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## Article

# How to Survive Intensive Harvesting: The High Recruitment Rates of the Precious Mediterranean Red Coral (*Corallium rubrum* L. 1758)

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**Abstract:** The recruitment process is a fundamental step in population life cycles that determines survival, population demographic structure, and dynamics. The success of recruitment events repeated over successive years greatly affects the survival of long-lived gorgonian populations. Here, we report the recruitment process of the precious, heavily harvested Mediterranean gorgonian *Corallium rubrum* (red coral) on both settlement tiles and natural substrates over different Mediterranean areas. Red coral is a gonochoric internal brooder that reproduces in early summer. Lecithotrophic planulae settle 15–30 days after release in semi-dark environments at depths between 15 and 800 m. In autumn, 0.58–0.68 mm-wide recruits can be observed on the vaults of small crevices and caves and on rocky cliffs and boulders. Owing to their small size, there is limited knowledge of *C. rubrum* recruitment in the field. In this study, we examined the recruitment density and distribution in Canadells (Banyuls sur Mer, France) and Calafuria (Livorno, Italy) and compared these findings with those collected over different Mediterranean areas. Red coral exhibited high recruitment values ranging from 0.43 to 13.19 recruits  $\text{dm}^{-2}$ . The distribution pattern of recruits, examined at a small spatial scale via nearest-neighbor distance analysis, revealed a significantly higher patch frequency on the natural substrate than on settlement tiles, presumably because of the scarcely available spots of free space on the former substrate, which are crowded by competitor species.

**Keywords:** precious corals; gorgonian corals; population recovery; recruitment; spatial distribution pattern; nearest-neighbor distances



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## 1. Introduction

Recruitment plays a fundamental role in community structuring and determines both diversity and dynamics [1]. In marine benthic sessile suspension feeders, which are characterized by the absence of migratory movements, variations in recruitment success can determine adult population abundance and population-age structure. After larval settlement, the populations of iteroparous sessile suspension feeders, which are characterized by “discrete” annual reproduction, remain stable or decrease, due to mortality, until the next reproductive event. Positive net recruitment rates are crucial to the survival and recovery of benthic and sessile species, whose populations have recently been affected by drastic mortality events linked to global climate change (GCC). In sessile benthic species, successful recruitment also provides an advantage when competing for free space on rocky bottoms [2–6]. A sharp increase in recruitment in the years following drastic mortality events is evidence of the recovery of coral populations subject to such events [7–9].

In the Caribbean Sea, octocoral populations show greater resilience to disturbances than scleractinians because of their higher fecundity, higher survival in early life stages, and higher recruitment rates [3,4,8,10]. The comprehension of the recovery dynamics in octocorals and their recruitment is limited, despite the fact that they are a major component

of the so-called “animal forests” [11,12] and of the highly biodiverse Mediterranean circalittoral “coralligenous” reef communities [13]. Gorgonian recruitment and early life stage dynamics are generally understudied because of the difficulty of identifying newly settled colonies, either by means of repeated sampling over time in a fixed area or by tagging early life stages. A common solution to this problem is the use of artificial substrates. For example, settlement plates have been used extensively to investigate the recruitment process in both scleractinians and octocorals, e.g., [14–16].

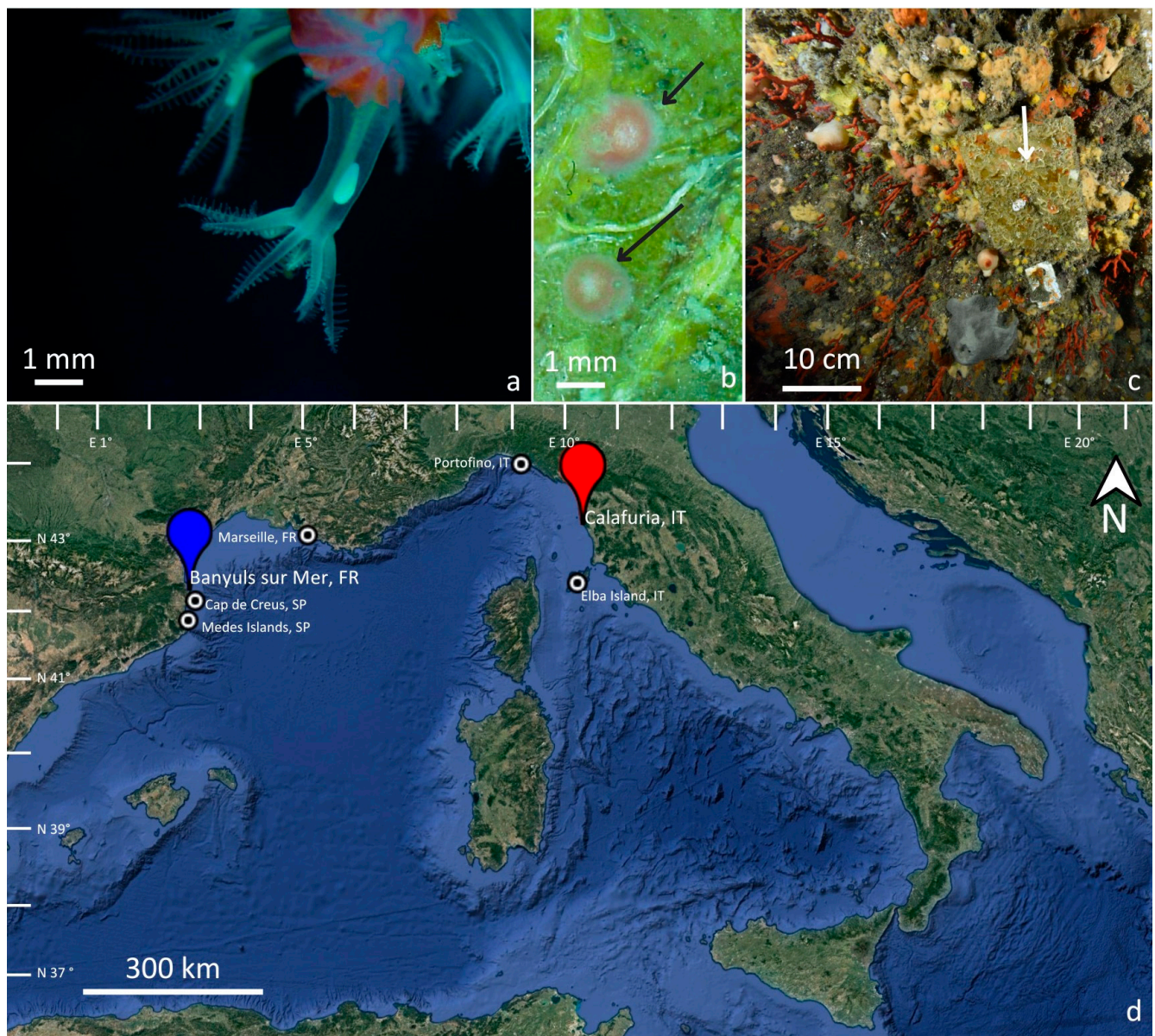
The highly valuable Mediterranean gorgonian coral *Corallium rubrum* (the red coral par excellence), which has been harvested for more than 2000 years, is a paramount example of an overexploited marine species (e.g., [17]). Even if local (and economic) extinctions occur in some areas [18], the wide geographic and bathymetric distribution of *C. rubrum*, together with its early age at sexual maturity [19,20], are likely key factors that allow this slow-growing, long-lived octocoral to survive the enduring exploitation in several Mediterranean areas [17,21]. Red coral is a gonochoric internal brooder that reproduces in early summer (Figure 1a). Lecithotrophic larvae (planulae) settle 15–30 days after release [22,23] in semi-dark environments, on the vaults of small crevices, overhangs, and caves, and on rocky cliffs and boulder sides at depths of 15–800 m [24].

Due to their small size (0.58–0.68 mm), identifying red coral recruits is extremely difficult in the natural environment (Figure 1b); however, some data have been collected on the recruitment and early life-cycle phases of this precious species on artificial settlement plates (Figure 1c). White marble tiles, the calcium carbonate composition of which is similar to that of the coralligenous substrate, have allowed researchers to identify the recruits and early life cycle stages of this octocoral [25–27]. As is typical for species with a highly localized distribution, the frequency of red coral patches (occupancy) and patch size are highly variable across geographic areas [12,28].

Several studies have focused on coral juveniles, including, within this large term, all new colonies produced by reproductive events. Here, we refer to the annual recruitment of red coral, considering “recruits” to be the newly settled colonies that are about six months old (belonging to the 0–1 year cohort), “juveniles” to be the non-reproductive colonies (belonging to the 1–2 years cohort), and “adult colonies” to be the older colonies (>2 years old).

We examined recruitment via macrophotographic sampling of marble tiles and natural substrates in two shallow (<50 m depth) red coral populations dwelling in the northwestern Mediterranean, one living at Banyuls sur Mer (France) and the other living in Calafuria (Italy). The obtained data were then compared with data collected from different red coral populations over different geographic areas, as well as with data concerning other gorgonians. The mathematical relationships between recruitment and adult colony density at different spatial scales and the spatial distribution pattern of red coral recruits were also examined using nearest-neighbor analysis on both settlement plates and the natural substrate.

Better knowledge of the recruitment rate of this precious gorgonian coral will improve demographic models established for this species, fostering both conservation and fishing regulations [29].



**Figure 1.** (a) Red coral polyps with planulae. (b) Two recruits on a marble tile (black arrows). (c) A settlement tile (white arrow) fixed on the vault of a crevice inhabited by red coral colonies. (d) Study areas: Canadells, Banyuls sur Mer (France) in blue and Calafuria, Livorno (Italy) in red. White spots mark other red coral populations mentioned in previous scientific publications.

## 2. Materials and Methods

### 2.1. Recruitment Density and Colony Size/Age Distribution

Marble tiles, 1 dm<sup>2</sup> each, were fixed by a central screw on the vaults of small crevices inhabited by red coral colonies [25] at the beginning of June between 24 and 29 m depth (water temperature at the fixing time: 15–16 °C) at Canadells, Banyuls sur Mer (France, 42°27.03' N, 03°09.59' E; Figure 1c,d). The Banyuls sur Mer red coral population dwells between 20 and 30 m depth, mostly inside small crevices. The area is characterized by high turbidity and has a highly diversified coralligenous community with thriving gorgonian populations (*Eunicella cavolini*, *Paramuricea clavata* and *Corallium rubrum*). No harvesting has occurred in the area for several years, thanks to the enforcement of the FAO-GFCM (General Fisheries Commission for the Mediterranean) recommendation to close red coral fisheries above 50 m depth [29].

In the study area, 18 marble tiles were randomly distributed at three randomly chosen sites (six tiles per site: west, east, and south Canadells) of approximately 10 m<sup>2</sup> each, approximately 100 m apart. Five months later, the tiles were photographed using a Canon G10 underwater-housed digital camera and a TTL strobe. To examine the local variability in recruitment density, the Kruskal–Wallis test was applied.

The density of adult red coral colonies on the natural substrate was measured in situ in thirty-three squares (4 dm<sup>2</sup> each) randomly distributed within each of the three sites, and 99 squares were examined for an overall surface area of 396 dm<sup>2</sup>. The variability between sites was examined using one-way ANOVA after Ln (X + 1) data transformation.

The correlation between adult and recruit density was examined at different spatial scales: at a meter scale (at each site at Canadells, Banyuls sur Mer), at a scale of hundreds of meters (different sites in Canadells, Banyuls sur Mer), and at hundreds of kilometers scale (different Mediterranean populations; data from [27,30]) by best fit R<sup>2</sup> and *r* Pearson's linear correlation coefficient.

The basal diameters of adult colonies were measured in situ using a caliper on a subsample of 62 randomly chosen specimens. The size/age distribution frequency of this population sample was based on the average annual growth rate of the basal diameter, previously measured in a red coral population dwelling in Cap de Creus, Spain [30].

## 2.2. Recruits, Juveniles, and Adult Colonies Spatial Distribution

Thirteen marble tiles (1 dm<sup>2</sup> each), were installed as described above, on the vault of small crevices inhabited by red coral within a 30 × 30 m area, at the beginning of June, between 25 and 38 m depth (water temperature at the fixing time: 15 °C) at Calafuria, Livorno (Italy 43°30' N, 10°20' E; Figure 1c). The Calafuria red coral population dwells between 22 and 43 m depths, below the summer thermocline, within a coralligenous community in which 40 sponge species have been identified [25]. This red coral population, dominating the small crevices and overhangs of a vertical cliff, is characterized by high density and a small colony size. Historically, this population was subjected to several studies and suffered intensive harvesting, which was prolonged until recent times [25,26,31].

Tiles were photographed at the end of November each year over four years using a Nikonos V underwater analogic camera with a 35 mm lens, TTL strobe, and macro 1:3 extension tube to which a 10 × 10 cm metallic frame was fixed by a stem. The frame, overlapping exactly with the tiles, allowed us to collect similar macrophotographs over time. The same procedure was followed to randomly collect photosamples of the natural substrate on which the frame was leaning. Thus, the collected photosamples were comparable to each other. This procedure provides a recruitment data series without removing the tiles from the substrate [31]. Tiles were recorded over a 4-year period, and data on four recruitment events for an overall number of 52 (13 × 4) photosamples of tiles and 52 of the natural substrate were thus collected [26,27].

Each macrophotographic sample (slide) was projected onto a screen and the point positions of red coral recruits, juveniles, and adults were identified and reported on a transparent sheet. The transparent sheets with the marked points were then processed using ADOBE PHOTOSHOP 7.0, to obtain a point pattern model on which the NIH-Image Program (USA National Institute of Health version 1.61) was applied [32]. A 79.89 pixel/cm scale was then tuned, and the distance of each recruit to the nearest neighbor (nearest neighbor distance; [33]) was calculated. Finally, the Clark–Evans aggregation test (with Donnelly correction for edge effects) was applied and the Clark–Evans index (R = observed/expected average NNDs) was calculated [34,35].

A 2 × 2 chi-square contingency table with Yeats correction [36] was used to test the observed proportion of aggregated/randomly distributed recruits on tiles and on the natural substrate.

### 2.3. *C. rubrum* Recruitment Data from the Literature

Overall, we analyzed nine scientific publications, one Master's thesis and one PhD thesis reporting on red coral recruitment density, some of them on juveniles (Table 1), collected in Italy (Portofino Marine Protected Area-MPA, Calafuria, and Elba Island), Spain (Cap de Creus MPA, Medes Islands MPA), and France (Marseille and Banyuls sur Mer). Some of these studies did not include *C. rubrum* recruitment as their main targets; however, they reported meaningful data on the early life stages of red corals.

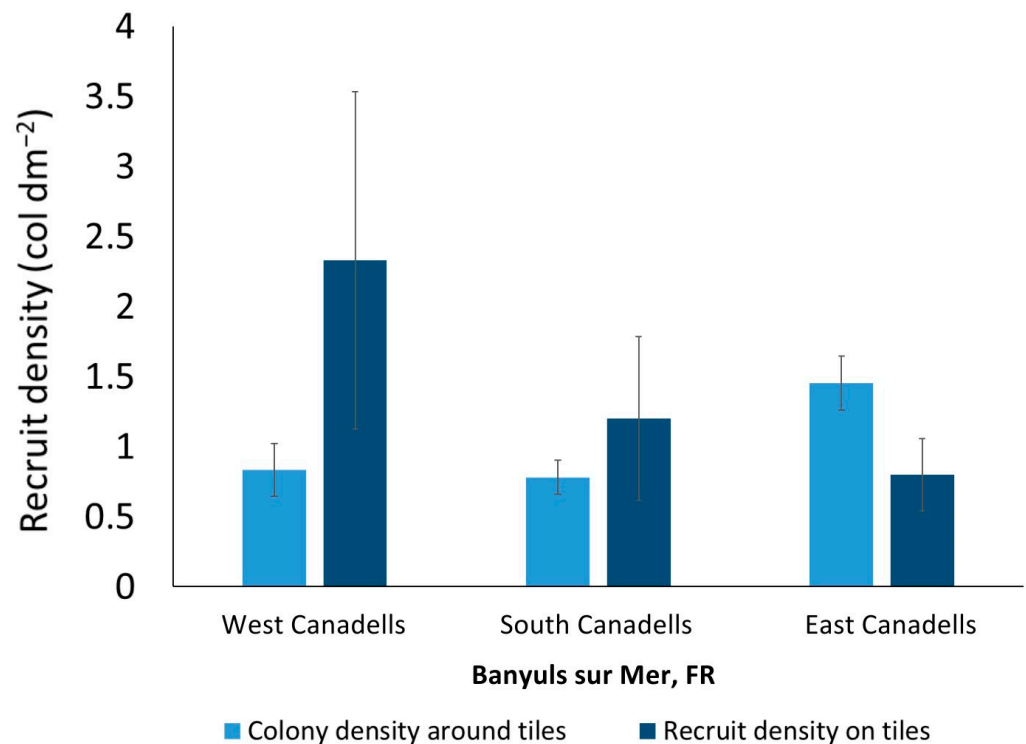
**Table 1.** Density of recruits and adults of *Corallium rubrum* from different areas of the Mediterranean Sea. \* MPA; § = Tiles electrically accreted by CaCO<sub>3</sub>.

Location	Depth (Meters)	Substrate	Recruit Density (col dm <sup>-2</sup> )	Adult Density (col dm <sup>-2</sup> )	Recruit Density/Adult Density	References
Portofino (It.) *	34	Natural	2.77 (11.11 over 4 years)	4.0	0.69	Cerrano et al., 1999 [37]
Portofino (It.) *	40–50	Fiber cement	1.6–11.7	ND		Cerrano et al., 1999 [37]
Marseille (Fr.)	27 (cave walls)	Local limestone	0.43	0.65 ± 0.3	0.66	Garrabou and Harmelin, 2002 [38]
Calafuria (It.)	25–35	Marble	12.3 ± 6.1–2.7 ± 2.4 (5.4 average over 4 years)	20	0.61–0.13	Bramanti et al., 2005 [25]
Calafuria (It.)	25–35	Natural	13.19 ± 4.7	29	0.48	Renieri, 2005 [39]
Calafuria (It.)	35	Marble—CaCO <sub>3</sub> §	3 ± 2.5–2.7 ± 1.1	20	0.15–0.13	Benedetti et al., 2011 [40]
Calafuria (It.)	35 ± 1	Marble	6.06 ± 1.75	20	0.33	Santangelo et al., 2012 [27]
Elba Island (It.)	35 ± 1	Marble	4.6 ± 1.01	ND		Santangelo et al., 2012 [27]
Medes Is. MPA (Sp.) *	35 ± 1	Marble	0.56 ± 0.21	ND		Santangelo et al., 2012 [27]
Cap de Creus (Sp.)	35	Natural	1.4 ± 0.7	3 ± 1.7	0.45	Bramanti et al., 2014 [30]
Portofino (It.) *	35	Natural	4.4 ± 1.20	9.9 ± 4.6	0.44	Bramanti et al., 2014 [30]
Portofino (It.) *	34–37 (cave ceiling)	PVC	0.92	3.5 ± 2.1	2.48	Costantini et al., 2018 [41]
Portofino (It.) *	34–37 (cave ceiling)	PVC	8.7 ± 5.96	3.5 ± 2.1	1.53	Costantini et al., 2018 [41]
Portofino (It.) *	34–70	PVC	1.87 ± 1.94–1.63 ± 0.5	2.5–3	0.75–0.54	Villechanoux, 2022 [42]
Banyuls sur Mer (Fr)	24–29	Marble	1.17 ± 1.0	1.11 ± 0.11	1.05	Benedetti MC PhD Thesis, 2018 [43]

### 3. Results

#### 3.1. Recruit, Juvenile, and Adult Densities

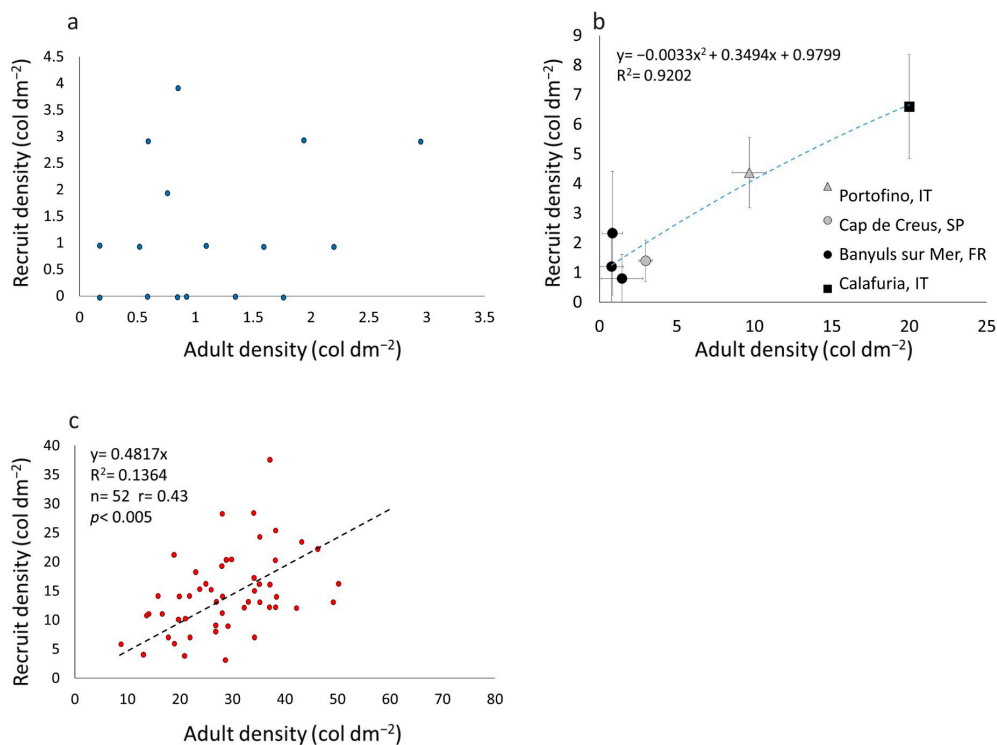
Overall, 21 red coral recruits were found in November on 11 of 18 marble tiles (61%) installed in Canadells, Banyuls sur Mer (France). The density of recruits was  $1.17 \pm 1.03 \text{ col dm}^{-2}$ , ranging between zero and four recruits/tile. According to the Kruskal–Wallis test, no significant differences were observed among the three sites examined (Figure 2).



**Figure 2.** Colony and recruit density of the 3 sites (west, south and east Canadells) in Canadells, Banyuls sur Mer (France); error bars represent SE.

At each of the three sites at which settlement tiles were fixed, thirty-three areas ( $4 \text{ dm}^2$ ) on the natural substrate around the tiles were examined in situ (corresponding to a  $396 \text{ dm}^2$  total area) to determine the density of adult and juvenile colonies. Overall, 441 colonies were counted, ranging between 0 and  $4 \text{ col dm}^{-2}$ , showing an average density of  $1.11 \pm 0.11 \text{ colonies dm}^{-2}$ . The recruit/adult ratio is 1.05, indicating a high recruitment rate. A one-way ANOVA showed significant differences in adult colony density among sites ( $p < 0.017$ ), indicating that adult colony density varied on a scale of a few hundred meters in the studied population (Figure 2).

No significant correlation was found between adult colonies and recruit density (Figure 3a) measured at each site within a ten-meter distance (the small spatial scale considered at Canadells, Banyuls sur Mer, France). However, a positive correlation was found between the densities measured at larger spatial scales in the three sites within the Canadells, Banyuls sur Mer area, and three other geographic areas (at distances ranging from hundred meters to hundred kilometres) (Figure 3b). A significant positive linear correlation between recruitment and adult density was also found at Calafuria, Livorno (Italy) at the smallest spatial scale considered (within  $1 \text{ dm}^2$  sampling quadrats; Figure 3c).

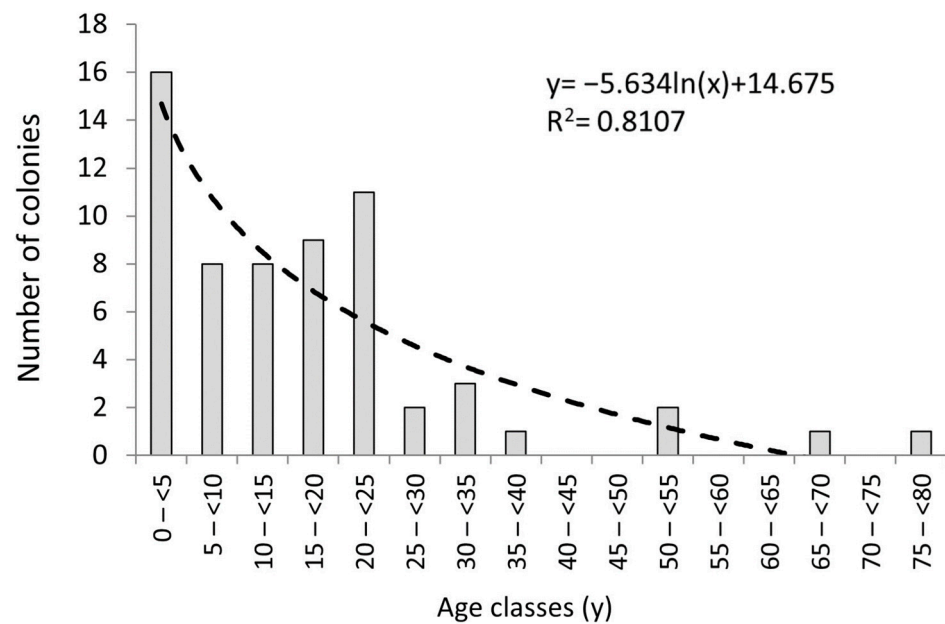


**Figure 3.** Relationship between recruit and colony density: (a) at a small spatial scale (1 m) in Canadells, Banyuls sur Mer (France); no relationship was found; (b) at a larger spatial scale (at a distance ranging from hundred meters to hundred kilometres), error bars represent SD; (c) at a small spatial scale (1 dm<sup>2</sup>) in Calafuria, Livorno (Italy). In (b,c) some correlation was found.

The average diameter of the adult colonies was  $4.09 \pm 0.3$  mm ( $n = 53$ ). Colonies with a diameter larger than 7 mm (the minimal harvestable size in Italy and several Mediterranean countries, FAO-GFCM 2011) represented 13% of the population of Canadells in Banyuls sur Mer (France).

The size classes of colonies were converted into size/age classes [44] based on the average colony growth rates measured in the neighboring red coral population dwelling at Cap de Creus, according to the power curve:  $y = 0.646x^{0.652}$  ( $y =$  diameter,  $x =$  age, after Bramanti and Coll. [30]). On this basis, the average size of the colonies of this population corresponded to an age of  $19 \pm 2$  years, and the size of the largest colony (10.8 mm) corresponded to a maximum lifespan of approximately 75 years (Figure 4). Due to the dominance of smaller/younger colonies, provided with a higher growth rate than the older ones [30], the average growth rate in the Canadells, Banyuls sur Mer population was higher than that in other populations (0.28 vs. 0.24; [30,45]). The size/age frequency distribution of this population was significantly skewed towards larger or older colonies ( $Sk = 1.17$ ,  $z = 2.22$ ,  $p = 0.027$ ). A monotonically decreasing function fitted this size/age–frequency distribution well (Figure 4).





**Figure 4.** Population size/age distribution represented by a monotonic decreasing curve.

### 3.2. Spatial Distribution Pattern

Recruits and juveniles were identified on 52 macro photo-samples of 13 marble tiles taken annually over 4 years and on 52 macro photo-samples of similar size taken on the natural substrate colonized by red coral at Calafuria, Livorno (Italy). We also examined the adult colony distribution in the latter samples. Data on recruitment density are reported in Table 1 and, together with mortality and early growth rates, have been mentioned in previous studies [25–27]. Here, we examined the distribution patterns of recruits on settlement tiles and recruits, juveniles, and adult colonies on a natural substrate at a small spatial scale (within 1 dm<sup>2</sup> samples). Nearest neighbor distance analysis allowed us to test the distribution pattern frequency on the settlement tiles and natural substrate using the Clark–Evans test and Point Pattern Index [34,35]. Overall, recruits were significantly aggregated in 37 of the 104 photographs examined (35.6%) and randomly distributed in 67 (64.4%). In particular, they showed significant aggregation in 6 out of 52 macro-photographic samples of tiles (11.5%), while their distribution was random in the remaining 46 (88.5%). In contrast, on the natural substrate, at the spatial scale considered (1 dm<sup>2</sup>), a significant aggregation of recruits was found in 31 out of 52 samples (59.6%) and a random distribution in the remaining 21 (31.4%). Based on a 2 × 2 chi-square contingency table, the difference between the tiles and natural substrates was highly significant ( $\chi^2 = 53.07$ ;  $n = 104$ ;  $p < 0.001$ ; Table S1 in Supplementary Materials).

Concerning the natural substrate, juveniles showed an aggregated distribution in only 1/52 (1.9%) and adults in 2/52 (3.8%) of the samples and a random distribution in all the others (98.1% and 96.2%, respectively). Recruits, juveniles, and adults did not show a regular distribution on either the artificial or natural substrates. The average NND of the recruits was higher than that of the adult colonies (1.13 cm vs. 0.98), suggesting an unsaturated population. Similar NND values for adult colonies were found in a shallow red coral population in the Medes Islands MPA [46].

### 3.3. *C. rubrum* Recruitment in Different Populations

Most of the research dealt with shallow red coral populations (<50 m depth) [47]; only one [42] reported recruitment to artificial (PVC) settlement plates located in deeper red coral populations (70 m deep). Recruits were identified and counted on ad hoc settlement plates of different materials, either natural (limestone and marble) or artificial (PVC and fiber cement). In another study [40], iron tiles covered with a calcium carbonate layer

accreted by a galvanic electrical current were used. Only two studies [30,37] and a master's thesis [39] dealt with recruits identified and counted on a natural substrate.

In all but one population, recruitment was recorded for all years during which they were examined (Table 1). The only exception was the Marseille population, for which the study was conducted by fixing limestone settlement plates on the walls of a 25 m-long horizontal cave at a depth of 27 m [38] over 23 years. This population showed sporadic recruitment, for which the initial density was 10 to 30 times lower than that found in the Calafuria population, at a similar depth [25–27,39,40], decreasing further in the following 21 years, when only 15 recruits were found ( $0.018 \pm 0.03 \text{ rec dm}^{-2} \text{ y}^{-1}$ ). During the study, limestone plates were progressively colonized by sponges and other encrusting fauna, which are putative competitors of red coral settlers for space [38].

Overall, recruitment on the settlement plates showed wide variability (Table 1), ranging from the lowest recruitment density in Marseille ( $0.43 \text{ rec dm}^{-2}$ ) [38] to the highest density ( $12.3 \pm 6.1 \text{ rec dm}^{-2}$ ), measured at Calafuria (Livorno) [25]. Local hydrodynamic features and irregular larval pulses may be key factors in this variability; however, the position at which the settlement plates have been installed (cave walls in Marseille or cave ceiling in Calafuria) and the structure of the substrate (semi-closed crevices) are likely the main factors fostering red coral recruitment [27,38,48].

The highest recruitment density for the natural substrate (Table 1) was recorded in the Calafuria population ( $13.19 \pm 4.7 \text{ rec dm}^{-2}$ ) [39], in which the highest adult density was also found ( $29 \text{ col. dm}^{-2}$ ). Lower values of both recruitment and adult density on the natural substrate were recorded in the Cap de Creus MPA ( $1.4 \pm 0.7$  and  $3 \pm 1.7 \text{ col. dm}^{-2}$ ) [30]. Recruit density on the natural substrate, measured at Portofino MPA after a 17-year interval [30,37], was comparable to that at Cap de Creus MPA ( $2.77\text{--}4.4 \pm 1.2 \text{ rec dm}^{-2}$ ). In general, these results confirm the positive relationship between recruitment and adult densities reported in Figure 3b,c.

#### 4. Discussion

Extensive, prolonged overfishing, to which anomalous mortality events linked to thermal anomalies have recently been added [25,44], has deeply affected many populations of the highly valuable Mediterranean red coral *Corallium rubrum*. Although several of these populations survive and thrive, their structures have shifted towards smaller sizes and higher densities than those found in the past [49,50]. A high recruitment rate may be a key factor that allows these populations to survive and recover slowly. In the present study, we analyzed the recruitment rates, size/age structure, and spatial distribution patterns of recruits in two shallow red coral populations and compared these findings with the recruitment rates reported for other red coral populations and octocoral species. A better understanding of the early dynamics of red coral populations could improve long-term management and conservation plans over the long run.

Red coral recruitment is characterized by large spatial and temporal variability; however, some general and local trends were identified. The data collected at Canadells, Banyuls sur Mer [43], describe a shallow population living in an unprotected area, with a recruit/adult colony ratio higher than that found in most of the populations examined. This finding was partly due to the low adult colony density in this area. Linares and Coll. reported a 20% higher density and average colony size for the neighboring Cerbere/Banyuls MPA population [51]. Higher densities were also reported for the Portofino and Cap de Creus MPAs [30,37]. The maximum life-span (75 years) of this population is similar to that reported for the Portofino MPA but 1/3 higher than that measured at the Cap de Creus MPA, at which the local red coral population has been subject to intensive harvesting [30,50]. The percentage of colonies exceeding the minimum legally harvestable size [29] found at Canadells, Banyuls sur Mer, was two-fold higher than that reported for these two MPAs. These findings, together with a high recruit/adult ratio, suggest a good conservation status for the French population, considering that it is thriving in an unprotected area. Recruits and juveniles represent the dominant classes within this

population; a ‘monotonous,’ decreasing curve well fits the size/age distribution, which is significantly skewed towards larger classes. Such a structure suggests a population in “steady state,” in which the mortality rates of the different classes are constant over time [52,53]. As observed in several red coral populations [30,44,45], the highest mortality affects younger classes, supporting the hypothesis that some self-thinning [54] may occur during the early stages of the red coral life cycle.

No correlation between recruitment and adult colony density was found at the small spatial scale (1 m) examined at Canadells, Banyuls sur Mer; however, some correlations were found at larger scales (from hundreds of meters to hundreds of kilometres). A significant correlation was also found in the Calafurian population at the smallest spatial scale (1 dm<sup>2</sup>) [39]. In general, these findings suggest that adult colony abundance, via an increased local planulae supply and/or some attractive effects of adult colonies, may foster larval settlement near the parental colonies [41,55]. However, at the highest adult colony densities, some density limitations may occur in relation to recruitment [30,44,46,56].

The highest densities of both recruit and adult colonies were found in the unprotected Italian population from Calafuria, Livorno. The spatial distribution patterns of red coral recruits, juveniles, and adult colonies in this area were examined at a small spatial scale (1 dm<sup>2</sup>) on both marble tiles and natural substrates using nearest-neighbor distance analysis [39]. This method, based on the measurement of the distance of each individual from its nearest neighbor, allows us to determine the frequency of random, clustered, and regular distributions. [33–35]. Our findings revealed a significantly higher frequency of clustered recruits on natural substrates than on settled marble tiles. The reason for this difference could be the greater availability of space, free from competitors, offered by the surface of the tiles for red coral planulae settlement. On natural substrates, only a limited number of spots are free from competitors (e.g., sponges, tunicates, and bryozoans) or are inhabited by encrusting organisms (such as serpulids) that selectively foster red coral planulae settlement [23,27,46]. The texture of the substratum is one of the factors affecting red coral recruitment; however, several other factors may be responsible for its temporal and spatial variability. The presence of aggressive, dominant early colonizers, such as the solitary oral *Leptopsammia pruvoti* [46], and micro- and macrodominant currents, may significantly affect recruitment rates. Moreover, high sedimentation rates and anomalous heat waves can disturb settlement [25,28].

Comparisons of recruitment data between studies are difficult because of the diversity of methodologies used by different authors; however, some main aspects can be highlighted. According to the data from literature, overall, red coral recruitment is about two orders of magnitude higher than that of the other octocorals here examined, suggesting that larvae could get “trapped” on the vault of caves and crevices where adult colonies dwell, and tend to settle in the proximity of their parent colonies.

Several different materials have been found to be suitable for red coral settlement [42], and even if the data dealing with recruitment on the natural substrate are limited, they are comparable with those obtained from ad hoc settlement plates located in the same areas.

Red coral, an internal brooder, is reported to have low fecundity [19,57]; however, it has high recruitment rates. Recruitment density data for 14 octocorals were extracted from 11 scientific papers and compared with the red coral data (Table S2, Supplementary Materials). The examined species covered all the main reproductive modalities (three internal brooders, six surface brooders, and four broadcast spawners). There was no clear difference between species, which were also provided by different reproductive modalities. All the species examined, with the exception mentioned below, show recruitment densities ranging between 0.0001 and 0.048 recruit dm<sup>-2</sup> [7,9,58–66], which are lower by at least one order of magnitude than the lowest values reported for *Corallium rubrum* (0.43 recruit dm<sup>-2</sup>) [38]. The only exception is the stony octocoral surface brooder *Heliopora coerulea*, which, like *C. rubrum*, belongs to the order Scleractinia. This surface brooder provided, like red coral, of a narrow dispersal range, showed a remarkably higher recruitment density

(3.5–3.7 recruits  $\text{dm}^{-2}$ ) [63] (Table S2 from Supplementary Materials), comparable with the values reported for red coral.

Among the other species, the highest recruitment densities (0.041–0.048 rec.  $\text{dm}^{-2}$ ) were found in populations of the Mediterranean gorgonian *Paramuricea clavata*, on the natural substrate, some years after they had been struck by catastrophic mortality events [64,65].

Unfortunately, almost all studies dealing with red coral recruitment have been carried out on shallow populations, while nothing is known about recruitment rates in deeper commercial populations dwelling below 50 m, which are currently the main target of harvesting. These populations, characterized by larger colonies and lower densities than shallower ones, have been studied for the last ten years and their demographic structure and reproductive features have been described [28,45,54,67,68]; however, nothing is known about red coral recruitment at deeper depths. The limited unpublished data at our disposal suggest lower recruitment rates for these populations.

## 5. Conclusions

- (1) The recruitment rates of *Corallium rubrum* are characterized by large fluctuations; however, all but one population analyzed in the present study regularly recruited each year.
- (2) All but one of the data points on red coral recruitment were at least two orders of magnitude higher than those of most of the octocoral species reported here.
- (3) The only octocoral showing recruitment rates comparable to those of the red coral is another octocoral brooder (*Heliopora coerulea*) belonging to the order Scleractinia.
- (4) Red coral tended to form monospecific patches, and at the smaller spatial scale examined (1  $\text{dm}^2$ ), patchiness occurred more frequently on natural substrates than on settlement tiles. This suggests that the availability of a limited suitable surface for larval settlement on the natural substrate, rather than the settlement of small clouds of planulae in the same microarea, may have determined the observed patchiness.
- (5) Overall, the data collected in this study highlighted that red coral, in the shallower portion of its bathymetric distribution, is a highly recruiting species. High recruitment rates, together with an early age at first reproduction and a wide geographic and bathymetric distribution, are likely key factors allowing the shallow populations of this slow-growing, long-lived octocoral to survive a long-lasting, intensive exploitation to which some drastic mortality events linked to the GCC have recently been added.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/oceans4030021/s1>, Table S1: Chi-square contingency table for the aggregation of recruits on the settlement tiles and on the natural substrate; Table S2: Recruit density of other octocorals extracted from literature.

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