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After the Fall: The Demographic Destiny of a Gorgonian Population Stricken by Catastrophic Mortality

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Abstract: In recent years, the frequency of mass mortality events in marine ecosystems has increased, and several populations of benthic organism have been affected, reducing their density and changing their size and age structure. Few details are known about the dynamics of these populations over long time intervals. In late summer of both 1999 and 2003 two drastic mass mortality events, co-occurring with anomalous temperature increases, affected the northwestern Mediterranean rocky coastal communities. Due to these events the *Paramuricea clavata* population living at the western edge of La Spezia Gulf (Italy) was stricken, and 78% of the colonies died. This population was monitored from 1998 (pre-mortality) until 2013. This paper deals with the photographic sampling of permanent plots carried out in 2013. The findings were compared with those from the previous sampling series. This long-term, non-destructive sampling highlights the demographic trajectory of the octocoral population there after two anomalous mortality events, indicating that some new drop-point between local extinction and complete recovery may be have been reached. Long-term monitoring (including pre-mortality data) could allow evaluating the effects of global climate change on the conservation of impacted populations.

Keywords: long-term mortality series; population dynamics; mass mortality; octocorals; habitat forming species; extinction; survival; equilibrium points

1. Introduction

Over the last few years, the frequency of mass mortalities in marine ecosystems linked to Global Climate Change (GCC) has increased greatly, and several authors have described the dramatic effects of such anomalous events on benthic communities and populations [1–4] among others. However, few research studies address the delayed effects on, and the long-term growth trends of the affected populations, whose complex dynamics cannot be adequately expressed through the narrow terms of "survival" or "extinction".

In marine ecosystems, temperature is one of the main factors controlling species distribution, and unusual deviations from typical seasonal patterns may represent the greater impacts of global change on such systems [5]. The effects of abnormal warming of the water column are clearly and easily observable not only at shallow depths as environmental degradation and the direct responses of the organisms (e.g., lower population growth rates), but also in the deep sea, where modifications of the water's physicochemical characteristics are impacting biodiversity [6].

Habitat-forming species such as sea grasses, kelps, corals, and oysters are among the main organisms profoundly influenced by thermal stressors [7], although neither all species nor all communities are equally affected or respond in the same way. For example, among tropical hexacorals, differential susceptibility and resistance to bleaching and mass

mortalities have been observed due to species peculiarity, the environmental variability between reefs, and even genetic differences between colonies of the same species on the same reef [8–10].

In recent decades, several worldwide populations of octocorals have been affected by stressors linked to GCC, making it essential that a demographic study of these populations is carried out in order to formulate reliable survivorship predictions [11–19]. It has been observed that the frequency of negative events may be a main factor determining the survival of such populations [17]. Even if they do endure, these populations could dramatically change their demographic structure and, depending upon their peculiar life-history traits, respond to anomalous mortality events in unexpected ways [13,20–23]. Octocorals are among the most common suspension feeders dwelling within the so-called animal marine forest *sensu* Rossi [24], where they often act as *habitat engineers*. Thus, the dynamics of their populations may have profound effects on the whole species assemblage. In the Mediterranean Sea, some populations of the temperate red gorgonian *Paramuricea clavata* (Risso 1826) have been affected by mass mortality events following unusual thermal stress [20,25–27] among others. Widely distributed along boulders and cliffs between 12 and 120 m depth in highly hydrodynamic areas [28,29], *P. clavata* is one of the main components of the coralligenous species assemblages [30] and determines the composition of the entire epibenthic community [31]. *P. clavata* is a large sea fan gorgonian (up to 1 m tall) that can form dense patches (up to 59 colonies per m^2, [32]) and is characterized by high reproductive output and long life cycle [21]. This species has recently been classified as a "bioindicator" [33] and "vulnerable" by the IUCN (International Union for Conservation of Nature). A recent genetic study has highlighted the strategic role of the *P. clavata* populations in the eastern Ligurian Sea (northwestern Mediterranean, Italy) for the persistence of the species at a regional level [34].

At summer's end of both 1999 and 2003, the benthic suspension feeders living along the coastal shores of the Ligurian Sea were affected by two mass mortality events co-occurring with exceptional warming of the water column [35,36]. Exposure to abnormal temperature increases was likely the cause of an ensuing outbreak of opportunistic pathogens such as bacteria, protozoans, and fungi on the *P. clavata* colonies, leading to their total or partial death [35,37]. The local population of this gorgonian living at the western edge of the Spezia Gulf (Figure 1) was stricken, and 78% of the colonies died or were heavily damaged [32]. This population was monitored from 1998 (pre-mortality) to 2010 [13,21]. In the years following the catastrophic events both adult and recruit density fell drastically, and the population size/age structure was altered due to the mortality disproportionally affecting the larger colonies, thereby shifting it towards the smaller ones [32]. Since 2007, a significant increase in adult and recruit density has occurred [13,20].

This paper analyzes the population size/age structure, the adult and annual recruit densities, and the percentage cover of *P. clavata* and the main organisms living in the area in 2013. The results have been compared with the previous findings to identify long-term variations affecting both the *P. clavata* population and the whole community after the catastrophic mortality events.
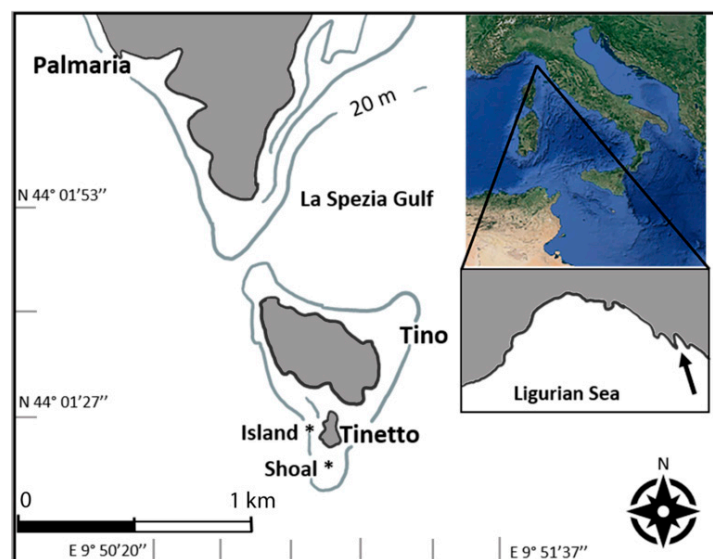
Figure 1. Sampling area, Tinetto islet: stars represent the sampling sites (Eastern Liguria Sea, NW Mediterranean, Italy).

## 2. Materials and Methods

2.1. Study Area and Sampling Design

The study area is located at Tinetto Islet (Figure 1), part of a small archipelago of the Ligurian Sea at the western edge of the La Spezia Gulf (NW Mediterranean, Italy), an area included in the World Heritage list and under the protection of the United Nations Educational, Scientific and Cultural Organization (UNESCO). Oriented from northwest to southeast, the Gulf is about 5 km wide and 10 km long, and its circulation is affected by several factors: the Ligurian current, seasonal weather changes, and the strength of the so-called 'Sirocco' warm southerly wind. The area is characterized by high turbidity due to the Magra river plume influencing the water and its hydrodynamics, especially during rainy seasons [21,38]. The northwest and western sides of Tinetto Islet are composed of vertical calcareous walls while the southern and the eastern sides are characterized by medium slopes. A more detailed description of the area has been previously published [13,21].

The population of *Paramuricea clavata* living on a sub-vertical rocky cliff between 17 and 25 m depth was monitored between 1998 (pre-mortality) and 2010 by identification and measurement during SCUBA diving [13,21]. This paper deals with the results of the photographic sampling carried out via a housed X 100 G10 Canon (Canon Inc., Tokyo, Japan) digital camera at a 1:1 magnification on the same population in July 2013.

In 2013, 24 of the permanent polyvinyl chloride (PVC) quadrates (1 × 1 m, thus 1 square meter each) previously fixed at 2 sites a few hundred meters from one another were sampled for analysis. Twelve were on the northwestern side (Tinetto Island) of Tinetto Islet (44°01′26′′ N, 09°51′03′′ E), and 12 at the Tinetto Shoal, on the southern side of the islet (44°01′23′′ N, 09°51′05′′ E; unfortunately, one of the quadrates fixed at this site was lost). At each site, the squares were randomly arranged at a few meters' distance. Of the 23 quadrates sampled for this study, 12 corresponded to the same ones used for the previous monitoring study. Four photos of a 0.25 m^2 area in each one-square meter quadrate were taken vertically to the cliff. Overall, 92 photos of 23 quadrates in the whole area have been analyzed for the present study.

The main taxa of the sessile organisms in each photo-sample (Figure 2) were identified, and their percent cover was measured by the graphic program Image J. The "TSH" substrate (including algal turf, *sensu* Connell et al. [39], sediment, and small hydrozoans) was considered as "free surface", putatively suitable for the settlement of *P. clavata*, as recruits and young colonies of this gorgonian have been frequently found emerging from this

substrate [20]. The remaining substrate, hereafter named "occupied substrate" was covered by sessile macro-benthos.
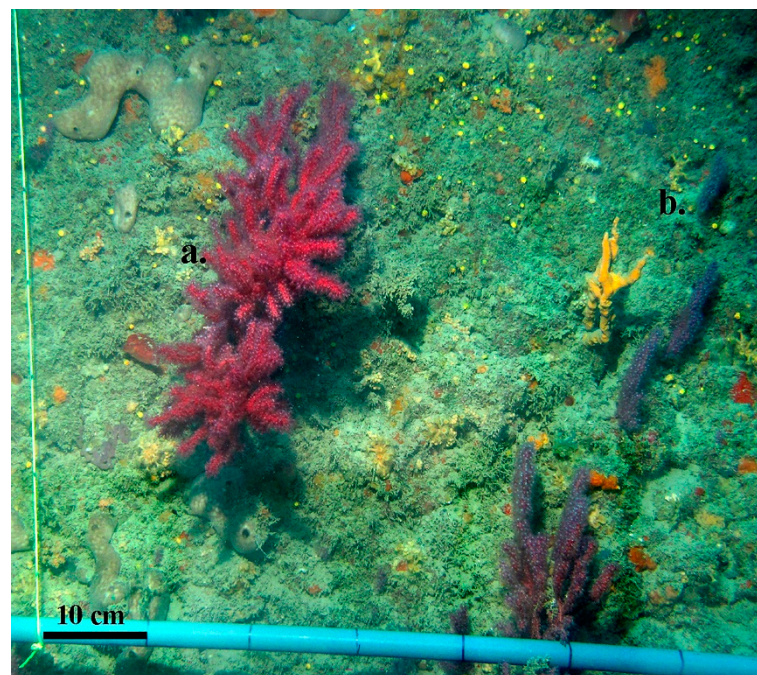
Figure 2. *P. clavata*: (**a**) a large/old adult and (**b**) a small/young colony.

2.2. Size Structure and Density of the P. clavata Population

The number of colonies of *P. clavata* in each plot ($n = 23$) was counted, and the densities (col m^{-2}) of adults and annual recruits recorded. Colony size (in width) was measured by a ruler reported on one side of each square in a top view image. Considering an average annual growth rate of 3 cm y^{-1} in width, all colonies were divided into annual age classes according to their size (i.e., size/age classes [12,40]), and all those <4.5 cm were assigned to the 0–1 age class (recruits) according to Cupido et al. [21]. The colonies assigned to classes 2 to 4 were defined as small/young adults, while colonies belonging to classes >5 were considered large/old adults (Figure 2).

Since time series data and the size/age structure of the population between 1998 and 2010 were available [20,21,32], a comparison was made with the data collected in 2013.

2.3. Data Analysis

Data normality and homogeneity have been tested using the Shapiro–Wilk test [41] and the Levene test [42], respectively. Non-normal data have been transformed into Log(x) and Log(x + 1), and the remaining non-normally distributed data have been analyzed by non-parametric tests.

The density variability in adult colonies and recruits over the years 1998 to 2013 has been analyzed via the non-parametric Friedman test [43]. Moreover, the population size/age structures over this period have been compared by multidimensional scaling (MDS): in the resulting configuration of points ($n = 9$, years of sampling), the closeness of one year's sample data to another's provides a measure of similarity. The MDS analysis has been performed using the free software Past4.03 and the Euclidean index of similarity has been used.

Differences in percent cover of TSH and occupied substrate between the two sites ($n = 12$ at Tinetto Island and $n = 11$ in Tinetto Shoal) sampled in 2013 have been tested via the *t*-test [44]. Percent cover and density differences in adult *P. clavata* colonies between sites have also been analyzed via the *t*-test, while those of the recruits with the Mann–Whitney test.

The relations between adult and recruit densities and between these data and free substrate have been tested by R^2 best fit coefficient, linear Pearson's coefficient and the *t*-test. The relations between recruit densities in the same quadrate on 2 subsequent years have been explored on the scatter plot: the density of one year was plotted against that of the following year in the same fixed plot (2007 vs. 2008 and 2009 vs. 2010), finally a linear trend has been calculated.

3. Results

3.1. Population Density and Size/Age Structure over the 1998–2013 Period

In 2013, the overall density of *P. clavata* adult colonies reached about half the 'pristine' 1998 values (Figure 3a), while the overall recruit density was 4.5 times higher than that in 1998 (Figure 3b). For both adults and recruits, 2004 was a crucial year in which the population was reduced by 78%, while 2007 was the turning point after which they underwent a rapid increase, remaining stable thereafter (Figure 3a,b), as no differences in adult colony and recruit density have been found over the period 2007–2013 (Friedman tests, adult $\chi^2 = 0.98$, $p > 0.05$ and recruit $\chi^2 = 5.98$, $p > 0.05$).

(**a**)

(**b**)
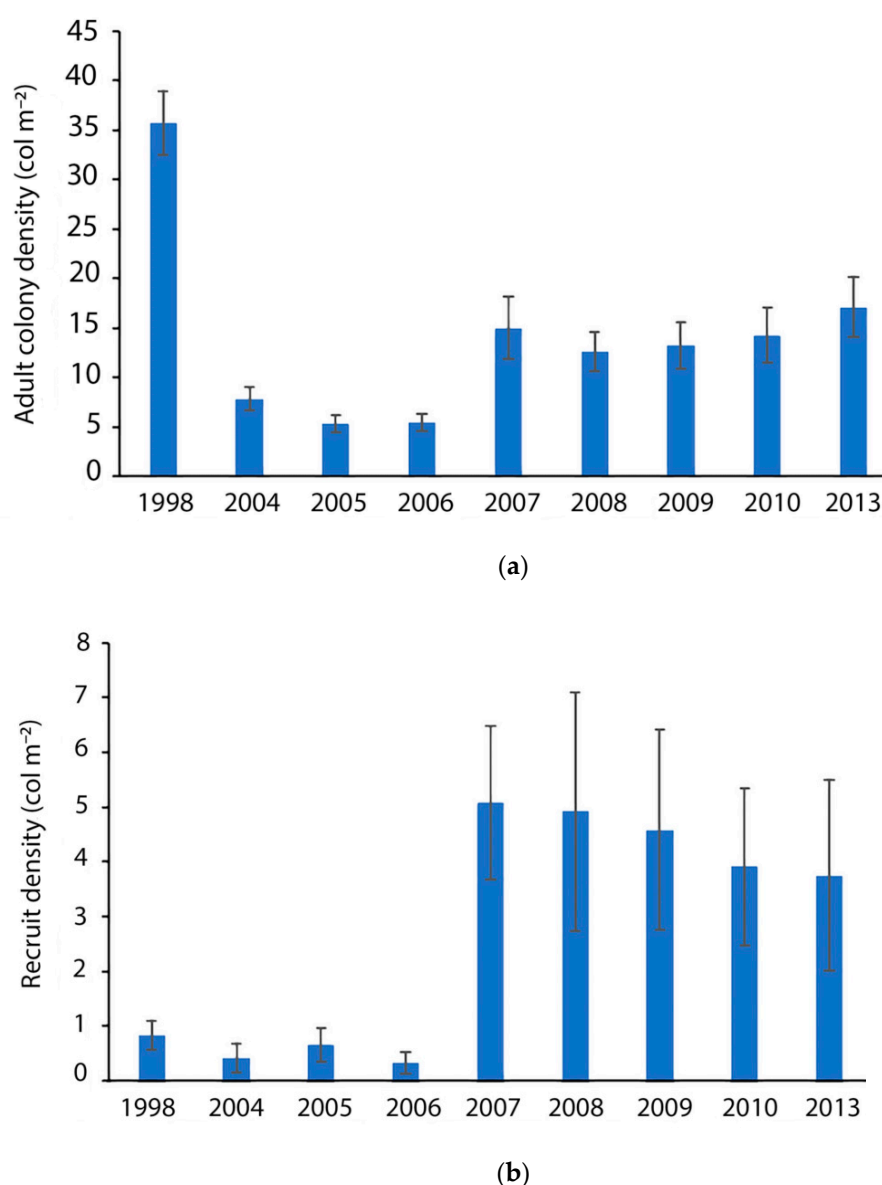
Figure 3. (**a**) Adult colony density and (**b**) recruit density during the observational period.

The size/age structures of the *P. clavata* population in 1998 (before the anomalous mortality events) and the following years 2004–2013 are reported in Figure 4a–i. The maximum size found (53.5 cm) corresponded to a maximum life span of about 18 years. The population was thus divided into 18 size/age classes based on the average annual colony growth rate [12,20].
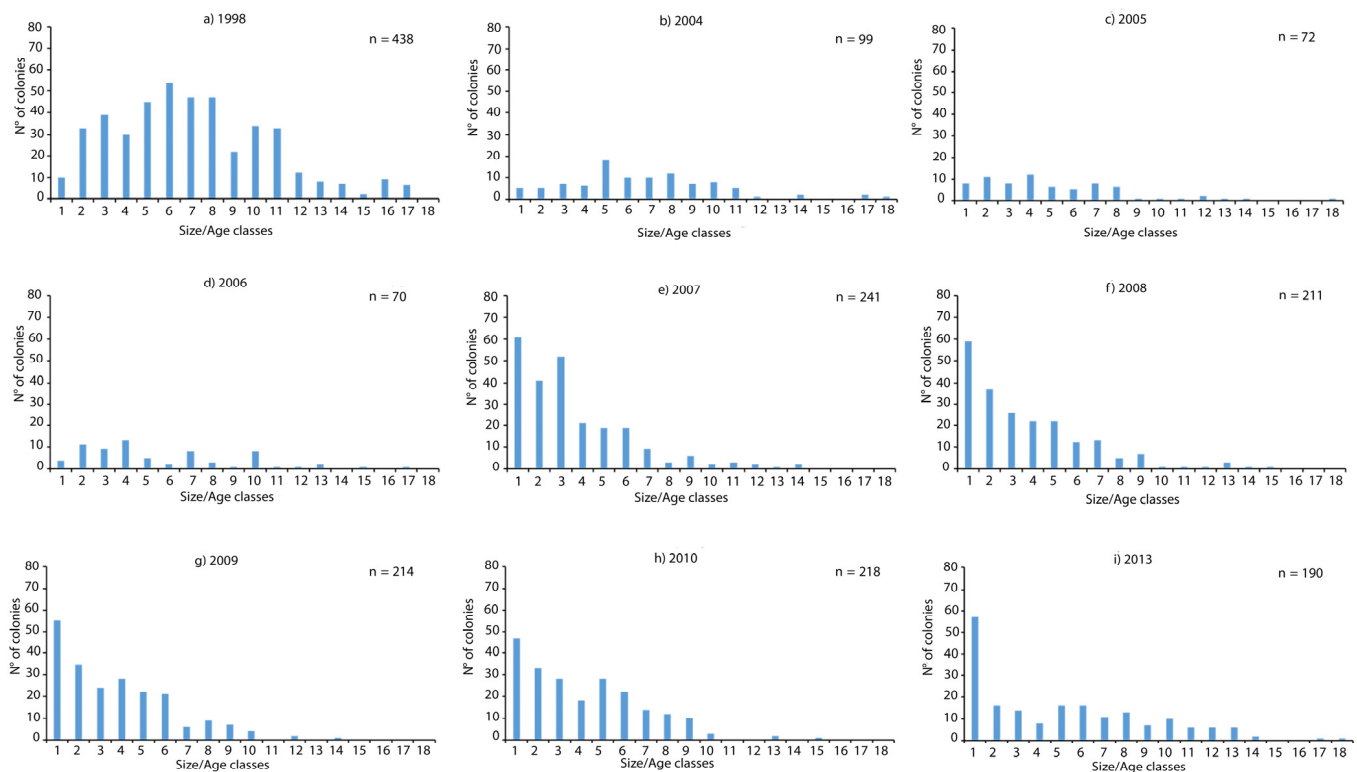
Figure 4. (**a**–**i**) Population size/age structure during the observational period.

The pre-mortality 1998 population (Figure 4a) exhibited a non-monotonic structure, skewed toward larger/older colonies (reaching class 17), in which classes 5–8 were dominant and recruitment (the first class) was low. In the following years (2004–2006; Figure 4b–d), recruitment, together with all classes, fell, and larger/older colonies nearly disappeared, being heavily impacted by the 1999 and 2003 mortality events. In 2007, and up to 2013 (Figure 4e–i), the population size/age structure changed again, following a monotonic, regularly decreasing pattern with dominant recruitment indicating, according to Caswell [45], a population in steady state. In 2013, the number of larger/older classes increased, and classes 17–18 were again represented (Figure 4i).

These findings are consistent with the results of the MDS analysis (Figure 5), which separated the 1998 pristine structure from the others and grouped together all the years between 2007 and 2013, which exhibited a similar demographic structure, characterized by dominant recruitment and a regularly decreasing abundance of larger/older classes. The population structure in 2004 (immediately after the second mortality event) is not grouped with the other years, but is instead set apart from them. The 2005–2006 cluster likely represents an intermediate point between the pristine structure and the partial recovery occurring in the following years.
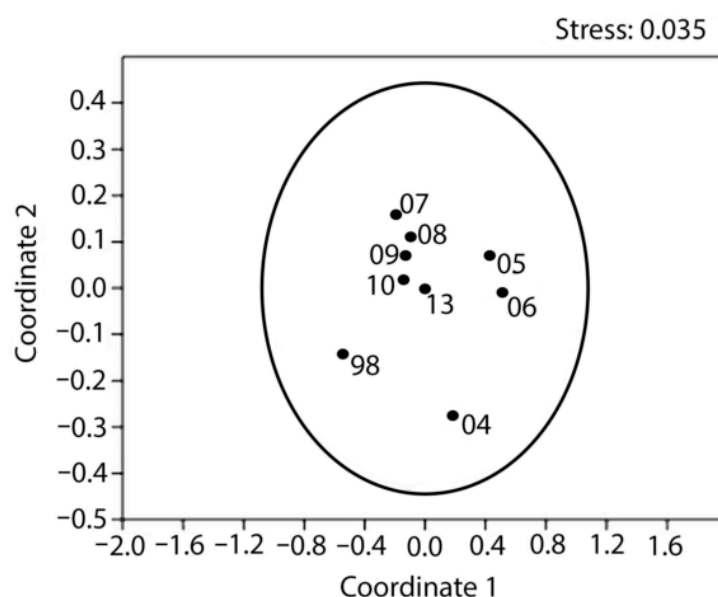
Figure 5. Multidimensional scaling (MDS) of population size/age structure in different years. The closeness of one sample to another (belonging to a different year) is a measure of similarity. The elliptical area represents 95% confidence. The 1998 pristine structure is set apart from the others, while all the years between 2007 and 2013 are grouped together. The 2005–2006 cluster likely represents an intermediate point between the pristine structure and the subsequent partial recovery.

3.2. Percentage Cover of Benthic Organisms and Density of Paramuricea Clavata

In 2013, the majority of the substrate (65%) was covered by TSH and the remaining 34% by sessile macro-benthonic organism (occupied substrate). It was impossible to read the remaining 1% of the photo-sample (undetermined area, Table 1). *P. clavata* (50%) and Porifera (27.7%) were the dominant organisms. Hexacorallia (mainly *Parazoanthus axinellae* and *Leptosamnia pruvoti*), Phaeophyceae, Rodophyceae, Ascidiacea, Bryozoa, and Polychaeta covered the remaining surface of the occupied cliff (22.3%).

Table 1. Percent cover (%) of the whole Tinetto Islet area and two sites (Tinetto Island and Tinetto Shoal) in 2013 and 1998 [46]. The TSH substrate is composed by algal turf, sediment, and small hydrozoans; occupied substrate includes sessile macro-benthonic organisms listed below. * = $p < 0.05$ level. TSH, occupied substrate, density of *P. clavata* adults and recruits (col m^{-2}) in the whole Tinetto Islet area in 2013 are compared with those measured in 1998 [46].

			2013			**1998**
			Tinetto Islet Area	**Tinetto Island**	**Tinetto Shoal**	**Tinetto Islet Area**
			n = 23	*n* = 12	*n* = 11	*n* = 24
% Cover $\bar{x} \pm$ ES		TSH	65.1 ± 1.4	65 ± 2.3	65.3 ± 1.7	39 ± 1
		Undetermined area	1.3 ± 1.4	1.5 ± 0.2	1 ± 0.2	0
		Occupied substrate	33.6 ± 1.5	33.5 ± 2.5	33.7 ± 1.8	61 ± 1
		Porifera	9.3 ± 0.7	10.9 ± 0.6 *	7.6 ± 1.2 *	-
		Hexacorallia	4 ± 0.4	5.8 ± 1 *	2 ± 0.2 *	-
		Algae	2 ± 0.04	1.1 ± 0.1 *	2.9 ± 0.6 *	-
		Ascidiacea, Bryozoa, and Polychetae	0.29 ± 0.06	0.4 ± 0.1 *	0.2 ± 0.03 *	-
		Paramuricea clavata	16.8 ± 1.7	14.0 ± 2.3 *	19.9 ± 2.4 *	52.0 ± 1
Colony density (col m^{-2}) $\bar{x} \pm$ ES		Recruits	3.75 ± 1.74	1.33 ± 0.48 *	6.18 ± 2.14 *	0.83 ± 0.27
		Adults	17.10 ± 3.01	12.07 ± 1.81*	21.30 ± 4.17*	35.67 ± 3.20

A comparison with the data collected in the same area in 1998 on a similar number of samples highlighted some major changes occurring within the community over the pre-mortality/post mortality transition, showing about a twofold increase in TSH and halving of the cover of benthic organisms (Table 1). The *P. clavata* % cover was reduced threefold, and the adult density decreased twofold, while during the same time interval recruitment increased by four and a half times.

In 2013, no significant difference in TSH % cover or the % of the occupied substrate by sessile organisms between the two sample sites was found ($t = -0.095$, $p > 0.05$ and $t = -0.07$, $p > 0.05$), while the % cover of Porifera was significantly higher at Tinetto Island than at Tinetto Shoal ($t = 2.56$, $p < 0.05$, Table 1).

Overall 355 colonies were counted in 23 m^2 of the study area (130 at Tinetto Island and 225 at Tinetto Shoal), reaching an average density of about 15 colonies per m^2. Recruits settled only on some of the plots (61.8%): overall, 64 recruits were found on 14 plots (6/12 plots at Tinetto Island and 8/11 plots at Tinetto Shoal), with an average density of 3.75 recruits per m^2. A significantly higher recruit density was found at Tinetto Shoal (6.18 ± 2.14 col m^{-2}) vs. at Tinetto Island (1.33 ± 0.48 col m^{-2}; Mann–Whitney $w = -2.06$, $p < 0.05$, Table 1). Moreover, adult colony cover and density were also significantly higher in this latter area (14.0 ± 2.3 vs. 19.9 ± 2.4% cover: $t = -1.80$, $p < 0.05$; 12.07 ± 1.81 col m^{-2} vs. 21.30 ± 4.17 col m^{-2}: $t = -2.08$, $p < 0.05$).

No correlation emerged between larger/older colony and recruit densities ($n = 23$, $r = 0.35$, $p > 0.05$, Figure 6a), but a significant positive linear correlation was found between the density of recruits and that of smaller/younger colonies ($n = 23$, $r = 0.78$, $p < 0.01$, Figure 6b). Some linear trend was also found in the recruitment density measured in the same plot in two consecutive years ($n = 24$, Figure 6c). Both the last findings suggest that samples showing high recruitment in one year show similar values in the following years, as well.

No correlation was found between colony density and Porifera % cover ($r = -0.34$, $p > 0.05$) or between recruit density and TSH % cover measured in the same plots ($r = 0.038$, $p > 0.05$). These results suggest that neither the density of adult colonies nor the kind of substrate (at the gross-grain level examined) likely have any linear effect on *P. clavata* recruitment.
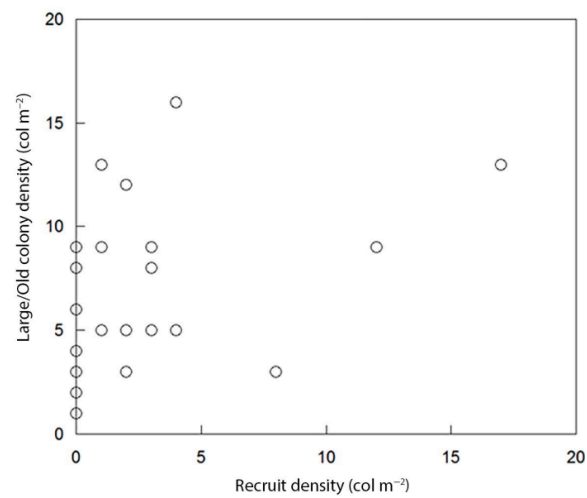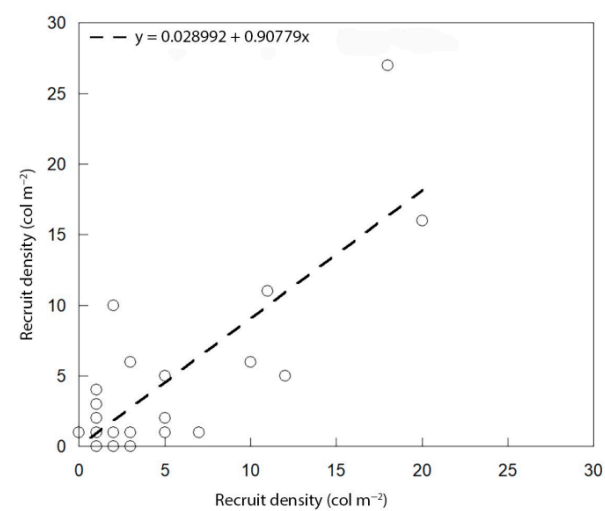
(a)
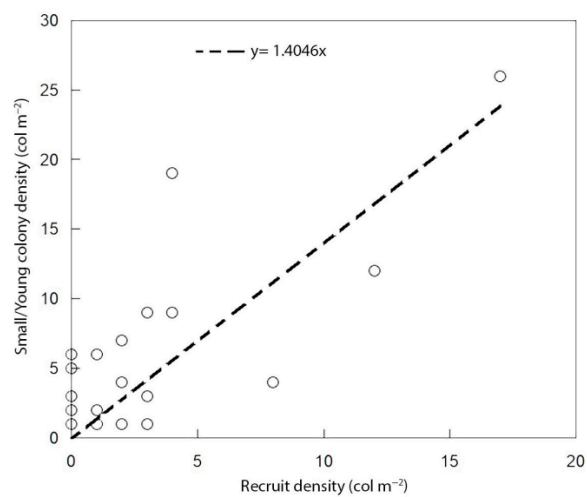
(b)

(c)

Figure 6. Trends of recruit and colony density: (**a**) density of recruits vs. that of larger/older colonies; no linear trend was found; (**b**) density of recruits vs. that of small/young colonies; a linear trend emerged; (**c**) recruit density measured in the same photo sample in two successive years (2007 vs. 2008 and 2009 vs. 2010) and the linear trend.

4. Discussion

Our understanding of the long-lasting effects of GCC on long-lived populations of marine benthic communities is quite limited. Generally, simulations try to fill this gap by devising possible scenarios of affected population trends [40,47] among others. An analysis of a dataset from 1998 to 2013 allowed us to follow the main trends of the community under study and the locally dominant gorgonian population before and after two dramatic mass mortality events occurring throughout the northwest Mediterranean during late summer in both 1999 and 2003.

The area where the temperate gorgonian *Paramuricea clavata* population examined here dwells is characterized by a sciaphilic epibenthic community settled on a vertical cliff. The entire area is affected by high sedimentation rates due to the outflow of the Magra river [38]. The high concentration of seston typical of this area is likely a factor favoring passive suspension feeders [32]. Cnidarians, and the gorgonian *P. clavata* in particular, are the dominant group, while the algal cover is poor, limited by the high turbidity of the area.

The *P. clavata* population of Tinetto Islet has been divided into 18 annual age/size classes, according to the mean annual colony growth rate [20]. The distribution of size classes observed in 1998 in the crowded, pre-mortality population with abundant larger (older) colonies could be driven, by the effect of the increasing density of larger/older colonies on recruitment rate, progressively affecting the population over some years, leading to a structure characterized by a low abundance of recruits and smaller/younger classes. After the 1999 and 2003 mortalities, only a few of the largest sized gorgonians survived, and the structure of the population drastically shifted towards the smaller/younger classes. In 2007, colony density significantly increased and remained stable subsequently. As mortality disproportionally affected the larger/older colonies and fecundity is strictly correlated with colony size [21], a drastic reduction in the larger classes could have decreased the population's reproductive output. However, the abundant egg and planulae production of this species could have attenuated the effects of the loss of larger colonies on population resilience [21].

Ten years after the last *P. clavata* anomalous mortality event (2003) a twofold increase was found in the substrate covered by TSH, indicating that a clear-cut change in the whole community occurred. Concerning the *P. clavata* population, both % cover and density of adult colonies were also reduced, albeit to different degrees, as they were respectively one third and half those recorded in 1998. Recruitment, on the other hand, was four and a half times higher than in the pre-mortality population. The difference between the reduction in adult colony cover and the density found could be due to the different size/age structure of the post-mortality population, in which the number of larger/older colonies fell disproportionally [20], thereby affecting colony cover more than density.

Several papers have reported that algal turf coverage and high sedimentation rates negatively affect recruitment and reproduction in benthic communities [48,49] among others. For example, in the gorgonian *Eunicella singularis*, algal turf seems to negatively affect the process of settlement by decreasing the larva's access to suitable substrate [50]. Contrary to this general finding, *P. clavata* recruitment density increased since 2007, despite a significant rise in TSH % cover between 1998 and 2004 [45], and remained substantially unchanged in the following years. However, the lack of any correlation between the TSH and *P. clavata* recruitment or adult colony density likely indicates the absence of any linear effect of TSH cover on the gorgonian population examined. This finding seems to be confirmed by the similarity in TSH % cover between the two sites sampled which, however, differ in *P. clavata* adult and recruit densities. As no correlation between these parameters and TSH cover was observed, other factors likely caused the difference found between the sites. According to Padròn et al. [34], who examined the genetic structure and connectivity of *P. clavata* populations across our sampling area and six other sites in the eastern Ligurian Sea, the locally dominant currents may have fostered a higher larval input in our more external site (Tinetto Shoal), thereby partly driving the dynamics of this population. Indeed, the input of larvae released in other areas may play an important role in the recovery of

benthic sessile populations affected by anomalous mortality events. In *P. clavata* the larval stage can span between 6 and 26 days under experimental conditions [45,51], and planulae are able to travel distances of up to tens of kilometers. Recent genetic analyses in the Ligurian Sea suggest that tight connectivity among *P. clavata* populations affected by anomalous mortality can avoid their collapse [34], while highly frequent mortality events may lead isolated octocoral populations even to extinction [12]. Thus, the strategic position of the population under study and the connectivity with the other neighboring populations could be a key factor in fast recovery after disturbing events [51].

There is some hint towards a small-scale spatial constancy of recruitment over time; this is based on two findings: (1) a significant positive linear correlation between the density of recruits and that of the cohort of small/young adult colonies measured in the same plot; (2) some linear trend of recruit density recorded in the same plot in two consecutive years. Both these findings suggest that the plots more intensively recruiting in one year will also recruit more in following years. Thus, some plots should likely, present particular features that make them more suitable for *P. clavata* settlement over time. It can be speculated that micro-scale hydrodynamics, local substrate texture, and/or chemical attractors produced by the local species associations could foster more abundant recruitment in some plots.

The lack of any relation between the density of recruits and that of larger/older colonies suggests some independence of recruitment from the density of these colonies, as well as the lack of any effect of their high fecundity on local recruitment [21]. Although these findings may appear to be in contrast with the initial relation between recruits and small/young adults, the selectively higher mortality affecting the larger/older classes may, over time, lead to an alteration of such relation.

The highly dense canopy made mainly by older colonies in the pre-mortality, over-crowded population may have had some "shadow effect" to avoid larval settlement in their surroundings by limiting the substrate suitable for recruits. After the 1999 and 2003 mortalities, reduction of the canopy by about 2/3 could have driven a clear-cut increase in recruitment. As the increase in recruitment was delayed by four years since the mortality events and co-occurred with the detachment of dead colonies from the cliff in 2007 [20], the shadow effect caused by the dead 'scaffold' of larger colonies could have been maintained until they detached. Only after the dead colonies fell off the cliff and their shadow effect disappeared did recruitment start to rise, remaining at similar values in the following years, as well.

Paramuricea clavata has been considered a species with low population turnover and recovery rates [52,53]. Moreover, according to a demographic model aimed at projecting the trends of this population over time by means of simulations based on an ad hoc Leslie-Lewis transition matrix [46], wide fluctuations in density that stabilize only after several decades have been described [13]. However, in the present study, we observed, in the real population, faster density stabilization than predicted by said model.

After 14 and 10 years since the two mortality events, the population of *P. clavata* is still alive and has partially recovered, although with severely reduced density and canopy. Moreover, the population structure, dominated in recent years by recruits, is quite different from the pre-mortality one, dominated by larger/older colonies. As these features have been maintained for 7 years, the population seems to have reached a new equilibrium point.

All the findings presented herein indicate that the effects of drastic mortality events on a long-lived gorgonian population cannot be limited to the narrow definitions of "extinction or recovery", but that a stricken population may reach a new equilibrium. The main concern regards the stability of such a new equilibrium reached at remarkably lower densities: repeated mortality events and undamped oscillations may even devolve the local population to extinction.

5. Conclusions

A decade after two mass mortality events in 1999 and 2003, the circalittoral community thriving on a vertical cliff has undergone some profound changes. In subsequent years, the TSH (algal turf, sediment and small hydrozoans) percentage cover increased twofold, and the cover and density of the dominant gorgonian population *P. clavata* was reduced by 2/3 and 1/2, respectively, while recruitment increased two and a half times. A tendency of some quadrates to recruit more intensely over time was found. No direct effect of TSH and *P. clavata* percentage cover on recruit and adult colony density resulted.

In 2013 the still surviving population had not recovered its pristine structure, and had only partially restored its canopy. In addition, although it had recovered, the population seemed to have reached a new equilibrium point, whose stability is as yet disturbingly unknown.

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