polyps.

2.3. Determination of age at first reproduction

The age of the smallest fertile colonies at each site was determined following a new ageing method recently developed for red coral. This method is based on the observation of annual growth rings after staining the organic matrix present in the skeleton (Marschal et al., in press). To obtain age estimates, transversal sections of the colonies' trunk (1 mm thick slices) were cut about 0.5–1 cm from the base of each colony. After the decalcification process, 4–5 h in 2% acetic acid solution, the organic matrix was stained with 0.05% Toluidine blue during 10–30 s (Marschal et al., in press). The number of growth rings in the colonies' sections was counted under the binocular microscope. Three different trained readers counted three times at different dates the number of growth rings in each colony. Age estimates of each independent reader were averaged to obtain age estimation for each small fertile colony. Average percentage error (APE) and index of precision (D) were used to describe intra- and inter-reader variability (Beamish and Fournier, 1981; Chang, 1982).

2.4. Reproduction parameters and colony size

Percentage of fertile colonies for each height class and fertility, i.e., percentage of gravid polyps within each colony, was quantified to study their variability with colony size.

3. Results

3.1. Mean size at first reproduction

Minimal size measurements of a fertile colony were 15.0 mm in height, 2.3 mm in basal diameter and 0.12 g in wet weight (Table 1). A large proportion of colonies of small-size class (<30 mm in height) were already fertile at both the Riou and Frioul sites (Fig. 1). In this

Table 1

Corallium rubrum – Height (mm), basal diameter (mm), wet weight (g) and mean age estimates (years) of fertile small-sized colonies (Height: <30 mm) of red coral (n : number of studied colonies for size measurements and age estimates are provided) sampled at Riou and Frioul sites

Sites	Measurements	n	Mean	SD	Minimum	Maximum
<i>Small-sized fertile colonies</i>						
Riou	Height		24.6	4.2	15.5	29.0
	Diameter	17	3.6	1.0	2.3	6.5
	Weight		0.55	0.34	0.12	1.17
	Age	12	7.0	3.5	3.0	13.0
Frioul	Height		23.4	5.1	15.0	29.5
	Diameter	18	3.6	0.9	2.3	5.3
	Weight		0.66	0.48	0.22	1.90
	Age	16	10.0	4.2	5.2	19.1
Riou + Frioul	Height		24.0	4.7	15.0	29.5
	Diameter	35	3.6	0.9	2.3	6.5
	Weight		0.60	0.42	0.12	1.90
	Age	28	8.7	4.11	3.0	19.1

Mean, standard deviation (SD), minimum (min) and maximum (max) data for all parameters are displayed.

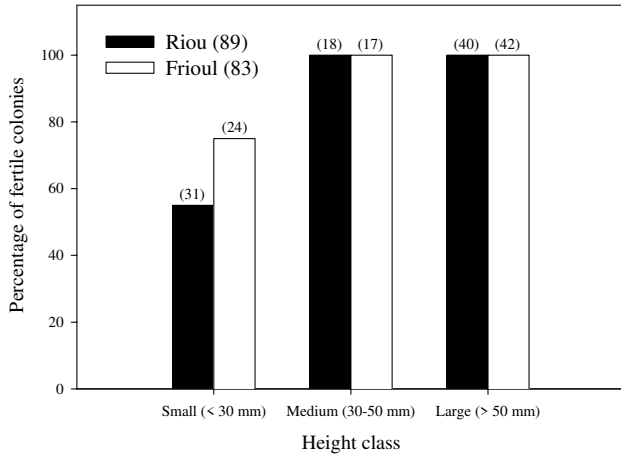


Fig. 1. *Corallium rubrum* – Percentage of fertile colonies in each height class at two sites, Riou and Frioul. Sample sizes for each site and each height class are noted in parenthesis.

height class, fertile colonies were on an average 24.0 mm in height, 3.6 mm in basal diameter and 0.60 g in wet weight (Table 1). Intersite differences in colony size in small fertile colonies were not detected for any of the three sizes parameters analysed (t -test; height, $t = 0.789$, $df = 33$, $p > 0.05$; basal diameter, $t = -0.281$, $df = 33$, $p > 0.05$; wet weight, $t = -0.789$, $df = 33$, $p > 0.05$; t -test were carried out after verifying the homogeneity of variances with a Levene's test).

3.2. Mean age at first reproduction

The youngest fertile colonies determined were 3.0 years and 5.2 years at Riou and Frioul sites, respectively (Table 1). The mean age (\pm SD) of fertile colonies in the small height class were similar at Riou (7.0 ± 3.5 years) and Frioul (10.0 ± 4.2 years) (t -test; age, $t = -2.007$, $df = 26$, $p > 0.05$; t -test were carried out after verifying

the homogeneity of variances with a Levene's test; Table 1). The large variability in age of colonies is worth noting. The age range found in the small-sized fertile colonies was about 3–13 and 5–19 years old in Riou and Frioul, respectively (Table 1). The APE for each reader was 5.8%, 9.4% and 9.1% with an index of precision (D) of 6.2%, indicating a good repetitiveness/precision of estimated age data. For seven of the 35 colonies examined, age could not be determined because the action of boring organisms had damaged their skeleton.

3.3. Variation of percentage of fertile colonies and fertility according to colony size

The proportion of fertile colonies was clearly size-dependent at Riou ($\chi^2 = 31.08$, $df = 2$, $p < 0.05$) and Frioul sites ($\chi^2 = 15.90$, $df = 2$, $p < 0.05$). Among small-sized colonies, the percentage of fertile colonies was 55% (Riou) and 75% (Frioul), while it reached 100% among medium-sized and large colonies at both sites (Fig. 1).

Differences in fertility (percentage of gravid polyps per colony) with size and site were tested with a two-way ANOVA after verifying the homogeneity of variances with a Bartlett's test. Fertility increased significantly with colony size (Factor height class, two-way ANOVA, $F_{(2,166)} = 21.45$, $p < 0.05$). Small colonies had about 30% gravid polyps, while large and medium-sized colonies had about 60% gravid polyps (Fig. 2). Post-hoc comparisons showed only significant differences between small-sized colonies versus medium and large colonies (Tukey's test, $F = 0.61$ and $F = 0.67$, $p < 0.05$). A significant difference on fertility between Riou and Frioul was detected (Factor site, two-way ANOVA, $F_{(1,166)} = 9.65$, $p < 0.05$). At Frioul, fertility was higher than Riou (Fig. 2). Finally, the interaction between size and site factors was not significant (height class \times site, two-way

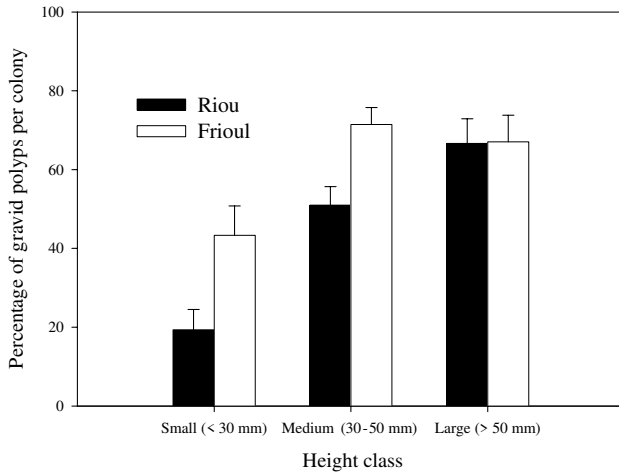


Fig. 2. *Corallium rubrum* – Mean (\pm SE) percentage of gravid polyps per colony (with immature and mature gonads or larvae) at Riou and Frioul, in male and female colonies in each height class.

ANOVA, $F_{(2,166)} = 1.65$, $p = 0.155$, ns), indicating that the variation of fertility with height class was similar between the two sites (Fig. 2).

4. Discussion

4.1. Age and size at first reproduction

Mean age at first reproduction of smallest fertile colonies in *Corallium rubrum* collected at Marseilles

was 7–10 years corresponding to colonies about 24.0 mm in height, 3.6 mm in basal diameter and 0.60 g in wet weight (Table 1). Our results on age at first reproduction contrast with the 2–4 years estimates found in previous studies (Abbiati et al., 1991; Santangelo et al., 2003). Methodological differences are behind this discrepancy, since previous methods using the mineralised part of the skeleton underestimated age of colonies as recently shown by Marschal et al. (in press). Actual age of colonies at first reproduction could be even higher because it seems that at least two or three years are required before the development of the first growth ring (Marschal et al., in press). Regarding size at first reproduction, our results showed similar minimum size values although they always corresponded to the upper limit of diameter class from in previous studies on Italian red coral populations, i.e., 1.4–2.3 mm in basal diameter (Santangelo et al., 2003). In this sense, our mean values, i.e., 3.6 mm in basal diameter, were about double those found on Italian red coral populations, i.e., 1.85 mm in basal diameter. Causes behind these inter population differences should be addressed in future research, since this could largely affect meaningful conservation plans in each Mediterranean region.

4.2. Colony size at first reproduction and mortality risks

Red coral, as many other gorgonian species, show a very slow growth rate and late reproduction (Table 2). Most gorgonian and antipatharian species dwelling in

Table 2
Age (years) and size at first reproduction in other octocorals

Species	First reproduction		Habitat, depth range, geographical location	Source
	Age (year)	Size (cm)		
<i>Corallium rubrum</i>	7–10	2.4 ^a , 0.36 ^b	Crevices in rocky walls, 36–41 m, NW Mediterranean (France)	This study
<i>Corallium rubrum</i>	2	0.14–0.23 ^b	Crevices in rocky walls, 25 and 35 m, N Tyrrhenian Sea (Italia)	Santangelo et al. (2003)
<i>Leptogorgia virgulata</i>	2	14 ^a	Limestone outcropping, 2 m, N Gulf of Mexico	Gotelli (1991)
<i>Briareum asbestinum</i>	2–3	10–20 ^a	Small back reef and reef flat complex, San Blas Islands (Panama)	Brazeau and Lasker (1990)
<i>Muricea fruticosa</i>	5	25 ^a	Rocky bottoms, 14–17 m, Baja California and Channel Islands (USA)	Grigg (1977a); Grigg (1977b)
<i>Plexaura flexuosa</i>	–	20–30 ^a	Patch reef, 2–4 m, San Blas Islands	Beiring (1997)
<i>Plexaura A</i>	5	20 ^a	Small back reef and reef flat complex, San Blas Islands	Brazeau and Lasker (1989); Kinzie (1970)
<i>Muricea californica</i>	10	25 ^a	Rocky bottoms, 14–17 m, Baja California and Channel Islands	Grigg (1977a); Grigg (1977b)
<i>Plexaura homomalla</i>	4–11	25–35 ^a	Small back reef and reef flat complex, N Gulf of Mexico	Martin (1982)
<i>Paramuricea clavata</i>	6–13	11 ^a	Rocky walls, 17–19 m, NW Mediterranean (Spain)	Coma et al. (1995)
<i>Antipathes dichotoma</i>	12–13	–	Rocky clean swept substrata, 30–110 m, Hawaii (USA)	R.W. Grigg, personal communication
<i>Antipathes fiordensis</i>	31	70–105 ^a	Rocky walls on fjords, 10–35 m, SW New Zealand	Parker et al. (1997)

^a Height (cm).

^b Basal diameter (cm).

stable environments such as dim-light habitats with low physical disturbance rates display maturity about 10 years or more contrasting with early maturity in species inhabiting environments with high rates of disturbance (Hall and Hughes, 1996, Table 2). Meanwhile, size at first reproduction in red coral is much smaller compared to other gorgonian species, i.e., usually about 15 cm in height (Table 2). Certainly, red coral have one of the slowest growth rates among gorgonian species (Garra-bou and Harmelin, 2002).

Delayed first reproduction in red coral is interpreted as a strategy to derive most colony's resources to growth in order to reach a refuge size minimizing mortality risks as in other clonal species (Babcock, 1991; Connell, 1973; Harvell and Grosberg, 1988; Hughes and Jackson, 1985; Kapela and Lasker, 1999; Sebens, 1987). Red coral populations occur in shaded habitats (overhangs, submarine caves and tunnels) which are dominated by rich invertebrate suspension-feeder assemblages (encrusting and massive sponges, bryozoans, ascidians and colonial and solitary antho-zoan species). In red coral, overgrowth, specially by sponges, is the main source of mortality of settlers and recruits (Garra-bou and Harmelin, 2002), as reported in other coral species from tropical habitats (Richmond, 1996). Therefore, our results indicated that despite the small size at first reproduction, it would be large enough to reduce most mortality risks by overgrowth regardless the age at the first reproduction.

4.3. Age and size at first reproduction: implications for red coral conservation and management plans

Maturity at small colony size can be pointed out as the main reason for the persistence of red coral populations in the NW Mediterranean despite long-standing fishing pressure. Our data show, though, that the danger for the persistence of red coral populations could arise from factors reinforcing the decrease of abundance and mean colony size of populations. This decrease would imply a reduction of the reproductive output enhancing the probability of local extinction for two main reasons.

Firstly, reproductive parameters of red coral (percentage of fertile colonies and fertility) were significantly lower in small-sized colonies than in medium and large colonies (Figs. 1 and 2). Overall, the same pattern has been found by other authors working on tropical and temperate gorgonian species (Beiring and Lasker, 2000; Brazeau and Lasker, 1990; Coma et al., 1995; Grigg, 1977b; Kapela and Lasker, 1999; Kinzie, 1974), although a previous study with red coral did not find a significant effect of colony size on fertility of colonies (Santangelo et al., 2003).

Secondly, age at first maturity was considerably older than previously reported and, since colonies are

mature at about 10 years, at least 20 years are needed to reach colony size able to ensure high reproductive potential (Garra-bou and Harmelin, 2002; Marschal et al., in press; Torrents, 2002). Furthermore, larger colonies have an enhanced survival likelihood (Kojis and Quinn, 1981; Martin, 1982; Szmant, 1986) and thus increased future reproductive success (Szmant-Froelich, 1985).

Reduction of abundance and mean size in harvested and non-harvested populations could be already occurring because recently we have been witnessing on one hand, red coral fishermen exploiting increasingly smaller colony sizes and using highly destructive methods affecting the whole size range in some areas (Santangelo et al., 2003; Gili, personal communication), and on the other hand, an increase in new sources of disturbance especially mass mortality events linked to elevated temperature anomalies and mechanical disturbance due to the recreational diving activities (Garra-bou et al., 1998, 2001, 2003). This scenario may be driving red coral populations, especially in shallow water habitats, to situations of risk of local extinction in the near future.

We contend that different management strategies focusing on the conservation of population's size structure allowing a good reproductive output should be adopted. These strategies may involve: (i) leaving free of harvesting shallow water habitats (<50 m) where negative effects of global change and recreational diving activities are more likely to occur; (ii) establishing minimal harvesting size (e.g., 10 cm in height or 0.8 cm in basal diameter depending on the biometric parameters of each population) and/or (iii) rotating closures (Caddy, 1993) for at least 10 years. Some regions in the NW Mediterranean (Spain, Corsica, Sardinia) have already partially adopted these initiatives. However, we contend that adoption of such regulations should be generalised and even reinforced in the NW Mediterranean region to guarantee the conservation of red coral populations to the face of possible increasing in the disturbance regime in the near future.

Acknowledgements

The authors gratefully acknowledge the helpful assistance of B. de Ligondes and R. Graille during sampling. Comments and suggestions from P. Chevaldonné, J. Vacelet and 2 anonymous reviews vastly improved the manuscript. We also thank Mr. M. Paul for revising the English version. This study was funded by the "Provence-Alpes-Côte d'Azur" region (O. Torrents Doctoral Fellowship) and partly by the IFB (Institut Français de la Biodiversité) and the Environmental Department of TOTAL-Fina-Elf group.

References

- Abbiati, M., Buffoni, G., Di Cola, G., Santangelo, G., 1991. Red coral population dynamics: stability analysis and numerical simulation of time evolution of perturbed states. In: Ravera, O. (Ed.), *Terrestrial and Aquatic Ecosystems: Perturbations and Recovery*. Ellis Horwood, New York, pp. 219–228.
- Abbiati, M., Santangelo, G., Novelli, S., 1993. Genetic variation within and between two Tyrrhenian populations of the Mediterranean alcyonarian *Corallium rubrum*. *Marine Ecology Progress Series* 95, 245–250.
- Babcock, R.C., 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classification. *Ecological Monographs* 61, 225–244.
- Beamish, R.J., Fournier, D.A., 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Aquatic Sciences* 38, 982–983.
- Beiring, E.A., 1997. Life history and reproductive success of a broadcast-spawning gorgonian coral and implications for conservation biology. PhD Thesis, State University of New York, Buffalo, New York.
- Beiring, E.A., Lasker, H.R., 2000. Egg production by colonies of a gorgonian coral. *Marine Ecology Progress Series* 196, 169–177.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. *Science* 277, 509–515.
- Brazeau, D.A., Lasker, H.R., 1989. The reproductive cycle and spawning in a Caribbean gorgonian. *Biological Bulletin* 176, 1–7.
- Brazeau, D.A., Lasker, H.R., 1990. Sexual reproduction and external brooding by the Caribbean gorgonian *Briareum asbestinum*. *Marine Biology* 104, 465–474.
- Caddy, J.F., 1993. Background concepts for a rotating harvesting strategy with particular reference to the Mediterranean red coral, *Corallium rubrum*. *Marine Fisheries Review* 55, 10–18.
- Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Aquatic Sciences* 39, 1208–1210.
- Charbonnier, D., Garcia, S., 1984. Consultation on red coral resources of the Western Mediterranean and their rational exploitation, General Fisheries Council for the Mediterranean, 13–16 December 1983, Palma de Mallorca, Spain, vol. 306, pp. 1–142.
- Coma, R., Zabala, M., Gili, J.-M., 1995. Sexual reproductive effort in the Mediterranean gorgonian *Paramuricea clavata*. *Marine Ecology Progress Series* 117, 185–192.
- Connell, J.H., 1973. Population biology of reef-building corals. In: Jones, O.A., Endean, R. (Eds.), *Biology and Geology of Coral Reefs*, vol. 2. Academic Press, New York, pp. 205–245.
- Crouse, D.T., 1999. The consequences of delayed maturity in a human-dominated world. In: Musick, J.A. (Ed.), *Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals*. American Fisheries Society Symposium, Bethesda, MD, vol. 23, pp. 195–202.
- Dayton, P.K., Thrush, S.F., Agardy, M.T., Hofman, R.J., 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5, 205–232.
- Dobson, A.P., 1998. *Conservation and biology*. Scientific American Library, New York.
- Fujiwara, M., Caswell, H., 2001. Demography of endangered North Atlantic right whale. *Nature* 414, 537–541.
- Garrabou, J., Harmelin, J.G., 2002. A 20-year study on life history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. *Journal of Animal Ecology* 71, 966–978.
- Garrabou, J., Perez, T., Chevaldonné, P., Bensoussan, N., Torrents, O., Lejeune, C., Romano, J.C., Vacelet, J., Boury-Esnault, N., Harmelin-Vivien, M., Verlaque, M., Boudouresque, C.F., Harmelin, J.G., 2003. Is global change a real threat for conservation of the NW Mediterranean marine biodiversity? *Geophysical Research Abstracts* 5, 10522.
- Garrabou, J., Perez, T., Sartoretto, S., Harmelin, J.G., 2001. Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). *Marine Ecology Progress Series* 217, 263–272.
- Garrabou, J., Sala, E., Arcas, A., Zabala, M., 1998. The impact of diving use on marine rocky sublittoral communities: a case study of a Mediterranean bryozoan population. *Conservation Biology* 12, 1–12.
- Gotelli, N.J., 1991. Demographic models for *Leptogorgia virgulata*, a shallow-water gorgonian. *Ecology* 72, 457–467.
- Grigg, R.W., 2001. Black coral: history of a sustainable fishery in Hawaii. *Pacific Science* 55, 291–299.
- Grigg, R.W., 1977a. Hawaii's Precious Corals. Island Heritage Ltd., Honolulu, HI.
- Grigg, R.W., 1977b. Population dynamics of two gorgonian corals. *Ecology* 58, 278–290.
- Hall, V.R., Hughes, T.P., 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* 77, 950–963.
- Harvell, C.D., Grosberg, R.K., 1988. The timing of sexual maturity in clonal animals. *Ecology* 69, 1855–1864.
- Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., Hofmann, E.E., Lipp, E.K., Osterhaus, A.D.M.E., Overstreet, R.M., Porter, J.W., Smith, G.W., Vasta, G.R., 1999. Emerging marine diseases – climate links and anthropogenic factors. *Science* 285, 1505–1510.
- Hereu, B., Linares, C., Zabala, M., 2001. Avaluació de l'impacte de l'episodi d'expoli de corall vermell (*Corallium rubrum*) de la zona protegida de les Illes Medes detectat durant l'hivern de 2000. In: G.d.C. (Ed.), *Departament de Medi Ambient, Seguiment temporal de la reserva marina de les Illes Medes. Informe anual 2001*. Barcelona, pp. 51–60.
- Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. *Ecological Monographs* 55, 141–166.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.B., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34, 201–352.
- Kapela, W., Lasker, H.R., 1999. Size-dependent reproduction in the Caribbean gorgonian *Pseudoplexaura porosa*. *Marine Biology* 135, 107–114.
- Kinzie, R.A., 1970. The ecology of the gorgonians (Cnidaria, Octocorallia) of Discovery Bay, Jamaica. PhD Thesis, Yale University, New Haven, Connecticut.
- Kinzie, R.A., 1974. *Plexaura homomalla*: Biology and ecology of a harvestable marine resource. *Studies on Tropical Oceanography* 12, 22–38.
- Kojis, B.L., Quinn, N.J., 1981. Aspects of sexual reproduction and larval development in the shallow water hermatypic coral, *Goniastrea australensis* (Edwards and Haime, 1857). *Bulletin of Marine Science* 31, 558–573.
- Laborel, J., Vacelet, J., 1960. Répartition bionomique du *Corallium rubrum* Lmck dans les grottes et falaises sous-marines. *Rapports et Procès-Verbaux des Réuniones de la C.I.E.S.M.* 16, 465–469.
- Lubchenco, J., Olson, A.M., Brubaker, L.S., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J., Risser, P.G., 1991. The sustainable biosphere initiative: an ecological research agenda. *Ecology* 72, 371–412.

- Marschal, C., Garrabou, J., Harmelin, J.G., Pichon, M. A new method for measuring growth and age in the precious red coral *Corallium rubrum* (L.). Coral Reefs (in press).
- Martin, E., 1982. Ciclo reproductivo, proporción sexual y fecundidad del coral blando *Plexaura homomalla* (Esper.) en el Mar Caribe Mexicano (Octocoralla: Plexauridae). Anales del Instituto de Ciencias del Mar y Limnología de la Universidad Nacional Autónoma de México 9, 359–380.
- Morel, J.P., Rondi-Costanzo, C., Ugolini, D., 2000. Corallo di Ieri – Corallo di Oggi. 13–15 Dicembre 1996, Ravello. Atti del Convegno, Centro Universitario Europeo per I Beni Culturali. p. 303.
- Musick, J.A., 1999. Ecology and conservation of long-lived marine animals. In: Musick, J.A. (Ed.), Life in the Slow Lane: Ecology and Conservation of Long-lived Marine Animals. vol. 23, American Fisheries Society Symposium, Bethesda, MD, pp. 1–10.
- Parker, N.R., Mladenov, P.V., Grange, K.R., 1997. Reproductive biology of the antipatharian black coral *Antipathes fiordensis* in Doubtful Sound, Fiordland, New Zealand. Marine Biology 130, 11–22.
- Richmond, R.H., 1996. Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland, C.E. (Ed.), Life and Death of Coral Reefs. Chapman and Hall, New York, pp. 175–197.
- Santangelo, G., Abbiati, M., 2001. Red coral: conservation and management of an over-exploited Mediterranean species. Aquatic Conservation of Marine and Freshwater Ecosystems 11, 253–259.
- Santangelo, G., Abbiati, M., Giannini, F., Cicogna, F., 1993. Red coral fishing trends in the Western Mediterranean Sea during the period 1981–1991. Scientia Marina 57, 139–143.
- Santangelo, G., Carletti, E., Maggi, E., Bramanti, L., 2003. Reproduction and population sexual structure of the overexploited Mediterranean red coral *Corallium rubrum*. Marine Ecology Progress Series 248, 99–108.
- Sebens, K.P., 1987. The ecology of indeterminate growth in animals. Annual Review of Ecology and Systematics 18, 371–407.
- Szmant, A.M., 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5, 43–53.
- Szmant-Froelich, A.M., 1985. The effect of colony size on the reproductive ability of the Caribbean coral *Montastrea annularis* (Ellis and Solander). In: Proceedings of the 5th International Coral Reef Congress, Tahiti, pp. 295–300.
- Torrents, O., 2002. Taille et âge à la première reproduction du corail rouge, *Corallium rubrum* (L.) (Anthozoa, Octocorallia) à Marseille (France, Méditerranée nord-ouest). Rapport DEA. Centre d’Océanologie de Marseille, Marseille, p. 34.
- Vighi, M., 1970. Ricerche sul ciclo riproduttivo del corallo rosso (*Corallium rubrum* (L.) del promontorio di Portofino. Atti Acc. Naz. Lincei Mem., S. VIII, vol. X, sez. 3. 10, pp. 1–26.
- Vighi, M., 1972. Etude sur la reproduction du *Corallium rubrum* (L.). Vie et Milieu 23, 21–32.
- Weinberg, S., 1979. The light-dependent behaviour of planula larvae of *Eunicella singularis* and *Corallium rubrum* and its implication for octocorallian ecology. Bijdragen tot de Dierkunde 49, 16–30.