Preprints.org

Article

Variation in the health status of the Mediterranean gorgonian forests: The synergistic effect of Marine Heat Waves and fishing activity

Martina Canessa [*] , Rosella Bertolotto , Federico Betti , Marzia Bo , Alessandro Dagnino , Francesco Enrichetti , Margherita Toma , Giorgio Bavestrello

Article

Variation in the Health Status of the Mediterranean Gorgonian Forests: The Synergistic Effect of Marine Heat Waves and Fishing Activity

Martina Canessa [1,*]**, Rosella Bertolotto** [2]**, Federico Betti** [1]**, Marzia Bo** [1,3,4]**, Alessandro Dagnino** [2]**, Francesco Enrichetti** [1,2]**, Margherita Toma** [1,5] **and Giorgio Bavestrello** [1,3,4]

[1] Dipartimento di Scienze della Terra dell'Ambiente e della Vita - DISTAV, Università di Genova, Corso Europa 26, 16132 Genova, Italy; giorgio.bavestrello@unige.it (G.B.); federico.betti@edu.unige.it (F.B.); marzia.bo@unige.it (M.B.); francesco.enrichetti@edu.unige.it (F.E.)

[2] 2Agenzia Regionale per la Protezione dell'Ambiente Ligure - ARPAL, Via Bombrini 8 - 16149 Genova, Italy; rosella.bertolotto@arpal.gov-it (R.B.); alessandro.dagnino@arpal.liguria.it (A.D.)

[3] Consorzio Nazionale Interuniversitario per le Scienze del Mare, Piazzale Flaminio 9, 00196 Roma, Italy

[4] National Biodiversity Future Center - NBFC, Piazza Marina 61, 90133 Palermo, Italy

[5] Istituto Superiore per la Protezione e la Ricerca Ambientale - ISPRA, Via Vitalino Brancati 48, 00144 Roma, Itay; margherita.toma@isprambiente.it (M.T.)

* Correspondence: martina.canessa@edu.unige.it

Simple Summary: Epibiosis on damaged gorgonians, particularly *Paramuricea clavata*, is generally used as an indirect indication of stressed conditions. Studying damaged colonies over time can help understand the temporal evolution of the phenomenon. Positive thermal anomalies recorded before 2019 were identified as the primary cause of damage to gorgonians. However, the decrease in epibiosis percentages after 2019, despite the episode in 2022, may be related to the resilience of the populations and a possible reduction in fishing activities due to the lockdown imposed during the COVID-19 pandemic. Long-term monitoring programs are fundamental in clarifying the trajectories of changes in marine benthic communities exposed to different stressors.

Abstract: Over the past thirty years, the red gorgonian *Paramuricea clavata* in the Mediterranean Sea has faced increasing threats, including heat waves and human activities such as fishing and diving. Epibiosis on damaged gorgonian colonies is generally used as an indirect indication of stressed conditions. The density and height of *P. clavata* and the percentage of colonies affected by epibiosis and entangled in lost fishing gear were studied to investigate the phenomenon and its trend over time in the Ligurian Sea. Analyses were based on transects collected during ROV campaigns between 2015 and 2022 at depths of 33-90 meters. A strong correlation was observed between fishing effort in the study area and the level of epibiosis. Maximal percentages of colonies affected by epibiosis and entanglement were recorded at depths of 50-70 meters. Temporally, marine heat waves before 2019 were identified as the primary cause of damage to *P. clavata*. The decrease in epibiosis percentages after 2019, despite the 2022 heat wave, may be due to a quick recovery ability of the populations and a reduction in fishing activities during the COVID-19 lockdown in 2020. Long-term monitoring programs are essential to understand the changes in marine benthic communities exposed to different stressors.

Keywords: structuring alcyonaceans; Marine Strategy Framework Directive; anthropic impact; global change; conservation; Ligurian Sea

1. Introduction

The red gorgonian *Paramuricea clavata* (Risso, 1827) (Cnidaria: Anthozoa) is among the main habitat-forming species in the Mediterranean circalittoral zone, and its aggregations are known to heavily influence the diversity and structure of the associated assemblage [1–3]. *P. clavata* forests constitute noteworthy seascapes attracting broad fluxes of SCUBA diving tourism, thus resulting in an important economic resource [4,5]. Moreover, they host significant populations of commercial fish such as the common dentex *Dentex dentex* (Linnaeus, 1758) and the dusky grouper *Epinephelus marginatus* (Lowe, 1834), typical targets of artisanal fishing [6].

P. clavata forests can be impacted by different kinds of pressures, mainly related to global warming and anthropogenic activities; therefore, the species is considered "vulnerable" according to the Red List of the International Union for Conservation of Nature (IUCN), and the reduction of some Mediterranean populations has been assessed in the last three decades [7]. The first pressure is related to the recent increase of positive thermal anomalies causing cascade effects such as the development of pathogenic bacteria and blooms of filamentous algae and mucilage. In turn, these phenomena affect the gorgonians with extensive diseases that favour the settling of invertebrate epibionts on the damaged colonies [8–16]. Marine Heat Waves (MHWs) also result in Mass Mortality Events (MMEs) that have been well-described for many organisms of the coralligenous assemblage [11,17–23], but mainly hit the red gorgonians [24–27].

In addition to climate-related impacts, it is well known that also boat anchoring and demersal recreational and artisanal fishing activities threaten *P. clavata* due to its large size, branched shape, and skeleton limited flexibility that favour the entanglement of fishing gear [20,28,29]. Bavestrello et al. [28] described the abrasive action by lost lines in contact with the gorgonian coenenchyme, producing suitable conditions for the settlement of several epibiotic organisms that ultimately cause the total or partial breaking of the colony under the current flow. In this regard, several authors employed the percentage of epibionted colonies as a biological index quantifying the fishing-induced stress of a gorgonian population [24,30–34]. Variable levels of epibiosis, hence the health status of the populations, have been reported in different Mediterranean sites. A study conducted in the Medes Islands (Catalan Sea) indicated that 10-33% of the colonies settled in unprotected areas were partially colonised by epibionts, whereas only 4-10% of the populations inside the borders of the Marine Protected Area (MPA) were involved in the phenomenon [35]. Along the eastern Adriatic coasts, in an area characterised by low fishing pressure, the colonies with denuded or epibionted branches were less than 10% [36]. On the contrary, inside the Portofino MPA (Ligurian Sea) and in the Tavolara - Punta Coda Cavallo MPA (Tyrrhenian Sea) colonies with epibiosis exceeded 50% of the total, suggesting a high fishing impact [6,37,38].

Monitoring programs on a broad spatial and temporal scale dedicated to the evaluation of the health status of gorgonian forests are lacking, and the recovery ability of populations after mass mortality episodes was followed only for a few years [39–42]. The Marine Strategy Framework Directive (MSFD 2008/56/EC) represents the EU's Integrated Maritime Policy tool to achieve the Good Environmental Status (GES) of marine waters, based on eleven qualitative descriptors. Within these, the descriptor "biodiversity" states that "*The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions (MSFD, 2008/56/EC, Annex I). Ecosystem components – groups of species and habitat types, such as the coralligenous – are recognised as indicators of environmental quality, becoming priority habitats target of study and monitoring activities*".

Thanks to the data obtained during the Marine Strategy project (2015-2022), the Ligurian Sea (NW Mediterranean Sea) is nowadays one of the best-known areas along Italian coasts [43]. During this project, 80 sites were explored (2015-2018) and then subjected to monitoring in the following years. The forests of *P. clavata* were widely distributed along the whole Ligurian arc, occurring on sloping outcroppings and coralligenous rocks up to 89 m. The forests dominated by this species represented over 13% of the sampling units considered in the study and were characterised by an average density of 7.4 ± 3.0 colonies m-2 with maximum values reaching 19 colonies m-2. This

gorgonian also consistently occurred in other communities, such as that dominated by *Corallium rubrum* (Linnaeus, 1758) [43].

Thanks to the large ROV footage collected during the Ligurian Marine Strategy surveys, this paper aims to give a comprehensive view of the level of epibiosis affecting the *P. clavata* forests along the whole Ligurian coastline and describe a pluriannual trajectory of their health status evolution.

2. Materials and Methods

2.1. Study Area

The Ligurian coast extends for over 350 km, from La Spezia in the East to Ventimiglia in the West, in the North-western sector of the Mediterranean Sea (Figure 1). The coast is densely populated with cities and large commercial harbours [44].

In this study, the Ligurian coast was divided into three macro-areas: East (A1), from Mesco Cape to Isuela Shoal (Portofino Promontory); Centre (A2), from Arenzano to Finale Ligure; West (A3), from Albenga to Mortola Cape (Ventimiglia) (Figure 1; Table 1).
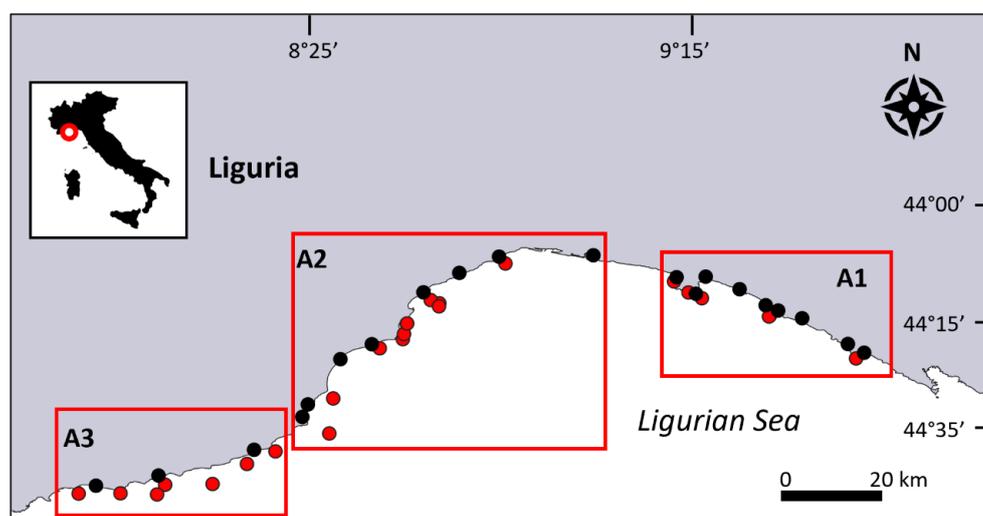

Figure 1. The Ligurian coast, with the localisation of the studied transects hosting the *Paramuricea clavata* forests (red dots), grouped into the three macro-areas. The black dots represent the fishing harbours.

Data coming from the European fleet register (https://webgate.ec.europa.eu) were used to obtain the number of fishing harbours and boats targeting on demersal fishing insisting on each identified macro-area.

Table 1. The repeated explored sites with occurrence of *Paramuricea clavata* forests in the three macro-areas of the Ligurian coast.

	Year	Site	Lat. (N)	Long. (E)	Transect ID	Depth (m)	N colony	Density (col m^{-2})	Epibiosis %	Entanglement %	Av. H ± SE (cm)
	2016	Mesco Cape	44.13108	9.63407	PMMN_S2_T2	47	64	1.3	9.4	7.8	28.8 ± 2.3
	2019						66	0.5	15.9	4.5	20.3 ± 1.3
	2022						66	0.8	9.1	3.0	23.6 ± 0.9
	2015	Manara Cape W	44.243216	9.40207	SLMO_S3_T1	59	82	0.9	20.7	3.7	38.4 ± 2.2
	2019						107	4.1	40.0	77.6	35.5 ± 1.7
Macroarea A1	2019				SLMO_S3_T3	41	198	2.0	73.0	21.2	30.2 ± 0.9
	2022						284	3.6	56.0	1.1	28.0 ± 1.1
	2015				SLMO_S3_T4	47	228	2.5	10.1	1.3	47.3 ± 2.2
	2019						95	1.4	89.4	46.3	35.0 ± 1.1
	2022						94	1.0	39.4	3.2	29.0 ± 1.7
	2015	Manara Cape E	44.24516	9.40409	SLMO_S2_T1	55	119	1.6	16.0	0.8	34.3 ± 2.3
	2019						212	2.6	76.0	22.2	35.3 ± 1.0
	2015				SLMO_S2_T2	64	97	1.0	9.3	4.1	32.2 ± 2.2

Macro-area	Year	Site	Latitude	Longitude	Code	Depth				
	2019						94	1.8	37.5	9.6	25.5 ± 1.1
	2016	Portofino Cape	44.2923	9.22313	AMPP_S1_T3	60	174	6.7	6.3	1.1	31.7 ± 1.2
	2019						115	1.2	58.8	9.6	32.7 ± 1.6
	2022						50	0.6	10.0	-	28.2 ± 1.3
	2016	Isuela Shoal	44.33713	9.14897	AMPP_S3_T2	33	838	10.6	24.6	2.7	24.2 ± 1.5
	2019						833	8.3	36.0	1.6	29.2 ± 1.0
	2022						649	6.6	8.8	-	30.8 ± 0.7
	2016				AMPP_S3_T3	52	332	3.8	15.1	6.9	24.9 ± 1.5
	2019						247	4.4	33.0	11.7	28.7 ± 1.5
	2022						104	1.2	53.1	1.0	28.5 ± 0.9
Macro-area A2	2015	Arenzano-Varazze	44.38512	8.6996	NOAR_S1_T2	40	337	4.3	11.6	2.1	34.3 ± 1.3
	2018						411	5.1	60.3	42.8	33.2 ± 1.2
	2021						315	3.6	79.0	31.0	21.0 ± 0.9
	2015	Vado Ligure	44.2603	8.46638	NOAR_S2_T1	48	277	3.4	12.3	9.0	34.6 ± 2.0
	2018						207	4.0	28.5	50.7	31.1 ± 1.4
	2015				NOAR_S2_T2	63	184	1.5	12.5	14.2	30.0 ± 2.0
	2018						144	3.0	78.5	22.2	34.5 ± 1.2
	2021						152	3.2	44.0	8.0	22.3 ± 1.0
	2015				NOAR_S2_T3	56	72	0.9	5.6	4.2	13.4 ± 1.5
	2018						81	1.5	66.7	76.5	25.3 ± 1.2
	2016	Savona A	44.28739	8.50042	SVCL_S3_T2	45	291	3.5	3.8	22.0	29.8 ± 1.6
	2019						158	3.9	51.0	21.5	28.7 ± 0.9
	2022						314	4.5	7.6	9.2	25.0 ± 0.6
	2016	Savona B	44.27878	8.52335	SVCL_S2_T3	58	309	3.3	6.1	37.5	25.6 ± 1.7
	2019						125	2.6	76.7	72.0	35.3 ± 1.7
	2022						482	12.4	38.0	19.9	25.1 ± 0.8
	2015	Maledetti Shoal	44.22381	8.43657	NOAR_S4_T1	58	610	5.3	1.7	47.3	21.7 ± 1.0
	2018						276	2.8	42.4	84.4	25.2 ± 1.0
	2015				NOAR_S4_T2	68	69	4.2	8.8	29.8	17.8 ± 1.5
	2018						179	2.3	7.8	97.2	27.8 ± 1.2
	2021						89	2.1	28.2	12.8	12.5 ± 1.2
	2018				NOAR_S4_T4	56	271	3.2	42.1	87.8	29.8 ± 1.4
	2021						138	1.6	36.0	14.0	19.1 ± 0.7
	2018				NOAR_S4_T5	62	382	3.8	20.7	79.8	26.3 ± 1.3
	2021						352	4.2	30.0	58.0	21.5 ± 0.7
	2018				NOAR_S4_T7	53	68	0.7	10.3	36.8	15.8 ± 0.8
	2021						84	0.8	12.9	21.4	11.6 ± 0.5
	2018				NOAR_S4_T8	59	640	6.6	10.8	60.0	15.8 ± 0.4
	2021						421	4.2	53.0	25.0	12.5 ± 0.3
	2017	Finale Ligure	44.15817	8.36462	BONO_S1_T2	83	163	2.0	4.9	12.3	24.2 ± 1.2
	2020						112	5.9	34.3	18.8	33.2 ± 3.4
	2017				BONO_S1_T3	77	405	5.1	3.6	35.3	32.9 ± 1.2
	2020						453	5.3	12.0	5.7	65.7 ± 2.6
Macro-area A3	2017	Albenga	44.02396	8.24063	ALGA_S3_T2	58	54	0.7	11.8	38.2	30.1 ± 1.5
	2020						72	1.2	70.8	1.4	35.4 ± 2.1
	2015	Diano Marina	43.88217	8.08675	SSDM_S1_T2	51	175	2.4	6.3	18.9	33.2 ± 1.5
	2018						119	2.0	55.5	68.9	39.4 ± 1.2
	2021						115	1.3	28.4	10.8	20.6 ± 1.0
	2018	Porto Maurizio	43.84858	8.01065	SSDM_S2_T3	36	76	1.2	1.3	-	37.8 ± 1.2
	2021						156	3.1	21.0	11.0	21.5 ± 0.9
	2017	Sanremo E	43.7929	7.79271	SRSST_S1_T2	69	265	3.3	18.1	46.2	27.7 ± 0.9
	2020						335	6.6	4.0	25.1	37.4 ± 1.3
	2017				SRSST_S1_T3	61	232	2.9	18.7	46.7	24.9 ± 1.2
	2020						135	3.5	7.0	26.7	31.7 ± 1.6
	2017	Sanremo W	43.76695	7.77113	BOSR_S3_T1	65	180	2.3	9.7	55.9	25.9 ± 1.1
	2020						181	4.4	10.4	1.7	38.3 ± 2.1
	2017				BOSR_S3_T2	49	54	0.7	9.7	55.9	32.9 ± 1.5
	2020						77	0.9	33.3	15.6	50.5 ± 2.2
	2016	Bordighera E	43.7699	7.67639	CMBO_S1_T1	49	155	1.9	4.5	5.8	19.5 ± 1.6
	2018						218	4.0	11.5	13.3	45.0 ± 1.2
	2021						556	8.4	7.0	3.4	21.7 ± 1.0
	2016				CMBO_S1_T2	60	179	1.9	8.4	13.4	26.8 ± 2.1
	2018						180	3.8	13.3	31.7	34.9 ± 1.6
	2021						823	13.1	49.0	6.0	24.8 ± 0.9
	2016				CMBO_S1_T3	66	400	5.0	2.8	11.3	22.5 ± 1.6
	2018						517	8.6	7.4	44.7	25.9 ± 1.2

2021						407	5.1	0.0	0.0	13.6 ± 1.1
2016	Mortola Cape	43.76952	7.56353	CMBO_S3_T2	35	302	3.8	29.1	3.3	28.1 ± 2.1
2020						243	4.5	39.3	7.4	43.1 ± 1.9

2.2. ROV Footage Analysis

The surveys were carried out following the indications reported on the Marine Strategy Framework Directive (MSFD) methodological sheet created in 2016 by the Ministero dell'Ambiente e della Tutela del Territorio e del Mare (MATTM) in collaboration with ISPRA and ARPA, relating to coralligenous habitats (Module 7, Rocky reefs), including all following modifications (Art. 11, D.lgs. 190/2010). From 2015 to 2022, 264 transects were performed in the 33-90 m depth range along the whole Ligurian coast and repeated to check putative differences after a span of time of 2-4 years.

Each ROV transect had a length of 200 m and a width of 50 cm, covering 100 m2 of seafloor. In each transect, all the colonies of *P. clavata* were counted, and their density was calculated, referring only to the percentage of hard bottom seafloor present in the transect, thus excluding soft bottom areas unsuitable for the settling of the gorgonian.

Sessile epibionts (sponges, anthozoans, bryozoans, annelids) and vagile fauna spotted associated with the colonies were noted. The percentage of colonies with epibiosis or entangled in fishing gear was used to estimate the health status of the populations. The height of 100 colonies randomly selected per transect was measured using the laser pointers as a reference (15 cm apart). In transects with less than 100 gorgonians, all the colonies were measured (Table 1).

Only the transects with more than 50 colonies were selected for the formal analysis. In particular, 13 transects replicated after 3-4 years in A1, 19 transects replicated after 3 years in A2, and 14 transects replicated after 2-3 years in A3 (Table 1).

Considering the entire database, putative differences in the percentage of epibionted colonies were investigated among macro-areas and compared with the number of fishing harbours and fishing vessels working with set gear (set longlines, set gillnets, and trammel nets). Differences across time (Before/After) were studied within each macro-area, comparing data of epibiosis and entanglement in the same transects replicated after 2-4 years. To evaluate if the putative trajectories of temporal variations were generalised at a spatial scale or linked to stochastic phenomena, we evaluated the percentage of transects that presented a positive (epibiosis/entanglement increasing) or negative (epibiosis/entanglement decreasing) variation in the percentage of affected colonies in each considered period.

2.3. Statistical Analysis

Differences in *P. clavata* density, colony height, and percentage of epibiosis in the whole study area were tested by one-way ANalysis Of VAriance (ANOVA). Temporal analysis of the replicated transects was performed by PERMutational ANalysis Of VAriance (PERMANOVA) [45] (factor "macro-area", fixed, 3 levels, and "time", i.e. Before/After, fixed, 2 levels; Bray–Curtis similarity Index measure, permutation = 9999). All statistical analyses were performed using PRIMER-e 7 with PERMANOVA+ Add On package.

3. Results

3.1. Health Status of Paramuricea clavata Forests in the Ligurian Sea

In total, 24834 colonies of Paramuricea clavata were observed, of which 6836 were affected by epibiosis (28%), and 6140 were entangled in lost fishing gear (25%).

The forests appeared homogeneously distributed along the Ligurian arc (Figure 1). The average density (about 3.3 ± 0.5 colonies m-2) showed no significant differences between the three macro-areas (Figure 2a; Table 2). On the contrary, the average height was significantly lower in A2 (26.6 ± 1.5 cm) than in the two other macro-areas (29.4 ± 1 cm and 31 ±1.5 cm respectively in A1 and A3) (Figure 2b; Table 2). Particularly the percentage of the epibionted colonies significantly decreased from the eastern area (A1, 36%) to the centre (A2, 30%) and to the western ones (A3, 18%) (Figure 2c; Table 2).
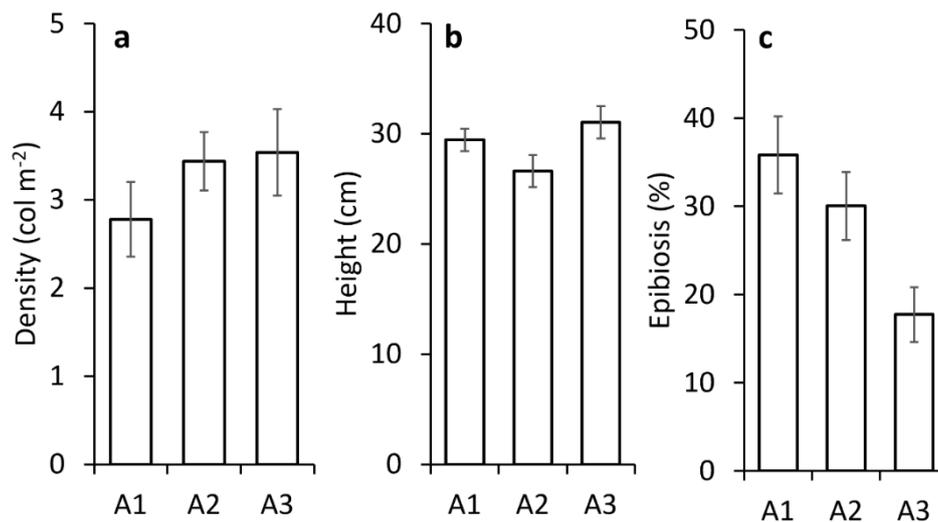
Figure 2. (**a**) Average density (± SE); (**b**) average height (± SE), and (**c**) average percentage of epibionted colonies (± SE) in the three macro-areas.

Table 2. Results of ANOVA and pair-wise comparisons of *Paramuricea clavata*, density, colony height, and percentages of epibionted specimens in each macro-area. Bray-Curtis similarity index used for the resemblance matrix construction; permutation n= 9999. Significant effects are in bold.

	df	SS	MS	Pseudo-F	P(perm)	Pair-wises	T	P(perm)
Density								
Macro-area	2	5201.1	2600.5	2.716	0.3686			
Res	107	1.0245E+05	957.5					
Total								
Height						**Height**		
Macro-area	2	1360.9	680.44	35.551	**0.0267**	A1 vs A2	20.462	**0.0357**
Res	107	20480	191.4			A1 vs A3	0.70001	0.5049
Total	109	21840				A2 vs A3	22.188	**0.0249**
Epibiosis						**Epibiosis**		
Macro-area	2	11824	5912.2	38.355	**0.006**	A1 vs A2	12.312	0.1907
Res	107	1.65E+09	1541.4			A1 vs A3	2.721	**0.0012**
Total	109	1.77E+09				A2 vs A3	16.747	0.0545
Entanglement						**Entanglement**		
Macro-area	2	25589	12795	68.677	**0.0001**	A1 vs A2	37.941	**0.0001**
Res	107	1.99E+09	1863			A1 vs A3	19.837	**0.0119**
Total	109	2.25E+09				A2 vs A3	16.131	0.0553

This trend was correlated with the fishing effort estimated per each macro-area: in fact, the fishing harbours were 11, 7, 3 respectively in A1, A2 and A3 and the fleets were represented by 121 vessels in A1, 136 in A2 and 98 in A3 (Figure 3a, b).
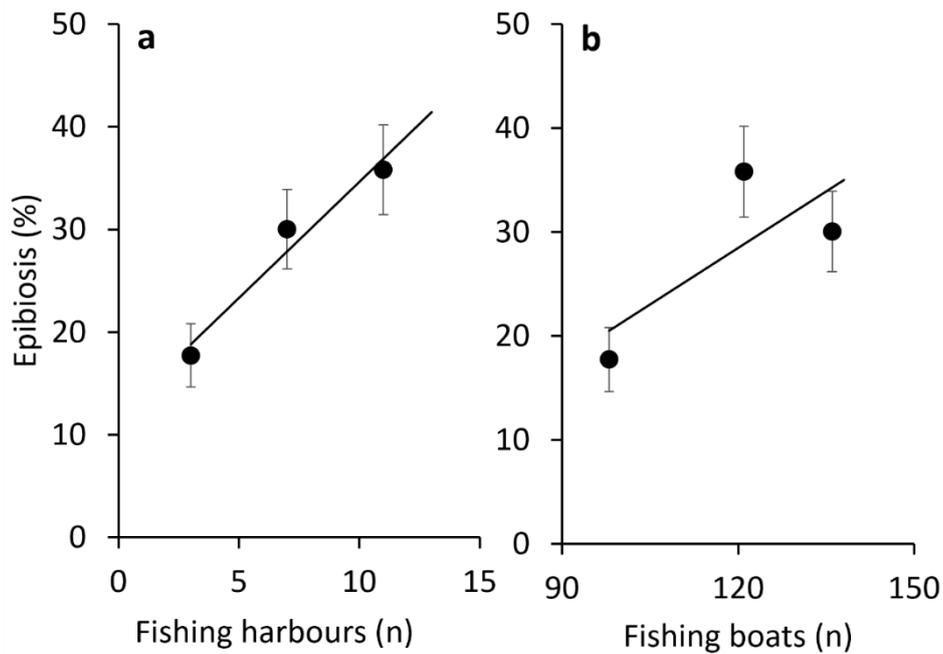
Figure 3. Correlation of the percentage of epibionted colonies in the three macro-areas with the number of fishing harbours ((**a**), r = 0.98) and fishing boats ((**b**), r = 0.75) insisting in each macro-area.

The bathymetric trend of the incidence of the epibiosis showed maximal values in the depth range 50-70 m (32-35% of the observed colonies), with a decrease at lower and higher depths (Figure 4a). The bathymetric distribution of the colonies entangled in lost fishing lines reflected a very similar trend (Figure 4b).
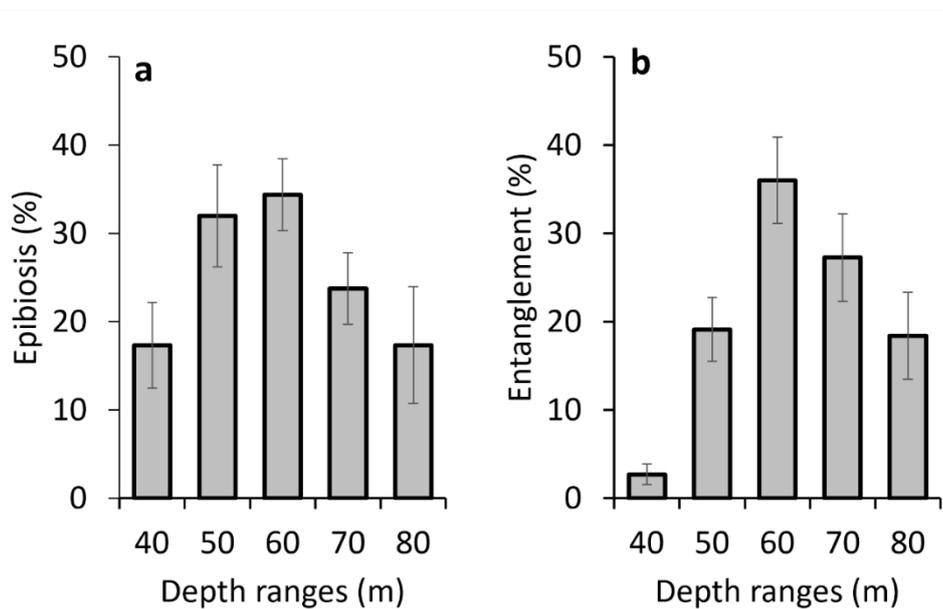
Figure 4. Bathymetric distribution of the percentage (**a**) of epibionted colonies and (**b**) of colonies entangled in lost fishing gear.

The species most frequently found as epibionts on *P. clavata* were the sponge *Pleraplysilla spinifera* (Schulze, 1879), the soft coral *Alcyonium coralloides* (Pallas, 1766), the bushy serpulids belonging to the *Filograna*/*Salmacina* complex, and the branched bryozoans *Adeonella calveti* Canu & Bassler, 1930,

Smittina cervicornis (Pallas, 1766), and *Turbicellepora avicularis* (Hincks, 1860). Finally, specimens of the passive filter-feeder echinoderm *Astrospartus mediterraneus* (Risso, 1826) were commonly observed.

3.2. Temporal Analysis of Epibiosis and Entanglement

The comparison of the same groups of transects replicated after 2-4 years revealed a similar trend in the three considered macro-areas.

In macro-area A1, the transects studied in 2015 and replicated in 2019 showed a significant increase in the percentage of epibionted colonies, shifting from 14% to 61%. A similar trend was observed in the transects made in 2016 and replicated in 2019, with values increasing from 13.8% to 35.9%. Differently, in the group of transects studied during 2019 and repeated in 2022, the incidence of epibiosis was not significantly different (Figure 5a; Table 3). These variations were homogeneously recorded among the considered transects, confirming the progressive shift. In fact, in the periods 2015-19 and 2016-19, almost all the studied transects showed positive variations (increase) of the epibiosis. Conversely, in the period 2019-22, 80% of the transects showed negative percentage variations (decrease) (Figure 5a inset). The percentage of entangled colonies significantly surged from 2.5% to 38.9% in the period 2015-19, while in both the following periods (2016-19; 2019-22), no significant differences were assessed (Figure 5b; Table 3). The trend of the percentage of transects with positive/negative variations showed 100% of positive variations in the first period while in the following periods, the percentage of negative variations progressively grew (Figure 5b inset).

Table 3. Results of PERMANOVA and pair-wise comparisons for the temporal analysis (Before/After) of percentage of epibiosis and entanglement of *Paramuricea clavata* in each replicated transect. Bray-Curtis similarity index used for the resemblance matrix construction; permutation n= 9999. Significant effects are in bold.

|	df	SS	MS	Pseudo-F	P(perm)	Pair-wises	t	P(perm)	Unique perms	P(MC)
A1										
Epibiosis										
Before/After	5	11612	2322.3	29.303	0.0228	2015/19	40.632	0.027	35	0.0024
Res	20	15850	792.52			2016/19	20.984	0.0532	35	0.0529
Total	25	27462				2019/22	0.79759	0.502	126	0.4923
Entanglement										
Before/After	5	18518	3703.6	21.411	0.0244	2015/19	27.952	0.0259	35	0.006
Res	20	34595	1729.7			2016/19	0.4955	0.7255	35	0.7313
Total	25	53113				2019/22	14.721	0.0794	126	0.1193
A2										
Epibiosis										
Before/After	5	23565	4713	46.103	0.001	2015/18	27.982	0.0135	462	0.0043
Res	32	32713	1022.3			2016/20	38.243	0.0287	35	0.0029
Total	37	56278				2018/22	0.516	0.709	8170	0.7162
Entanglement										
Before/After	5	15630	3125.9	32.804	0.0031	2015/18	2.362	0.0203	461	0.0157
Res	32	30493	952.92			2016/20	0.59803	0.8289	35	0.6893
Total	37	46123				2018/22	30.371	0.0046	8150	0.0043
A3										
Epibiosis										
Before/After	5	9829.4	1965.9	12.736	0.2349	2015/18	18.318	0.0536	35	0.0779
Res	22	33959	1543.6			2016/20	11.444	0.2483	91	0.2815
Total	27	43788				2018/21	0.83113	0.6803	126	0.5607
Entanglement										
Before/After	5	17345	3469	19.534	0.0293	2015/18	21.685	0.0855	35	0.0435
Res	22	39068	1775.8			2016/20	15.939	0.1094	91	0.1148
Total	27	56413				2018/21	15.329	0.0403	91	0.0872
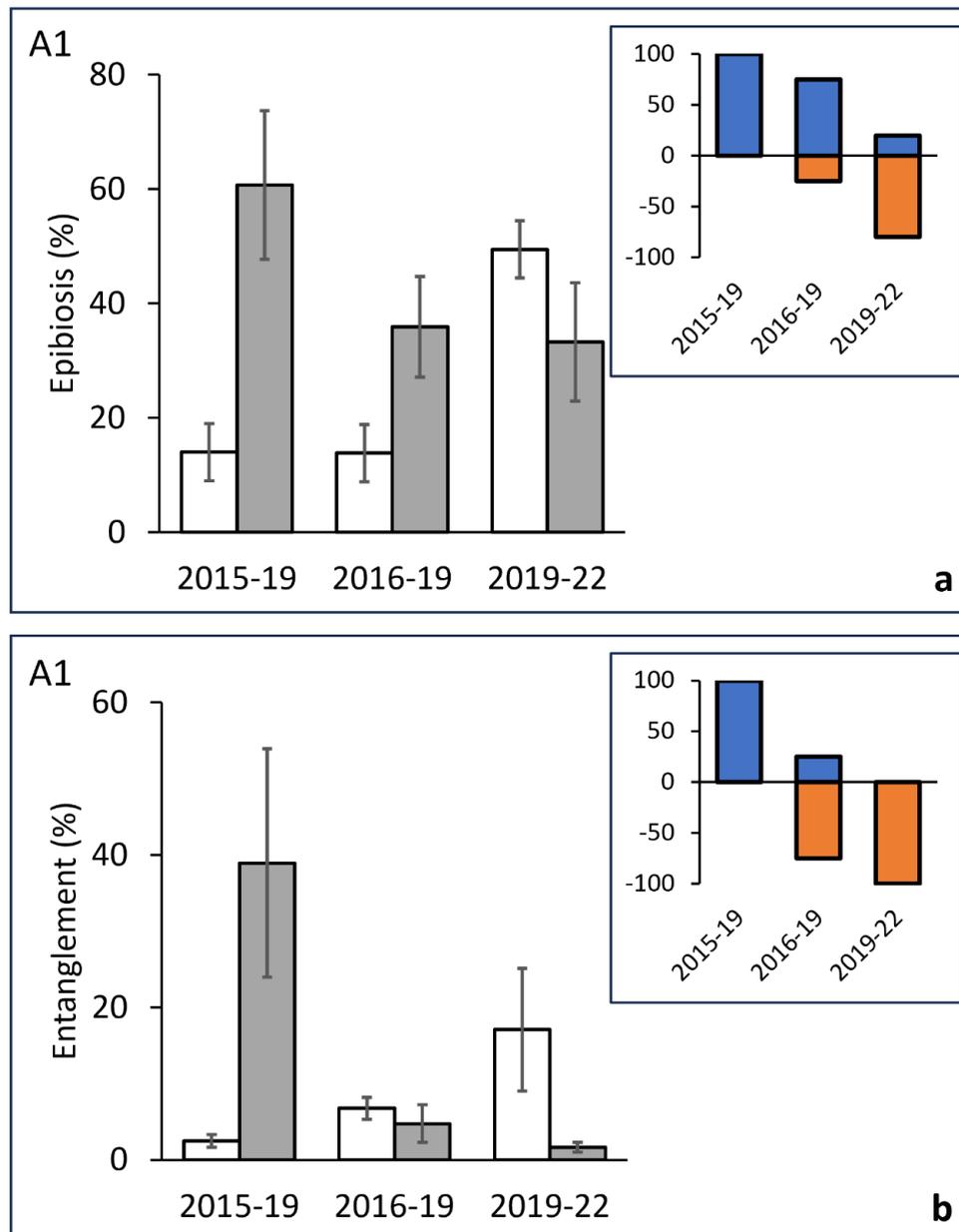
Figure 5. Eastern macro-area (A1). Differences across time (Before, white bars/After, grey bars) obtained comparing data of (**a**) epibiosis and (**b**) entanglement in the same groups of transects replicated after 3-4 years. Inset: Percentage of transects that presented a positive (epibiosis/entanglement increasing, blue bars) or negative (epibiosis/entanglement decreasing, red bars) variation in the value of affected colonies in each considered period.

A similar situation was observed for macro-area A2. The comparison of the transects carried out in the periods 2015-18 and 2016-20 showed a progressive steady rise in the percentage of colonies affected by epibiosis, from 8.7% to 47% and from 4.6% to 43.5%, respectively. In the period 2018-22, no significant differences were detected (Figure 6a; Table 3). In the first two periods, the totality of studied transects showed soaring values, while in the third period, this value decreased to 50% (Figure 6a inset).
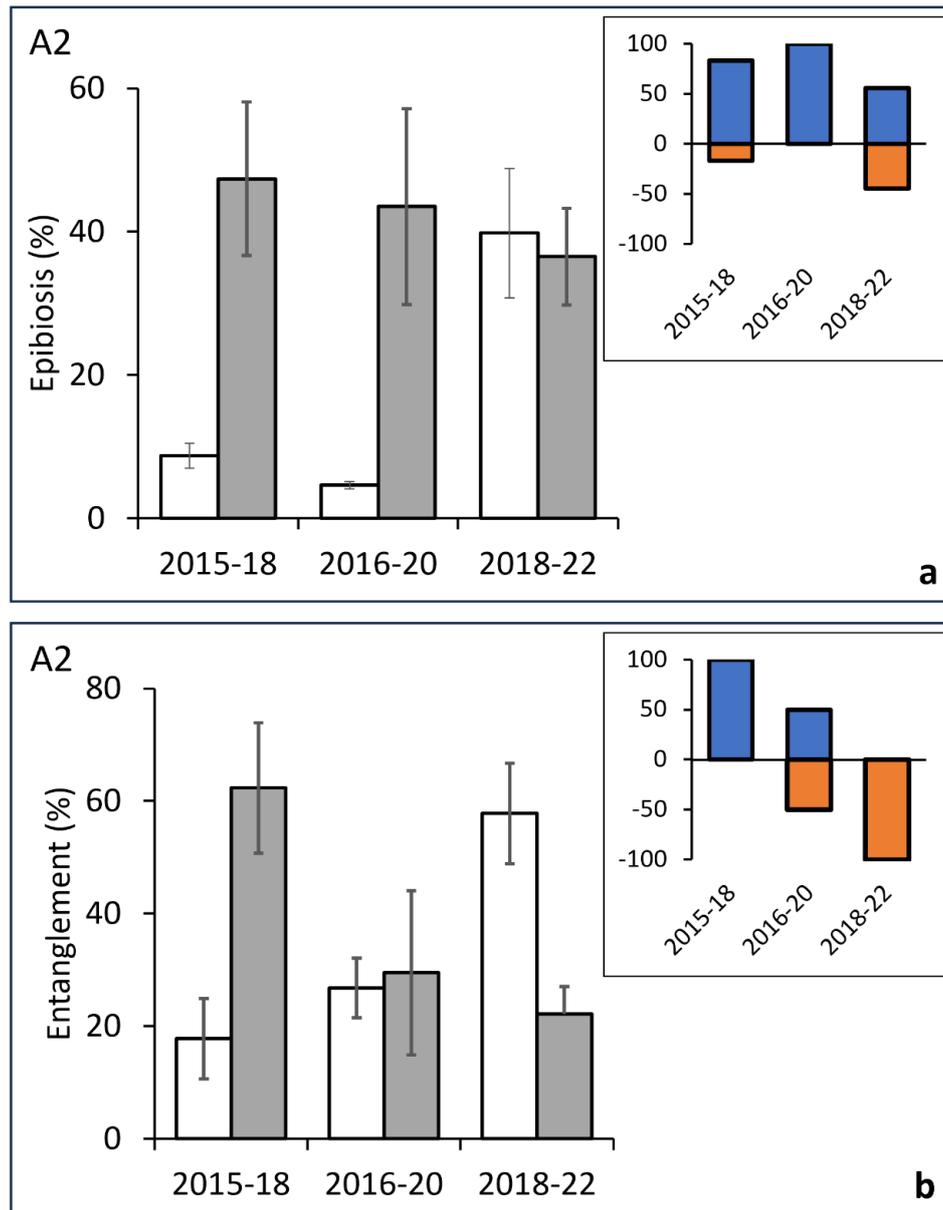
Figure 6. Central macro-area (A2). Differences across time (Before, white bars/After, grey bars) obtained comparing data of (**a**) epibiosis and (**b**) entanglement in the same groups of transects replicated after 3-4 years. Inset: Percentage of transects that presented a positive (epibiosis/entanglement increasing, blue bars) or negative (epibiosis/entanglement decreasing, red bars) variation in the value of affected colonies in each considered period.

Considering the entanglement percentages, a strong increase was observed in the first period, followed by a period without significant variations and, finally, by a third period characterised by a significant decrease (Figure 6b; Table 3). The analysis of the homogeneity of the variations across time showed a regular trend from 100% of transects with positive variations in the period 2015-18 to 100% of transects characterised by a negative variation in the period 2019-22 (Figure 6b inset).

Finally, regarding macro-area A3, the diachronic analysis highlighted a significant upsurge of the epibionted colonies in the first period, followed by two periods without significant variations (Figure 7a). The corresponding trend of the percentage of transects with positive variation progressively decreased from 100% in the first period to 33% in the third one (Figure 7a inset). Finally, the trend of the entanglement showed a significant increase in the first period followed by a significant decrease in the other two periods (Figure 7b; Table 3), also confirmed by a specular trend of the percentage of transects with positive/negative variations (Figure 7b inset).
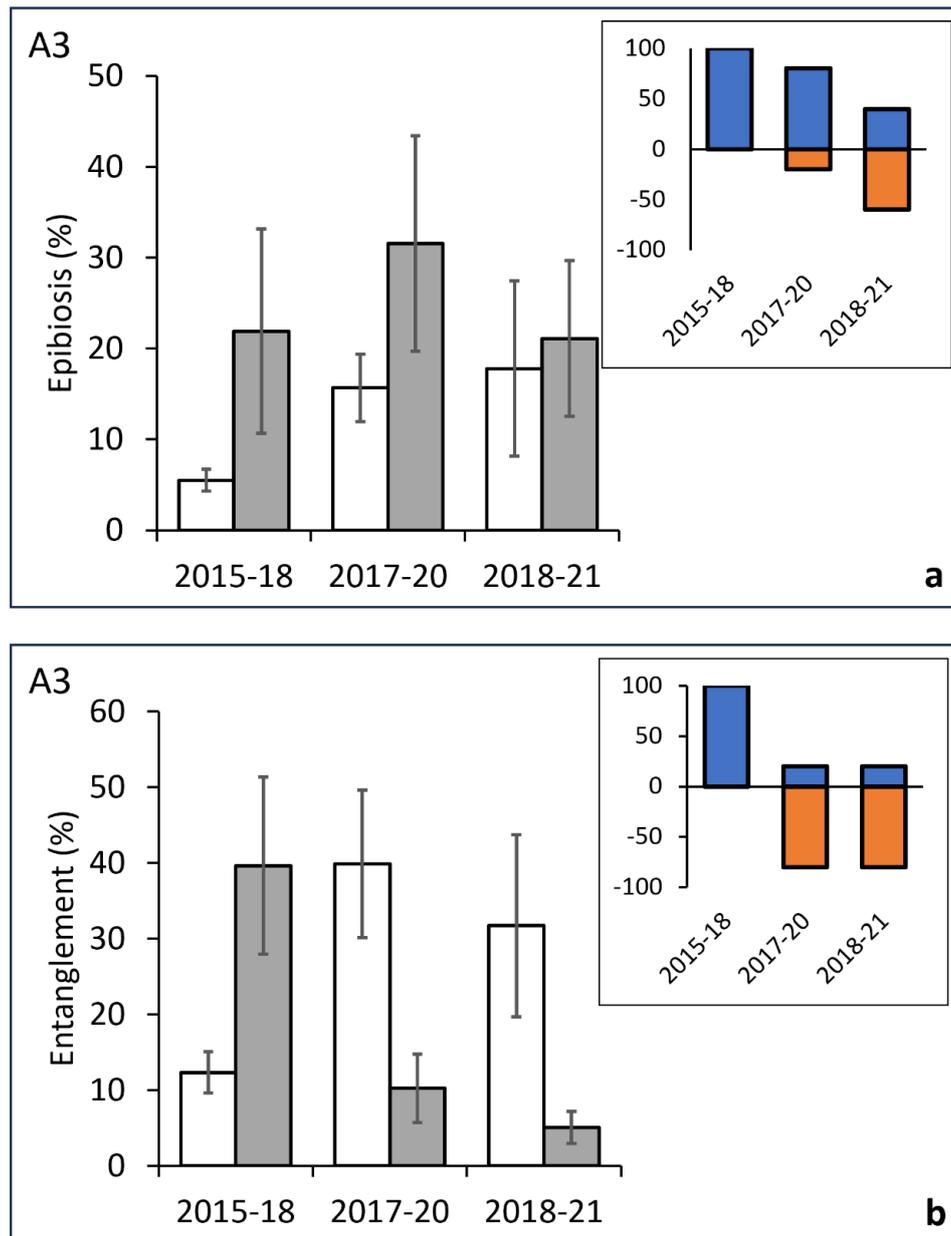
Figure 7. Western macro-area (A3). Differences across time (Before, white bars/After, grey bars) obtained comparing data of (**a**) epibiosis and (**b**) entanglement in the same groups of transects replicated after 3-4 years. Inset: Percentage of transects that presented a positive (epibiosis/entanglement increasing, blue bars) or negative (epibiosis/entanglement decreasing, red bars) variation in the value of affected colonies in each considered period.

4. Discussion

The diseases hitting the gorgonian populations in the Mediterranean Sea are generally attributed to the acute stress produced by positive thermal anomalies that have progressively increased in frequency and intensity in the last decades [22,42]. During the period of our observations, MHW events were recorded in 2015, 2016, 2018, and 2022 [22; –46].

Our study revealed that the epibiosis affecting *Paramuricea clavata* in three macro-areas along the Ligurian coast had an overlapping temporal trajectory that can be generalised at the regional scale. The percentage of involved colonies strongly increased from 2015 until 2019, while in the following period (2019-2022), the level remained unvaried or decreased. This pattern agrees with the trend of MHWs in the western Mediterranean Sea. In fact, the significant sharp increase between 2015 and

2019 could be related to the intense MHWs that took place between 2015 and 2018. Iborra et al. [42] investigated the gorgonian population of the Gulf of Calvi (NW Corsica Island) over a 15-year period (2004, 2014, and 2019) and the observed changes in the level of necrosis of the colonies were related to the trend of MHWs occurring in that period. According to these authors, the effect of MHWs on the gorgonian integrity reached relatively deep coastal waters (down to 40 m), where temperature increases are generally not recorded [42]. The shallow water temperature rise induces a strong stratification of the water column with a consequent low availability of trophic resources and a high respiratory demand [47,48]. This hypothesis agrees with the bathymetric distribution of the level of epibiosis observed during our study in the Ligurian Sea, where the maximum values were recorded below 50 m. In the same area, previous diseases involving cnidarians and sponges were already observed up to 70 m [17,49–51]. At the same time, the bathymetric distribution of the maximum level of epibiosis and entanglement (50-70 m) can be also related to the bathymetric distribution of *P. clavata* forests in the Ligurian Sea, being mainly concentrated between 45 and 65 m [43].

A remarkable quickness in the evolution of the levels of epibiosis emerges from the present study. In the eastern Ligurian Sea, in four years (2015-2019), the percentage of epibionted colonies increased more than three times, and in the central area increased six times. This evidence supports the damages inflicted by mass diseases following MHWs. In fact, during the 2003 episode, almost 80% of the studied colonies in the Gulf of Genoa developed epibiosis in a few weeks [21]. A long-term monitoring conducted on the *P. clavata* populations in the period 2003–2017 in the Scandola MPA highlighted a substantial decline in density and a slight loss of mean colony biomass after 15 years, and all populations were farther from recovery in 2017-2018 than in 2008. On average, in 2003, values decreased by around 71% and 80%, despite no significant changes in the size structure were observed in any population immediately after the 2003 MHW [41]. On the other hand, Cupido et al. [50] observed a strong recovery of the populations in the La Spezia Gulf after the late-summer 1999 and 2003 large mortality events due to thermal stress. The long-term observation (1998 to 2008) confirmed that a positive net recruitment and canopy reestablishment could start some years after a high-mortality event, also under naturally stressed environmental conditions.

Despite this evidence, our data strongly suggest that also human activities are deeply involved in the development of epibiosis in *P. clavata*. The correlation, at the regional scale, between the level of epibiosis with the number of fishing vessels and harbours evidences the role of fishing activities. Moreover, the overlapping of the bathymetric trend of epibiosis with that of the entanglement indicates a strong correlation also with this kind of impact. The depth range of epibionted colonies overlaps that of fishing with settled gear targeting spiny lobsters, sparids (common dentex, gilthead seabreams), and groupers [52]. Finally, the influence of fishing on the level of epibiosis was also supported by the temporal correlation of the two parameters in all the studied areas. In some cases (e.g., A3) it appears evident that a reduction in the entangled colonies anticipates that of epibionted ones.

These data strongly enforce the idea that the observed variations in the Ligurian forests are due to a synergistic effect of natural and anthropogenic causes. Probably, the damages caused by fishing activities pile up on colonies already deeply stressed by thermal diseases. A further indication is that, in the period 2018-2022, despite the occurrence of one of the strongest MHW ever observed [46], the epibiosis remained stable or decreased concomitantly with a period of strong reduction in the percentage of entanglement supporting a decrease in the fishing effort.

Unfortunately, data about the annual trend of artisanal fishing and, particularly, recreative fishing are virtually impossible to obtain, and therefore, only a hypothesis can be formulated. We suggest that the reduction of the fishing activity speculated for the period 2019-22 could be due to the COVID-19 pandemic lockdown imposed from March to May 2020. Fisheries were limited by the coronavirus pandemic at a global scale. In that period, the lockdown, followed by a strong shrinking in seafood requests, determined a decrease in fishing activities. For example, a recent study demonstrated a reduction of about 50% of the fishing effort for the Adriatic Sea [53]. In the eastern Mediterranean Sea, from December 2019 to February 2020, the average monthly gross margin for fishermen was 2.5 times less than the usual average [54]. The fishing effort in an exploited area of the

north-western Mediterranean coast (Spain) during the lockdown dropped by 34%, landings were down by 49%, and revenues declined by 39% in comparison with the same period in 2017–2019 [55]. This scenario well represents also the conditions of the Ligurian fishing economy in that period, an economy based on traditional activities carried out by small artisanal communities, mainly targeting high-value resources [56].

In addition, during the lockdown period, the media reported the presence of iconic large marine animals, such as marine mammals, elasmobranchs and marine turtles, in unexpected areas, such as very coastal areas or harbours [55]. Despite the wide interest in the effects of the COVID-19 pandemic on marine habitats and fisheries, no data are available about benthic organisms: our observation could be the first suggestion of an improvement in the health status of *P. clavata* forests resulting from a short-term strong reduction of fishing activities. The vulnerability of habitat-forming species is influenced by their low resilience to mechanical impacts, driven by modest to slow growth rates [57]. This work supports the potential effectiveness of Fisheries Restricted Areas (FRAs) on these complex habitats.

5. Conclusion

In conclusion, the importance of long-term monitoring programs must be underlined to understand the trajectories of modification of marine communities prone to different stressors. This kind of monitoring can provide evidence of unsuspected drivers of benthic community health, together with possible mitigation strategies.

Author Contributions: F Conceptualization, G.B. and M.C.; methodology, M.C., A.D., F.E., M.T.; formal analysis and investigation, M.C., F.E., M.T.; resources, R.B.; data curation, M.C., F.E., M.T.; writing—original draft preparation, G.B., F.B., M.B., M.C., A.D., F.E., M.T.; writing—review and editing, G.B., F.B., M.B., M.C., A.D., F.E., M.T.; visualization, F.B; supervision, G.B., M.B.; project administration, G.B.; funding acquisition, R.B. All authors have read and agreed to the published version of the manuscript.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The authors confirm that the data supporting the findings of this study are available within the article. The video dataset collected and analyzed during the present study is available from the corresponding author upon request.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Gori, A., Bavestrello, G., Grinyó, J., Dominguez-Carrió, C., Ambroso, S., Bo, M. *Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. Marine Animal Forests: the ecology of benthic biodiversity hotspots* 2017; pp.: 207-233.

2. Rossi, S., Bramanti, L., Gori, A., Orejas, C. *An overview of the animal forests of the world. Marine animal forests: the ecology of benthic biodiversity hotspots* **2017**, 1-28.

3. Piazzi, L., Atzori, F., Cadoni, N., Cinti, M.F., Frau, F., Pansini, A., Pinna, F., Stipcich, P., Ceccherelli, G. Animal Forest mortality: Following the consequences of a gorgonian coral loss on a Mediterranean Coralligenous assemblage. *Diversity* **2021**, *13(3)*, 133. https://doi.org/10.3390/d13030133

4. Linares, C., Doak, D.F. Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: a case study of *Paramuricea clavata*. *Mar Ecol Prog Ser* **2020**, *402*, 59-68. DOI: https://doi.org/10.3354/meps08437

5. Cerrano, C., Milanese, M., Ponti, M. Diving for science-science for diving: volunteer scuba divers support science and conservation in the Mediterranean Sea. *Aquat Conserv Mar Freshw Ecos* **2017**, *27(2)*, 303-323. https://doi.org/10.1002/aqc.2663

6. Betti, F., Bavestrello, G., Bo, M., Ravanetti, G., Enrichetti, F., Coppari, M., Cappanera, V., Venturini, S., Cattaneo-Vietti, R. Evidences of fishing impact on the coastal gorgonian forests inside the Portofino MPA (NW Mediterranean Sea). *Ocean Coast Manag* **2020**, *187*, 105105. https://doi.org/10.1016/j.ocecoaman.2020.105105

7. Otero, M.M., Numa, C., Bo, M., Orejas, C., Garrabou, J., Cerrano, C. et al. *Overview of the Conservation Status of Mediterranean Anthozoans; IUCN*, Málaga, Spain, 2017; pp. 1–73. ISBN 978-2-8317-1845-3. DOI: 10.2305/IUCN.CH.2017.RA.2.en. ISBN: 978-2-8317-1845-3. URI: http://hdl.handle.net/10261/150115

8. Martin, Y., Bonnefont, J.L., Chancerelle, L. Gorgonians mass mortality during the 1999 late summer in French Mediterranean coastal waters: the bacterial hypothesis. *Water Res* **2002**, *36(3)*, 779-782. https://doi.org/10.1016/S0043-1354(01)00251-2

9. Giuliani, S., Lamberti, C.V., Sonni, C., Pellegrini, D. Mucilage impact on gorgonians in the Tyrrhenian sea. *STOTEN* **2005**, *353(1-3)*, 340-349. https://doi.org/10.1016/j.scitotenv.2005.09.023

10. Schiaparelli, S., Castellano, M., Povero, P., Sartoni, G., Cattaneo-Vietti, R. A benthic mucilage event in North-Western Mediter- ranean Sea and its possible relationships with the summer 2003 European heatwave: Short term effects on littoral rocky assemblages. *Mar Ecol* **2007**, *28*, 341–353. https://doi.org/10.1111/j.1439-0485.2007.00155.x

11. Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M. et al. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Glob Chang* **2009**, *Biol 15*, 1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x

12. Vezzulli, L., Previati, M., Pruzzo, C., Marchese, A., Bourne, D.G., Cerrano, C., VibrioSea Consortium. *Vibrio* infections triggering mass mortality events in a warming Mediterranean Sea. *Environ Microbiol* **2010**, *12(7)*, 2007-2019. https://doi.org/10.1111/j.1462-2920.2010.02209.x

13. Vezzulli, L., Pezzati, E., Huete-Stauffer, C., Pruzzo, C., Cerrano, C. 16SrDNA pyrosequencing of the Mediterranean gorgonian *Paramuricea clavata* reveals a link among alterations in bacterial holobiont members, anthropogenic influence and disease outbreaks. *PLoS One* **2013**, *8(6)*, e67745. https://doi.org/10.1371/journal.pone.0067745

14. Piazzi, L., Atzori, F., Cadoni, N., Cinti, M.F., Frau, F., Ceccherelli, G. Benthic mucilage blooms threaten coralligenous reefs. *Mar Environ Res* **2018**, *140*, 145-151. https://doi.org/10.1016/j.marenvres.2018.06.011

15. Verdura, J., Linares, C., Ballesteros, E., Coma, R., Uriz, M.J., Bensoussan, N., Cebrian, E. Biodiversity loss in a Mediterranean ecosystem due to an extreme warming event unveils the role of an engineering gorgonian species. *Sci Rep* **2019**, *9(1)*, 5911. https://doi.org/10.1038/s41598-019-41929-0

16. Ceccherelli, G., Pinna, F., Pansini, A., Piazzi, L., La Manna, G. The constraint of ignoring the subtidal water climatology in evaluating the changes of coralligenous reefs due to heating events. *Sci Rep* **2020**, *10(1)*, 17332. https://doi.org/10.1038/s41598-020-74249-9

17. Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P.G., Schiaparelli, S., Siccardi, A., Sponga, F. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (North-western Mediterranean), summer 1999. *Ecol Let* **2000**, *3(4)*, 284-293. https://doi.org/10.1046/j.1461-0248.2000.00152.x

18. Garrabou, J., Perez T., Sartoretto, S., Harmelin, J.G. Mass mortality event in red coral *Corallium rubrum* populations in the Provence region (France, NW Mediterranean). *Mar Ecol Progr Ser* **2001**, *217*, 263-272. doi:10.3354/meps217263

19. Cebrian, E., Uriz, M.J., Garrabou, J., Ballesteros E. Sponge mass mortalities in a warming Mediterranean Sea: are cyanobacteria-harboring species worse off? *PLoS One* **2011**, *6(6)*, e20211. doi:10.1371/journal.pone.0020211

20. Cebrian, E., Linares, C., Marschal, C., Garrabou, J. Exploring the effects of invasive algae on the persistence of gorgonian populations. *Biol Inv* **2012**, *14*, 2647-2656. https://doi.org/10.1007/s10530-012-0261-6

21. Garrabou, J., Gómez-Gras, D., Ledoux, J.B., Linares, C., Bensoussan, N., López-Sendino, P. et al. Collaborative database to track mass mortality events in the Mediterranean Sea. *Front Mar Sci* **2019**, *6*, 478167. https://doi.org/10.3389/fmars.2019.00707

22. Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R. et al. Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Glob Chang Biol* **2022**, *28*, 5708–5725. https://doi.org/10.1111/gcb.16301

23. Cocito, S., Sgorbini, S. Long-term trend in substratum occupation by a clonal, carbonate bryozoan in a temperate rocky reef in times of thermal anomalies. *Mar Biol* **2014**, *161*, 17-27. https://doi.org/10.1007/s00227-013-2310-9

24. Linares, C., Coma, R., Diaz, D., Zabala, M., Hereu, B., Dantart, L. Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. *Mar Ecol Prog Ser* **2005**, *305*, 127–137. doi:10.3354/meps305127

25. Cerrano, C., Bavestrello, G. Medium-term effects of die-off of rocky benthos in the Ligurian Sea. What can we learn from gorgonians? *Chem Ecol* **2008**, *24*, 73–82. https://doi.org/10.1080/02757540801979648

26. Huete-Stauffer, C., Vielmini, I., Palma, M., Navone, A., Panzalis, P., Vezzulli, L., Misic, C., Cerrano, C. *Paramuricea clavata* (Anthozoa, Octocorallia) loss in the Marine Protected Area of Tavolara (Sardinia, Italy) due to a mass mortality event. *Mar Ecol* **2011**, *32*, 107–116. https://doi.org/10.1111/j.1439-0485.2011.00429.x

27. Teixidó, N., Casas, E., Cebrian, E., Linares, C., Garrabou, J. Impacts on coralligenous outcrop biodiversity of a dramatic coastal storm. *PLoS One* **2013**, *8*, e53742. https://doi.org/10.1371/journal.pone.0053742

28. Bavestrello, G., Cerrano, C., Zanzi, D., Cattaneo-Vietti, R. Damage by fishing activities to the Gorgonian coral *Paramuricea clavata* in the Ligurian Sea. *Aquat Conserv Mar Freshw Ecosyst* **1997**, 7, 253–262. https://doi.org/10.1002/(SICI)1099-0755(199709)7:3<253::AID-AQC243>3.0.CO;2-1

29. Coma, R., Pola, E., Ribes, M., Zabala, M. Long-term assessment of temperate octocoral mortality patterns, protected vs. unprotected areas. *Ecol Appl* **2004**, *14*, 1466–1478. https://doi.org/10.1890/03-5176

30. Bo, M., Bava, S., Canese, S., Angiolillo, M., Cattaneo-Vietti, R., Bavestrello, G. Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. *Biol Conserv* **2014**, *171*, 167–176. https://doi.org/10.1016/j.biocon.2014.01.011

31. Angiolillo, M., di Lorenzo, B., Farcomeni, A., Bo, M., Bavestrello, G., Santangelo, G., Cau, A., Mastascusa, V., Cau, A., Sacco, F., Canese, S. Distribution and assessment of marine debris in the deep Tyrrhenian Sea (NW Mediterranean Sea, Italy). *Mar Pollut* **2015**, 92, 149–159. https://doi.org/10.1016/j.marpolbul.2014.12.044

32. Angiolillo, M., Fortibuoni, T. Impacts of marine litter on Mediterranean reef systems: From shallow to deep waters. *Front Mar Sci* **2020**, *7*, 581966. https://doi.org/10.3389/fmars.2020.581966

33. Sini, M., Kipson, S., Linares, C., Koutsoubas, D., Garrabou, J. The yellow gorgonian *Eunicella cavolini*: Demography and disturbance levels across the Mediterranean Sea. *PLoS One 10* **2015**, *e0126253*. https://doi.org/10.1371/journal.pone.0126253

34. Enrichetti, F., Bo, M., Morri, C., Montefalcone, M., Toma, M., Bavestrello, G., Tunesi, L., Canese, S., Giusti, M., Salvati, E., Bertolotto, R.M., Bianchi, C.N. Assessing the environmental status of temperate mesophotic reefs: A new, integrated methodological approach. *Ecol Ind* **2019a**, *102*, 218-229. https://doi.org/10.1016/j.ecolind.2019.02.028

35. Tsounis, G., Martinez, L., Bramanti, L., Viladrich, N., Gili, J.M., Martinez, Á., Rossi, S. Anthropogenic effects on reproductive effort and allocation of energy reserves in the Mediterranean octocoral *Paramuricea clavata. Mar Ecol Prog Ser* **2012**, *449*, 161–172. DOI: https://doi.org/10.3354/meps09521

36. Kipson, S., Linares, C., Cˇižmek, H., Cebrián, E., Ballesteros, E., Bakran-Petricioli, T., Garrabou, J. Population structure and conservation status of the red gorgonian *Paramuricea clavata* (Risso, 1826) in the Eastern Adriatic Sea. *Mar Ecol* **2015**, *36*, 982–993. https://doi.org/10.1111/maec.12195

37. Canessa, M., Amedeo, I., Bavestrello, G., Panzalis, P., Trainito, E. The diversity, structure, and development of the epibiont community of *Paramuricea clavata* (Risso, 1826) (Cnidaria, Anthozoa). *Water* **2023**, *15*, 2664. https:// doi.org/10.3390/w15142664

38. Enrichetti, F., Bavestrello, G., Cappanera, V., Mariotti, M., Massa, F., Merotto, L., Povero, P., Rigo, I., Toma, M., Tunesi, L., Vassallo, P., Venturini, S., Bo, M. High megabenthic complexity and vulnerability of a mesophotic rocky shoal support its inclusion in a Mediterranean MPA. *Diversity* **2023**, *15(8)*, 933. https://doi.org/10.3390/d15080933

39. Cerrano, C., Arillo, A., Azzini, F., Calcinai, B., Castellano, L., Muti, C., Valisano, L., Zega, G., Bavestrello, G. Gorgonian population recovery after a mass mortality event. *Aquat Conserv Mar Freshw Ecos* **2005**, *15(2)*, 147-157. https://doi.org/10.1002/aqc.661

40. Fava, F., Bavestrello, G., Valisano, L., Cerrano, C. Survival, growth and regeneration in explants of four temperate gorgonian species in the Mediterranean Sea. *Ital J Zool* **2010**, *77(1)*, 44-52. https://doi.org/10.1080/11250000902769680

16

41. Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J. S., Brambilla, V., Ledoux, J. B. et al. Climate change transforms the functional identity of Mediterranean coralligenous assemblages. *Ecol Lett* **2021**, *24(5)*, 1038-1051. https://doi.org/10.1111/ele.13718

42. Iborra, L., Leduc, M., Fullgrabe, L., Cuny, P., Gobert, S. Temporal trends of two iconic Mediterranean gorgonians (*Paramuricea clavata* and *Eunicella cavolini*) in the climate change context. *J Sea Res* **2022**, *186*, 102241. https://doi.org/10.1016/j.seares.2022.102241

43. Enrichetti, F., Dominguez-Carrió, C., Toma, M., Bavestrello, G., Betti, F., Canese, S., Bo, M. Megabenthic communities of the Ligurian deep continental shelf and shelf break (NW Mediterranean Sea). *PLoS One* **2019b**, *14(10)*, e0223949. https://doi.org/10.1371/journal.pone.0223949

44. Enrichetti,F., Dominguez-Carrió, C., Toma, M., Bavestrello, G., Canese, S., Bo, M. Assessment and distribution of seafloor litter on the deep Ligurian continental shelf and shelf break (NW Mediterranean Sea). *Mar Pollut* **2020**, *151*, 110872. https://doi.org/10.1016/j.marpolbul.2019.110872

45. Anderson, M.J. Permutation tests for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat* **2001**, *58(3)*, 626-639. https://doi.org/10.1139/f01-004

46. Estaque, T., Richaume, J., Bianchimani, O., Schull, Q., Mérigot, B., Bensoussan, N. et al. Marine heatwaves on the rise: One of the strongest ever observed mass mortality event in temperate gorgonians. *Glob Chang Biol* **2023** *29(22)*, 6159-6162. DOI: 10.1111/gcb.16931. PMID: 37681400.

47. Previati, M., Scinto, A., Cerrano, C., Osinga, R. Oxygen consumption in Mediterranean octocorals under different temperatures. *J Experim Mar Biol Ecol* **2010**, *390(1)*, 39-48. https://doi.org/10.1016/j.jembe.2010.04.025

48. Ezzat, L., Merle, P.L., Furla, P., Buttler, A., Ferrier-Pages, C.The response of the Mediterranean gorgonian *Eunicella singularis* to thermal stress is independent of its nutritional regime. *PLoS One* **2013**, *8(5)*, e64370. https://doi.org/10.1371/journal.pone.0064370

49. Rodolfo-Metalpa, R., Bianchi, C.N., Peirano, A., Morri, C. Tissue necrosis and mortality of the temperate coral *Cladocora caespitosa. Ital J Zool* **2005**, *72(4)*, 271-276. https://doi.org/10.1080/11250000509356685

50. Cupido, R., Cocito, S., Barsanti, M., Sgorbini, S., Peirano, A., Santangelo G. Unexpected long-term population dynamics in a canopy-forming gorgonian coral following mass mortality. Mar *Ecol Progr Ser* **2009**, *394*, 195-200. DOI: https://doi.org/10.3354/meps08260

51. Rivetti, I., Fraschetti, S., Lionello, P., Zambianchi, E., Boero, F. Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. *PLoS One* **2014**, *9(12)*, e115655. https://doi.org/10.1371/journal.pone.0115655

52. Enrichetti, F., Bava, S., Bavestrello, G., Betti, F., Lanteri, L., Bo, M. Artisanal fishing impact on deep coralligenous animal forests: A Mediterranean case study of marine vulnerability. *Ocean Coastal Manag* **2019c**, *177*, 112-126.https://doi.org/10.1016/j.ocecoaman.2019.04.021

53. Russo, E., Anelli Monti, M., Toninato, G., Silvestri, C., Raffaetà, A., Pranovi, F. Lockdown: how the COVID-19 pandemic affected the fishing activities in the adriatic sea (Central Mediterranean Sea). *Front Mar Sci* **2021**, 8, 685808. https://doi.org/10.3389/fmars.2021.685808

54. Giannakis, E., Hadjioannou, L., Jimenez, C., Papageorgiou, M., Karonias, A., Petrou, A. Economic consequences of coronavirus disease (COVID-19) on fisheries in the eastern Mediterranean (Cyprus). *Sustainability* **2020**, *12(22)*, 9406. https://doi.org/10.3390/su12229406

55. Coll, M., Ortega-Cerdà, M., Mascarell-Rocher, Y. Ecological and economic effects of COVID-19 in marine fisheries from the Northwestern Mediterranean Sea. *Biol Conserv* **255**, 108997. https://doi.org/10.1016/j.biocon.2021.108997

56. Dapueto, G., Massa, F., Costa, S., Cimoli, L., Olivari, E., Chiantore, M., Federici, B., Povero, P. A spatial multi-criteria evaluation for site selection of offshore marine fish farm in the Ligurian Sea, Italy. *Ocean Coast Manag* **2015**, *116*, 64-77. https://doi.org/10.1016/j.ocecoaman.2015.06.030

57. FAO. International Guidelines for the Management of Deep-Sea Fisheries in the High Seas. Rome, 2009; 73 pp.