

## Article

# Animal Forest Mortality: Following the Consequences of a Gorgonian Coral Loss on a Mediterranean Coralligenous Assemblage

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**Abstract:** In this work, the consequences of a local gorgonian coral mortality on the whole coralligenous assemblage were studied. A Before/After-Control/Impact sampling design was used: the structure of the coralligenous assemblage was compared before and after the gorgonian mortality event at the mortality site and two control sites. At the mortality site, a relevant decrease in alpha and beta diversity occurred, with a shift from a stratified assemblage characterized by gorgonians and other invertebrates to an assemblage dominated by algal turfs; conversely, neither significant variations of the structure nor decrease in biodiversity were observed at the control sites. The assemblage shift involved the main taxa in different times: in autumn 2018, a large proportion of the plexaurid coral *Paramuricea clavata* died, but no significant changes were observed in the structure of the remaining assemblage. Then, in autumn 2019, algal turfs increased significantly and, one year later, the abundance of the gorgonian *Eunicella cavolini* and bryozoans collapsed. Although the mechanisms of the assemblage shift following gorgonian loss will remain uncertain and a cause-effect relationship cannot be derived, results suggest the need for detecting signs of gorgonian forests stress in monitoring programs, which should be considered early indicators of their condition. In the coralligenous monitoring programs for detecting any sign of gorgonian forests stress which should be considered an early indicator of the assemblage condition.



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## 1. Introduction

Mass mortality events (MMEs) in marine systems are of an increasing ecological concern, as their intensity and frequency are rising worldwide due to global changes mostly related to climate anomalies, such as sea surface temperature rise [1–3]. Consequences of mass mortality may be more serious than the mere loss of the concerned taxa, as some of them are habitat-forming species and their regression may lead to severe biodiversity erosion and changes in the whole system functioning [4,5]. The ability of marine systems to recover after MMEs is greatly variable due to differences in the taxa concerned, propagule availability, and the occurrence of further stressors [6–8]; thus, different systems may take different trajectories of community change following a MME [9].

In the Mediterranean Sea, MMEs have been first evidenced in the 1980s in the Western Basin and the Aegean Sea [10–12], but probably, the most recent impressive MME that has involved more than thirty species from different phyla has happened in 1999 along the French and Italian coasts [13,14]. Since then, other numbered MMEs have been reported of a range of scales, with respect to geographic extend and number of affected species [15–17].

Because MMEs have generally been associated with strong and recurrent marine heat waves (MHWs) [1,18–20], a collaborative data base has been created to examine the relationship between the thermal conditions and other environmental variables (such as the number of MHW days) possibly linked with thermal anomalies (e.g., occurrence of the proliferation of filamentous algal blooms and mucilage) and the MME [21].

The main Mediterranean MMEs, besides the mortality of the giant mussel *Pinna nobilis* (Linnaeus 1758) [22], concerned the coralligenous habitat [23], a typical Mediterranean biogenic subtidal seascape mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions and in relatively calm waters, mostly at depths of 30–130 m [24]. Calcareous encrusting algae constitute a secondary substrate where stratified assemblages including erect algae, sponges, bryozoans, gorgonian corals, and other alcyonaceans develop [24]. The maintenance of coralligenous organisms is likely related to relatively steady environmental conditions, and therefore they are particularly sensitive to local and global stressors [25–29]. MMEs have been described for many coralligenous species [30–33], but gorgonian corals and *Paramuricea clavata* (Risso, 1826) in particular appear to be mostly affected [34–37]. Indeed, Mediterranean gorgonians may be threatened by many local human pressures, such as pollution, sedimentation, introduced species, and mechanical destruction by fishing gears or scuba divers [38–40]. However, the most severe threats are often related to stressors acting at large scale, such as climatic anomalies [15,41,42], benthic mucilage [43–45], diseases [46,47], and synergisms among them [48]. Recovery of populations is slow and almost always partial [34,49–52]. Gorgonians are habitat-forming species whose presence is known to influence the structure of the associated assemblage and form an animal forest [53–58]. Thus, gorgonian loss is thought to induce changes in species composition of coralligenous assemblages and to reduce species diversity [42,59]. Although some common patterns have been described [42,59], the ecological consequences of gorgonian loss are variable [50,52,60,61] and far from being understood.

In this work, the diversity and structure of a coralligenous assemblage affected by a local gorgonian mortality (GM) was compared through time to nearby unaffected assemblages. Here, a Before/After-Control/Impact (BACI) sampling design [62,63] was used to compare the coralligenous assemblage before and after the GM event at the mortality site and two control sites. We hypothesized that the diversity of the coralligenous assemblages over time would change differently at the GM site rather than at the controls. Variations in taxa abundance following the mortality event was also evaluated to detect changes due to gorgonian loss, both identifying the taxa involved and measuring taxa vulnerability, by estimating the time needed to detect changes since GM.

## 2. Material and Methods

The study was done in the Marine Protected Area (MPA) of Capo Carbonara, located in South-Eastern Sardinia (Italy, Western Mediterranean). Three granite rocky bottom sites were considered: Cavoli Island (D, disturbed), where a widespread mortality of the gorgonian *Paramuricea clavata* was detected in late October 2018, and Serpentara and Santa Caterina (C1 and C2, controls Figure 1), where no mortality events have been recorded within the same period (LP, personal observation). The three sites are monitoring stations for the assessment of the MPA coralligenous reefs, and data before and after the GM event were therefore available. The D site was monitored annually between November 2016 and November 2020, while C1 and C2 were sampled in 2017 and 2020.



**Figure 1.** Map of the study sites. D = disturbed site, C1 and C2 = control sites.

During each sampling period, three plots (4 m<sup>2</sup> in size), tens of metres apart, were randomly selected on vertical substrates at about 33 m depth at each site. In each plot, 10 photographic samples of 0.2 m<sup>2</sup> were collected [64]. Photographic samplings were analyzed to evaluate the percentage cover of the main taxa or morphological groups using ImageJ software [65]. Organisms easily detected by photographic samples were identified to the lowest possible taxonomic level, while those not easily recognizable were identified according to morphological groups [66].

The diversity of the assemblages was evaluated both as taxa/morphological group number per sample (alpha diversity) and as heterogeneity (beta diversity) calculated through the PERMDISP analysis (Primer 6 + PERMANOVA) [67], using the mean distance of photographic samples from centroids as a measure of the beta diversity of the system [67].

Temporal and spatial differences in the structure of assemblages were analyzed by a permutational analysis of variance (Primer6 + PERMANOVA) [68] based on a Bray–Curtis resemblance matrix of untransformed data. Data were not transformed in order to stress the importance of the abundance of taxa/groups in determining the differences among conditions. The alpha and beta diversity and the abundance of the main taxa were analysed by PERMANOVA based on Euclidean distance. The Pair-wise test was used to discriminate between levels of significant factors.

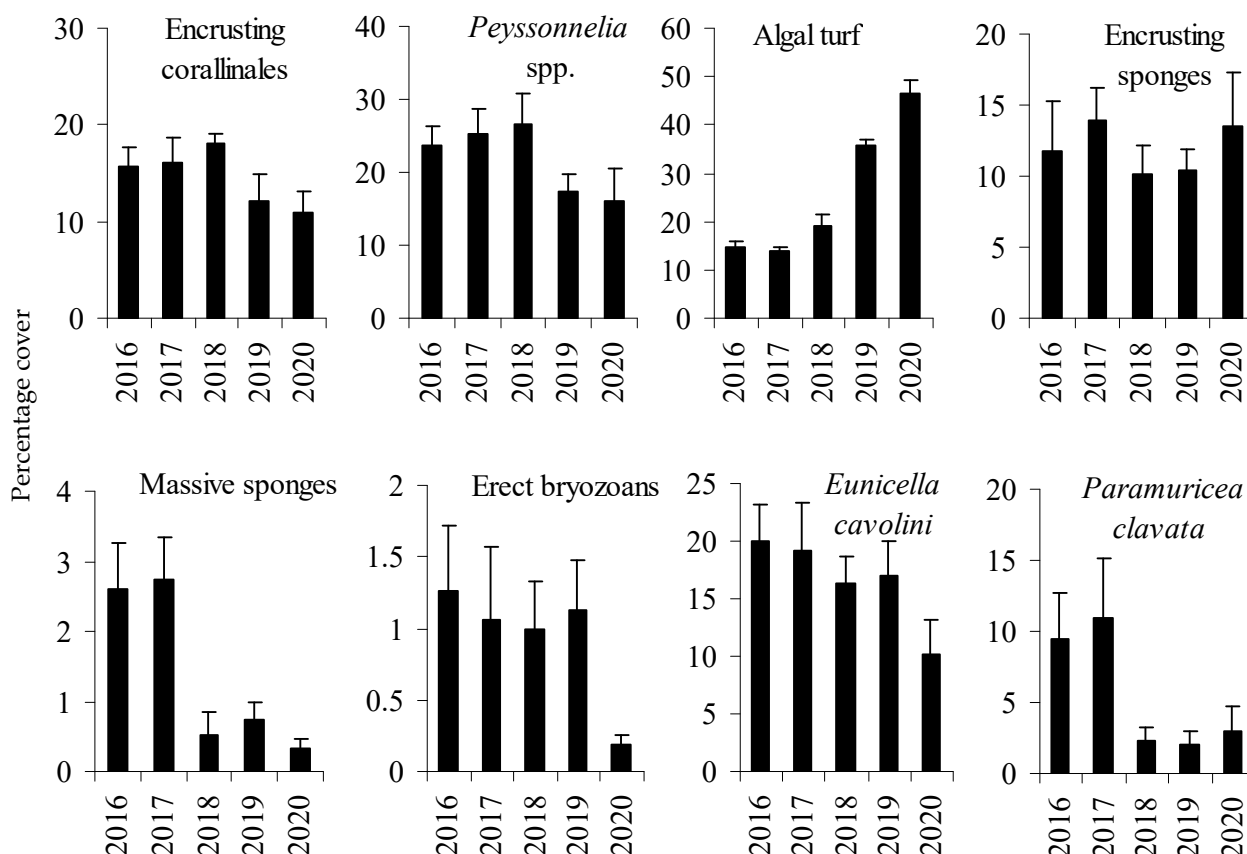
The structure of the D assemblage and the abundance of the main taxa were analyzed through a two-way model with the factors Time (2016, 2017, 2018, 2019, 2020, treated as fixed) and Plot (3 levels, treated as random and orthogonal). An nMDS was performed for a graphical representation of dissimilarities among assemblages through time.

To compare the D assemblage with the Cs between 2017 and 2020, a three-way PERMANOVA was used with Time (before vs. after, i.e., 2017 vs. 2020) and Site (D, C1 and C2) as fixed and orthogonal factors, while Plot (3 levels) as random and nested in Site. Gorgonians were not included in the analyses to test the hypothesis that their mortality affected the structure of assemblages. The same model of multivariate analysis was used for the alpha diversity, while beta diversity was analysed through a two-way model with Time and Site as fixed and orthogonal factors, while sampling plots were used as replicates.

### 3. Results

Before mortality (in 2016–2017) at the D site, the coralligenous assemblage was characterized by a stratified structure: the erect layer constituted by the gorgonians *Paramuricea clavata* and *Eunicella cavolini* (Koch, 1887), the intermediate layer by erect bryozoans (mostly *Smittina cervicornis* (Pallas, 1766)) and massive sponges, while the basal layer consisted of encrusting coralline algae, encrusting sponges, and prostrate red algae *Peyssonnelia*

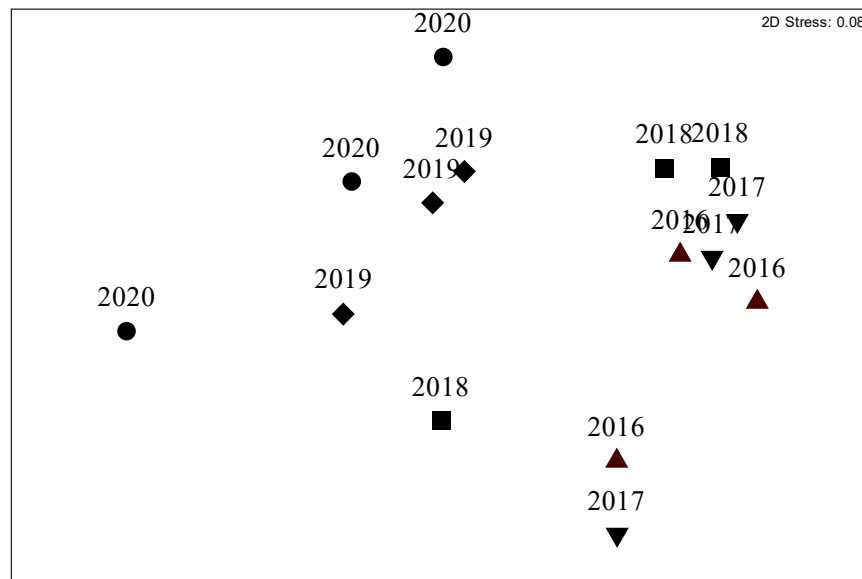
spp. (Figure 2). A small variability between 2016 and 2018 at D site in the structure of the coralligenous assemblage was identified (PERMANOVA, MDS and the Pair-wise test) compared to the variations found both in 2019 and 2020 (Table 1, Figure 3). Variations were mostly due to *P. clavata* that decreased between 2017 and 2018, the algal turf that increased between 2018 and 2019, and the erect bryozoans and *E. cavolini* that decreased between 2019 and 2020 (Table 1, Figure 2). The abundance of massive sponges, encrusting coralline algae and *Peyssonnelia* spp. also decreased during the study period, but variations were not significant (Table 1, Figure 2).



**Figure 2.** Percentage cover (mean  $\pm$  SE,  $n = 30$ ) of the main taxa groups of the coralligenous assemblages at the D site throughout the whole the study period.

**Table 1.** Effects of Time in PERMANOVA for the Cavoli (D site) coralligenous assemblage and its main taxa/groups. Significant  $p$ -values are in bold.

Taxa/Group	Pseudo- $F_{4,8}$	P (Perm)	Pair-Wise Test
Multivariate analysis	4.44	<b>0.003</b>	2016 = 2017 = 2018 $\neq$ 2019 $\neq$ 2020
encrusting coralline	2.88	0.090	
<i>Peyssonnelia</i> spp.	0.33	0.810	
algal turf	49.02	<b>0.001</b>	2016 = 2017 = 2018 < 2019 = 2020
encrusting sponges	0.10	0.981	
massive sponges	2.90	0.073	
erect bryozoans	14.36	<b>0.004</b>	2016 = 2017 = 2018 = 2019 > 2020
<i>Paramuricea clavata</i>	17.07	<b>0.003</b>	2016 = 2017 > 2018 = 2019 = 2020
<i>Eunicella cavolini</i>	4.98	<b>0.028</b>	2016 = 2017 = 2018 = 2019 > 2020



**Figure 3.** MDS: temporal variation of similarities throughout the study period (from 2016 to 2020) of the Cavoli (D site) coralligenous assemblage.

Based on the BACI design, on the before (2017) and after (2020) parameters, both the multivariate and univariate PERMANOVA analyses have found the interaction Time × Site to be significant (Tables 2–4). Particularly, the Pair-wise test showed that the structure of assemblages significantly varied at the D site from before to after GM, but not at the controls where assemblages did not change significantly through time (Table 2). The change in the structure of the coralligenous assemblage has led to a reduction of both alpha and beta diversity at the disturbed site; a different pattern was found at controls as alpha diversity increased in C2 and beta diversity did not change (Tables 3 and 4; Figure 4).

**Table 2.** PERMANOVA on the coralligenous assemblage: Time (before and after GM, T1 and T2 GM), Site (D, C1 and C2) and Plot (3 levels). Significant *p*-values are in bold.

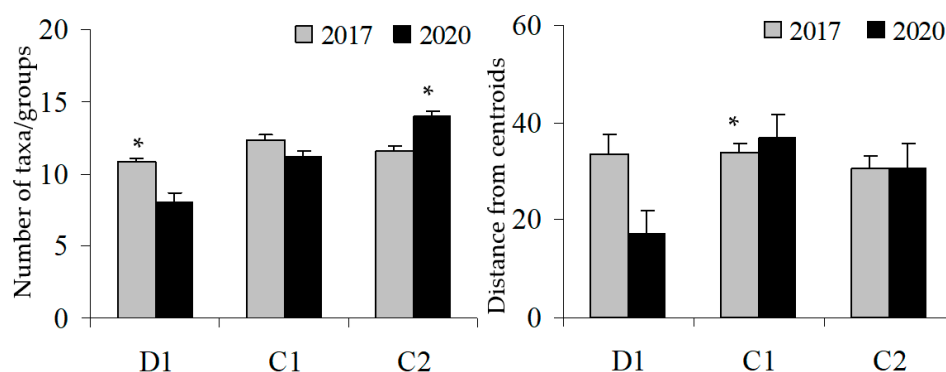
Source	df	MS	Pseudo-F	P (Perm)
Time = T	1	10,175	5.59	<b>0.007</b>
Site = S	2	53,273	28.66	<b>0.003</b>
Plot(S) = P(S)	6	1858	4.13	<b>0.001</b>
TxS	2	13,359	7.34	<b>0.002</b>
TxP(S)	6	1818	4.04	<b>0.001</b>
Residual	162	449		
Pair-wise test (TxS)	D:	T1 ≠ T2		
	C1:	T1 = T2		
	C2:	T1 = T2		

**Table 3.** PERMANOVA on alpha diversity: Time (before and after GM, T1 and T2), Site (D, C1 and C2) and Plot (3 levels). Significant *p*-values are in bold.

Source	df	MS	Pseudo-F	P (Perm)
Time = T	1	12.8	9.4	<b>0.028</b>
Site = S	2	175.5	13.21	<b>0.011</b>
Plot(S) = P(S)	6	13.2	2.9	<b>0.013</b>
TxS	2	96.2	70.72	<b>0.001</b>
TxP(S)	6	1.3	0.29	0.941
Residual	162	4.5		
Pair-wise test (TxS)	D:	T1 > T2		
	C1:	T1 = T2		
	C2:	T1 < T2		

**Table 4.** PERMANOVA on beta diversity: Time (before and after GM, T1 and T2) and Site (D, C1 and C2). Significant *p*-values are in bold.

Source	df	MS	Pseudo-F	P (Perm)
Time = T	1	95.6	5.37	<b>0.028</b>
Site = S	2	150.7	8.47	<b>0.009</b>
TxS	2	164.2	9.24	<b>0.004</b>
Residual	12	17.7		
Pair-wise test (TxS)	D:	T1 > T2		
	C1:	T1 = T2		
	C2:	T1 = T2		

**Figure 4.** Before (2017) and after (2020) GM: alpha (left) and beta diversity (right) at Cavoli (D) and at two control sites (C1 and C2). Asterisks indicate significant effects.

#### 4. Discussion

The results of the study showed relevant differences in coralligenous assemblage structure and biodiversity patterns after the mortality event of the gorgonian *Paramuricea clavata* that in 2018 has happened in the Capo Carbonara MPA only at the D site. Important clues about the role of *P. clavata* on the whole coralligenous assemblage come from the evidence that the changes only concerned the site affected by the mortality event, while no significant variations of the structure and biodiversity decrease were observed at the control sites.

Indeed, the most relevant changes have occurred locally at the D site where a decrease in alpha and beta diversity was highlighted. Particularly, the modifications have involved the stratified structure as the assemblage characterized by large erect gorgonian corals and other invertebrates has shifted to an assemblage dominated by low-growth algal turfs. Overall, the assemblage shift has involved all the main taxa, although in different times and with different significance levels, and it has occurred across three years since the onset of the GM: in autumn 2018, a large proportion of *P. clavata* had died but no significant changes were observed in the structure of the remaining assemblage; in autumn 2019, algal turfs increased significantly and, one year later, the abundance of the gorgonian *E. cavolini* and bryozoans collapsed. This kind of successional pattern was previously described in a similar way [42,59]. Moreover, the temporal pattern of change depicted here is in agreement with previous observations [42] that highlighted delayed severe effects due to GM after 2.5 years (rather than the immediately), overall suggesting that the collapse of this habitat does not happen immediately.

The shift in a coralligenous assemblage following a gorgonian mortality resembles the collapse of a community following the loss of its foundation species [69–71]. The mechanisms (whether direct or indirect) involved in this shift are not easy to understand. A concurrent mortality of multiple taxa would be expected as consequence of a severe environmental stress as several macro-invertebrates and coralline algae, usually inhabiting gorgonian forests, are considered to be affected by the same factors as gorgonians [13,27,30,33]. However, different organisms may have different responses to stress, and sublethal effects



or physiological stress may also occur, although the mortality happens in the subsequent years [50]. On the other hand, the lack of habitat-forming organisms may lead to further consequences: gorgonian forests can create complex three-dimension structures and offer protection to fragile calcareous colonies, supporting high species diversity [53,59]. Moreover, when the density of gorgonians is high, the altered environmental conditions (light, currents, sediment deposition rates, etc.) [53,72] offer several micro-habitats promoting high biodiversity [56]. Gorgonian forests may be considered structured habitat where smaller environmental modifications occur slower than in the surrounding 'unforested' environment, which provide positive effects on diversity, distribution, and abundance of a large proportion of organisms [53,56]. Finally, gorgonians are known to limit the settlement and spread of opportunistic species such as algal turfs and serpulid calcareous worms [56] and enhance the growth of calcareous algae and invertebrates [59]. Thus, the loss of gorgonians may explain itself the shift of assemblages dominated by erect invertebrates and encrusting algae to assemblages dominated by turf-forming species [42].

Nevertheless, a crucial role in this shift might be related to the spread of algal turfs which seems to be the first consequence of gorgonian loss [42]. In fact, turf algae have the capacity to affect the population dynamics of sessile invertebrates by reducing recruitment and juvenile survival [73]. The effects of turf algae on the invertebrate recruitment may be due either to a decrease of suitable substrate area for larval settlement and to algal overgrowth, as observed in coral reefs [74,75]. Thus, turfs, once established, can reduce the resilience of gorgonian forests preventing recruitment and stabilize an un-forested condition [73]. This effect may be more severe if invasive turf species are involved [40], such as the introduced Rhodophyta *Womersleyella setacea* (Hollenberg) R.E. Norris which has been described as a relevant component of coralligenous algal turfs in the Capo Carbonara MPA [76].

Although the mechanisms of the assemblage shift following gorgonian loss will remain uncertain and a cause-effect relationship cannot be derived, the present effort through a BACI approach has linked the loss of *Paramuricea clavata* with the decrease of biodiversity and structural complexity of coralligenous assemblages. Marine animal forests are declining worldwide with deep ecological consequences [77] mostly related to a shift towards less structurally complex systems [78]; the present study, in accordance with previous investigations [42,59], suggests the crucial role of animal forests in the maintenance of biodiversity of the Mediterranean coralligenous system. This study has documented the shift of assemblages two years after the GM, although long-term monitoring would be needed to detect the future development of the system, as different scenarios may be hypothesized: (i) the turf dominated assemblages can stabilize, (ii) gorgonians may recover their population or (iii) a new type of assemblage can develop, as high quality coralligenous reefs dominated by invertebrates or macroalgae may also occur in absence of an erect layer [79]. The trajectory of system evolution is expected to be strictly related to environmental conditions, as pressing stressors, such as climatic warming, thermal anomalies, and benthic mucilage, may preclude the spread of sensitive organisms, eroding the resilience of the system. Within the actual global change scenario, where environmental stress may be independent of local protection measures, raising the frequency of surveys is increasingly needed. Although the presence, size and status of gorgonians have already been proposed as descriptors of the ecological quality of coralligenous reefs [80–82]; the surveillance of gorgonian forest stress should be implemented, as they should be considered an important early indicator of the whole assemblage condition.

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