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Population structure and partial mortality of the gorgonian *Paramuricea clavata* (Risso) in the North-Western Mediterranean (France, Port-Cros Island)

Structure de la population et mortalité partielle de la gorgone Paramuricea clavata *(Risso) en Méditerranée nord-occidentale (France, Île de Port-Cros)*

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***Mots clés** : Gorgonacea, coralligène, structure démographique, nécroses, détachement de colonies, protection.*

***Key-words** : Gorgonacea, coralligenous community, demographic structure, injuries, colony toppling, conservation.*

ABSTRACT

Harmelin Jean-Georges, J. Marinopoulos, 1994 - Population structure and partial mortality of the gorgonian Paramuricea clavata *(Risso) in the North-Western Mediterranean (France, Port-Cros Island).* Mar. Life **4** (1) : 5 - 13.

The population size structure of the large gorgonian Paramuricea clavata *and the frequency of two forms of damage, injury and toppling, endured by the colonies were assessed in the national park of Port-Cros (French Mediterranean) within a* 18-44 m *depth range. The mean site density ranged from 12.4 to 13.8 colonies m^{-2} (maximum patch density: 67 col. m^{-2}). The size structure was markedly variable according to local conditions (patch and site scales). The height of the largest colonies clearly increased with depth within the upper half of the* Paramuricea *depth distribution range (10-45 m). Injuries (bare branch segments) affected one third of the sampled colony stock (41% in one site) with various age and size conditions, which suggests repeated limited events. The cause of injuries are clearly multiple. Among the possible agents, natural and man-induced mechanical processes are likely frequent causes of tissue loss, but increased temperature-related vulnerability may also be hypothesized. The phenomenon of colony toppling, commonly observed in the steepest sites, much exposed to surge and overloaded with diving and fishing activities, is facilitated by the nature of the local substrate (micashist); it is ascribed to mechanical actions, generated by hydrodynamic forces, as well as by man (anchors, fishing apparatus, handling by divers).*

RÉSUMÉ

Harmelin Jean-Georges, J. Marinopoulos, 1994 - [Structure de la population et mortalité partielle de la gorgone Paramuricea clavata *(Risso) en Méditerranée nord-occidentale (France, Île de Port-Cros)].* Mar. Life **4** (1) : 5 - 13.

La structure en classes de taille de la population de la grande gorgone Paramuricea clavata *et la fréquence de deux types de dommages, blessures et détachement du substrat, subis par les colonies ont été évaluées dans les eaux du parc national de Port-Cros (Méditerranée, France) entre 18 et 44 m de profondeur. La densité moyenne par site était de 12,4 à 13,8 colonies m^{-2} (densité maximale par tache : 67 col. m^{-2}). La structure en tailles était nettement variable selon les conditions locales (à l'échelle des taches ou des sites). La hauteur des colonies les plus grandes augmente avec la profondeur dans la première moitié du domaine vertical de* Paramuricea *(10-45 m). Des blessures (segments de branches dénudés) affectent un tiers du stock des colonies échantillonnées (41 % dans un site) avec des conditions d'âge et de taille variées qui suggèrent l'intervention répétée d'événements limités. L'origine des blessures est à l'évidence multiple. Parmi les agents possibles, des processus naturels* ou *induits par l'homme sont probablement des sources fréquentes de pertes de tissus ; mais l'hypothèse d'une vulnérabilité accrue en relation avec la température peut être évoquée. Le phénomène de détachement des colonies, communément observé dans le site le plus abrupt, très exposé à la houle et soumis à une pression importante de plongée et de pêche, est facilité par la nature du substrat local (micaschiste)* ; *il est imputé à des actions mécaniques, générées par les forces hydrodynamiques autant que par l'homme (ancres, engins de pêche, manipulations par les plongeurs).*

INTRODUCTION

Paramuricea clavata (Risso, 1826) (Cnidaria; Anthozoa; Gorgononacea) is widely distributed in the western basin of the Mediterranean and the Adriatic but apparently absent from the Eastern Mediterranean (Carpine and Grashoff, 1975). It is considered as a Mediterranean endemic but it can be found in Atlantic areas proximate to Gibraltar Straits (Portugal, Sagres: Weinberg, 1994; Morocco, Asilah: red coral fishermen, pers. com.). It typically lives on shadowed rocky substrates roughly from 10 m to at least 110 m depth (Carpine and Grashoff, 1975; Weinberg, 1991), often in dense aggregations on deep vertical walls. It is the largest of the five sea-fans occurring in the sublittoral zone (with *Eunicella cavolinii, E. singularis, E. verrucosa, Lophogorgia sarmentosa;* Weinberg, 1976). It is a typical member of the coralligenous community in the Western Mediterranean (Pérès and Picard, 1964; Pérès, 1967), dominating all other components by its biomass (True, 1970) and large size (height up to 150 cm, unpublished personal data). Therefore, it has a key role in structuring three-dimensionally the coralligenous community. Its growth rate is relatively low (12.5-60 mm yr^{-1}: Weinberg, 1991; 27-30 mm yr^{-1}: Mistri and Ceccherelli, 1994; 18 mm yr^{-1}: Coma i Bau, 1994). As demonstrated by Coma i Bau (1994) through photographie monitoring of colonies of different ages, growth is discontinuous, with a peak between January and April. Though growth rate shows a high between - and within - colony variability, colony height is considered to be well correlated to age (Coma i Bau, 1994); large colonies (H > 90 cm) are estimated to be at least 50 years old (Weinberg, 1991; Coma i Bau, 1994).

Several cases of mass mortality have been recently reported for *P. clavata* in the North-Western Mediterranean. In France, the deep-water population (> 80 m) off the French Riviera has been reduced early in the eighties, especially on the east side of steep rocky bottoms (Rivoire, 1991; Arnoux *et al.,* 1991). In Italy, populations of *P. clavata* were impacted in shallower localities: in the Ligurian Sea

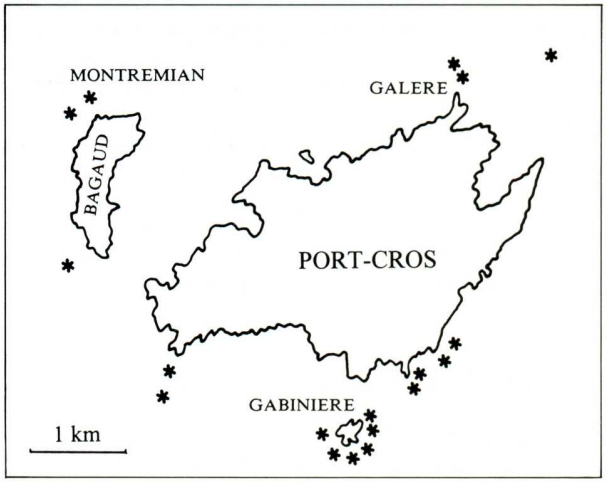

Figure 1 - Geographical distribution of the main habitats of *Paramuricea clavata* around the islands of Port-Cros and Bagaud and location of the three study sites. / *Distribution géographique des principaux habitats de* Paramuricea clavata *autour des îles de Port-Cros et de Bagaud, et localisation des trois sites d'étude.*

(Bavestrello *et al.,* 1994), near Elba Is. (Giglio Is., fall 1990, M. Abbiati, pers. com.), and in the Tyrrhenian Sea (Cinelli, 1992; Rinaldi, 1992; Mistri and Ceccherelli, 1994). In Medes Islands (Catalonian coast, Spain), the *Paramuricea* population of sites overloaded with divers shows an alarming mortality rate (Coma i Bau, 1992; Pola *et al.,* 1994).

As shown by Mistri and Ceccherelli (1994) and Coma i Bau (1994), *P. clavata* is characterized by a low P/B ratio, suggesting a long turnover time and consequently a slow population replenishment after a mortality event.

Thanks to its attractive shape, impressive size and density, this sea-fan contributes greatly to the aesthetic value of the Mediterranean underwater landscapes and therefore to the success of the most famous scuba diving sites. Particular attention should be paid to any additional cause of mortality in local populations of this emblematic species, especially in protected areas. In the national park of Port-Cros, large populations of *P. clavata* occur in several steep rocky sites (Figure 1) heavily frequented by scuba divers, while injuries (coenenchyme

Table I - Number and depth (range and mean) of quadrats (Q) and transects (T) made in the three studied sites, number of *Paramuricea* colonies (N *P.c.)* sampled with each method and density per m^2 of *Paramuricea* colonies (mean and standard deviation SD) present in the quadrats. / *Nombre et profondeur (bornes et moyenne) des quadrats (Q) et transects (T) faits dans les trois sites étudiés, nombre de colonies de* Paramuricea *(N* P.c.) *échantillonnées avec chaque méthode et densité par* m^2 *des colonies de* Paramuricea *(moyenne et écart-type SD) présentes dans les quadrats.*

	N quadrats (Q)	Depth (Q) range, *mean*	N *P.c.* (Q)	*P.c.* density *mean* (SD)	N transects (T)	Depth (T) range, *mean*	N P.c. (T)
Gabinière	19	16-44m *32.8 m*	437	*13.8 (14.5)*	45	16-45 m *34.1 m*	135
Montrémian	7	17-25 m *21.5 m*	183	*13.1* (6.5)			
Galère	18	22-30 m *26.6 m*	444	*12.4* (3.7)			
Total	44	16-44 m *28.5 m*	1064	*13.0 (9.8)*	45		135

partially removed and axis exposed) and individual detachment of colonies are commonly observed.
The aim of this study was to analyse the size structure of the *Paramuricea* local population, to evaluate the proportion of injured colonies, the size, location and age of these injuries and to characterize the colony detachment phenomenon. The potentially active sources of damage to sea-fans, such as predation, hydrodynamics, senescence, anchoring, nets, and violent behaviour by divers, are discussed.

MATERIAL AND METHODS

The national park of Port-Cros was founded in 1963; its marine part (1800 ha) is a semi-protected area: only some activities (e.g., spearfishing, angling from shore, anchoring in some sites, trawling) are forbidden. On the other hand, other forms of professional fishing and diving are authorized, except in a very limited area. Marine leisure activities and more especially scuba diving are on the increase around Port-Cros. Thousands of divers visit the park waters every year (about 16 300 dives made during July and August 1990; Richez, 1992). Most of the diving activity is concentrated in sites where the coralligenous community is well developed, that is in the *Paramuricea* habitats. These sites are also particularly intensively fished.
Sampling was carried out in June and October-November 1992 in three sites (Figure 1, Table I). The Gabinière islet, off the south coast of Port-Cros, shelters the largest population of *P. clavata,* which spreads over a wide depth range (15-80 m) on rocky walls and large boulders (Figure 2). This site is one of the most highly frequented by divers on the whole French Mediterranean coast. The Galère population extends from 22 to 32 m on the eastern, steep side of the immersed part of Galère headland, north coast of Port-Cros. The Montrémian population is relatively small and shallow (18-30 m), limited to the east side of rocks that form the underwater extension of a headland on the west coast of Bagaud Island.
The *Paramuricea* population's density and size structure were sampled by SCUBA diving, mostly within 2 m^2 quadrats. In each quadrat the sea-fans were counted and measured (height); the presence, relative extent (10, 25, 50, 75, 100 %), location (apical, median, basal), and age (recent: without apparent fouling, old: fouled) of injuries were noted. Detached colonies were counted, measured and their condition (proportion of exposed axis and vitality of living tissues) assessed by swimmers moving slowly along 5 m wide transects during 3 min. fractions (area sampled during each 3 min. fraction: 200 m^2). The frequency of toppled colonies was assessed along the east side of Gabinière islet where the *Paramuricea* population spreads over an area large enough for representative sampling. Depth of each quadrat or transect was noted (electronic depth gauge).

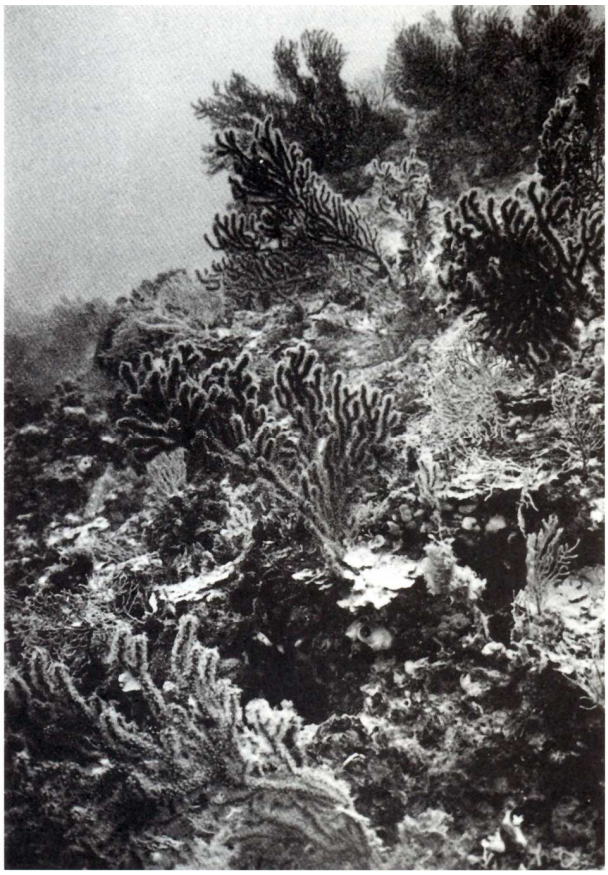

Figure 2 - Coralligenous community with *Paramuricea* on the Gabinière slope (45 m). / *Coralligène avec* Paramuricea *sur la pente de la Gabinière* (45m). *Ph. J.-G. Harmelin.*

RESULTS

1 - **Population density and size structure**

Average values of colony density were similar in the three sites (Table I) but the between-quadrat variability was notably higher in the Gabinière site (coefficient of variation > 100 versus 30 and 50 in Galère and Montrémian). There were clear between-site differences in the size structure of the local populations of *P. clavata* (Figure 3). The Montrémian site was characterized by a greater proportion of small colonies: 74.3 % of them were smaller than 36 cm (Gabinière: 57.0 %, Galère: 51.1 %). Conversely, the Galère site presented a higher proportion of old colonies (> 75 cm: 9.0 % *versus* Gabinière: 3.7 %, Montrémian : 0 %) and smaller proportion of young colonies (< 15 cm: 15.5 % *versus* Gabinière: 20.4 %, Montrémian: 21.9 %). The within-site (between-quadrat) variability in size structure was particularly marked in Gabinière site where the *Paramuricea* population was exposed to a wide range of environmental conditions: quadrats without young colonies contrast with nearby quadrats with numerous colonies < 15 cm located at the same depth. There was a significant positive relation between the proportion (%) of young colonies (H < 15 cm)

and the overall density in *Paramuricea* colonies ($r = 0.628$, d.f.: 42, $p < 0.001$). Thus the highest proportion of young colonies (H < 15 cm: 30 %; H < 20 c: 51 %) was observed in the sub-population with the highest density (67 col. m^{-2}); this situation corresponded to a shallow site (Gabinière NE corner, 21-24 m) also characterized by a lack of large colonies and affected by strong currents. No significant relation was evidenced between the proportion of young colonies and habitat depth. In the sampled part of the Gabinière population (18-44 m), the height of the largest colonies occurring within each quadrat was positively related to depth (Figure 4).

2 - Patterns of injuries

One third of the *Paramuricea* population off Port-Cros was affected by injuries (Table II). The highest proportion was observed at Galère site (41 %). These injuries consisted in loss of coenenchym around branch portions, the exposed axis being susceptible to fouling by sessile organisms (Figure 5). New injuries (exposed axis without macroscopic fouling) were frequently located at the branch tips (Figure 6), 62 % of them occurring on colonies already bearing old injuries (axis encrusted with *Parerythropodium*, serpulid polychaetes, bryozoans, etc). The average size of colonies bearing both old and young injuries (H = 54.1 cm ± 21.1) was larger than the whole injured stock (H = 44.6 cm ± 13.5) and even the intact stock (34.2 cm ± 12.5). The proportion of injured *P. clavata* increased with the colony size (8 size classes), i.e. with age ($r = 0.922$, d.f.: 6, $p < 0.01$; Table II). Recent injuries occupied

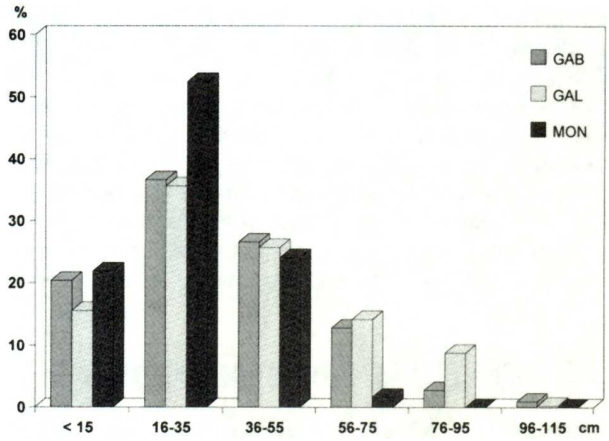

Figure 3 - Size structure of the *Paramuricea* population in the three sampled sites. GAB : Gabinière, GAL : Galère, MON : Montrémian. / *Structure en tailles de la population de* Paramuricea *dans les trois sites échantillonnés. GAB: Gabinière, GAL : Galère, MON : Montrémian.*

notably smaller colony portions than older ones: most of them (85 %) occupied 10 % or less of the colony area while 49 % of the old injuries covered at least 50 % of the colony area (Figure 7). Both parameters of injury rate (proportion of injured colonies and injury relative size) were not significantly related to habitat depth.

3 - Patterns of colony detachment

The frequency distribution of the 135 detached colonies recorded over 9000 m^2 of rocky bottom off the Gabinière site was typically contagious as shown by a variance to mean density ratio clearly

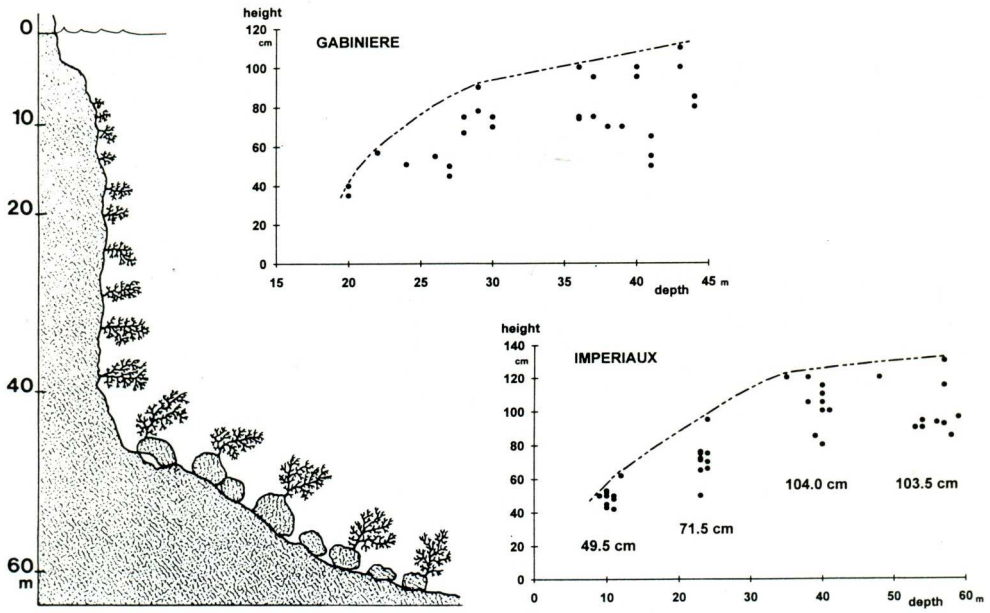

Figure 4 - Relationship between depth and within-patch maximum height of *Paramuricea* colonies in two steep rocky sites: Gabinière (Port-Cros) and Impériaux (Marseille, Riou island: illustrated bottom profile) with mean maximum height values at four depth levels (Impériaux). / *Relation entre la profondeur et la taille maximale de* Paramuricea *dans les taches de peuplement de deux sites rocheux abrupts : Cabinière (Port-Cros) et Impériaux (Marseille, Riou : profil de fond illustré), avec la taille maximale moyenne à quatre niveaux de profondeur (Impériaux).*

Figure 5 - Large *Paramuricea* colony with an extended old injury: axis colonized by serpulid polychaetes, hydroids and bryozoans. / *Grande colonie de* Paramuricea *avec une blessure ancienne : axe largement dénudé et colonisé par des polychètes serpulides, des hydraires et des bryozoaires.*

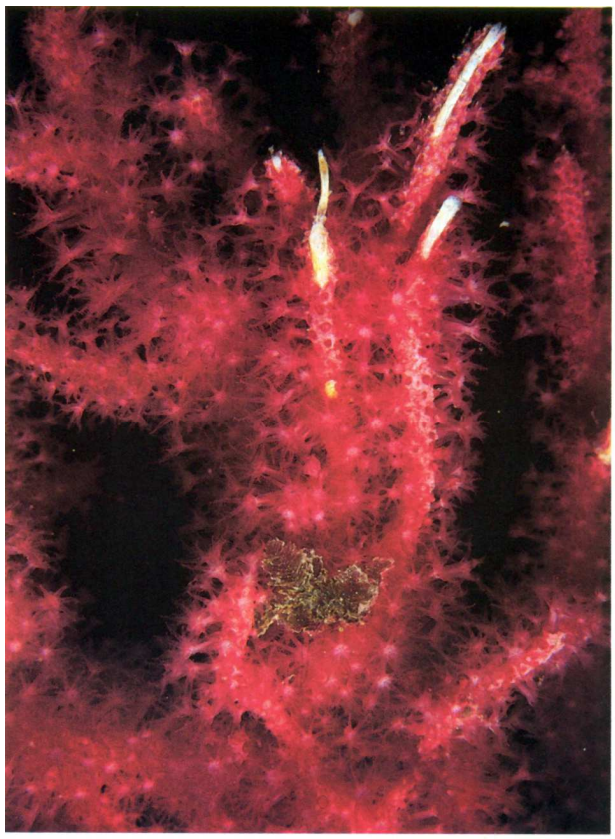

Figure 6 - Apical injuries on a colony from a shallow-water high-energy station (Gabinière, 20 m). / *Blessures apicales sur une colonie d'une station peu profonde en mode agité.*

Table II - Number of intact colonies and number and proportion (%) of injured colonies in the overall *Paramuricea clavata* population of Port-Cros Island. / *Nombre de colonies intactes en nombre et proportion (%) de colonies blessées dans l'ensemble de la population de* Paramuricea clavata *de l'Île de Port-Cros.*

	< 15 cm	16-35 cm	36-55 cm	56-75 cm	76-95 cm	96-115 cm	Total
Intact *P.c.*	188	277	172	54	19	3	713
Injured *P.c.*	10	137	102	68	32	2	351
% injured	5.05	33.09	37.23	55.74	62.75	-	32.99

higher than 1 (Elliott, 1971; average number of detached colonies per 200 m^2 = 3,0 ± 2,8 SD). However, within the sampled vertical range (16-45 m), the density of detached colonies showed no significant relation with depth ($p > 0.05$). Most detached colonies drifted in nooks down walls and at the bottom of large boulders though some isolated ones were also found on flat rocks. As indicated by their diverse condition, the sampled detached colonies had obviously issued from multiple toppling events spread over a long period of time. A notable proportion of detached colonies (28.1 %) presented no or little loss of living tissues (Table III). Old secondary colonization stages were generally observed on toppled sea-fans with totally bare axes or very little remaining living cortex. There was no significant difference in mean colony size between the four categories of detached colonies with different stages of injury (Table III). Several colonies toppled on the rocky slope survived without any injury during several weeks as indicated by the occurrence

Table III - Detached *Paramuricea clavata* colonies (N = 135) sampled at Gabinière Is. (16-45 m): classification according 4 vitality levels (% of colony area occupied by denuded axis). Number and percentage of sampled colonies in each category and corresponding mean height (H ± standard deviation). / *Colonies détachées de* Paramuricea clavata *(N = 735) échantillonnées à la Gabinière (16-45 m) : classification selon quatre niveaux de vitalité (% de la surface de la colonie avec un axe dénudé). Nombre et proportion des colonies dans chaque catégorie et hauteur moyenne correspondante (H ± écart -type).*

	N (%)	H ± SD (cm)
No denuded axis	18 (13.3)	53.8 ± 21.4
Denuded axis : 10-30%	20 (14.8)	46.8 ± 21.0
Denuded axis : 50-90%	44 (32.6)	54.2 ± 18.1
Denuded axis : 100 %	53 (39.3)	49.3 ± 18.9

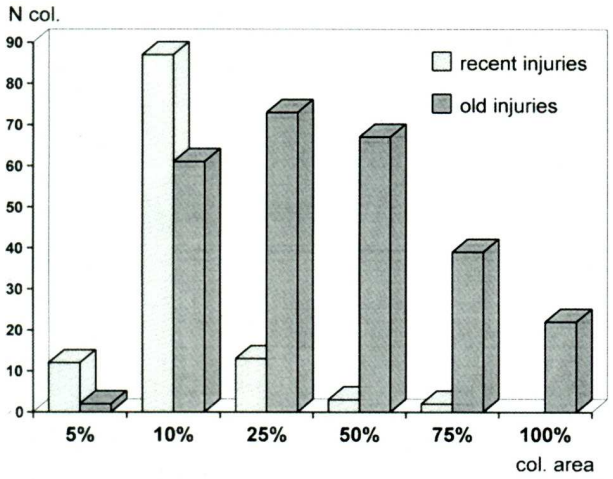

Figure 7 - Distribution of the sampled *Paramuricea* colonies with recent or old injuries according to 6 classes of injury extension (percent coverage of the colony area). / *Distribution des colonies échantillonnées de* Paramuricea *avec des blessures anciennes et récentes selon six classes d'extension des blessures* (*% de couverture de la surface des colonies).*

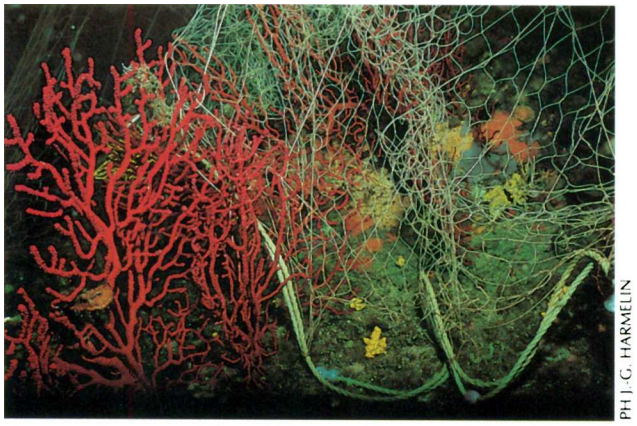

Figure 8 - *Paramuricea* colonies entangled in a fishing net. Gabinière, 35 m. / *Colonies de* Paramuricea *emmêlées dans un filet de pêche. Gabinière,* 35 m.

of spirorbid polychaetes fouling the reverse side of their holdfast basal disk. Partial detachment of colonies from the rocky wall has been observed on several occasions, mostly in a high energy station (19-32 m, NE corner of Gabinière); most of these colonies were not injured.

DISCUSSION

Quadrat sampling of *P. clavata* population density revealed a wide but not surprizing range of variation at Port-Cros (2.5-67 colonies m^{-2}): gorgonians have a clearly patchy distribution (Weinberg, 1978) like most sessile invertebrates. Average density was calculated within patches and not for the whole site area. This implies that some low density values may have no real signification as the patch limits become severely blurred when density decreases below certain limits. This distribution pattern argues for precisely delimited permanent census spots or transects instead of random sampling when population monitoring is required. Local populations characterrized by a combination of markedly high density and strong predominance of small colonies, observed here at shallow depth in a typically high energy station (E Gabinière), were reported for similar conditions by Weinberg (1978) in Banyuls-sur-Mer (Rédéris) and by Coma i Bau (1992) in Medes Islands. On the other hand, the largest colonies, exceeding 1 m in height, are found in deeper, quieter stations. The tight relation between maximum colony size and depth observed across the subvertical walls of Gabinière has been verified in the steepest site of the Marseilles' area (Impériaux): the height of the largest colonies (H-max) distributed on a vertical wall from 9 to 45 m depth clearly increases with depth, as shown by the mean H-max values and by the correlation coefficient (r = 0.900, n = 30; Figure 4). The same pattern was noticed for *Eunicella singularis* in Banyuls-sur-Mer by Weinberg and Weinberg (1979). This size-depth relationship is particularly pronounced in the upper part of the *Paramuricea* depth range, especially when the environmental gradient is simple (vertical flat wall). However, below a particular depth level, the maximum colony size seems to reach a local limit. In the deep-water Impériaux population (48-60 m) established on large blocks on a slope down to the wall, the size of the largest *Paramuricea* colonies displayed no depth-related gradient (Figure 4) and the mean H-max was similar to that observed in the 35-45 m zone (103.5 cm ± 14.9 SD *versus* 104.0 cm ± 13.5 SD). The tallest *Paramuricea* colony (130 cm) was observed there at 57 m.

Injury is a common phenomenon among gorgonians, occurring routinely at moderate levels or in relation with catastrophic events and partly balanced by regeneration processes (Bavestrello and Boero, 1986; Wahle, 1983, 1985). The exposed axis portions are typically colonized by sessile species with three-dimensional arborescent growth (bryozoans *Turbicellepora avicularis, Pentapora fascialis,* etc.) or developing sheaths (alcyonarian *Parerythropodium coralloides).* Natural causes of axis denudation, such as mechanical effects of strong water movements and storm events (Woodley *et al.,* 1981, Yoshioka and Yoshioka, 1987) and predation are frequently evoked, but direct or indirect consequences of human activities have also to be considered. Causes of gorgonian mass mortality recorded in the Caribbean region (Garzón-Ferreira and Zea, 1992; Guzman and Cortés, 1984; Peters, 1993) and in the Mediterranean (Rivoire 1991; Arnoux *et al.,* 1992; Bavestrello *et al.,* 1994) were not explicitly identified but lethal action was probably limited in time. The mortality events observed in Tyrrhenian Sea were attributed to massive deposits of mucillaginous aggregates produced by filamentous algae, mainly *Tribonema marinum* (Tribonemales, Chrysophyta) and *Acinetospora crinita* (Ectocarpales, Phaeophyta) (Sartoni and Sonni, 1992); the same phenomenon was reported from

southern Corsica in 1992 by sport divers. The unidentified lethal agent responsible for the mass mortality of the deep population of *Paramuricea* (80-100 m) on the east side of St Julien shoal, off St Tropez, only 23 nautical miles from Port-Cros Island, was assumed to have been brought west with particulate matter by the Ligurian current (Arnoux *et al.,* 1992).
In the Port-Cros population, the injury phenomenon is obviously not related to a major catastrophic event but rather to diffuse or repeated, and probably mutiple causes: variously aged injuries frequently co-occur in the same colony. The increase of injury rate with colony size (i.e. with age = time of exposure to injury agents) also argues for repeated limited attacks. However, the injury frequency (33 % of injured colonies in the whole sampled stock, 41 % in the Galère stock) reveals an alarming tendency among the Port-Cros *Paramuricea* population.

According to Wahle (1985), the main cause of injury in Caribbean gorgonian populations is abrasion. In Port-Cros, some cases of injury apparently result from natural mechanical processes. For instance, mutual abrasion of terminal branchlets shaken about by strong water turbulence may generate the apical tissue losses observed on colonies from particularly high energy spots (Figure 6). As the primary segments contribute 50 % towards gross colony growth (Coma i Bau, 1994), breakage of these denuded apical portions before regeneration of the tissues may lead to reduced or even negative colony growth. Man-induced mechanical causes of cortex injuries are suspected to be relatively frequent in Port-Cros. Fishing nets and lines entangled in large *Paramuricea* colonies were repeatedly observed on the Gabinière walls (Figure 8). Repeated impacts of divers' fins with rigid plastic blades on the *Paramuricea* branches could perhaps be serious source of wounds in much frequented sites, such as Gabinière. The role of predation in partial mortality of gorgonians seems to be less acute in the Mediterranean than in the Caribbean (Wahle, 1985). We found no evidence that predation was a regular source of cortex loss in the Port-Cros population. In his study of *Paramuricea* growth in Medes Islands, Coma i Bau (1994) hypothesized that disappearance of terminal segments from photographically monitored colonies was due to predation, but the predator was not identified. The carnivorous polychaete *Hermodice carunculata* which feeds on gorgonians in the Caribbean (Wahle, 1985; Vreeland and Lasker, 1989) and has been observed on *Paramuricea* in the Strait of Messina, southern Italy (Mistri *et al.,* 1994) has never been recorded in the Northern Mediterranean. Predation by Ovulidae gasteropods was reported to be a notable source of injury for *Eunicella singularis* in Banyuls-sur-Mer (Theodor, 1967; Weinberg, 1978) but seems to be absent or exceptional on *Paramuricea.* There are no asserted records of gorgonian predation by fish in the Mediterranean (Weinberg and Weinberg, 1979; personal observations).

Slight temperature rise and unusual freshwater discharge may have been responsible of a bleaching event which affected Caribbean reef organisms and particularly gorgonians (Zea and Duque, 1989). Similarly, in Banyuls-sur-Mer, Weinberg (1975) related mortality of shallow-water *Eunicella stricta* (= *singularis)* to exceptionally warm temperature (> 24° C) above the thermocline during summer 1973. *Paramuricea* was noticed to be not sensitive to warm temperature (Weinberg, 1975, 1991) but temperature sensitivity may likely vary between local populations. The quasi-total exclusion of gorgonians from the Eastern Mediterranean (Carpine and Grasshoff, 1975) is most probably related to the thermic regime of this basin. There is some evidence from several biological indicators that thermophilic southern species are increasingly successful in the northern part of the Western Mediterranean, probably in relation with a temperature rise of the sea water (Francour *et al.,* 1994). Temperature stress is hypothesized to be an important factor of development of diseases in various groups of invertebrates (Peters, 1993). The geographic distribution and depth limit of the disease which affected the horny sponges in the Mediterranean during 1986-1990 suggest that the virulence of the bacterial attack may have been related to a temperature rise (Vacelet *et al.,* 1994). Abnormal temperature rise or other environmental stresses might also have an indirect deleterious effect on Mediterranean gorgonians by diminishing their resistance to other factors, such as pollutants and pathogens and/or by generating proliferation of these pathogens (e. g., bloom of filamentous algae). The apparently lower proportion of injured colonies in the *Paramuricea* population from Marseilles' area, obviously more polluted than Port-Cros but slightly colder, may have some temperature-related significance. It may be predicted that a general water temperature rise (global change) in the Western Mediterranean will have a prolonged impact on the whole gorgonian populations.

Colony toppling appears to be a common phenolmenon, at least in Gabinière site. Three general features are evidenced by this study: (1) colony detachment and injury outcome are independant phenolmena; (2) toppling does not result from breakage of the colony axis but involves the holdfast detachment from the substrate; (3) detached colonies are able to survive for a long time if not burried or eroded. Thus, the down-to-slope dispersal of detached fertile colonies by currents and gravity may contribute to the spatial expansion of the population. However, this propagation mode, common among clonal organisms (Jackson, 1986), is probably less efficient than for biotas with ramified calcified colonies such as erect bryozoans, which can produce a large amount of fragments with high regeneration potential. Colony detachment involves relatively large individuals (Table III) though small colonies (20-35 cm) are also concerned. The resistance thre-

shold of the gorgonian holdfasts to drag generated by currents and swell depends on colony shape and area (Birkeland, 1974; Kinzie, 1974) and determines the decrease of colony height as depth dimishes (Weinberg and Weinberg, 1979). This trend is obviously accentuated by the geological nature of the substrate in Port-Cros: the Gabinière walls are made of micashists (Bronner, 1986) offering flat surfaces from which gorgonian holdfasts are easily torn off. The impact of the hydrodynamic forces is thus severely exaggerated by the character of this substrate, particularly in shallow high energy stations where biogenic calcareous concretions are poorly developed on the rocky substrate. On the other hand, the accretion of a biogenic calcareous substrate that occurs in deeper water implies a higher frequency of borers *(Cliona* sponges, sipunculids, etc.), whose long-term action can induce fragmentation of the substrate and detachment of the sessile organisms. Man-induced sources of sea-fan detachment comprise mainly anchors, fishing apparatus (Figure 8), predation and unvoluntary handling by divers. Though this kind of damage is not easily testable, field observations suggest that its frequency is increasing strongly along the tourism impacted coasts of the Mediterranean. Limitation of the deleterious impact through prohibition of anchoring and education of divers is recommanded, specially in marine reserves open to visitors whose popular success results in overloading their most representative sites.

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