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Michele Mistri & Victor Ugo Ceccherelli

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Effects of a mucilage event on the Mediterranean gorgonian *Paramuricea clavata*. I - Short term impacts at the population and colony levels

MICHELE MISTRI

Dipartimento di Biologia, Sezione di Biologia Evolutiva,
Università di Ferrara,
via L. Borsari 46, I-44100 Ferrara (Italy)

VICTOR UGO CECCHERELLI

Dipartimento di Biologia Evoluzionistica e Sperimentale,
Università di Bologna,
via Selmi 3, I-40126 Bologna (Italy)

ABSTRACT

A *Paramuricea clavata* population thriving between 29 and 39 m depth on a shoal at the northern entrance to the Strait of Messina (Tyrrhenian Sea) was affected by mucilage coverage at the end of summer 1993. Mucilage became entangled in projecting branches and necrotized the coenenchyme below, leaving the axial skeleton bare. The entire population was heavily affected, extent of injuries being negatively correlated with size of colonies. Colony size, scale and location of damage were related to successful regeneration after six months. Smaller colonies showed a higher mortality, while colonies with over 50-60% of their total branch length damaged were overgrown by invaders and died. The extent of injuries in the central part of the colony was found to be a critical parameter in determining colony regrowth. A number of injured colonies grew during the six months following the disappearance of mucilage, which shows that their regrowth was apparently not influenced by stress due to mucilage.

KEY WORDS: Mucilage - Cnidaria - *Paramuricea clavata* - Growth - Regeneration - Mediterranean Sea.

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INTRODUCTION

In the Mediterranean Sea, a number of studies have reported the occurrence of flocculent, amorphous aggregates known as mucilage. The settling of flocculent material of pelagic origin on the sea bottom is likely to act as a stressing agent. Disturbance episodes may have different effects on benthic fauna: in low densities, mucilage flocs can be actively removed from the body surface of benthic organisms or may even be utilized as food source (Stachowitsch *et al.*, 1990), but larger aggregates have a greater impact, and may cause benthic fauna to die (Zavodnik *et al.*, cited in Stachowitsch *et al.*, 1990).

The effect of the mucilage on benthic communities has been particularly studied in the Adriatic Sea (Stachowitsch, 1984), where its periodic presence has been known since the 17th century (Molin *et al.*, 1992). In the Tyrrhenian Sea, along the western Italian coast, data concerning the occurrence of mucilage are lacking, probably because extensive macroscopic phenomena of surface accumulation of floating gelatinous masses (like those occurring in the upper Adriatic) have never been observed. Nevertheless, mucilage is often present also in the Tyrrhenian Sea. In fact, in recent years (Cinelli, 1992; Rinaldi, 1992), benthic communities were impacted by deposits of mucilage produced by filamentous algae, mainly Tribonemales and Ectocarpales (Sartoni & Sonni, 1992).

In the lower Tyrrhenian Sea, an unusual occurrence of mucilage phenomenon was observed by amateur divers and fishermen at the northern entrance to the Strait of Messina, off the Calabrian coast near the small town of Scilla, at the end of summer 1993. It was first recorded at the beginning of September. Around the end of that month, mucilage sank to the bottom covering benthic sessile organisms with a whitish cobweb. Before and during this phenomenon, high temperatures were recorded throughout the water column. In September 1993, the thermocline, usually at about 18-20 m depth, broke apart, and very unusual high temperatures (> 25° C) were recorded at the foot of the shoal. The stiffling coverage of benthic sessile fauna lasted about two weeks, then, around mid-October, the mucilage aggregations broke apart.

Corals may be harmed by environmental conditions, and exogenous factors like pollution and sedimentation may play an important role in influencing the growth of colonies (Dodge & Lang, 1983; Tomascik & Sanders, 1985; Riegl, 1995). The main, macroscopic effect of these agents on corals is necrosis of the living tissue and, consequently, the skeleton being laid bare. Injured tissues may regenerate or become more or less immediately colonized by overgrowing organisms, hydroids, serpulid polychaetes, bryozoans, and, mostly, algae (Naim, 1993). However, the ability of stony corals to regenerate injured parts of the colony has been well documented (Bak & Steward van Es, 1980; Meesters *et al.*, 1994). Injury ap-

parently results in a reallocation of resources to regeneration and a consequently decreased investment in growth (Guzman *et al.*, 1994). During coral tissue regeneration, many life history traits, such as survival, growth, and reproduction, seem to be affected (Wahle, 1983; Meesters & Bak, 1993; Van Veghel & Bak, 1993).

In the waters off the town of Scilla there are dense patchy populations of the Mediterranean gorgonian *Paramuricea clavata*. One patch on the shoal called «La Montagna», under observation since 1991, was heavily affected by the September-October 1993 mucilage coverage. Fluffy stringers entangled in projecting branches caused widespread lesions to the colonies. The coenenchymal layers covered by entangled aggregates became necrotic, and when mucilage broke apart, injured colonies were clearly recognizable by the wide portions of exposed axial skeleton. Naked skeletal parts were susceptible to fouling by overgrowing organisms. The present investigation quantifies the damage of the mucilage event on the Scilla population of *P. clavata*, evaluates its influence on the gorgonian's growth, and estimates the ability of injured colonies to regenerate.

MATERIALS AND METHODS

Study site

Field work was conducted at «La Montagna» (38°15'00 N, 15°43'18 E) (Fig. 1), a granitic shoal with walls descending steeply downwards from the 18-m-top to a depth of 39 m, some hundreds of meters off the Rock of Scilla (Reggio Calabria, southern Italy). The shoal is directly affected by strong tidal currents from the Strait of Messina. The uppermost ten meters of the shoal slope are dominated by Dictyotales, while from 29 m downwards, a dense population of *P. clavata* thrives. More information about the characteristics of the study site can be found in Mistri (1994).

Sampling

In situ observations on the *P. clavata* population were carried out immediately after the disappearance of mucilage from colonies, in November 1993, and six months after, at the end of May 1994. Further observations were made in December 1994.

In November 1993, the depth distribution and percentage of damaged colonies in the *P. clavata* population was estimated in two series of 1-m² frames arranged along two parallel depth transects. Five frames were examined per transect, at depths of 30, 32, 35, 37, and 39 m, respectively. All colonies inside each frame were counted and visually examined for the presence of injuries. For simplicity, colonies were grouped into two classes: 'heavily' injured (damaged surface >50% of the whole colony surface) and 'slightly' injured (damage <50%).

Four more frames were then randomly chosen along a depth transect (30 to 37 m), and all colonies comprised within each frame were tagged with plastic markers. The colonies were photographed with a Nikonos V underwater camera, placing behind each one a white plastic 50-cm-sided graduate square. This kind of photographic survey was repeated in May 1994.

Back in the laboratory, slides of the colonies were viewed with a projector equipped with a built-in monitor, and the perimeters of the photographed colonies were traced. The traced outlines were transferred to a PC, using a Hewlett Packard ScanJet IIcx image digitizer, and filed according to specimen and date. For each gorgonian, the total linear development of all branches (TBL, total branch length), the part of the colony still covered by coenenchyme

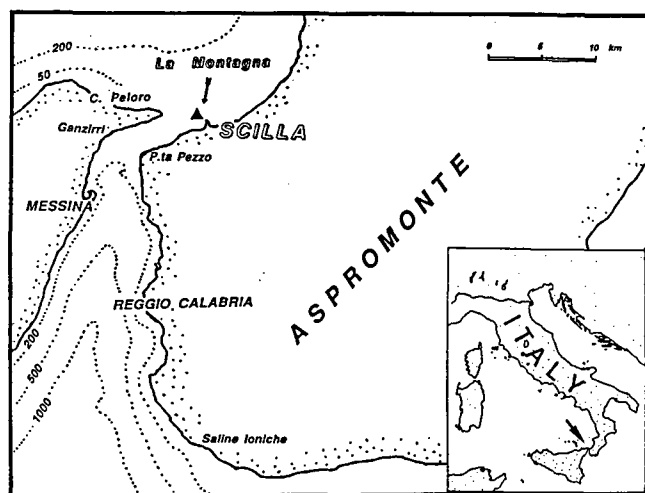


Fig. 1 - Study site location of *Paramuricea clavata* population. Arrow indicates position.

(LTL, living tissues length), and the linear development of bare branches (INJ, injured part length) were measured on the digitized outlines with a Kontron KS300 image analyser. According to the position, the extent of bare branches (INJ) in the November colonies was split into two further sets of measurements: the length of bare branches which do not further ramificate, or endbranchlets (DISTAL), and the length of the naked skeletal parts in the rest of the colony (CENTRE). In Figure 2, a drawing of the general shape of *P. clavata* with the recorded measurements is given. Measurements of TBL, LTL, and INJ were then repeated on the May data set.

In order to check the accuracy of the adopted method of collecting data (i.e., to determine the bias induced by a possible angle distortion due to the lens), 10 randomly chosen tagged colonies were photographed *in situ* and then collected in December 1994. Collected colonies were kept in 15-litre tanks filled with 10% neutralized formalin in seawater and brought back to the laboratory. In the studio, colonies were photographed again with an Olympus OM2 camera equipped with an Olympus Zuiko 50 mm lens, keeping the camera perpendicularly on each subject by means of a fixed arm. TBL measurements were then taken on both sets of slides with the above mentioned procedure. Studio measurements were regressed on those obtained on the same colonies from field photos, and checked for difference (ANOVA).

Statistical analysis

Since quantitative data on the ecological features of this gorgonian population before the disturbance event were available (Mistri & Ceccherelli, 1994), statistical analysis depended both on those data and on those recorded afterwards.

To determine the vertical distribution of gorgonians affected by mucilage, the rank class 'heavily injured' was utilized. The average relative frequency of heavily injured colonies on the total number of colonies per frame (after arcsin-square root transformation) was tested by means of ANOVA on depth (five levels).

In order to test the hypothesis that a relationship existed between colony size and resistance to physical damage (Connell, 1973), total branch length measurements of the November tagged colonies were grouped in seven TBL size classes (0-1000; 1001-2000; 2001-3000; 3001-4000; 4001-5000; 5001-6000; > 6001 mm), and the INJ average percentages for each class were then regressed on size ranks. Regression significance was tested by means of ANOVA. The same procedure was repeated on the May data set.

The ability of *P. clavata* to resist damage was investigated by comparing the November and May TBL and LTL measurements from the two sets of photographed colonies. At the end of May 1994, some of

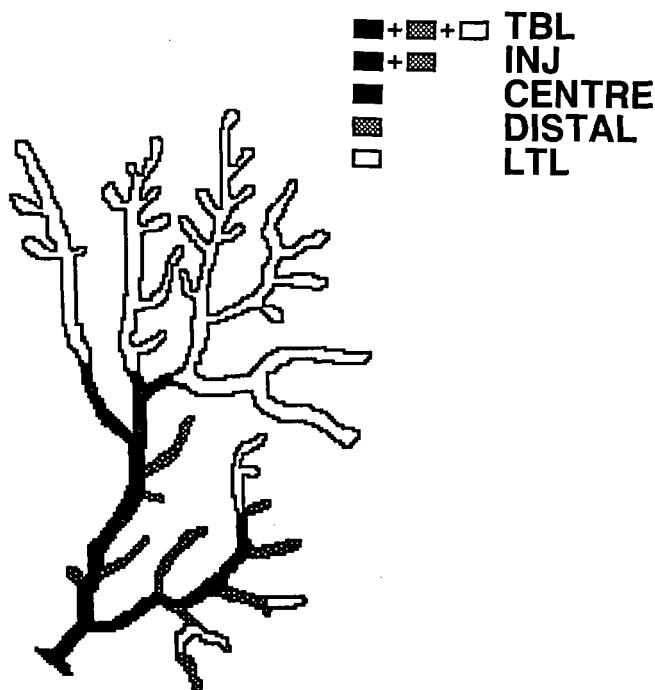


Fig. 2 - Drawing of the general shape of *Paramuricea clavata* with the measurements taken. TBL, total branch length; INJ, extent of bare branches; LTL, living tissues length.

the tagged colonies were completely covered by overgrowing organisms, and were thus dead (LTL = 0; status: DEAD). Others showed a significant further coenenchyme withdrawal ($TBL_{May} < TBL_{Nov}$; *t*-test for paired data: $t = 2.34$, $df = 11$, $P < 0.05$; $LTL_{May} < LTL_{Nov}$; $t = 3.05$, $df = 11$, $P < 0.01$; status: WITHDRAWN), while a number were found to have significantly increased the extent of living tissues ($TBL_{May} > TBL_{Nov}$; $t = 3.28$, $df = 26$, $P < 0.005$; $LTL_{May} > LTL_{Nov}$; $t = 3.67$; $df = 26$; $P < 0.001$; status: GROWN). Colonies were grouped according to the health status in which they had been found in May (DEAD, GROWN, WITHDRAWN). It must be stressed that in this study 'dead colonies' are colonies which suffered complete mortality, while colonies which underwent partial mortality (*sensu* Hughes & Jackson, 1980) are 'withdrawn colonies'.

Stepwise discriminant function analysis (SDFA) was used to determine which variable among colony size (TBL), and extent of damage in the periphery (DISTAL) or in the central part (CENTRE) of the colony, mostly influenced the recovery success of the November injured gorgonians. Colonies were labelled according to their May status (DEAD, GROWN, WITHDRAWN), and, after log-transformation of variable values, were submitted to the analysis.

The effect of the stress due to mucilage on the growth rate of colonies which had shown a significant growth (GROWN) was investigated on the May set of measurements. By means of the specific growth equation calculated for the same population (Mistri, 1995), each colony's theoretical TBL after a period of six months (November-May) was calculated. Then, theoretical TBL estimates were compared with observed TBL measurements by means of a *t*-test for paired data, in order to check the agreement between sampled (May TBLs) and theoretical (TBLs of undisturbed colonies) values.

RESULTS

The mean difference between total branch length measurements taken both from studio and field

photographs was -2.4% (± 6.1 SD). The regression between studio and field TBLs was highly significant ($F = 2534$; $df = 1, 9$; $P < 0.001$), as shown by the high value of the coefficient of determination ($R^2 = 0.997$). Subsequent *t*-test for paired data run between field TBL measurements and their respective theoretical TBL values, obtained by means of the regression equation, was not significant ($t = 1.49$; $df = 9$; $P = 0.170$). This means that no macroscopic bias due to angle distortion was introduced when positioning the camera over the same specimen in the field.

A total of 161 colonies were counted in the frames arranged along depth transects. Table I reports the mean density and the mean percentage of colonies visually injured for more than 50% of their fan surface at the five depths considered. ANOVA showed that the extent of tissue damage in the observed colonies was independent of depth ($F = 1.02$; $df = 4, 8$; $P = 0.493$).

Fifty-eight colonies were tagged, photographed and measured for parameters (TBL, LTL, INJ, length of bare skeleton at the edge (DISTAL) and in the central part (CENTRE) of the colony) in November 1993. Randomly chosen quadrats were at 33, 34, 35 and 37 m depth. The relative extent of injured parts ranged from 0.0 to 96.2% of the colony TBL. Colonies were grouped in TBL size classes (see Materials and Methods) and plotted against mean injury extent. In Figure 3, the Box-and-Whisker plot of the relative percentage of fan injury per size class is reported: smaller size classes seemed to have suffered heavier tissue damage. The negative regression between the two parameters ($R^2 = 0.803$), shown in Figure 4, was highly significant ($F = 20.41$; $df = 1, 6$; $P < 0.001$). In Table II, TBL size classes and measured parameters of the 58 colonies photographed in November 1993 are reported.

Out of 58 colonies tagged in November, only 55 were found in May: 16 colonies (29.1%) were dead, 27 (49.1%) had significantly grown, and 12 (21.8%) showed a further LTL withdrawal (see Materials and Methods for statistical tests). Some colonies had regenerated the in-

TABLE I - Percent of *Paramuricea clavata* colonies visibly injured in more than 50% of their TBL, and average densities at various depths.

Depth (m)	Density (col·m ⁻²)	% colonies injured > 50%
30	15.0	43.3
32	12.5	24.0
35	26.0	48.1
37	17.5	8.6
39	19.0	21.1

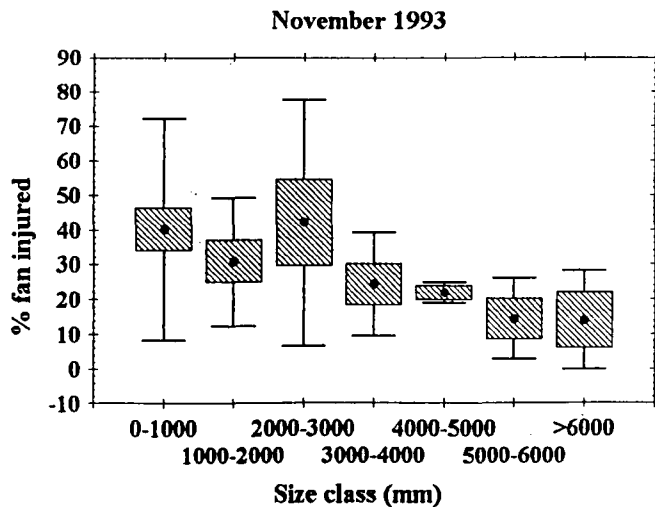


Fig. 3 - November 1993: Box-and-Whisker plot of colony size class and relative percentage of colony injury (means, SD, and SE are reported).

jured coenenchymal parts, while others showed extended areas of the colony overgrown with sessile organisms. Some of the latter colonies were completely overgrown. The May status (DEAD, GROWN, WITHDRAWN) of the tagged colonies, together with each colony's relative scale of injury (IRS) calculated in November and May, is reported in Table III. At first sight, the temporal trend of each colony's injury relative size does not seem to be consistent with the status assigned in May to the colony itself. For example, colony 1 increased the scale of injured parts from 0 to 5.2% in the six months between the two sampling dates. In spite of this, it was assigned to the GROWN group because in May 1994, TBL was found increased in length, but 5.2% of it was denuded. Here partial predation is probably the cause of branch denudation, since (1) lesions consisted of loss of coenen-

chyme around endbranches (see Discussion), and (2) injuries were new, since exposed axial tips were still not fouled by organisms. The case of colony 56 is different: the extent of the fan's injured parts was greatly reduced (from 30.0% to 13.7%, Table III), but it was, however, assigned to the WITHDRAWN group. It must be stressed that status was assigned as a consequence of the increase or decrease of the extent of living coenenchyme (LTL) from one sampling date to the other, while injury relative size (IRS) was calculated as a percentage of TBL. So, if a fan loses one or more bare branches, as a few WITHDRAWN colonies did, TBL will, of course, be reduced, and so will IRS, if we assume that dead parts of the colony (INJ) are more brittle and, thus, more easily subject to breakage.

Out of 16 dead colonies, 12 (75%) belonged to the 0-1000 mm size class, 1 (6.25%) to the 1001-2000 mm size class, and 3 (18.75%) to the 2001-3000 mm size class. The May Box-and-Whisker plot of the relative percentage of fan injury per size class of the 39 surviving colonies is reported in Figure 5; the regression between the two parameters ($R^2 = 0.642$, graph not shown) was not statistically significant ($F = 3.50$; $df = 1, 5$; $P = 0.120$). In the first size class (TBL: 0-1000 mm) a significant reduction (t -test: 2.93; $df = 39$; $P < 0.01$) of the extent of injured parts was observed. This may be due to the recovery and growth processes exhibited by some colonies, but, most likely, to the elimination of the more heavily damaged colonies. In fact, the numbers in this class were found almost halved. t -tests run for the other size classes showed no statistically significant differences between the November and May extent of injured parts.

Stepwise discriminant function analysis (SDFA) was adopted to determine which variable, TBL, CENTRE, or DISTAL, discriminated most in defining the May status of previously injured colonies. The overall discrimination between variables was significant (Wilks' $\lambda = 0.531$; $F = 6.212$; $df = 6, 100$; $P < 0.001$). In Table IV, the independ-

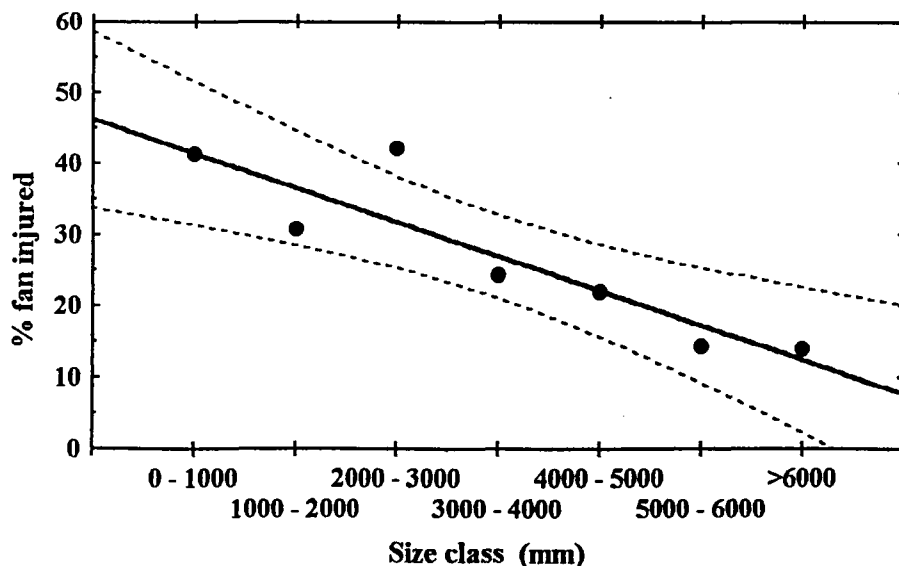


Fig. 4 - November 1993: regression between colony size class and mean relative percentage of colony injury (dotted line: 95% confidence limits).

TABLE II - Parameters of November 1993 photographed colonies of *Paramuricea clavata* total branch length (TBL), living tissue length (LTL), total injured length (INJ), extent of damage in the central part (CENTRE) and at the edge (DISTAL) of the colony.

colony No	size class (mm)	TBL (mm)	LTL (mm)	INJ (mm)	CENTRAL (mm)	DISTAL (mm)
1	0-1000	83	83	0	0	0
2	0-1000	103	103	0	0	0
3	0-1000	126	13	113	64	49
4	0-1000	161	32	129	49	80
5	0-1000	169	92	77	0	77
6	0-1000	209	48	161	113	48
7	0-1000	210	81	129	129	0
8	0-1000	241	178	63	21	42
9	0-1000	243	205	38	0	38
10	0-1000	244	90	154	65	89
11	0-1000	278	236	42	0	42
12	0-1000	308	200	108	46	62
13	0-1000	321	132	189	113	76
14	0-1000	326	43	283	283	0
15	0-1000	446	338	108	92	16
16	0-1000	477	154	323	216	107
17	0-1000	530	508	22	0	22
18	0-1000	554	554	0	0	0
19	0-1000	600	538	62	0	62
20	0-1000	603	23	580	464	116
21	0-1000	604	170	434	208	226
22	0-1000	629	629	0	0	0
23	0-1000	670	512	158	115	43
24	0-1000	675	367	308	126	182
25	0-1000	749	491	258	26	232
26	0-1000	984	903	81	0	81
27	1000-2000	1107	644	463	0	463
28	1000-2000	1124	769	355	0	355
29	1000-2000	1215	1169	46	15	31
30	1000-2000	1246	803	443	319	124
31	1000-2000	1246	877	369	277	92
32	1000-2000	1580	1434	146	70	76
33	1000-2000	1800	1453	347	125	222
34	1000-2000	1860	1094	766	651	115
35	1000-2000	1887	677	1210	847	363
36	2000-3000	2033	973	1060	604	456
37	2000-3000	2151	2038	113	57	57
38	2000-3000	2203	2169	34	0	34
39	2000-3000	2423	1963	460	193	267
40	2000-3000	2452	1742	710	391	320
41	2000-3000	2500	264	2236	1342	894
42	2000-3000	2501	1356	1145	676	469
43	2000-3000	2866	166	2700	1350	1350
44	3000-4000	3117	2166	951	476	476
45	3000-4000	3135	1879	1256	615	641
46	3000-4000	3194	2772	422	63	359
47	3000-4000	3316	3017	299	15	284
48	3000-4000	3400	2004	1396	824	572
49	3000-4000	3822	3400	422	283	139
50	4000-5000	4146	3329	817	90	727
51	4000-5000	4523	3446	1077	227	850
52	5000-6000	5196	4144	1052	705	347
53	5000-6000	5287	5090	197	32	165
54	5000-6000	5497	3982	1515	631	884
55	5000-6000	5657	5360	297	15	282
56	>6000	6886	4820	2066	186	1880
57	>6000	9471	8688	783	337	446
58	>6000	11470	11078	392	39	353

TABLE III - Injury relative size (IRS) in *Paramuricea clavata* as percentage of TBL measured in November 1993 and in May 1994. Status of colonies recorded in May is also reported.

colony No.	IRS Nov. (% of TBL)	IRS May (% of TBL)	status (May 94)
1	0.0	5.2	GROWN
2	0.0	0.0	GROWN
3	89.7	100	DEAD
4	80.1	100	DEAD
5	45.6	100	DEAD
6	77.0	100	DEAD
7	61.4	100	DEAD
8	26.1		(not found)
9	15.6	0.0	GROWN
10	63.1	100	DEAD
11	15.1	0.0	GROWN
12	35.1	9.4	GROWN
13	58.9	100	DEAD
14	86.8	100	DEAD
15	24.2	15.1	GROWN
16	67.7	100	DEAD
17	4.2	0.0	GROWN
18	0.0	0.0	GROWN
19	10.3	13.2	GROWN
20	96.2	100	DEAD
21	71.9	100	DEAD
22	6.0	0.0	GROWN
23	23.5	30.6	WITHDRAWN
24	45.6	100	DEAD
25	34.4	26.4	WITHDRAWN
26	8.2	14.8	WITHDRAWN
27	41.8	65.6	WITHDRAWN
28	31.6	25.0	WITHDRAWN
29	3.8	1.1	GROWN
30	35.6	61.8	WITHDRAWN
31	29.6	28.0	WITHDRAWN
32	9.2	9.0	GROWN
33	19.3	21.5	WITHDRAWN
34	41.2	100	DEAD
35	64.1	57.0	GROWN
36	52.1	100	DEAD
37	5.3	0.6	GROWN
38	1.5	0.0	GROWN
39	19.0	19.4	GROWN
40	29.0	51.2	WITHDRAWN
41	89.4	100	DEAD
42	45.9	44.4	GROWN
43	94.2	100	DEAD
44	30.5	38.5	WITHDRAWN
45	40.1	37.6	GROWN
46	13.2	6.3	GROWN
47	9.0	1.5	GROWN
48	41.1	70.0	WITHDRAWN
49	11.0	3.6	GROWN
50	19.1	2.4	GROWN
51	23.8		(not found)
52	20.3	3.9	GROWN
53	3.7	15.7	GROWN
54	27.6		(not found)
55	5.3	0.6	GROWN
56	30.0	13.7	WITHDRAWN
57	8.3	2.8	GROWN
58	3.4	0.2	GROWN

ent contribution to the prediction for each variable in the model are reported. The partial Wilks' λ indicate that SIZE contributes most ($P < 0.0001$), followed by CENTRE ($P < 0.001$). The DISTAL variable ($P < 0.05$) contributes least to the overall discrimination. Since there were three variables in the model, two discriminant functions were extracted; Table V reports the step-down test of canonical roots: only the first discriminant function was statistically significant ($P < 0.0001$). This function discriminated mostly between GROWN (mean of canonical variables: 0.751) versus DEAD (-1.123). In Figure 6, the plot of the individual scores for the two discriminant functions is shown. Again, function 1 seems to discriminate mostly between GROWN and DEAD. Posterior classification probability of each colony was calculated using the Mahalanobis distance from each of the group centroids. Correct classifications were 93.8% for DEAD and 85.2% for GROWN. A large number of misallocations (only 25.0% correctly classified) were found for WITHDRAWN, confirming the low discriminatory power of this group.

Theoretical and measured TBL values of grown colonies did not differ significantly (*t*-test for paired data: $t = 1.45$; $df = 26$; $P = 0.159$).

DISCUSSION

Injury occurs quite commonly among Mediterranean gorgonians. In the northwestern Mediterranean basin, many local gorgonian populations have recently been severely injured by unidentified exogenous factors (Bavestrello & Boero, 1986; Rivoire, 1991; Bavestrello *et al.*, 1994). Harmelin & Marinopoulos (1994), investigating a *Paramuricea clavata* population in the national park of Port-Cros (southern France), reported a co-occurrence of diffuse and multiple injuring events, such as simultaneous abrasion by water turbulence and mechanical man-induced factors. In the central Tyrrhenian Sea, major catastrophic events occurred in summer 1990 and 1991, when, as a consequence of an extremely large-scale occurrence of mucilage, several

TABLE IV - Stepwise discriminant function analysis (SDFA): independent contribution for each *Paramuricea clavata* measured variable (SIZE, CENTRE, DISTAL) to the overall discrimination between status (DEAD, GROWN, WITHDRAWN) of colonies.

Variable	Partial λ	F-to-remove ($df = 2, 50$)	P
Size	0.682	11.664	< 0.0001
Centre	0.777	7.169	< 0.001
Distal	0.870	3.804	< 0.05

gorgonian populations suffered great damage (Rinaldi, 1992). Off the Calabrian coast of the Strait of Messina, mucilage appeared and impacted benthic communities about two years later, at the end of summer 1993. Gorgonian coenenchymal necrosis was probably caused by prolonged anoxic conditions due to mucilage entangled in branches. Although it is not the aim of this

TABLE V - Stepwise discriminant function analysis (SDFA): step-down test of canonical roots among colonies of *Paramuricea clavata* of different status.

Roots removed	Wilks' λ	χ^2	df	P
0	0.531	32.311	6	< 0.0001
1	0.896	5.573	2	0.062

study to comment on the specific causes of gorgonian damage, it is, however, a matter of fact that very few colonies of the *P. clavata* population at «La Montagna» were found to be unaffected by tissue necrosis.

Injuries to the colonies resulted in the denudation of more or less wide parts of the axial skeleton. In benthic communities, where competition for space is very strong, such bare branches constitute an immediately available, free substratum on which overgrowing organisms can settle. Sessile species with three-dimensional arborescent growth (like the bryozoans *Turbicellepora avicularis* and *Pentapora fascialis*) or developing sheaths (like the alcyonarian *Parerythropodium coralloides*) have been found to typically

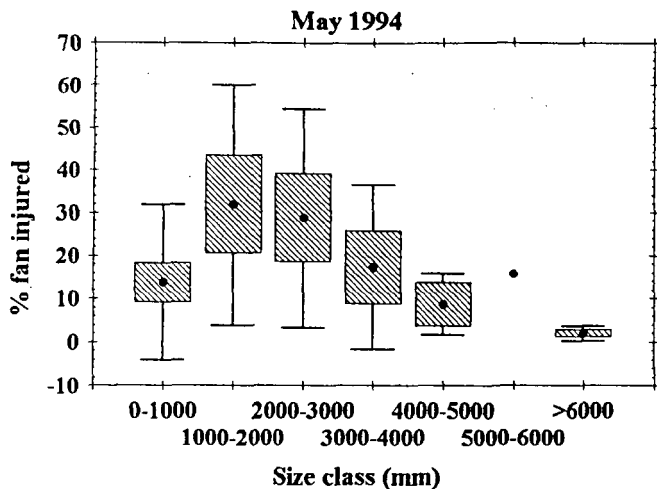


Fig. 5 - May 1994: Box-and-Whisker plot of colony size class and relative percentage of colony injury (means, SD, and SE are reported).

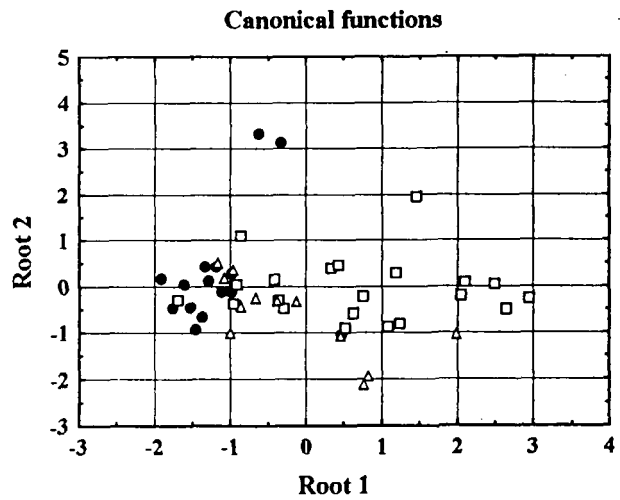


Fig. 6 - Scatter plot from Stepwise Discriminant Function Analysis of variables (see text) for three groups (● DEAD; □ GROWN; △ WITHDRAWN).

colonize gorgonian bare branches (Harmelin & Marinopoulos, 1994). Loya (1976) reported that the initial response of the scleractinian *Stylophora pistillata* to branch breakage was the rapid coverage of the exposed areas with living tissues to prevent settlement of fouling organisms. Lang da Silveira & Van't Hof (1977), simulating predation on the tropical gorgonian *Plexaura flexuosa*, observed four to eight weeks for complete tissue regeneration in 4-cm-long denuded branches.

In the Mediterranean Sea, a few studies have dealt with gorgonians ability to withstand overgrowers' colonization. Theodor (1964) observed that the plexaurid *Eunicella singularis* was able to form coenenchymal «bubbles» in which epibionts were still surviving. One of us (M. M.) observed coenenchymal bubbles covering epibionts in colonies of *Eunicella cavolinii* extirpated by fishermen's trawling nets from deep waters (80-100 m) off the isle of Linosa (southern Sicily). Bavestrello & Boero (1986) reported autoctomy phenomena in necrotized branchlets of *E. cavolinii* from Portofino Promontory (Ligurian Sea). In the present study, the ability of the gorgonian *P. clavata* to regenerate injured parts of the colony was investigated considering several factors: colony size, and scale and location of injury. The factors that appeared to affect regeneration may also have an effect on the competitive ability of the gorgonian.

Colony size

Connell (1973) proposed that larger colonies may have a better capacity to resist damage than smaller ones of the same species. Hughes & Jackson (1980) found that the pattern of mortality of the scleractinian *Agaricia agaricites* was strikingly related to colony size. Meesters et al. (1994) recently suggested that successful regeneration in the reef-building coral *Montastrea annularis* depends on the amount of tissue bordering the

lesion. These apparently contradictory statements are not mutually exclusive. Larger colonies may have more energy available and regeneration can depend on the amount of tissue bordering the lesion, while small colonies may have too little energy available for regeneration because there is not enough tissue bordering the lesion. In the *P. clavata* population, complete mortality was mostly observed in smaller colonies (0-1000 mm as TBL), while only a few gorgonians comprised in the larger TBL size classes (> 1000 mm) died during the six months following the mucilage event. Damage in smaller colonies probably leaves too little coenenchyme to supply enough energy for regeneration. In fact, all organisms must allocate energy to various biological functions such as growth, regeneration, reproduction, and maintenance (Charnov & Schaffer, 1973). Assuming that regrowth of the coenenchyme and regeneration of injuries require additional metabolic resources, and that energy is limited in gorgonians, exhaustion of metabolic reserves may result in the death of smaller colonies. In contrast, Wahle (1983) found that small, experimentally injured *Plexaura homomalla* colonies did not regenerate significantly slower than larger ones; however, the level of injury tested was very low: as will be discussed below, a primary role in gorgonian regeneration ability is played by the scale of injury.

Scale of injury

Whether or not *P. clavata* successfully regenerates tissues after injury mostly depends on the scale of injury. If coenenchyme damage is sufficiently large, recovery may not be rapid enough to exclude colonization by fouling organisms. Lang da Silveira & Van't Hof (1977) found a direct relationship between the time during which the bare axial skeleton of *Plexaura flexuosa* was available as a free substratum, and the settlement of algae and planulae of the fire-coral *Millepora* spp. They also observed successful settlement of invaders when the skeleton remained bare for more than two weeks. In our *P. clavata*, the average monthly growth in length was estimated to be about 2.5 mm (Mistri & Ceccherelli, 1994). Even if it is reasonable to suppose that the coenenchyme could grow faster because that value is inclusive of axis growth, it clearly testifies for a slow rate of growth. Because most lesions on *P. clavata* branches were larger than a few millimeters, most of the skeleton remained uncovered long enough to allow settlement to occur. Fouling organisms settling on the *P. clavata* bare skeleton were mostly algae, hydroids, and bryozoans.

Gorgonians are able to regenerate tissues efficiently under low levels of natural injury, but repeated injury among colonies can inhibit future regeneration (Lang da Silveira & Van't Hof, 1977). Table III summarizes injury relative size and status of the November *P. clavata* tagged colonies. Gorgonians injured in more than 50-60% of their TBL are apparently not able to withstand competition from overgrowing invaders. Regrowth of the

coenenchyme over the damaged areas is probably inhibited by fouling organisms and the colony dies completely in a few months. On the other hand, colonies damaged in less than 20% of their TBL are able to restore injuries quickly. As said above, slightly injured gorgonians are likely to have enough living tissue left to furnish a sufficient amount of energy to allocate to regeneration: an energetic constraint on regeneration probably becomes important among colonies with large and numerous injuries. The fate of colonies injured in 20-50% of TBL does not seem to be predictable: some colonies regenerated, even if the scale of damage was high, while other colonies showed further tissue degeneration.

It is not clear whether *P. clavata* is able to eliminate bare branches by autoctomy processes. Comparing the November with the May 'healthy' (i.e., the GROWN group) *P. clavata* colony outlines, the detachment of bare branchlets was clearly evident only in two specimens. Withdrawn gorgonians, on the contrary, showed slightly larger missing portions in the colony. Reduction in size exhibited by some 'ill' colonies, as demonstrated by the significance of the statistical test on TBL values, (see Materials and Methods) may probably be due, however, to some kind of mechanically-induced causes. For example, breakage of dead, fouled branches could result from divers' flippers (at the «La Montagna» shoal, because of the aesthetic value of the *P. clavata* population, scuba diving activities are on the increase; P. Barone, pers. comm.). Harmelin & Marinopoulos (1994) reported such a cause as one of the possible sources of wounds to *P. clavata* colonies in Port-Cros. From the present data, however, it is not possible to ascertain whether *P. clavata* is able to detach dead branches from the colony by autoctomy processes.

Location of injury

This study points out that a major role in defining the ability of colonies to successfully regenerate injured parts is also played by the physical location of the damage on the colony itself. In fact, colonies injured in the central area of the fan showed lesser ability to regenerate and, thus, to withstand epizoan colonization, while regeneration at branch ends was in most cases successful. Meesters & Bak (1995), investigating the regeneration potential of the branching coral *Acropora palmata*, found that regeneration ability decreased rapidly, from tip to base, along branches: they observed that tissues in basal regions of colonies were more vulnerable and less vigorous than at branch ends. The separation of the colony into two distinct areas (upper branches and lower stem) probably reflects differences in the physiological functioning of the colony (Jackson, 1979). Our findings seem to be in agreement with that evidence. A slower regeneration in the central and basal parts of the colony of *P. clavata* may facilitate colonization of overgrowing invaders. At the distal parts of the colony the case is dif-

ferent, since coral growth takes place at the tips and a relation of regeneration of the coenenchyme to the main centres of growth (i.e., endbranches) may exist (Meesters & Bak, 1995).

Harvell (1984) showed that, in some bryozoans, predator attacks on the centre of the colony more often prevent colony regeneration than attacks on the distal parts. The majority of the gorgonians which successfully regenerated injured parts of the colony were not at all, or only slightly, wounded in the central area of the fan. Injuries in distal branches do regenerate successfully: distal injuries do not play a significant role in the mortality of the colony. This may also reflect a coadaptative strategy exhibited by colonies and their predators. At the «La Montagna» shoal, in fact, lesions due to predators do not occur randomly within *P. clavata* colonies, but they tend to be located on the periphery of the colony and particularly on endbranches and tips: all observed attacks of the major gorgonian grazer at the study site, the polychaete *Hermodice carunculata*, were centred on endbranchlets (pers. obs.). For any predator to be successful it is important not to reduce the population of its prey too much, and it can do this by consuming parts that will quickly regenerate.

Growth

The growth of a gorgonian is the end result of several physiological processes that can be altered by environmental conditions. Since growth can vary between colonies of the same population under similar environmental conditions (Mistri & Ceccherelli, 1994), statistical analysis and interpretation of results can be difficult. Dodge & Lang (1983) found the growth rate of the scleractinian *Montastrea annularis* to be negatively correlated with sedimentation in the Gulf of Mexico. In Panama, Guzman *et al.* (1994) observed that growth after an oil spill declined significantly for the coral *Siderastrea siderea*, but not for *Porites astreoides*. At our study site, injuries did not seem to affect short-term growth of those *P. clavata* colonies which were not lethally affected by mucilage. Colonies grew during the six months following the disappearance of mucilage, and the observed TBL growth was similar to that of colonies growing under natural conditions (i.e., by considering the growth rate of an unstressed theoretical population).

The *P. clavata* population at «La Montagna» was heavily affected by a mucilage event. This study, which is the first of this kind in the Mediterranean basin, points out that multiple factors were responsible for successful regeneration in injured colonies. Colonies that lost more than 50-60% of their total branch length were not able to withstand competition from overgrowing organisms and died. The location of injuries was important for successful regeneration in colonies affected to a lesser degree. Colonies injured in less than 20% of their TBL in distal branches restore injuries quickly and grow normally.

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