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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

J. GARRABOU and J. G. HARMELIN

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

Summary

1. Long-lived species play a paramount role in the structure and functioning of terrestrial and marine ecosystems. The dramatic increase of human-induced disturbances may be irremediably affecting populations of long-lived species. Data on life-history traits on these species taking into account relevant temporal and spatial scales are very scarce for marine ecosystems, though these data are key to guarantee the conservation of these species and the communities that they shape.

2. This study examined long-term data on life-history traits of the precious red coral (*Corallium rubrum* L., 1758) in the NW Mediterranean. This was performed by surveying the fate of 67 red coral colonies during 21 years in a shallow-water habitat (27 m depth).

3. Photographic monitoring provided data on survivorship, whole and partial mortality, recruitment and growth of colonies allowing about 1000 observations on life-history traits.

4. Red coral showed a high survivorship, 60% of colonies reaching 22 years of age. Whole mortality was significantly higher in juvenile colonies while partial mortality displayed the inverse pattern. Recruitment showed a pulse mode with a single peak at the beginning of the study and low rates thereafter. Average growth rates over the study period were extremely low: $0{\cdot}24 \pm 0{\cdot}05$ mm year^{-1} for the basal diameter, $1{\cdot}78 \pm 0{\cdot}7$ mm year^{-1} for colony height and $3{\cdot}40 \pm 0{\cdot}31$ branches in 22 years.

5. This study also examined size-related effects of harvesting on red coral populations since shallow-water populations (between 10 and 40 m depth) have long been submitted to intensive harvesting.

6. Measurements (basal diameter and height) of 400 colonies corresponding to the largest ones dwelling in 10 currently harvested and two non-harvested populations were compared to analyse the effects on the population's recovery and potential colonies' maximum sizes. Harvested populations showed values that were about twice as low on average and up to four times lower for maximum values in colony size than in the non-harvested populations.

7. Our study provides indisputable data on the longevity of colonies and the parsimonious population dynamics of *C. rubrum*. Current populations have shown a dramatic shift in their size structures characterized by the absence of large colonies. Taking into account results obtained in this study full recovery time of shallow-water harvested populations may be measured by several decades or even centuries.

Key-words: red coral, *Corallium rubrum*, long-term study, growth, sublittoral habitats, benthos.

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Introduction

A dramatic increase in human-induced disturbances has been observed in the past decades in terrestrial as well as in marine coastal habitats (e.g. Vitousek *et al.* 1997;

Correspondence: J. Garrabou, Centre d'Océanologie de Marseille, UMR-CNRS 6540 DIMAR, Station Marine d'Endoume, rue Batterie des Lions, F-13007 Marseille, France. Fax: 33 4 91 04 16 35;
E-mail: garrabou@com.univ-mrs.fr

Harvell *et al.* 1999; Jackson 2001). The terrestrial realm has been impacted by large-scale effects including significant diversity losses and changes in ecosystem functioning (Vitousek *et al.* 1997). Most marine ecosystems have also been affected by profound, although generally more recent, changes (Botsford, Castilla & Peterson 1997; Harvell *et al.* 1999; Jackson *et al.* 2001). For instance, overfishing has severely reduced the abundance of targeted stocks resulting in truncated age structures by selective fishing of large-sized individuals (e.g. Dayton *et al.* 1995; Jennings & Kaiser 1998). Long-term consequences of strong disturbances are highly dependent on the life history of species. Effects are particularly severe on species with low dynamics and long life span (Dayton *et al.* 1995; Russ & Alcala 1998).

Long-lived species play a paramount role in the structure and functioning of many sublittoral communities through their trophic activity, biomass and perennial biogenic structures that significantly shape the habitat (Dayton *et al.* 1974; Hughes & Jackson 1985; Sebens 1991). For these reasons these species are often called ecosystem engineers (Jones, Lawton & Shachak 1994). Changes in their abundance can have a significant influence on community organization and eventually promote important shifts in the communities (Hughes 1994). However, data on life-history traits of long-lived species based on relevant temporal and spatial scales are scarce in marine ecosystems (Hughes & Connell 1999). In most cases data on their life-history traits come from short-term studies or are based on indirect measurements. For instance, studies on recruitment rates of reef corals hardly span beyond 5 years (Connell, Hughes & Wallance 1997; Hughes & Connell 1999). Knowledge of long-term trends in the life history of long-lived species subjected to both human harvesting and natural disturbances is an essential prerequisite for the conservation and rational management of those organisms.

The Mediterranean red coral, *Corallium rubrum* (L., 1758) (Gorgonacea, Octocorallia), is a colonial, sessile cnidarian with an arborescent growth form, which can reach 50 cm in height (mass > 2 kg) although colonies taller than 20 cm and thicker than 2 cm in basal diameter are today very rare because of harvesting (Barletta, Marchetti & Vighi 1968; Marin & Reynal de Saint-Michel 1981; Liverino 1989). Red coral is essentially distributed in the western basin of the Mediterranean Sea but it is also present in some areas of the eastern Mediterranean and African Atlantic coast (Marchetti 1965; Zibrowius, Monteiro-Marques & Grasshoff 1984; Chintiroglou, Dounas & Koukouras 1989). It is typically associated with animal-dominated communities growing in dimly lit habitats, such as caves and smaller cavities, vertical cliffs and overhangs, from 10 to 200 m in depth (Carpine & Grasshoff 1975; Weinberg 1978).

Red coral is characterized by a solid red carbonate axial skeleton, which has been highly valued since antiquity for jewellery (Morel, Rondi-Constanzo & Ugolini 2000). More recently recreational divers are being increasingly attracted by the aesthetic quality of red coral populations. Intensive harvesting (Santangelo *et al.* 1993a; FAO 1998) is the major and oldest source of disturbance in red coral populations. Although partial, data on fisheries (Cudoni, Chessa & Pais 1992; Marin & Reynal de Saint-Michel 1981; Santangelo, Abbiati & Caforio 1993b) attest that harvesting has driven a dramatic shift in the size structure of red coral populations in the Mediterranean, i.e. from virgin mature populations comprising large-sized colonies to populations only composed of colonies below the smallest commercial size. Besides harvesting, large-scale mortality events probably associated with climatic change (Harmelin 1984; Cerrano *et al.* 2000; Perez *et al.* 2000; Garrabou *et al.* 2001) or pollution (Arnoux *et al.* 1992) have recently been documented.

In spite of being both an emblematic and a commercial species, little is known regarding the biology and life history of red coral (Charbonnier & Garcia 1984). The few studies available depict red coral as a long-lived species (decades) with slow growth rate (Lacaze-Duthiers 1864; Harmelin 1984; Garcia-Rodriguez & Masso 1986; Abbiati *et al.* 1992; Allemand 1993). A long-term colonization experiment in a semi-dark cave started in 1969 (Harmelin *et al.* 1970), and surveyed photographically for more than 20 years, offered a unique opportunity to study red coral life-history traits for the first time over two decades. This study has provided long-term data on red coral's survivorship, whole and partial mortality, recruitment and growth. Furthermore, since red coral populations in the study region are submitted to intensive harvesting (legal and poaching), size-related effects of this activity on populations were examined through comparison with non-harvested populations. Data provide new insights for the conservation and management for this precious coral which could be applied to species with similar life histories and harvesting pressure.

Materials and methods

STUDY AREA

The study area is the limestone rocky coast around Marseilles, France. Habitat characteristics, i.e. frequent occurrence of submerged cavities and overhangs (Laborel & Vacelet 1961), together with instability of water column during summer and other oceanographic features in the study area, favour the development of red coral at shallow depths. The study area is characterized by active seawater circulation and relatively high productivity because of the combined effects of the northern current, strong wind-induced upwellings and the vicinity of the river Rhone.

LONG-TERM COLONIZATION EXPERIMENT SITE

The experiment site is a submarine cave located at the bottom of a vertical cliff on the south coast of Riou

Island (43°10′40″N, 5°23′50″E). Although widely open (entrance ceiling-floor depths: 20–32 m, horizontal extension: 25 m) this cave receives only dim light. At the surface of the experimental panels (see below) light was 2·3 ± 1·9% of that measured at the same depth in open water and 0·2 ± 0·1% of that at the subsurface (average of six measurements made at noon in May, July, August and October with a quantum photometer Li-Cor Li 185B and a spherical sensor SPQA 0308); Li-COR Nebraska, USA). The mean temperature in 2000 at 25 m depth in the study area was 12·88 ± 0·15 °C in February (coldest month) and 19·41 ± 3·02 °C in August (warmest month) (*in situ* measurements with Hugrun temperature logger (Hugrun, Reykjavik, Iceland), measurement interval: 2 h).

The cave walls harbour the succession of sessile invertebrate assemblages whose composition and spatial distribution from the entrance to the interior are typical of sublittoral cavities of the NW Mediterranean (Laborel & Vacelet 1958; Harmelin, Vacelet & Vasseur 1985). At the experiment location, the community was dominated by thick encrusting (e.g. *Oscarella* spp., *Reniera fulva* Topsent, 1893, *Pleraplysilla spinifera* (Schulze, 1878), *Crella mollior* Topsent, 1925) and massive (e.g. *Aplysina cavernicola* (Vacelet, 1959), *Cacospongia scalaris* Schmidt, 1862, *Petrosia ficiformis* (Poiret, 1789)) sponges. The other main macroscopic components of the community included the anthozoans *Caryophyllia inornata* (Duncan, 1878), *Hoplangia durotrix* Gosse, 1860, *Leptopsammia pruvoti* Lacaze-Duthiers, 1897 and *Corallium rubrum*, the ascidian *Aplidium fuscum* (Drasche, 1883), and numerous small-sized serpulid and bryozoan species.

COLONIZATION EXPERIMENT AND PHOTOGRAPHIC SURVEY

A colonization experiment was set up in 1969. Twelve 20 × 20 cm^2 panels were installed on the eastern lateral wall of the cave at 27 m depth and 20 m from the entrance. This experiment was part of a project aiming to study the colonization of sublittoral hard substrates under natural conditions (Harmelin *et al.* 1970). The panels were made of Urgonian (Lower Cretaceous) limestone, i.e. of the same geological nature as the local coast, in order to facilitate the outcome of natural processes of substrate colonization, including bioerosion by borers. They were attached together within a frame roped off to the wall. Two panels were lost accidentally during the 1980s, leaving a total of 10 panels for analysis, i.e. 4000 cm^2. Two photographs per panel, corresponding to the upper and lower panel halves, were taken at distinct sampling intervals from 1979 to 2000 (i.e. 21 years of monitoring), quarterly from 1979 to 1985, and quarterly to annually from 1985 to 2000. Photographs (colour slides) were taken with diverse Nikonos cameras (Nippon Kogaku, Tokyo, Japan) fitted with UW 28 mm and close-up lenses, and an electronic strobe. A fixed frame ensured constant picture field (21 × 12·7 cm) and parallelism between the panel and film planes.

LIFE-HISTORY TRAITS STUDY

The life-history traits of *C. rubrum* colonies growing on the panels were surveyed on selected photographs corresponding to about 1-year intervals. Slides were projected with an inverse projector and each *C. rubrum* colony observed was mapped and registered with an individual identification number. The first red coral colonies settled on the panels in 1976 after 7 years of submersion (Harmelin 1980). By then the panels were already completely colonized, predominantly by various thin encrusting demosponges, some anthozoan species and various sets of small-sized erect and encrusting invertebrates, similar to those found on the adjacent walls. However, massive sponges that predominate in the mature communities were still absent from the panels (Harmelin 1980, 1984). Unfortunately no photographic information was available on the first red coral recruits at the time of their settlement. The survey of the 67 red coral colonies that recruited onto the 10 panels during the 1976–2000 period allowed about 1000 observations on the following life-history traits.

Survival and mortality

The life table of the 52 colonies recorded in 1979 on the first photographs was set out on the assumption that those colonies settled between 1976 and 1978. This settlement time was indicated by the small size of those colonies in 1979 (height < 1 cm: 49 colonies, *c.* 1·5 cm: 3 colonies) and the growth rate displayed by the later recruits. Each case of whole and partial mortality that occurred between 1979 and 2000 was noted with its presumed cause.

Former observations on the causes of mortality of red coral colonies indicated that overgrowth by other components of the community could have a significant impact on young colonies (Harmelin 1984). For this reason we noted all ongoing overgrowth events at each sampling date and identified the overgrowing species when possible.

Recruitment

Juvenile colonies not mapped in the previous panel photographic sequences were considered as recruits. Recruitment rate was considered as the total number of recruits apparent at each sampling date (i.e. roughly each year) in the 10 panels (4000 cm^2).

Growth rate

Growth rate was assessed in colonies used in the life table through two approaches. Firstly, the mean annual growth rates of all colonies that recruited during the 1976–78 period, choosing arbitrarily 1978 as the

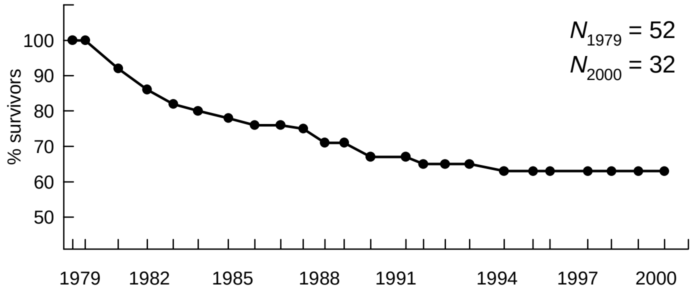

Fig. 1. Survival curve for red coral (*Corallium rubrum*) colonies settled in the experimental panels between 1976 and 1979.

recruitment year for calculations, and were still alive in 2000 were calculated by measuring *in situ* their basal diameter with callipers and their maximum height with a ruler. In these calculations it was assumed that colonies had no axial skeleton at recruitment time and that thickness of the coenchyme was negligible in the colonies measured in 2000. Secondly, the temporal pattern of development of branching was examined in the same colonies. We noted arbitrarily 0 branch when non-ramified colonies were smaller than about 1 cm in height. This allowed us to distinguish recently recruited from older colonies with a single branch.

COMPARISON OF PANEL AND MATURE COMMUNITY SUBPOPULATIONS

The size structure and density of colonies occurring in the 10 panels and in the mature community beside the panels were recorded in June 2000 in order to compare the degree of development of both subpopulations and to give insights into population dynamics at the study site. The mature community features were assessed by counting and measuring as above all colonies found in 20 quadrats (20×20 cm^2) placed at random on the wall beside the panels.

HARVESTING IMPACT ON SIZE STRUCTURE OF RED CORAL POPULATIONS

In the study area, red coral populations have been reputed and exploited (using different kinds of gear and techniques) since the ancient and medieval ages (Morel *et al.* 2000). At present, harvesting is only authorized for registered divers, but poaching is likely to be common. Official fishing files reporting harvesting localities indicate that our study area has been recently harvested. Harvesting by divers threatens principally the largest, most attractive, colonies. Therefore, we contend that the size of the largest colonies observed in the populations are good indicators of the harvesting level and provide reliable information on the potential size reached by red coral colonies in populations free of harvesting.

Eleven local populations were surveyed in 1998, 10 regularly harvested in the Riou archipelago (including the experiment site) and one in the only non-harvested area in the study region, the marine reserve of Carry-le-Rouet (see Table 4 for characteristics of each site). In this marine reserve, situated about 20–24 km from Riou archipelago, all human activity has been prohibited since 1983 (Francour *et al.* 2001). At each surveyed site, after an inspection of the whole local population, about 30 of the largest colonies were selected and their basal diameter and height were measured as above. This data set was completed with measurements on large-sized colonies from a presumably pristine population. These colonies, belonging to a private collection, were collected in 1962 in shallow-water habitats (25–35 m depth) on the northern face of the Cap de Creus (NE Spain).

Results

SURVIVORSHIP AND MORTALITY

The survivorship of the 52 colonies that settled on the panels in 1976–78 is illustrated by the cumulative survival plot of these colonies (Fig. 1). This survival curve shows three successive phases in the mortality rate during the 21-year period: (i) a phase of high mortality during the three first years, (ii) gradual decrease and stabilization of the mortality rate during the following 10 years (cumulative survival was around 0·6), and (iii) lack of mortality among the remaining colonies during the 1994–2000 period.

Mortality affected 31 colonies out of the 67 that were recorded on the panels between 1979 and 2000. According to the results of the life table, all colonies that died were younger than 15 years, almost 80% of them were 0–9-year-old colonies, the youngest (<3 years old) being the most severely affected by mortality (Fig. 2). The possible relationships between age and mortality were examined pooling data on colonies' age at death or undergoing partial mortality (see below) into a two-way table analysed by homogeneity tests (taking into account all colonies found on the panels during the 21-year survey). The age-related mortality pattern was statistically significant ($\chi^2 = 59{\cdot}8$; d.f. = 3; $P < 0{\cdot}001$; Fig. 2).

Overgrowth was the most common cause of death (about 55%), followed by colony toppling (9·7%). Other causes of mortality included complete coenchyme loss (Table 1) and non-identified causes, which probably also correspond, in most cases, to overgrowth processes.

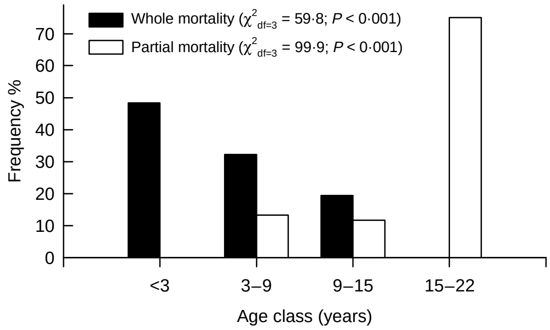

Fig. 2. Effect of age on whole and partial mortality in red coral (*Corallium rubrum*) colonies settled in the experimental panels (1976–2000).

Table 1. Causes of whole and partial mortality by age classes

Age class	Overgrowth	Breakage	Others
Mortality			
<3	29·0	0·0	19·4
3–9	19·4	0·0	12·9
9–15	6·5	9·7	3·2
15–21	0·0	0·0	0·0
Total	54·8	9·7	35·5
Partial mortality			
<3	0·0	0·0	0·0
3–9	8·3	1·7	5·0
9–15	8·4	10·0	1·7
15–21	43·3	0·0	21·6
Total	60·0	11·7	28·3

Table 2. Species and categories identified in overgrowth events and percentages of events where those species were implied in overgrowth events (total number of overgrowth events = 124)

Species	Percentage
Sponges	54·8
Cacospongia scalaris	17·7
Cacospongia scalaris + other	7·3
Pleraplysilla spinifera	9·7
Oscarella spp.	4·8
Crella mollior	4·8
Other sponges	10·5
Ascidian	25·8
Aplidium fuscum	19·4
Aplidium fuscum + sponge	5·6
Aplidium fuscum + other	0·8
Fouling	8·9
Other	10·5

PARTIAL MORTALITY

Sixty partial mortality events were recorded on 29 colonies out of 67 monitored in this study. This result indicates that some colonies suffered several events during their life span while 38 colonies were spared by this disturbance. The oldest colonies accounted for almost 80% of all partial mortality events while younger colonies suffered far fewer (age < 15 years) or no (age < 3 years) partial mortality events (Fig. 2). The probability of partial mortality occurrence increased significantly with age ($\chi^2 = 99{\cdot}9$; d.f. = 3; $P < 0{\cdot}001$; Fig. 2). The main causes of partial mortality were breakage of branches (60·0%), followed by overgrowth (11·6%) and coenchyme loss (11·6%) (Table 1).

OVERGROWTH

A total of 124 overgrowth events were observed, involving or not whole or partial mortality in 38 different colonies. Thus some colonies were overgrown more than once. In many cases colonies older than 5 years remained partially overgrown during several consecutive years, especially when massive overgrowers were involved. For instance, overgrowth by the sponge *Cacospongia scalaris* usually lasted more than 4 years (up to 9 years in one case). Sponges and the ascidian *Aplidium fuscum* were responsible for most overgrowth events (Table 2). Among sponges *C. scalaris* accounted for most interactions followed by *Pleraplysilla spinifera, Oscarella* spp. and *Crella mollior* (Table 2).

RECRUITMENT

Most recruits (n = 52: 77·6%) appeared during the 1976–78 period and afterwards the annual recruitment observed on the panels was nil or limited to one or two recruits until June 2000 (Fig. 3). Only 15 recruits appeared during this 21-year long period of low recruitment and the mean recruitment rate was only 0·71 ± 1·27 recruit year^{-1} 0·4 m^{-2}.

GROWTH RATE

The mean basal diameter of the oldest colonies in the panels still alive in June 2000 (n = 32) was 0·53 ± 0·12 cm and their mean height was 3·92 ± 1·48 cm (Table 3). Thus, growth over 22 years averaged 0·24 ± 0·05 mm year^{-1} for the basal diameter, with a maximum and minimum of 0·36 and 0·18 mm year^{-1}, respectively. Whereas average growth rate was 1·78 ± 0·67 mm year^{-1} for colony height, with a maximum and minimum of 3·18 and 0·59 mm year^{-1}, respectively. On the other hand, the mean number of branches in the same set of 22-year-old colonies increased steadily from 0 to 4·5 branches during the 1979–94 period, and decreased afterwards fluctuating between 3 and 4 branches (Fig. 4). The range of sizes observed among colonies having the same age was particularly wide. In 22-year-old colonies, size of colonies ranged from 0·4 to 0·8 cm for basal diameter, from 1·3 to 7·0 cm for height and from 1 to 8 for the branch number.

COMPARISON OF SIZE STRUCTURE AND DENSITY BETWEEN PANEL AND ADJACENT WALL SUBPOPULATIONS

Differences in density and size of colonies between both subpopulations were compared with a t-test after

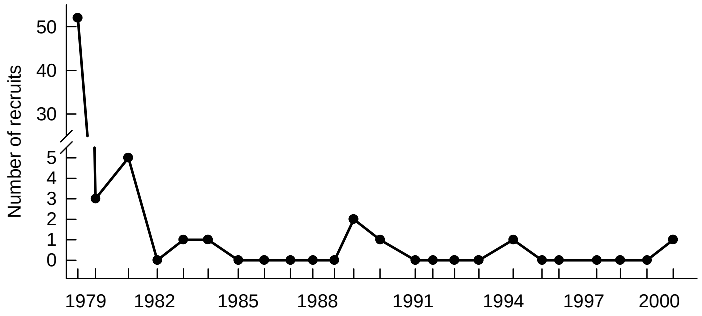

Fig. 3. Recruitment rate of red coral (*Corallium rubrum*) on the experimental panels (1976–2000).

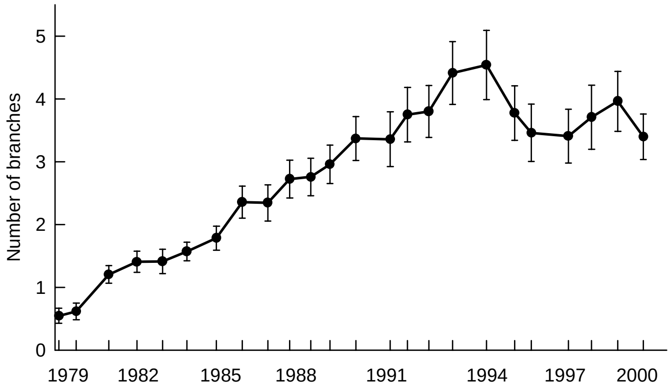

Fig. 4. Means (± ES) of number of branches of red coral (*Corallium rubrum*) colonies settled on the experimental panels between 1976 and 1979.

Table 3. Descriptive statistics for density (number of colonies per 400 cm^2 quadrats), diameter (cm) and height (cm) in June 2000 of red coral (*Corallium rubrum*) colonies on the panels (i.e. those recruited between 1976 and 1979 and later) and on the adjacent wall. N: number of quadrats (density) and colonies (diameter and height)

	Experimental panels			Mature community		
Site	*N*	Mean ± SD	Range	*N*	Mean ± SD	Range
Whole colonies						
Density	10	3·6 ± 1·2	2–7	20	2·6 ± 1·2	0–5
Diameter	36	0·52 ± 0·13	0·2–0·8	61	0·42 ± 0·14	0·2–0·7
Height	36	3·73 ± 1·63	0·2–7·0	61	3·51 ± 2·03	0·5–9·0
22-year-old colonies						
Diameter	32	0·53 ± 0·12	0·4–0·8			
Height	32	3·92 ± 1·48	1·3–7·0			

testing the homogeneity of variances with Levene's test. Colony densities on the panels (3·6 ± 1·2 col. 400 cm^{-2}) and the cave wall (2·6 ± 1·2 col. 400 cm^{-2}) were not significantly different ($t = 1{\cdot}87$, d.f. = 28, $P = 0{\cdot}07$). On the panels the average size of colonies was larger and less variable than on the cave wall (Table 3, Fig. 5). However, differences were clearly significant for diameter ($t = -3{\cdot}42$, d.f. = 95, $P < 0{\cdot}001$, panels > wall) but not for height ($t = -0{\cdot}54$, d.f. = 95, $P = 0{\cdot}055$) (Fig. 5).

HARVESTING IMPACT ON MAXIMUM COLONY SIZE IN RED CORAL POPULATIONS

Differences in the maximum size of colonies between harvested populations and the two non-harvested populations (Carry-le-Rouet reserve and private collection) were examined with a one-way ANOVA after testing the homogeneity of variances with Levene's tests. Whenever the homogeneity of variances was not met, a log transformation was applied to data, successfully removing their heterogeneity. Clear-cut significant differences in maximum basal diameter ($F_{2,397} = 331{\cdot}86$, $P < 0{\cdot}001$) and maximum height ($F_{2,397} = 162{\cdot}1$, $P < 0{\cdot}001$) were found between harvested and non-harvested (data from a Marine Reserve and private collection) populations (Figs 6 and 7, Table 4). Tukey's post-hoc comparisons denoted significant differences between the three groups of populations for basal diameter ($P < 0{\cdot}001$) and between non-harvested and harvested populations for maximum height

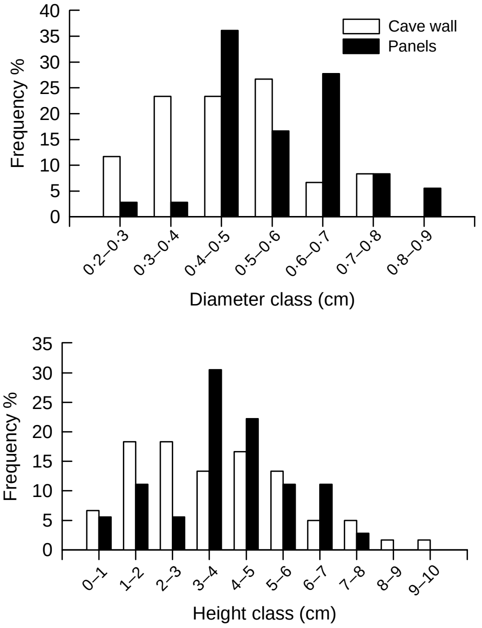

Fig. 5. Size structure distribution (basal diameter and height) of red coral colonies (*Corallium rubrum*) dwelling in the experimental panels and in the mature community at the study site in June 2000.

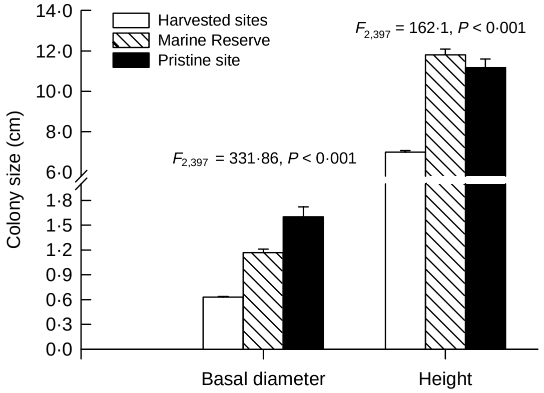

Fig. 6. Means (± ES) of maximum basal diameter and height of red coral (*Corallium rubrum*) colonies in harvested populations (10 populations) and in two non-harvested populations. Data from Carry-le-Rouet marine reserve and from a private collection of large-sized colonies collected in 1962 in the same habitat. For site characteristics and descriptive statistics see Table 4.

($P < 0{\cdot}001$) but not between the two non-harvested populations.

The largest basal diameter observed in the harvested populations was 1·1 cm (1 case over 325 colonies measured), i.e. smaller than the average value observed in the protected site (1·16 cm) and the minimum value in the private collection (Table 4). The largest maximum basal diameter (4·5 cm) observed from the presumed pristine population (private collection) was 2·6 cm larger than the maximum diameter occurring at the site protected for 15 years. Overall, these results stress the evidence that harvesting dramatically affects the size structure of red coral populations, preventing the colonies from reaching their potential maximum size.

Discussion

For the first time long-term data on the life history of red coral are provided from direct observations of the fate of individual colonies. Our study provides indisputable data on the longevity of colonies and the parsimonious population dynamics of *C. rubrum*. The red coral populations are shaped by the pulse mode of

Table 4. Characteristics of study sites and descriptive statistics for maximum sizes diameter (cm) and height (cm) in harvested and non-harvested red coral (*Corallium rubrum*) populations. Measurements were made *in situ* during summer 1998 except for colonies from the private collection which were collected in 1962 and measured in the lab

				Maximum basal diameter (cm)		Maximum height (cm)	
Site	Habitat	Depth (m)	*N*	Mean ± SD	Range	Mean ± SD	Range
Harvested							
Maire	Overhangs	40	31	0·65 ± 0·13	0·4–0·9	7·3 ± 1·15	5·8–10·0
Ile Plane, Grotte Pérès	Cave interior	10–15	33	0·56 ± 0·09	0·4–0·7	6·23 ± 1·04	4·0–9·0
Ile Plane	Overhangs	35–40	32	0·61 ± 0·17	0·3–1·0	6·59 ± 1·4	4·2–10·0
Ile Riou, Moyade	Cave interior	23	31	0·58 ± 0·1	0·4–0·8	5·99 ± 1·07	4·2–8·0
Ile Riou, Moyade	Overhangs	35–40	31	0·65 ± 0·15	0·4–1·0	6·19 ± 0·86	5·0–8·0
Ile Riou, Grotte Sud*	Cave entrance	23–27	34	0·6 ± 0·09	0·4–0·8	9·72 ± 1·7	7·0–13·0
Imperial du Milieu	Overhangs	28–45	27	0·7 ± 0·18	0·4–1·1	5·67 ± 0·87	4·0–7·5
Pointe Caramasaigne	Overhangs	47–50	31	0·63 ± 0·09	0·5–0·9	7·08 ± 1·5	5·0–11·0
Grand Conglue	Overhangs	38–45	41	0·71 ± 0·13	0·5–1·0	7·6 ± 1·25	5·0–11·0
Petit Conglue	Overhangs	27–30	35	0·67 ± 0·13	0·5–1·0	6·95 ± 1·66	4·0–10·5
Overall harvested			325	0·64 ± 0·05	0·3–1·1	6·93 ± 1·16	4·0–13·0
Non-harvested							
Marine Reserve Carry-le-Rouet	Overhangs	23	45	1·16 ± 0·28	0·8–1·9	11·81 ± 1·93	8·0–17·0
Private collection Cap de Creus	Overhangs	25–35	30	1·60 ± 0·39	1·0–4·5	11·45 ± 2·49	6·0–15·5

*Experiment site.

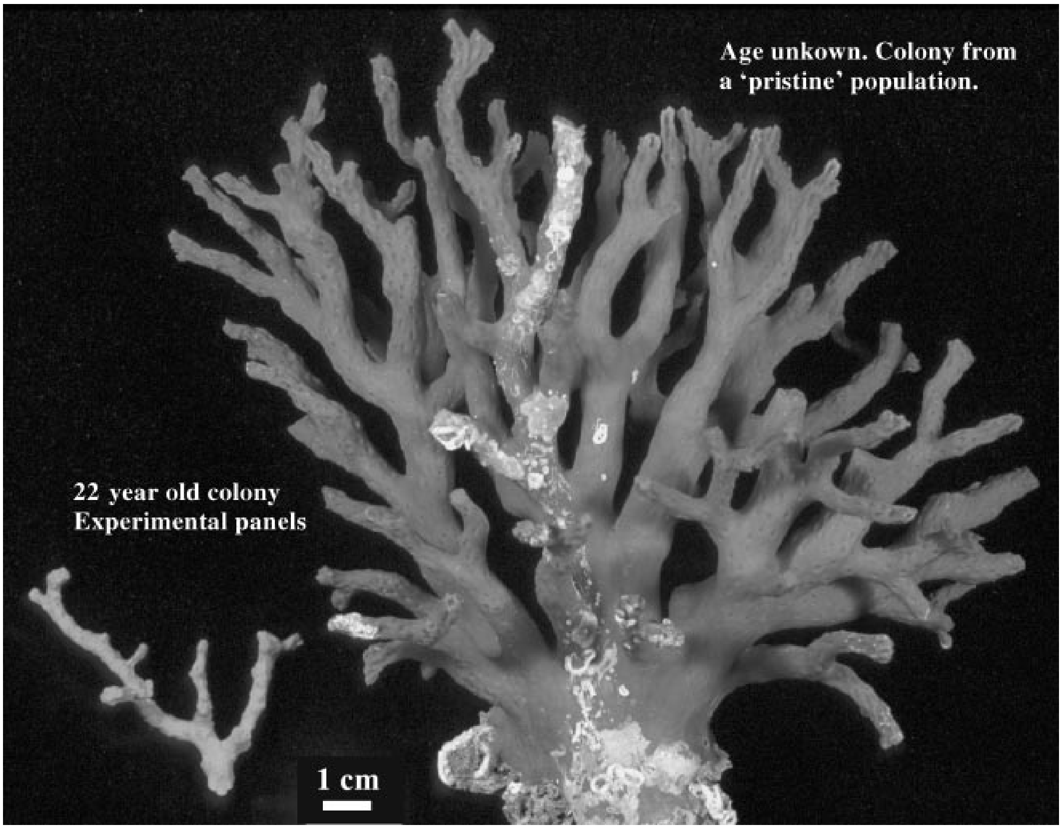

Fig. 7. A 20-year-old red coral colony collected in 2000 from the experimental panels and a colony from a pristine site (age unknown) collected at the same depth in 1962 from the private collection.

recruitment, the high mortality rate of juvenile colonies, and the very slow growth rate of surviving colonies, whose potential life span can reach many decades. Thus, the combination of high adult survivorship with pulse recruitment and high early postrecruitment mortality is consistent with the 'bet-hedging' interpretation of life-history patterns (Stearns 1992).

SURVIVORSHIP AND MORTALITY

The mortality rate decreased clearly over the first 15 years of life while older colonies only underwent partial mortality (Figs 1 and 2). This pattern has also been found in other long-lived benthic clonal invertebrates such as corals (Hughes & Jackson 1985; Garrabou 1999; Hughes & Tanner 2000). In red coral, as in other sessile clonal organisms, lower vulnerability of large colonies may result from higher ability (i) to withstand complete overgrowth by competitors for space and (ii) to compensate biomass losses, whatever their causes (e.g. predation, partial overgrowth, necrosis) (Buss 1980; Connell 1973; Jackson 1979; Sebens 1982, 1986; Sousa 1984).

Overgrowth was the major cause of mortality of the young red coral colonies living on the panels, as reported for other sessile invertebrates (Richmond 1997). Various sponges or one ascidian species were responsible for most overgrowth events (Table 2). This outcome is consistent with the phyletic hierarchy observed elsewhere in interactions among sessile components of animal-dominated communities (Jackson & Buss 1975; Jackson & Winston 1982; Russ 1982; Nandakumar, Tanaka & Kikuchi 1993).

In older colonies (>5 years) breakage of branches was another major cause of partial mortality. The causes of this biomass loss were not identified but the action of microborers and shocks, e.g. by exceptional sea-storms or large fish (e.g. resident conger eel) or divers are the most probable factors. Fragmentation of branch tips by autotomy may also have occurred since it was observed in red coral colonies reared in aquarium (Russo, Ulianich & Cicogna 1997). More generally, cryptic communities are devoid of active grazers (e.g. sea urchins, herbivorous fish) (Jackson & Kaufmann 1987) that could induce strong disturbances and affect the community development, as commonly observed in well-lit communities (Sala, Boudouresque & Harmelin-Vivien 1998 and references therein). No sign of predation was observed on the monitored colonies throughout the whole study period. Predators of red coral are scarce (Santangelo *et al.* 1993b) and, as in other sessile invertebrate dominated communities (Garrabou *et al.* 2002), predation appears to play a minor role in the red coral community. The temperature-induced mortality that affected red coral populations in the study area in 1999 (Garrabou *et al.* 2001) also affected the colonies monitored in this study. About

40% of colonies suffered coenchyme loss but none died. Many of the affected colonies recovered partially through coenchyme recolonization of axes within the year following the event but they also suffered partial or complete lost of some of their branches. Injuries and regeneration are widespread and variously scaled processes among gorgonian species (e.g. Wahle 1983; Bavestrello & Boero 1986). As stressed by Wahle (1983), long disruption of the colony-wide integration of physiological functions, such as reproduction and nutrition, may have severe consequences on the growth dynamics and long-term survival of colonies.

GROWTH RATES

The long-term monitoring of colonies of known age made it possible to record indisputable data on the basal diameter growth rate. These values are considerably lower than those reported in the literature (i.e. 0·24 mm year^{-1} vs. 0·91 mm year^{-1} in Abbiati *et al.* 1992 and 1·32 mm year^{-1} in Garcia-Rodriguez & Masso 1986). We contend that this strong difference probably resulted from an overestimation of growth rates introduced by non-validated sclerochronology methods applied in previous studies. According to those growth rates estimations, the basal diameter of 22-year-old colonies would have reached 2·0 cm or 2·9 cm, instead of 0·5 cm, as observed. A 10-year study (1991–2001) of the size structure of several red coral local populations in the Medes Islands protected area (Linares, Hereu & Zabala 2000) also attests to the overestimation of the previous growth rates. The same indication is given by the comparison of sizes reached by the largest red coral colonies in the marine reserve of Carry-le-Rouet after 15 years of strict protection.

However, part of this discrepancy may also result from interhabitat environmental differences. In general, water flow and trophic inputs are reduced in caves (Fichez 1991; Garrabou & Flos 1995; Harmelin 2000). Our experimental site, although widely open and exposed to hydrodynamics from the strong easterly wind, may be more sheltered than the habitats sampled by Garcia-Rodriguez & Masso (1986) and Abbiati *et al.* (1992). These poor flow conditions could limit growth in passive suspension-feeders such as red coral (Leversee 1976; Patterson 1991). In any case, efforts should be focused on sclerochronology methods that could supply reliable information on red coral growth rate and its variations under different conditions.

Even within the relatively homogeneous panel microcosm, the colonies showed a high variability in growth as denoted by the wide array of sizes (especially in height and branch number) reached within the same cohort (Fig. 4). However, the coefficient of variation of the mean basal diameter is relatively low (22·6%). Biotic and physical interactions acting at the panel and smaller spatial scales, such as food depletion, allelopathy, overgrowth by neighbours or alterations of microflow conditions, are the most likely sources of this variability (Buss 1979; Leichter & Witman 1997). In fact, such high individual variability in dynamics appears to be a typical feature of most clonal organisms inhabiting the same kind of community (e.g. Turon & Becerro 1992; Coma *et al.* 1998; Garrabou 1999).

RECRUITMENT

The recruitment of red coral on the panels was characterized by a 21-year period of extremely low yearly rates preceded by one relatively early peak corresponding to the recruits that founded the panel subpopulation between 1976 and 1978 (Fig. 3). The same pattern was reported from long-term monitoring (>5 years) of recruitment in other long-lived invertebrate species attached to hard bottoms (Yoshioka 1996; Connell *et al.* 1997; Hughes & Tanner 2000).

The short period of high recruitment, assumed to be centred on the year 1977, may result from a pulse supply of larvae, or/and from the brief occurrence of habitat conditions particularly suitable to settlers during the early successional stages of the panel community. On the other hand, further pulse recruitment events may have been prevented by the monopolization of space by thick encrusting and massive sponges during later successional stages.

Pulse recruitment events involving the supply of water-borne larvae are often linked to more or less episodic variations in the climatic-oceanographic conditions, such as storms and associated water transfer, upwellings or meanders of mesoscale currents (Roughgarden, Gaines & Possingham 1988; Letourneur *et al.* 1998). This may apply to the present situation in spite of the small scale at which the supply side processes (Fairweather 1991) act locally due to the habitat type and the probable self-sustaining nature of the local population (see below). For instance, a swarm of larvae might have been concentrated and advected to the panels by exceptional storm-induced water movements during red coral spawning.

In any case, saturation of space and interference competition appear to be a major controlling factor in red coral recruitment as attested by the small proportion of small-sized colonies observed in the study site (Fig. 5) as well as in other red coral populations (Santangelo, Abbiati & Caforio 1988; Garrabou *et al.* 2001). This could explain why recruitment rates were higher after harvesting events (Santangelo, Bongiorni & Buffoni 1997; Linares, Hereu & Zabala 2000).

Dispersal of red coral lecitotrophic planulae is probably restricted to short distances because of their free life is brief, reaching 4–12 days under laboratory conditions but probably much less in the field (Vighi 1972; Weinberg 1979; Grillo & Chessa 1992). Low natatory capability and geonegative behaviour tend to confine larvae to the vicinity of parental colonies within cavities (Weinberg 1979). These philopatric dispersal features are reflected in the frequent aggregative distribution of red coral colonies (Harmelin 1985) and by the limited gene flow between populations (Abbiati, Santangelo & Novelli 1993).

Thus, the long-term recruitment pattern observed on our panels appears to be based on two successive phases – foundation pulse and sustaining regime – that may be typical of the population dynamics and spatial distribution of the long-lived organisms dominant in dimly lit habitats.

RED CORAL POPULATION RESTORATION CAPABILITY AND CONSERVATION

In the studied site, more than 20 years were necessary for the red coral subpopulation established on the panels to reach the development (colony size and density) of that harboured by adjacent walls (Fig. 5 and Table 3). One may note that this local population is itself obviously not at a mature state because of harvesting and poaching by divers. For instance, the experiment site was harvested by a professional coral fisherman in 1977 (fishing records provided by the Marine administration). The largest colonies occurring on the walls in 2000 as well as the 22-year-old colonies from the panels had not yet reached commercial size. This evidence and the striking differences in maximum size between harvested and non-harvested sites (marine reserve and 'pristine' site) (Fig. 6; Linares *et al.* 2000; J. Garrabou & J. G. Harmelin personal observation) attest that harvesting is the major cause of mortality of large colonies. Thus, this activity keeps red coral populations in a 'young' state with regard to potential longevity and maximum size of colonies.

Mediterranean marine protected areas offer an excellent opportunity to observe the recovery of red coral populations in shallow-water habitats in the absence of harvesting. Unfortunately, baseline information on the prefishing status of populations (size structure and density of colonies) in shallow-water habitats is lacking. However, some rare historical fishing records, accounts from old divers who harvested red coral during the 1950s, and sizes of colonies collected in 1962 at Cap de Creus attest that size of colonies was considerably larger in shallow-water habitats than today (Audivert 1971; Santangelo *et al.* 1993a; Fig. 6 and Table 4). It seems reasonable to consider that colonies double the size of those found today in marine reserves (i.e. 2 cm in basal diameter) were abundant in the past. Bearing in mind the results of this study, such colony sizes might require at least 80 years of uninterrupted growth. This scenario suggests that the full recovery of red coral populations requires decades or centuries of effective absence of harvesting. The few Mediterranean marine reserves that harbour red coral are younger than 30 years old and thus still a long way from complete recovery (Francour *et al.* 2001). More research should be devoted to population baselines in order to provide more reliable management plans for the harvesting and conservation of red coral.

Red coral populations are not at risk of extinction under the present harvesting pressure since reproductive maturity occurs in small-sized (<3 cm in height), non-commercial colonies (Abbiati *et al.* 1992; O. Torrents, J. Garrabou & J. G. Harmelin, unpublished data). Sport diving activities are expected to have a limited impact on populations, e.g. breaking tips of branches. However, the potential risks of mechanical disturbance and poaching events will increase in the near future with the predicted increase of diving (Sala, Garrabou & Zabala 1996; Garrabou *et al.* 1998). Management initiatives, including the education of divers are desirable to limit the damage induced by excessive frequentation. The major risk for the conservation of red coral may come from very strong disturbances affecting local populations. For instance, red coral was affected by massive mortality in 1999 in some shallow local populations (Garrabou *et al.* 2001). This unusual mortality event was linked to a temperature anomaly reported in the NW Mediterranean (Cerrano *et al.* 2000; Perez *et al.* 2000; Romano *et al.* 2000). Under the global change scenario the repetition of this kind of disturbance is predictable in future decades in shallow-water habitats (Hughes 2000; Garrabou *et al.* 2001). Recovery from such events seems uncertain considering the slow dynamics and recruitment limitation, and the low rate of exchange among local populations (Abbiati *et al.* 1993), particularly if source populations for replenishment are in deep-water habitats. Therefore, reinforced management strategies (e.g. complete prohibition of harvesting at shallow depths) should be adopted if we want to preserve near-shore red coral populations.

Conclusion

Long-lived organisms, such as red coral, usually display slow population dynamics, rendering them vulnerable to strong disturbance events (Hughes & Connell 1999; Hughes & Tanner 2000). Marine habitats are exposed to new disturbances sources for which they are not adapted. Among them the direct and indirect effects of overfishing and global change could be pointed to as the most important. These kinds of disturbances have already caused dramatic changes in various marine coastal systems and threaten their conservation (Jackson 2001; Knowlton 2001). It has highlighted the need for long-term, large-scale studies in marine habitats for a better comprehension of the functioning of marine communities (Yoshioka 1994; Hughes & Connell 1999; Jackson *et al.* 2001). However, little research has been devoted to this goal. We contend that we will be able to furnish relevant data for the conservation and management of marine species and communities only through a renewed effort in furnishing data over larger temporal and spatial scales.

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