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Effects of a mucilage event on the Mediterranean gorgonian *Paramuricea clavata*. II - Population recovery after two years

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ABSTRACT

A population of the Mediterranean gorgonian *Paramuricea clavata* was heavily damaged by a mucilage coverage of colonies at the end of summer 1993, and suffered a relatively high mortality. Gorgonian population structure before (summer 1992), and two years after (summer 1995) the mucilage event was compared in order to assess the recovery of the population. Despite gorgonian mean density being practically identical on both dates, suggesting that the local population had fully recovered its effectives, the demographic structure of the *P. clavata* population showed changes from one sampling date to the other. The most striking effect of disturbance due to mucilage was the rejuvenation of the population: in 1995, juveniles constituted 26.1% of the population, while in 1992 they were only 4.2%.

KEY WORDS: Cnidaria - *Paramuricea clavata* - Disturbance - Recovery - Population structure - Mediterranean Sea.

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INTRODUCTION

The Mediterranean purple gorgonian Paramuricea clavata (Risso, 1826) is an aposymbiontic, sciaphilic Octocorallia which lives on vertical and overhanging rocky surfaces, roughly from 10 m to over 100 m in depth (Carpine & Grasshof, 1975). It is widely distributed in the western Mediterranean basin and in the Adriatic Sea, but distribution is highly specific, temperature, low irradiance and high water turbulence being among the most important limiting factors to the species (Weinberg, 1978). Dense, patchy populations of P. clavata have been reported in the Banyuls area (Weinberg, 1979), around the Port-Cros marine park (Harmelin & Marinopoulos, 1994), in the Medes Island (Coma et al., 1994), and at the northern entrance to the Strait of Messina (Mistri, 1994), where the population, which thrives on a shoal called «La Montagna», has been under observation by us since 1991.

P. clavata is characterized by a low P/B ratio (Mistri & Ceccherelli, 1994), indicating that the species might be less resilient than others to environmental perturbations (Tumbiolo & Downing, 1994). Occasional mass mortality might have long-lasting effects (i.e., a slow population replenishment) on *P. clavata* populations. The chance to verify that in the field was given by a mucilage phenomenon affecting the benthic community of «La Montagna» at the end of summer 1993.

In recent years (1990, 1991) large scale occurrence of mucilage had been observed in the central and lower Tyrrhenian Sea (Cinelli, 1992; Innamorati, 1992), around Sicily (Giaccone, 1992), and on the Lavezzi Archipelago (Corsica) (M. Mistri & M. Bergamini Mistri, personal observation). Moreover, more or less conspicuous patchy occurrence of mucilage was observed along Sicilian coasts also in 1993 and 1994 (G. Giaccone, personal communication). Off the Calabrian coast of the Strait of Messina, an area which had never been subject previously to mucilage events (P. Barone & F. Turano, personal communication), mucilage appeared and affected benthic communities at the end of summer 1993. Whitish flocs and stringers floating in the water column were first observed by amateur divers and fishermen at the beginning of September 1993; around the end of that month, mucilage sank to the bottom and covered benthic sessile organisms with a whitish cobweb. The stifling coverage of the benthic sessile fauna lasted about two weeks, then, around mid-October, mucilage aggregations broke away, leaving the P. clavata population heavily affected; fluffy stringers entangled in projecting branches caused wide lesions to the colonies. As a consequence of prolonged anoxic conditions, the coenenchymal layers covered by entangled aggregates became necrotic and died, leaving large parts of exposed axial skeleton. Naked skeletal parts of gorgonians are susceptible to fouling by overgrowing organisms: coenenchymal tissues may regenerate or become more or less immediately colonized by invaders; this competiton inhibits regrowth of the coenenchyme over the damaged areas, and may

eventually result in the complete destruction of the colony. Very few colonies of the *P. clavata* population at «La Montagna» were found to be unaffected by tissue necrosis. In November 1993, just after the disappearance of mucilage, a large amount of the sampled population exhibited denuded skeletal parts over 50% of the linear development of the whole colony. Whether or not successful tissue regeneration occurred in *P. clavata* colonies after coenenchyme necrosis, depended on the size of the injured colony, and on the scale and location of the damage (Mistri & Ceccherelli, 1996).

Large-scale catastrophic disturbance events exert profund effects on benthic communities (Woodley et al., 1981; Glynn, 1988; Genin et al., 1995), but smaller-scale disturbance episodes, too, may have important effects on the community structure of benthic populations (Hughes, 1984). Describing such a catastophic event on a population requires collection of samples which span the time course of the event, including a) the prepollution condition, b) the immediate effect of the impact, and c) the recovery phase. Data from the site prior to the event have been reported in Mistri & Ceccherelli (1994), and Mistri (1994, 1995), while data from the immediate effect of the impact have been recently published (Mistri & Ceccherelli, 1996). This paper describes point c) by comparing the population structure of P. clavata before and after the catastrophic event. Opportunities for this kind of work rarely occur in field ecology, but are increasingly important in view of looming environmental problems in polluted coastal waters.

MATERIALS AND METHODS

Field work was conducted at «La Montagna» (38°15'00 N, 15°43'18 E), 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 subjected to strong tidal currents which flow from the Strait of Messina every 6 h; for this reason, underwater work was necessarily carried out only between flood tides. The uppermost ten meters of the shoal are visually dominated by Dictyotales; from 29 downwards, a dense population of the purple gorgonian *P. clavata* thrives.

Paramuricea clavata population density was estimated by direct counting of the number of colonies per 1-m² quadrat along three depth-transects in August 1992. Along each transect, four quadrats, at depths of 30, 34, 36, and 38 m, respectively, were examined; a total of 213 colonies were counted and their total heights measured to the nearest mm. Using height is perhaps not the best method to evaluate colony size in gorgonians: Brazeau & Lasker (1988) and Mitchell et al. (1993) have demonstrated total branch length (TBL) to be a better determinator of colony size. Anyway, in a previous study (Mistri, 1995) TBL and colony height of P. clavata were related, and a fairly good relationship between these two morphometric traits was found. Height can be easily and quickly measured in the field, which is not of secondary importance when operating in the troubled and often dangerous conditions of the Strait of Messina.

Density counts were repeated in July 1995, about two years after the mucilage event which impacted the gorgonian population. Again, along three depth-transects, four quadrats were examined at depths of 30, 33, 37, and 39 m, respectively; a total of 207 colonies was counted and measured for height. The depth of each quadrat was noted with an electronic depth gauge.

At each sampling date, the eventual correlation between mean colony density and depth was investigated by means of regression analysis followed by ANOVA, after arcsin-square root transformation of frequency data. ANOVA was also used to investigate whether a relationship existed between the size of colonies and the vertical distribution of gorgonians on the shoal. In the latter case pertaining, height measurements were log-transformed prior to being submitted to the analysis.

Spacing measurements of colonies of the undisturbed population (i.e., before the mucilage event) were taken in August 1992: these data are reported elsewhere (Mistri, 1994). In July 1995, spacing measurements of colonies were repeated. The 1-m² frame, whose sides were 20-cm graduate, was randomly positioned on the shoal at four different depths (30, 33, 35 and 39 m), and the whole area inside the frame was photographed with a Nikonos V underwater camera equipped with a Nikkor 15 mm lens. This enabled us to get very close to the subject and, thus, to identify the recruits and very small colonies. At the laboratory, slides of frames were viewed with a projector equipped with a built-in monitor, and the position of each colony inside each frame was traced onto drawing paper. The nearest-neighbour distance was then calculated using the method of Clark & Evans (1954) following Krebs (1989).

To investigate whether the population structure of gorgonians had modified after the 1993 disturbance event, the size distribution of the *P. clavata* population at each sampling date (August 1992 and June 1995, i.e., before and after the mucilage) was checked against a series of theoretical distributions (normal, gamma, binomial, geometric and Poisson): the Kolmogorov-Smirnov nonparametric test was then run to evaluate the fit of the observed data to each hypothesized distribution. The Kolmogorov *D-max* statistic is the largest absolute difference between the cumulative observed and expected distribution (Siegel, 1956).

RESULTS

Colony density in August 1992 and in July 1995, determined by quadrat sampling, was 19.36 (±9.20 SD) and 17.25 (\pm 9.42 SD) colonies m⁻², respectively. The *t-test* for unpaired data showed no statistical significance, between mean colony density, on the two dates (t = 2.03; df = 21; NS). In August 1992, the regression between average colony density and depth ($R^2 = 0.72$) was found not to be statistically significant (F = 5.14; df = 1, 3; NS). July 1995 was a different case, a strong significant relationship being found between the two parameters ($R^2 = 0.925$; F = 24.75; df = 1, 3; P < 0.05). The spatial distribution of the gorgonian population on both dates was first tested against the H_o of randomness by means of the goodnessof-fit test for agreement with a Poisson series (Elliott, 1977); as some expected frequencies were less than 1, the values in both tails of the distribution were combined. Since H_o was rejected on both dates at 99.9% probability level (August 1992: $\chi^2 = 39.6$, df = 3; July 1995: $\chi^2 = 20.4$, df = 3), the dispersion of gorgonians was investigated by computing the variance-to-mean ratio (index of dispersion, I) and by testing it with a χ^2 (Elliott, 1977). Values of indexes of dispersion and of χ^2 test at both sampling dates (August 1992: I = 4.37, $\chi^2 =$ 43.7, df = 10; July 1995: I = 5.14, $\chi^2 = 56.6$, df = 11) suggested a contagious distribution of gorgonians on the shoal.

In August 1992, colony height ranged from a minimum of 3.2 cm to a maximum of 71.7 cm. At the considered

depths (30, 34, 36 and 38 m), mean colony size was 33.6 cm (± 11.9 cm SD), 30.8 cm (± 14.7 cm SD), 31.7 cm (± 17.7 cm SD), and 27.9 cm (±14.9 cm SD) respectively. Figure 1 reports the Box-and-Whisker plot of P. clavata size statistics at the sampled depths. Gorgonian size distribution was found to be unaffected by depth (F =0.81; df = 3, 209; NS). In July 1995, colony height ranged from 1.5 to 70.6 cm. At the sampled depths (30, 33, 37 and 39 m), mean colony size was 22.67 cm (±18.7) cm SD), 20.1 cm (±13.5 cm SD), 24.1 cm (±15.7 cm SD), and 22.0 cm (±16.9 cm SD), respectively. In Figure 2, the Box-and-Whisker plot of size statistics is shown. In this case too, the size distribution of P. clavata was not influenced by depth (F = 0.62; df = 3, 203; NS). The average height of the sampled population was 30.3 cm (±15.8 cm SD) in August 1992, and 22.3 cm (±15.9 cm SD) in July 1995. The t-test for unpaired data revealed a statistical significant difference between mean gorgonian height on the two sampling dates (t = 5.17; df = 418; P < 0.001).

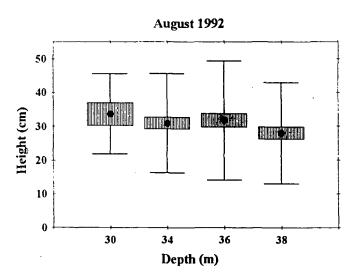


Fig. 1 - August 1992: Box-and-Whisker plot of *Paramuricea clavata* colony size at the sampled depths (means, SD, and SE are reported).

Spacing measurements taken in August 1992 are reported elsewhere (Mistri, 1994): briefly, mean distance between *P. clavata* neighbouring colonies measured at two different depths (30-31.5 and 36-37.5 m) was 18.5 cm (\pm 6.0 cm SD) and 14.4 cm (\pm 5.0 cm SD), respectively. In July 1995, mean distance between neighbouring colonies at the considered depths (30, 34, 36 and 38 m) was 11.3 cm (\pm 6.4 cm SD), 13.7 cm (\pm 4.9 cm SD), 10.5 (\pm 3.3 cm SD) and 9.6 (\pm 3.2 cm SD), respectively. On each date, distances between neighbouring colonies were averaged (August 1992: 16.45 \pm 1.76 cm; July 1995: 11.28 \pm 1.76 cm) and checked for difference: a *t-test* for unpaired data evidenced a statistical significant difference between average distance among colonies (t = 2.84; df = 4; P < 0.05).

Population size structure of P. clavata on both sam-

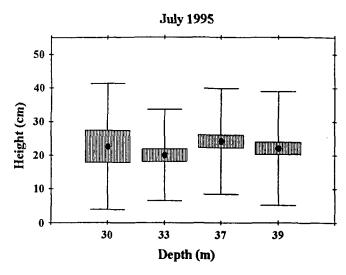


Fig. 2 - July 1995: Box-and-Whisker plot of *Paramuricea clavata* colony size at the sampled depths (means, SD, and SE are reported).

pling dates was obtained by assigning colonies to 5 cmheight classes. These particular categories were chosen to encompass the range of colony height, in centimeters, observed in the population, while maintaining at least a minimum number of colonies in each size class. Figure 3 shows the histogram of the August 1992 height class observed frequencies. The population structure fitted a normal, bell-shaped distribution (Kolmogorov-Smirnov test: D-max = 0.07; NS), even if an area of discrepancy between observed and theoretical distribution was evident at the 15-cm size class; in Figure 3, the theoretical expected frequencies are superimposed onto the plot. The July 1995 P. clavata population size structure was different (Fig. 4): observed data were rightward skewed and fitted a hypothesized gamma distribution best (Kolmogorov-Smirnov test: D-max = 0.05; NS).

In a previous study (Mistri & Ceccherelli, 1994), we calculated *P. clavata* mean annual height growth rate at «La Montagna» shoal, both by field measurements (tagging) and by fitting a Bertalanffy growth equation for

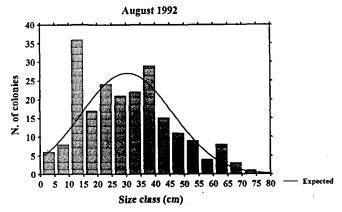


Fig. 3 - August 1992: population size structure of *Paramuricea clavata*. The fitted theoretical distribution (normal-type) is superimposed onto the histogram.

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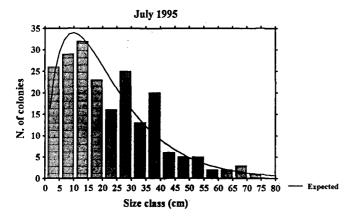


Fig. 4 - July 1995: population size structure of *Paramuricea clavata*. The fitted theoretical distribution (gamma-type) is superimposed onto the histogram.

the species. Considering both the variability of growth speed shown by different colonies of the same age, and that younger colonies on average grow faster than older ones (Mistri & Ceccherelli, 1994), we assumed that any colony of height up to 10 cm had been recruited in the current and in the preceeding year (1991-1992 and 1994-1995), while any larger size was older. Since in many gorgonian species, asexual is as important as sexual recruitment, as was observed in several tropical species, our assumption could be biased by the difficulty of discerning whether small colonies came from asexual or sexual recruitment. On the contrary, Coma et al. (1995b) recently demonstrated that, in contrast to tropical gorgonians, P. clavata bases the maintenance of its populations on sexual reproduction, while asexual reproduction is negligible. For this reason the bias introduced by our assumption should be negligible. So, in August 1992, out of 213 colonies, only 9 (4.2%) were juveniles, while out of 207 colonies measured in July 1995, 54 (26.1%) were new recruits. A t-test for independent samples showed the abundance of juveniles to differ significantly between the two sampling dates (t = 3.37; df = 6; P < 0.05). In July 1995, younger colonies abundance was found to be slightly correlated with depth (R² = 0.83); on that date, relative percentage abundances of new recruits on their total number were: 11.1% at 30 m depth, 24.1% at both 33 m and 37 m depth, and 40.7% at 39 m depth. All colonies <10 cm in height appeared to be original rather than remnants of larger colonies.

DISCUSSION

The settling of flocculent material of pelagic origin on the sea bottom has been shown to act as a stressing agent: mucilage coverage may lead to death of benthic fauna (Stachowitsch *et al.*, 1990), and thus disrupt community or population structure. At the «La Montagna» shoal, on the Calabrian side of the northern entrance to the Strait of Messina, the *P. clavata* population was affected by the

stifling effect of mucilage aggregations at the end of summer 1993. In a previous study (Mistri & Ceccherelli, 1996) we demonstrated the effects of mucus on the vitality of the species by selecting a number of specific colonies and following these over a reasonable period of time.

About two years after the mucilage phenomenon, the gorgonian population at «La Montagna» was found to be quite healthy: visual signs of the previous disturbance event (e.g., colonies heavily overgrown, or bare gorgonian skeletons covered by epizoans) were not evident. Ecological features of the gorgonian population showed some changes from one sampling date to the other. However, mean colony density was similar on both dates, indicating that, notwithstanding the relatively high mortality exhibited by the smallest size class in 1993 (small colonies: 0-100 cm as total branch length; Mistri & Ceccherelli, 1996), the population seemed to have recovered its effectiveness.

Unlike in August 1992, in July 1995 a statistically significant positive correlation was found between colony density and depth: gorgonians were more dense at the deeper levels than at the shallower ones. Fleshy algae are the dominant species in the uppermost 10 m of the shoal, where gorgonians are absent, while P. clavata constitutes the visually dominant macrozoobenthic taxon from 29 m downwards. In the range of depth comprised between 29 and 32 m, the distribution range of brown algae and gorgonians overlaps. The lower gorgonian density at shallower depths could be the result of competition processes for substrate occupation between P. clavata and Dictyotales. At the end of spring, corresponding with the warming of the waters and the development of large fleshy algal facies, P. clavata colonies spawn in the Mediterranean (Coma et al., 1995b): since algae grow faster, the gorgonian recruitment pattern could have been affected by strong competition with brown algae for attachment space in the depth range where the two species coexist. In fact, 88.9% of newly recruited colonies were found in the 33-39 m depth range (i.e., below the brown algae distribution horizon), while only 11.1% were at the 30 m depth level. This hypothesis is, however, purely speculative, and fresh studies are required for testing it. A similar conclusion was drawn by Gotelli (1988) while studying the recruitment pattern of the gorgonian Leptogorgia virgulata in the northern Gulf of Mexico.

On both dates, we found that the pattern of spatial distribution of gorgonians was generally aggregated, but, in July 1995, the average distance between *P. clavata* colonies on the shoal was less than in August 1992. This pattern could have been generated by the mode of juveniles recruitment: it is reported (Coma *et al.*, 1995b) that the short free-living existence and the limited locomotive ability of *P. clavata* larvae enhance the likelihood of their settlement in the close vicinity of the colonies of the parent population. This hypothesis agrees with the distribution pattern of colonies on the shoal,

which proved to be contagious. A similar pattern was found by Lewis (1970, 1974) on Barbados reef crests: three out of four species of corals showed contagious distribution, and, moreover, planulae of *Flavia fragum* and *Agaricia agaricites* were gregarious and tended to settle where conspecific colonies existed.

As a consequence of the mucilage stressing event, the population structure of *P. clavata* changed. The comparison between August 1992 and July 1995 P. clavata population structure was carried out by splitting the population into size classes rather than age classes. It has been demonstrated (Mistri, 1995) that intraspecific variations in gorgonian growth are relatively large: to avoid any possible error introduced in estimating gorgonian age from field morphometric measurements by back-calculation methodology, in the present study height measurements were directly utilized. Population size classes structure on the two sampling dates differed significantly. In August 1992, the P. clavata population was representative of an assemblage of gorgonians in which the majority of colonies were relatively large. Size class distribution followed a normal curve, with central size classes comprised between 25 and 40 cm height; the population showed fairly scarce recruitment and a low number of very large colonies. July 1995 was a different case, when size classes followed a gamma, rightward skewed distribution. In July 1995, the population structure was characterized by a lower number of larger colonies and by a greater amount of small ones. Since smaller colonies should be younger on average than larger colonies, a major consequence of the mucilage disturbing event on the gorgonian population has probably been to allow a conspicuous settlement of new recruits.

Small-sized disturbance events (i.e., predators grazing, smothering of small colonies due to sedimentation, substrate failure, abrasion etc.) occur frequently, and probably constitute the level of stress that naturally affects the gorgonian population. Together with intraspecific and interspecific competition processes, disturbance contributes in shaping demography and dispersion of a population (Connell & Keough, 1985): the population structure observed in 1992 may probably be representative of a gorgonian population shaped in time by a 'normal' disturbance (in the 1980's, no catastrophic event such as the 1993 mucilage coverage was remembered; P. Barone, pers. comm.). In contrast, intense disturbance events, like the 1993 mucilage one, occur less frequently, but may have a larger role in shaping population structure. P. clavata is a clonal organism whose growth pattern tends toward a theoretically high size asymptote (Mistri & Ceccherelli, 1994), and whose natural populations seemingly show absence of senescence (Coma et al., 1995a), although the latter statement probably needs further confirmation; nevertheless, it is generally accepted that the life span of such organisms is ecologically, rather than genetically limited (Sebens, 1987). In the Caribbean Sea and in the Great Barrier Reef, hurricanes are known to be the most important intense disturbance events for shaping coral populations, but in the Mediterranean Sea such catastrophic events are absent. Mucilage has proved to play an important role in shaping *P. clavata* population structure, since, after the disturbance, the population was found rejuvenated.

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