Introduction

The coralligenous habitats are among the most typical ones in the Mediterranean Sea. They are biocconstructions, which host the highest level of benthic species diversity in the Mediterranean Sea [1], and Porifera is the richest taxon [2]. Coralligenous habitat structure has been clearly described by Riedl [3], who outlined a microscale zonation: an infaunal layer (boring and cryptic species) and an epibenthic layer with two main levels of complexity, one microscale zonation: an infaunal layer (boring and cryptic species) and an epibenthic layer with two main levels of complexity, one

Abstract

Mediterranean gorgonian forests are threatened by several human activities and are affected by climatic anomalies that have led to mass mortality events in recent decades. The ecological role of these habitats and the possible consequence of their loss are poorly understood. Effects of gorgonians on the recruitment of epibenthic organisms were investigated by manipulating presence of gorgonians on experimental panels at 24 m depth, for Eunicella cavolinii, and at 40 m depth, for Paramuricea clavata, at two sites: Tavolara Island (Tyrrhenian Sea) and Portofino Promontory (Ligurian Sea). After 4 months, the most abundant taxa on the panels were encrusting green algae, erect red algae and crustose coralline algae at 24 m depth and encrusting brown algae and erect red algae at 40 m depth. Assemblages on the panels were significantly affected by the presence of the gorgonians, although effects varied across sites and between gorgonian species. Species diversity and evenness were lower on panels with gorgonian branches. Growth of erect algae and recruitment of serpulid polychaetes were also affected by the presence of the gorgonians, primarily at Tavolara. Crustose coralline algae and erect sponges were more abundant on E. cavolinii panels at 24 m depth, while encrusting bryozoans were more abundant on P. clavata panels at 40 m depth. Effects of gorgonians on recruited assemblages could be due to microscale modification of hydrodynamics and sediment deposition rate, or by a shading effect reducing light intensity. Gorgonians may also intercept settling propagules, compete for food with the filter-feeders and/or for space by producing allelochemicals. Presence of gorgonians mainly limits the growth of erect algae and enhances the abundance of encrusting algae and sessile invertebrates. Therefore, the gorgonian disappearances may cause a shift from assemblages characterised by crustose coralline algae to filamentous algae assemblages, decreasing complexity and resilience of coralligenous bioconstructions.

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Ecological Shifts in Mediterranean Coralligenous Assemblages Related to Gorgonian Forest Loss

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experimentally manipulated in two locations, to quantify specific changes associated with their loss.

Materials and Methods

Experimental Set-up and Study Sites

Possible effects of the presence of *Eunicella cavolinii* (Koch, 1837) and *Paramuricea clavata* (Risso, 1826) (Anthozoa, Plexauridae) on the early recruitment of epibenthic organisms were investigated by a manipulative field experiment carried out from June to October, 2010. To limit the impact of the experiments 10.5 x 15.0 cm foamed PVC (Forex) panels were used to quantify the recruitment. Although artificial panels cannot exactly mimic natural substrates, they are commonly used in experimental ecology to investigate early-stage recruitment and succession processes. This method is simple, inexpensive to implement, and provides results very similar to natural substrates [20,21,22,23]. Gorgonian ‘forests’ were simulated by transplanting three 20 cm long ramified apical branches on each artificial panel. Branches were collected from 40–50 cm high colonies to avoid detaching whole specimens from the nearby populations. The collected apical branches were maintained in continuously renewed seawater without exposing them to air during the transplant operations, which lasted a few hours on the boat. The simulated processes are calcu-

Table 1. Mean values (± s.e., observations number in brackets) of the main water physical and chemical parameters at Tavolara (August 2008–July 2009, from the database of the Italian Ministry of Environment and Protection of Land and Sea, http://www.sidimar.tutelamare.it/) and Portofino (August 2008–August 2009, from the database of the Liguria Region’ Environmental Agency, http://www.ambienteinliguria.it).

| Parameter | Tavolara | Portofino |
|-----------|---------|----------|
| Temperature | °C | 18.73±1.38 (12) | 17.90±1.10 (12) |
| Salinity | psu | 37.71±0.23 (12) | 37.88±0.22 (12) |
| pH | | 8.20±0.06 (10) | 8.24±0.05 (10) |
| O₂ | % sat | 114.50±3.56 (11) | 101.92±3.42 (11) |
| Chl | µg L⁻¹ | 0.26±0.01 (10) | 0.25±0.01 (10) |
| Transparency | m | 19.00±3.43 (12) | 11.93±2.01 (7) |
| Nitrates | µM L⁻¹ | 0.06±0.02 (5) | 0.92±0.49 (7) |
| Nitrites | µM L⁻¹ | 0.05±0.04 (5) | 0.11±0.11 (7) |
| Ammonia | µM L⁻¹ | 0.61±0.21 (5) | 0.35±0.22 (7) |
| N₂O | µM L⁻¹ | 12.70±4.08 (5) | 7.53±1.18 (7) |
| Phosphates | µM L⁻¹ | 0.07±0.04 (5) | 0.01±0.01 (7) |
| Po₄ | µM L⁻¹ | 0.15±0.08 (5) | 0.01±0.01 (7) |
| Silicates | µM L⁻¹ | 2.10±0.93 (5) | 2.12±0.64 (7) |

Habitat Loss Effects on Temperate Biogenic Reefs

Ligurian Sea, Lat. 44° 17’ 54” N–Long. 9° 13’ 09” E). Tavolara Island is a limestone-dolomite massif with steep cliffs, while Portofino Promontory bedrock is made of a conglomerate of heterogeneous pebbles, mainly of marly limestone, in a sandy-limestone matrix. Compared to Portofino, Tavolara waters are generally more transparent and richer in oxygen, ammonia, total nitrogen and total phosphorus. Portofino waters are richer in nitrates, nitrites and phytoplankton, in terms of Chlorophyll concentration, especially at greater depth (Table 1). To reduce possible anthropogenic disturbances, study sites were selected within Marine Protected Areas.

Panels were collected after 4 months, before the storms season. Panels were brought to the surface in individual plastic zip-bags and preserved in a buffered solution of formaldehyde (4%) until observation.

Ethics Statement

Sampling at Tavolara and Portofino was done in accordance with Italian laws, and authorisations were granted by the “Marine Protected Area Tavolara - Punta Coda Cavallo” (www.amptavolara.com) and the “Marine Protected Area of Portofino” (www.portofinoamp.it). This study did not involve endangered or protected species.

Laboratory and Data Analyses

Sessile species that recruited on the panels were identified to the lowest possible taxonomic level and their percent covers on the upper side was estimated by superimposing a reference grid of 400 equal sized squares [25]. Species richness (as number of species, S), species diversity (as Hill’s diversity number N1 = Exp H’, where H’ is the Shannon’s index based on natural logarithm) and the corresponding evenness component (as N10 = N1/S) were calculated for each panel [26]. Differences in assemblage structures were represented using Principal Coordinate Analysis (PCoA unconstrained ordination plot; [27]) based on Bray-Curtis similarities of square root-transformed percent cover data.
Subsequently, taxa were pooled into main ecological and taxonomic groups and their contribution to similarity patterns of the assemblages were investigated by multivariate multiple regression using the DistLM procedure [28] and represented by correlation vectors on the PCoA ordination plots.

Differences in community structures, species abundances, ecological and taxonomic group abundances and species diversity indices between forestation treatment (Fo: fixed factor with 2 levels: presence/absence of gorgonian forest), sites (Si: fixed factor with 2 levels: Tavolara/Portofino), and plots (Pl: random factor nested in Fo×Si with 4 levels) were assessed by permutational multivariate analysis of variance (PERMANOVA, α = 0.05; [29]). When less than 999 unique values in the permutation distribution were available, asymptotical Monte Carlo P-values was used instead of permutational P-values. Multivariate tests were performed on Bray-Curtis similarities of square root-transformed percent cover data, while univariate tests were run on untransformed data using the Euclidean distance. Significant interactions among main factors were investigated by post-hoc pair-wise tests. Statistical analyses were performed using PRIMER 6 with PERMANOVA+ add-on package [30].

Results
The experiment was monitored periodically and at the end, all transplanted gorgonian branches were alive and in good condition.
Unfortunately, one panel with transplanted branches of *P. clavata* and an entire plot without gorgonian branches associated to the *E. cavolinii* experiment were lost at one site, Portofino. Measurements carried out at the end of the experiment confirmed that the simulated gorgonian density and biomass on the panels were consistent between forested plots and sites. In particular the mean dry mass of *P. clavata* was $827 \pm 66$ g m$^{-2}$ (s.e.), which correspond to an ash free dry mass of $91$ g m$^{-2}$ (according to the conversion factor provided by [31]).

Overall, assemblages recruited on the experimental panels included 233 taxa, of which 146 occurred at 24 m depth, 160 at 40 m depth and 73 were common to both depths. The effect of the two gorgonian species on the recruitment of sessile assemblages was analysed separately.

**Effects of *Eunicella cavolinii***

The most abundant taxa on the panels at 24 m depth were encrusting green algae (88.6% ± 2.0 s.e.), erect red algae (57.6% ± 4.1 s.e.) and crustose coralline algae (55.4% ± 1.4 s.e.), followed by foraminifera (29.2% ± 1.9 s.e.), hydroids (15.3% ± 1.8 s.e.), erect brown algae (11.0% ± 1.1 s.e.) and calcareous tube worms (10.2% ± 0.7 s.e.). Overall, the benthic assemblages differed between plots and sites and were significantly affected by the presence of the gorgonian *E. cavolinii* (Table 2a).

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**Table 2. Summary of PERMANOVA test on the effects of (a) *Eunicella cavolinii* and (b) *Paramuricea clavata* forests (Fo) on the recruitment of sessile assemblages at different sites (Si) and among plots (Pl) within Fo × Si (Bray-Curtis similarities on square root transformed data).**

| Source            | df | SS    | MS    | Pseudo-<i>F</i> | <i>P</i> (perm) | Unique perms |
|-------------------|----|-------|-------|-----------------|---------------|--------------|
| (a) *E. cavolinii*|    |       |       |                 |               |              |
| Fo                | 1  | 2'058 | 2'058 | 1.817           | 0.0347        | 9'926        |
| Si                | 1  | 21'566| 21'566| 19.045          | 0.0001        | 9'914        |
| Fo × Si           | 11 | 1601  | 1'601 | 1.413           | 0.1586        | 9'928        |
| Pl (Fo × Si)      | 45 | 13'807| 307   |                 |               |              |
| Total             | 59 | 51'597|       |                 |               |              |
| (b) *P. clavata*  |    |       |       |                 |               |              |
| Fo                | 1  | 5'345 | 5'345 | 3.690           | 0.0001        | 9'930        |
| Si                | 1  | 33'061| 33'061| 22.823          | 0.0001        | 9'929        |
| Fo × Si           | 12 | 17'425| 1'452 | 2.754           | 0.0001        | 9'703        |
| Pl (Fo × Si)      | 47 | 24'779| 527   |                 |               |              |
| Total             | 62 | 84'386|       |                 |               |              |

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**Figure 2. Effects of *Eunicella cavolinii* on benthic assemblages structures.** a) PCoA unconstrained ordination plot (i.e. metric MDS) based on Bray-Curtis similarities of square root-transformed sessile assemblages percent cover on recruitment panels with (Y) and without (N) *Eunicella cavolinii* forest after 4 months in Tavolara and Portofino; b) significant correlations of main ecological groups with PCoA Axes, represented by superimposed vectors (DistLM, marginal test <i>P</i>&lt;0.01). doi:10.1371/journal.pone.0102782.g002
Table 3. Summary of PERMANOVA test on the effects of *Eunicella cavolinii* forests (Fo) on the recruitment of ecological and functional groups and diversity indices at different sites (Si) and among plots (Pl) within Fo × Si.

| Forest (Fo)                      | Site (Si) | Fo × Si | Plot (Fo × Si) | Res       |
|----------------------------------|-----------|---------|----------------|-----------|
|                                  | (1 df)    | (1 df)  | (1 df)         | (11 df)   | (45 df)  |
|                                  | MS        | F       | P              | MS        | F       | P       | MS        | F       | P       | 45 df    | MS       |
| Erect blue-green algae           | 377.74    | 3.25    | 0.0949 ns      | 65.39     | 0.56    | 0.4905 ns | 57.55     | 0.50    | 0.5193 ns | 116.14   | 3.65    | 0.0006*** |
| Erect red algae                  | 6'238.30  | 4.89    | 0.0337*        | 280'740.00 | 22.03   | 0.0001*** | 90.40     | 0.07    | 0.8214 ns | 1'274.50 | 4.19    | 0.0005*** |
| Encrusting red algae             | 0.12      | 0.06    | 0.8071 ns      | 9.14      | 4.93    | 0.0510 ns | 0.02      | 0.01    | 0.9251 ns | 1.85     | 2.55    | 0.0096**  |
| Crustose coralline algae         | 1'611.40  | 8.76    | 0.0113*        | 1'210.90  | 6.58    | 0.0266*   | 113.60    | 0.62    | 0.4505 ns | 183.99   | 4.83    | 0.0002*** |
| Erect brown algae                | 686.49    | 5.00    | 0.0475*        | 333.96    | 2.43    | 0.1419 ns | 224.16    | 1.63    | 0.2367 ns | 137.22   | 4.11    | 0.0002*** |
| Encrusting brown algae           | 7.46      | 0.78    | 0.4479 ns      | 50.63     | 5.29    | 0.0105*   | 7.80      | 0.81    | 0.4364 ns | 9.58     | 9.95    | 0.0001*** |
| Encrusting green algae           | 1'069.00  | 2.42    | 0.1427 ns      | 2'025.50  | 4.58    | 0.0567 ns | 16.43     | 0.04    | 0.8566 ns | 442.65   | 2.84    | 0.0002**  |
| Erect green algae                | 7.36      | 11.22   | 0.0057**       | 5.82      | 8.88    | 0.0117*   | 0.00      | 0.01    | 0.9317 ns | 0.66     | 1.64    | 0.1153 ns |
| Foraminifera                     | 703.38    | 3.12    | 0.1119 ns      | 7'915.90  | 35.06   | 0.0001*** | 406.27    | 1.80    | 0.2165 ns | 225.79   | 4.85    | 0.0001*** |
| Erect sponges                    | 1'124.00  | 3.85    | 0.0056**       | 429'980.00 | 14.42   | 0.0001*** | 1'358.40  | 0.47    | 0.8051 ns | 2'919.30 | 3.82    | 0.0001*** |
| Hydroids                         | 462.56    | 1.07    | 0.3229 ns      | 1'002.10  | 2.33    | 0.1493 ns | 135.47    | 0.31    | 0.5824 ns | 430.45   | 3.85    | 0.0006*** |
| Calcareous tube worms            | 44.43     | 1.87    | 0.2001 ns      | 769.63    | 32.48   | 0.0003*** | 135.71    | 5.73    | 0.0358*   | 23.70    | 2.19    | 0.0315*   |
| Bivalves                         | 0.14      | 3.07    | 0.1112 ns      | 0.63      | 14.01   | 0.0002*** | 0.14      | 3.07    | 0.1008 ns | 0.04     | 1.06    | 0.4171 ns |
| Encrusting bryozoans             | 10.13     | 1.89    | 0.2187 ns      | 234.47    | 43.70   | 0.0001*** | 5.48      | 1.02    | 0.3367 ns | 5.47     | 1.78    | 0.0649 ns |
| Stoloniferous bryozoans          | 0.67      | 0.01    | 0.9110 ns      | 0.89      | 0.02    | 0.9010 ns | 128.35    | 2.68    | 0.0343 ns | 47.86    | 2.26    | 0.0183*   |
| Erect bryozoans                  | 4.09      | 0.36    | 0.5626 ns      | 316.64    | 27.66   | 0.0002*** | 15.08     | 1.32    | 0.2861 ns | 114.5    | 4.28    | 0.0002*** |
| S                                | 513.39    | 3.34    | 0.0923 ns      | 1'773.60  | 11.54   | 0.0029*** | 27.08     | 0.18    | 0.6911 ns | 153.66   | 6.43    | 0.0001*** |
| N1                               | 135.93    | 5.40    | 0.0370*        | 512.72    | 20.38   | 0.0003*** | 4.10      | 0.16    | 0.7033 ns | 25.16    | 4.98    | 0.0001*** |
| N10                              | 0.01      | 9.91    | 0.0087**       | 0.04      | 39.23   | 0.0001*** | 0.00      | 0.81    | 0.3903 ns | 0.00     | 0.79    | 0.6509 ns |

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Despite the large local variability, the mean percent cover of several groups was significantly different between the two sites (Table 3). Erect red algae (including 44 taxa, Fig. 3), green algae (12 taxa) and crustose coralline algae (Fig. 3) were significantly more abundant at Portofino, while encrusting brown algae (2 taxa) were more abundant at Tavolara. Among invertebrates, foraminifera (4 taxa), bivalves (i.e. *Anomia ephippium* Linnaeus, 1758), encrusting bryozoans and erect bryozoans (10 and 9 taxa respectively) showed greater percent cover at Portofino. In contrast, erect sponges were more abundant at Tavolara. On panels with *E. cavolinii*, a significant reduction in percent cover of erect red algae (Fig. 3), brown algae (12 taxa, Fig. 3) and green algae was observed, whilst recruitment of crustose coralline algae and erect sponges was enhanced. The mean percent cover of calcareous tube worms (14 taxa, Fig. 3) was significantly reduced by the presence of the gorgonian, but only at one site, Tavolara. Similarly, at the same site, the serpulid polychaete *Hydroides stoichadon* Zibrowius, 1971 was also significantly less abundant in the presence of the gorgonian (pair-wise test: $P<0.05$). However, in contrast at Portofino *H. stoichadon* was occasionally observed but only on the panels which had transplanted gorgonian branches (Fig. 4).

Overall, species richness ($S$) was significantly higher at Portofino, but was not affected by the presence of the *E. cavolinii*.
The groups of erect algae were more abundant on the panels without gorgonians at Tavolara, yet were significantly more abundant on the panels without gorgonians at Portofino (pair-wise test: $P < 0.05$). Encrusting sponges (3 taxa) were present at Tavolara, while hydroids (12 taxa), bivalves (i.e., Anomia ephippium Linnaeus, 1758) and stoloniferous bryozoans (2 taxa) were much more abundant at Portofino. Encrusting bryozoans (7 taxa) were facilitated by gorgonians at both sites. Even with different mean percent covers, erect brown (15 taxa, Fig. 6) and green algae (10 taxa), along with calcareous tube worms (18 taxa), were significantly more abundant on panels without gorgonians at Tavolara (pair-wise test: $P < 0.01$), whilst these effects were not observed at Portofino. Conversely, encrusting brown algae (5 taxa) were facilitated by the gorgonian at Tavolara (pair-wise test: $P < 0.05$), and reduced at Portofino (pair-wise test: $P < 0.05$). Encrusting sponges (3 taxa) were absent at Tavolara, yet were significantly more abundant on the panels without gorgonian at Portofino (pair-wise test: $P < 0.05$). As observed in the experiment with E. cavolinii, at 24 m depth, even if less abundant at 40 m depth, the serpulid polychaete Hydroides stoechadon was significantly reduced by the gorgonian at Tavolara (pair-wise test: $P < 0.05$) (Fig. 7).

Overall, species richness ($S$) was significantly higher at Tavolara, but it was not affected by the presence of the gorgonian (Table 4). Furthermore, species heterogeneity ($N1$) and evenness ($N10$) were significantly higher in absence of the gorgonian at Tavolara (pair-wise test: $P < 0.01$) whilst no effects were found at Portofino (Fig. 6).

**Discussion**

Owing to the use of experimental panels, in 4 months of deployment it was possible to detect the effects of the two most common Mediterranean gorgonians on the early-stage recruitment of the epibenthic assemblages. The newly recruited assemblages differed amongst plots and between sites, both in Eunicella cavolinii (24 m depth) and in Paramuricea clavata (40 m depth) treatments. Analyses of the recruitment highlighted site-specific and species-specific effects of the gorgonian forests. Overall, the presence of gorgonians limited the growth of erect algae and, at Tavolara, the recruitment of serpulid polychaetes. Moreover, the presence of gorgonians, lowered species diversity and evenness of the assemblages on the experimental panels. These effects may be related to both biological and physical effects. Being passive filter feeders (they cannot create currents on their own [32]) and active predators (polyps capture prey by nematocysts) the gorgonians can intercept and feed on drifting larvae before settlement. Coma et al. [33] documented that P. clavata has a broad and heterogeneous diet with prey species ranging from 3.8 μm (nauculacean zoas) to 700 μm (copepods). Protozoans and microalgae are the main items caught by the polyps. Capture of detrital and live particulate organic carbon is minimal in the summer, due to the scarcity of suspended food during this season [34]. Gorgonians may also compete with other filter-feeders for food and/or for space, producing allelochemicals [35]. On the other hand, gorgonians could affect settlement and
Table 4. Summary of PERMANOVA test on the effects of *Paramuricea clavata* forests (Fo) on the recruitment of ecological and functional groups and diversity indices at different sites (Si) and among plots (Pl) within Fo×Si.

| Forest (Fo)                       | Site (Si) | Fo × Si | Plot (Fo × Si) | Res       |
|-----------------------------------|-----------|---------|----------------|-----------|
|                                   | (1 df)    | (1 df)  | (1 df)         | (12 df)   | (47 df)   |
|                                   | MS        | F       | P              | MS        | F       | P       | MS        | F       | P       | MS |
| Erect red algae                   | 7211.80   | 6.45    | 0.0311*        | 65548.00  | 58.60   | 0.0002*** | 761.73    | 0.68    | 0.4255 ns | 1'121.20 | 2.51    | 0.0107** |
| Encrusting red algae              | 245.90    | 0.78    | 0.3867 ns      | 138.87    | 0.44    | 0.5185 ns | 1'093.20  | 3.49    | 0.0845 ns | 314.50   | 3.47    | 0.0015** |
| Crustose coralline algae          | 33.10     | 0.08    | 0.7776 ns      | 521.02    | 1.22    | 0.2757 ns | 903.81    | 2.11    | 0.1727 ns | 428.53   | 3.46    | 0.0009*** |
| Erect brown algae                 | 4513.00   | 14.80   | 0.0030**       | 7803.00   | 25.59   | 0.0006*** | 3'003.60  | 12.48   | 0.0064**  | 305.48   | 2.01    | 0.0443*  |
| Encrusting brown algae            | 2006.70   | 1.55    | 0.2372 ns      | 6170.20   | 4.75    | 0.0553 ns | 17609.00  | 13.56   | 0.0025**  | 1'303.10 | 4.11    | 0.0001*** | 316.47 |
| Erect green algae                 | 117.86    | 17.48   | 0.0020**       | 106.08    | 15.74   | 0.0027**  | 76.62     | 11.37   | 0.0078**  | 6.75     | 1.37    | 0.2077 ns | 49.44 |
| Encrusting green algae            | 2070.00   | 4.48    | 0.0591 ns      | 6343.10   | 13.74   | 0.0024**  | 33.45     | 0.07    | 0.7881 ns | 462.91   | 3.03    | 0.0027**  | 152.79 |
| Foraminifera                       | 1'317.80  | 23.27   | 0.0010**       | 1'023.40  | 18.07   | 0.0026**  | 1.84      | 0.04    | 0.9076 ns | 56.53    | 0.65    | 0.7833 ns | 86.61 |
| Encrusting sponges                 | 0.11      | 12.33   | 0.0055**       | 0.44      | 49.32   | 0.0003*** | 0.11      | 12.33   | 0.0057**  | 0.01     | 0.18    | 0.9993 ns | 0.05  |
| Solitary polyps                    | 0.01      | 0.62    | 0.4943 ns      | 0.12      | 8.28    | 0.0114*   | 0.01      | 0.62    | 0.4918 ns | 0.01     | 1.28    | 0.2409 ns | 0.01  |
| Hydroids                           | 1'305.10  | 1.27    | 0.2843 ns      | 20'172.00 | 19.61   | 0.0011**  | 757.75    | 0.74    | 0.4075 ns | 1'032.10 | 5.39    | 0.0002*** | 191.32 |
| Calcareous tube worms              | 21.72     | 0.30    | 0.6199 ns      | 107.14    | 1.47    | 0.2578 ns | 851.29    | 11.71   | 0.0018**  | 72.90    | 3.31    | 0.0015**  | 22.04 |
| Bivalves                           | 49.73     | 1.52    | 0.2550 ns      | 1256.40   | 38.30   | 0.0001*** | 72.87     | 2.22    | 0.1639 ns | 32.90    | 4.48    | 0.0001*** | 7.35  |
| Encrusting bryozoans               | 184.08    | 8.60    | 0.0121*        | 44.36     | 2.07    | 0.1715 ns | 1.91      | 0.09    | 0.7676 ns | 21.45    | 2.60    | 0.0094*** | 8.24  |
| Stoloniferous bryozoans            | 88.99     | 1.74    | 0.2201 ns      | 4594.2    | 9.00    | 0.0079**  | 116.52    | 2.28    | 0.1627 ns | 51.12    | 1.95    | 0.0473*  | 26.26 |
| Erect bryozoans                    | 55.41     | 0.32    | 0.5747 ns      | 608.17    | 3.47    | 0.0898 ns | 63.02     | 3.62    | 0.5509 ns | 175.83   | 3.86    | 0.0009*** | 45.50 |
| S                                 | 253.39    | 2.78    | 0.1171 ns      | 4474.30   | 49.00   | 0.0033*** | 40.33     | 0.44    | 0.5259 ns | 91.50    | 2.27    | 0.0198*  | 40.23 |
| N1                                | 524.67    | 27.65   | 0.0004***      | 1'487.80  | 78.41   | 0.0033*** | 233.77    | 12.32   | 0.0054**  | 19.01    | 1.92    | 0.0562 ns | 9.88  |
| N10                               | 0.11      | 26.09   | 0.0005***      | 0.04      | 10.50   | 0.0112*   | 0.04      | 9.72    | 0.0062**  | 0.00     | 1.31    | 0.2454 ns | 0.00  |

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recruitment processes by modifying microscale hydrodynamic conditions, sediment deposition rates by limiting resuspension processes, and algal development by creating shading effects that may reduce the availability of light. In the mesophotic zone, gorgonian forests are considered to be of paramount importance to support surrounding species diversity. It was observed that they significantly increased the deposition of bioavailable substrates and enhanced benthic diversity, compared to areas without colonies [5]. As a result, organisms living in habitats characterised by the presence of these ‘ecosystem engineers’ (sensu [36]) may experience a sort of buffer zone where environmental modifications occur more slowly and within narrower ranges with respect to the surrounding ‘unforested’ environment.

In the present study, significant spatial variation of recruitment patterns was observed between Tavolara and Portofino. These differences could be related to variability in larval supply, chemical-physical parameters, sediment deposition and hydrodynamic conditions between sites. For example, in Portofino the value of nitrites and nitrates is higher compared to Tavolara. These differences are likely related to the fact that Tavolara is further from rivers and densely populated areas. Furthermore, at the specific study site (i.e. Punta del Faro) the Portofino Promontory receives a secondary branch of the main Ligurian...

**Figure 6. Effects of *Paramuricea clavata* on selected groups and species diversity indices.** Mean (±s.e.) percent cover of selected groups recruited on panels and species diversity indices (Hill’s diversity number N1 and corresponding evenness component N10) for each experimental plot at Tavolara and Portofino, with (Y) and without (N) *Paramuricea clavata* at 40 m depth. doi:10.1371/journal.pone.0102782.g006

**Figure 7. Effects of *Paramuricea clavata* on the serpulid polychaete *Hydroides stoichadon*.** Mean (±s.e.) percent cover of the serpulid polychaete *Hydroides stoichadon* on panels for each experimental plot at Tavolara and Portofino, with (Y) and without (N) *Paramuricea clavata* at 40 m depth. doi:10.1371/journal.pone.0102782.g007

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**Habitat Loss Effects on Temperate Biogenic Reefs**

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current [17], transporting urban waste-waters from the Tigullio Gulf, especially during the tourist summer season.

Longer experiments are needed to better understand the temporal dynamics of coralligenous assemblages; nevertheless, this short-time experiment has provided clear indications on the effect of gorgonians on the recruitment trajectories. In the study sites, the presence of gorgonians mainly reduces the initial growth of erect algae in favour of encrusting ones, which are the most important builders of the coralligenous frameworks [1], and some sessile invertebrates. Therefore, depending on the trophic conditions and turbidity of the water, rarefaction of gorgonians may favour a simplification of the coralligenous assemblages and a shift toward more autotrophic communities, dominated by fast growing filamentous algae instead of the slow accretion of crustose coralline algae.

Coralligenous habitats are threatened by several global stressors. The most evident, are climate change (massive mortalities related to temperature anomalies) and fishing activities (mechanical injuries and sediment re-suspension). Recently potential synergism between these stressors have been hypothesized [12], resulting in a fragmentation of the habitat that can open new space available for invasive species. Unfortunately, the dearth of information available on the interactions between octocorals and associated fauna prevents predicting any effect of gorgonian loss on the trophic structure. Owing to natural or anthropogenic causes, the loss of the 3D structure of the epibenthic layer in coralligenous assemblages [3], may affect both the established assemblages and the settlement and recruitment processes. The main question addressed by this study is whether the rapid loss of complexity due to extensive Mediterranean gorgonian mortalities [37], can affect the early-stage recruitment of coralligenous assemblages. Although the biological interaction between gorgonians and the other species deserve further studies, modifications of the edaphic conditions caused by the gorgonian forests influences larval settlement and recruitment processes of the benthic assemblages.

Coralligenous habitats are mainly built by deposition of calcareous thalli of crustose coralline algae, a process that has lasted for thousands of years [1]. These assemblages are generally characterised by high spatial heterogeneity and limited temporal variability, possibly related to the longevity and slow growth rates of the most abundant and structuring species [38], [39],[41]. If the local disappearance of gorgonians causes a shift of the epibenthic assemblages from crustose coralline algae to filamentous algae dominated, complexity decreases. In absence of gorgonians, the resilience of coralligenous bioconstructions could be compromised due to the reduced recruitment of the main builder organisms and other key species. As another possible consequence, the establishment of non-indigenous species, such as the erect green algae Caulerpa cylindracea Sonder and the turf forming red algae Womersleyella setacea (Hollyberg) R.E.Norris, may be facilitated [42,43], irreversibly altering these unique Mediterranean underwater landscapes. A regional scale assessment of coralligenous habitats taking in account not only the biological component but also the three-dimensional arrangement [44] is needed to develop adequate management plans.

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Author Contributions

Conceived and designed the experiments: MP CC. Performed the experiments: MP RAP VV DG CC. Analyzed the data: MP RAP VV DG CC. Wrote the paper: MP CC. Provided input into the manuscript: MA.

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