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Ecological observations on a population of the Mediterranean gorgonian *Paramuricea clavata* (Risso, 1826)

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ABSTRACT

The gorgonian *Paramuricea clavata* grows below 29 m water depth in a station located at the northern entrance of the Strait of Messina. Colonies are randomly spaced, and show an abrupt change in orientation below 36 m depth. A turbulence zone caused by the current flowing downslope along the bottom is likely to be the main factor responsible for the 90° change in orientation. The relationship between growth and development of a fan was investigated in terms of change of fractal dimension. The latter gradually evolves in complexity with age, suggesting that a high fractality could set a limit to the life span of the species.

KEY WORDS: *Paramuricea clavata* - Growth pattern - Fractals - Coelenterata.

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INTRODUCTION

Colonial shallow-water gorgonians are a common component of rocky benthic communities of the western Mediterranean (Weinberg, 1979, 1980; Gili *et al.*, 1989). *Paramuricea clavata* (Octocorallia, Gorgonacea) is a sciaphilic gorgonian which thrives on vertical and overhanging surfaces forming large colonies with thick irregularly ramifying branches.

Although *Paramuricea clavata* is one of the most common gorgonian species in infra-circumlittoral rocky bottom communities of the Mediterranean, little is known of its life history, pattern of growth and energetic contribution to the benthic community. Mistri & Ceccherelli (1994) investigated growth and secondary production of the species. Mean annual linear growth rates were calculated both by field measurements (tagging) and by fitting a Bertalanffy growth equation for the species. Growth rates were 2.7 and 3.0 cm yr^{-1} respectively. Secondary production was estimated in 3.0 g AFDW m^{-2} yr^{-1}.

Some gorgonian species exhibit growth patterns revealing fractal properties (Burlando *et al.*, 1991; Mistri & Ceccherelli, 1992). Fractal objects are conceptual or concrete objects that achieve a certain degree of occupation of a euclidean space, and the fractal dimension (D) is considered the measure of that degree of occupation (Mandelbrot, 1982).

In this study, observations were made on spatial distribution, orientation and geometry of *Paramuricea clavata*. In addition, the relationship between age and development of a fan was investigated.

MATERIALS AND METHODS

Paramuricea clavata colonies were collected 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-deep top to a depth of 39 m, a few hundred meters off the Rock of Scilla (Reggio Calabria). The uppermost ten meters of the shoal are visually dominated by Dictyotales; from 29 m downwards a dense population of *P. clavata* thrives (Mistri & Ceccherelli, 1994).

A stratified sample collection was carried out in August 1992 and in November 1993: at two different depths (30 and 36 m), a minimum number of colonies (34), compatible with statistical reliability, were collected by hand by SCUBA diving. Orientation of *Paramuricea clavata* was recorded while diving: an orientation parallel to the sea surface was used as 0°. Depths were determined using a digital depth gauge. Spacing measurements were made within a 2.5 m × 1.5 m strip between 30 and 31.5 m (Area 1) and 36 and 37.5 m (Area 2). The nearest-neighbour distance was calculated using the method of Clark & Evans (1954) following Krebs (1989).

In the laboratory, the 34 collected colonies were photocopied and measured to the nearest millimeter for height (i.e., the distance between the base and the furthest point of the endbranches of the colony), and width (the largest dimension orthogonal to height). Gorgonians' rectangular area (i.e., the product of colony height by width) was then calculated. Colonies were then mounted on graph paper and their outlines were traced onto the paper. The effective gorgonian area was determined by counting squares occupied by the trace.

Colonies of *Paramuricea clavata* were age-dated by counting an-

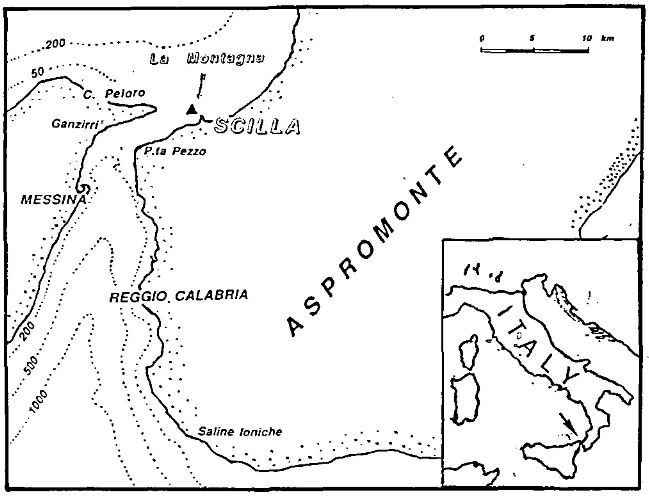

Fig. 1 - Study site location of *Paramuricea clavata* population.

nual growth rings from thin sections taken from the first centimeter of the skeleton at the base of each colony.

Fractal dimension of colonies was measured using the counting box method: scaled photographs (in order to make the size of each colony suitable for grid size) of *Paramuricea clavata* were randomly placed under six 256 mm side grids respectively, partitioned into 2^n squares along each edge, with n varying from 2 to 7. For each colony, the fractal dimension «D» is given by the slope of the regression line obtained by plotting the log of the number of squares entered by the outline of the colony against the log of the number of squares along one side of the grid (Morse *et al.*, 1985).

The relationship between D values and colony age was investigated by fitting several regression models (i.e., linear, multiplicative, and exponential); statistical significance was tested by means of ANOVA.

RESULTS

The gorgonian *Paramuricea clavata* was not observed at depths of less than 29 m. Sea fans were present at depths from 29 m to the bottom of the shoal at 39 m. Spacing measurements (Table I) showed that *P. clavata* colonies were randomly spaced at both depths. Mean distance between neighbouring colonies was 18.5 cm (± 6.0 cm SD) at Area 1, and 14.4 cm (± 5.0 cm SD) at Area 2.

TABLE I - Paramuricea clavata: *spacing data.*

Depth (m)	*n*	r_a (cm)	r_e (cm)	R	Spacing
30-31.5	38	18.5	11.4	1.62	random
36-37.5	41	14.4	11.4	1.26	random

n, sample size; r_a, mean observed distance to nearest neighbour; r_e, mean expected distance to nearest neighbour; R, index of aggregation.

All colonies growing between 29 and 36 m were oriented perpendicular to the sea surface; below 36 m their orientation changed abruptly by 90°, and colonies were, without exception, parallel to the sea surface.

The age of *Paramuricea clavata* colonies, calculated by counting annual growth rings, ranged from 0-1 yr to 21-22 yr. Each annual ring is made up by two alternating growth bands: light bands correspond to the faster period of growth, whereas dark bands are indicative of slower growth, as commonly observed in other gorgonian species (Grigg, 1974; Mistri & Ceccherelli, 1993).

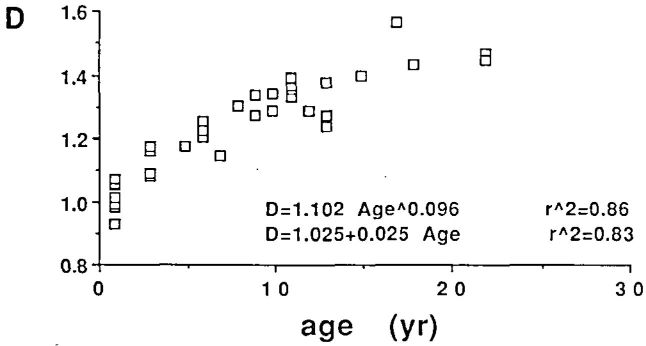

Fig. 2 - Plot of measured D values versus colony age. Parameters of regression models are also given.

The rectangular area of a fan is a measure of its obstruction to water flow. The effective area is the hydrodynamically effective surface of the fan. In this study, the ratio between rectangular and effective area varied between 10.2 and 22.7%, with a mean of 16.5% (± 3.9 SD). Four of the youngest, unbranched colonies, were not included in the calculations. The rectangular area ranged from 0.18 cm^2 (age class 0-1 yr) to 2984 cm^2 (age class 21-22 yr). No significant correlation between rectangular area and height/width ratio was found (r^2 = 0.02; NS). The effective area ranged from 0.15 cm^2 (0-1 yr) to 490 cm^2 (21-22 yr). The effective area of colonies collected at both sites was compared by means of t-tests: no statistical difference was found (t = 1.15; d.f. = 32).

Figure 2 plots the estimated fractal dimension (D) and age of each collected colony. D values of a few of the youngest, unbranched colonies, although scaled, are likely to have been underestimated (D < 1). D exhibited a general tendency to gradually increase with growth. Among regression models tested to investigate the relationship between colony age and increasing D values, both multiplicative and linear regression proved to be highly significant (r^2 = 0.86, $P < 0.01$; r^2 = 0.83, $P < 0.01$, respectively).

DISCUSSION

At «La Montagna» shoal, Scilla, at the northern entrance to the Strait of Messina, *Paramuricea clavata* was not observed at depths less than 29 m. It is reported (Weinberg, 1978) that low irradiance and high water turbulence are the most important limiting factors to the species distribution. *P. clavata* was randomly spaced throughout all depths: the average distance between neighbouring colonies at 30 to 31.5 m was similar to that at the 36 to 37.5 m depth range.

Colonies growing on the walls of the shoal between 29 and 36 m were oriented perpendicular to the sea surface; at the foot, gorgonians were oriented parallel to the sea surface. Grigg (1972) showed that gorgonian orientation is affected by different components of water motion at different depths. Moreover, gorgonian orientation has been used as an indicator of tidal current patterns (Riedl, 1972). Because of depth, the growth of *Paramuricea clavata* at «La Montagna» is not influenced by vertical water motion due to wave action. Gorgonians grow in a horizontal unidimensional flowing zone and orient themselves normally to the prevailing tidal current, unlike what occurs at the foot of the shoal, where the current flowing downslope along the bottom encounters the shoal and causes a turbulence zone of a few meters (Magazzù, pers. comm.). The result is that between 36 and 39 m depth gorgonians are oriented without exception parallel to the sea surface.

One of the fundamental components of the interaction between an organism and its environment is the organism's morphology. In gorgonians, colony morphology affects resistance to wave and current action (Wainwright & Dillon, 1969; Velimirov, 1976), feeding (Leversee, 1976), and even reproduction (Brazeau & Lasker, 1992). Except for the younger, unbranched colonies, the ratio between effective area and rectangular area of *Paramuricea clavata* was quite constant. No significant correlation was found between rectangular area of colonies and height/width ratio. This is in contrast with Russo (1985), who found that in the plexaurid *Eunicella cavolinii*, colony width increased as the rectangular area of the gorgonian increased. The author explained the negative correlation between rectangular area and height/width ratio suggesting that a faster growth in length would be disadvantageous for the colony, because of the increased bending moment.

Flexibility in gorgonians is a topic of much interest. Shallow-water gorgonians on coral reefs, such as *Gorgonia* sp., appear to be very flexible. The skeleton of *G. ventalina* branches is elliptical in cross section with the long axis parallel to the plane of the fan, facilitating bending with the waves (Wainwright & Dillon, 1969). In contrast, deeper-water, fan-shaped antipatharians living in moderate and uniform flow regimes have the long axis of the skeleton at right angles to the plane of the fan, in order to increase resistance to bending (Warner, 1981). *Paramuricea clavata* growing in the Strait of Messina, where tidal currents are of exceptional force, shows a slightly elliptical skeleton when viewed in cross section, with the long axis parallel to the plane of the fan. Unfortunately, there is no data in the literature about the shape of cross sections of the skeleton of *E. cavolinii*. I collected a few colonies of this species ($n = 5$) at Tavolara Isle, northeastern Sardinia, at a depth of 15 m, and observed thin cross sections of the skeleton taken from the base of each colony. *E. cavolinii* showed a slightly elliptical skeleton with the long axis parallel to the plane of the fan. The number of sections observed is clearly too small to allow any final conclusion to be drawn, yet it would seem that *P. clavata* and *E. cavolinii* adopt the same strategy (a fairly elliptical skeleton with the long axis parallel to the plane of the fan) to support the stress of bending due to strong tidal current or wave action.

The relationship between colony growth and development of the fan (which is, in turn, related to environmental forcing factors) was investigated through simple elements of fractal geometry. *Paramuricea clavata* growth mechanism retains a self similar design: axes are orthotropic and ramification is lateral and diffuse; additional structures reiterate the basic architectural model. Starting from a simpler branching pattern ($D \approx 1$, age class 0-1), colonies seem to increase their ramification complexity with age (D tending to 1.45 in the oldest one, Fig. 2). Regression analysis showed a positive correlation between D values and colony age.

In the considered age interval, the branching pattern of the gorgonian constantly increases with aging. The consequence of a constantly increasing D is an ever higher degree of occupancy of the colony plane (*Paramuricea clavata* strictly grows in two dimensions, and never gives rise to bushy colonies). At a certain age, D will approximate 2.0, which is the value of a surface. Such a complex branching pattern would result in a too densely filled canopy that could hinder water circulation (and thus oxygen diffusion, food supply, metabolic exchanges etc.) among polyps, and might lead to the death of the colony. Moreover, it enhances the probability of branch fracture during periods of extremely strong current: Yoshioka & Yoshioka (1991) reported breakage of the axial skeleton as one of the main causes of mortality among Caribbean shallow-water gorgonians in physically highly disturbed habitats. In the study area, but also in other Mediterranean sites (Ligurian Sea, Lavezzi Archipelago, Sardinia, Giannutri Isle, southern Calabrian coast), down to 70 m of depth, I have never observed *P. clavata* colonies bigger than 50-60 cm (approximately 20-25 yr; Mistri & Ceccherelli, 1994).

The overall structure of a branching gorgonian represents the trade-off between maximizing surface area for metabolic exchanges and minimizing hydrodynamic forces on the colony (Koehl, 1984). A lower ramification complexity (and thus a low fractal value) probably allows the most suitable interaction between *Paramuricea clavata* and its environment. With growth, D would increase to higher values: such a high fractality could set a limit to the life span of the species.

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