

Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*

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ABSTRACT: Growth and secondary production of the shallow-water gorgonian *Paramuricea clavata* (Risso, 1826) were investigated at an infralittoral rocky station located at the northern entrance of the Strait of Messina (Tyrrhenian Sea, southern Italy). Colonies were aged by counting the number of annual growth rings at the base of the skeleton. 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 by means of an increment-summation method. The estimate was quite conservative, because it did not take into account production lost by nonlethal predation, and yielded 3.0 g ash-free dry weight (AFDW) m⁻² yr⁻¹. Standing stock biomass was 22.5 g AFDW m⁻². Annual *P/B* ratio was 0.13, and turnover time 7.5 yr.

KEY WORDS: *Paramuricea clavata* · Cnidaria · Growth · Secondary production · Mediterranean Sea

INTRODUCTION

Colonial shallow-water gorgonians are common in rocky benthic communities of the western Mediterranean (Weinberg 1979, 1980, Gili et al. 1989). They are suspension feeders, as defined by Jørgesen (1966), and may play a significant role in the energy transfer processes between planktonic and benthic communities. Only a few reports deal with the age and growth of these organisms (Velimirov 1975, Weinberg & Weinberg 1979, Mistri & Ceccherelli in press) and, to date, no study has addressed their role in production in the Mediterranean basin.

Paramuricea clavata (Risso, 1826) (Octocorallia, Gorgonacea) is a sciaphilic gorgonian which lives on vertical and overhanging surfaces and forms large colonies with thick, irregularly ramified branches. Dense populations of this species have been reported in the Banyuls area (up to 55 colonies m⁻²; Weinberg 1979), and the gorgonian is common all along northwestern Mediterranean rocky bottoms (True 1970, Weinberg 1980, Gili et al. 1989). Low irradiance and high water turbulence are probably the most important factors limiting distribution (Weinberg 1978).

In the present paper we investigate growth and secondary production of a population of *Paramuricea clavata* at a rocky, infralittoral station located at the northern entrance of the Strait of Messina, Tyrrhenian Sea.

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 some hundreds of meters off the Rock of Scilla (Reggio Calabria, southern Italy). The walls of the shoal descend steeply downwards from the 18 m deep top to a depth of 39 m. The shoal is subjected to strong tidal currents (>4 knots) which flow from the Strait of Messina every 6 h (Magazzù 1989); for this reason, underwater work was necessarily carried out only between flood tides. The top of the shoal appears dominated by Dictyotales and, from 29 m downwards, a dense population of *Paramuricea clavata* thrives on the shoal walls (Mistri et al. 1993).

Growth. Linear growth was measured from colony height increments over a 1 yr period. Thirty colonies of

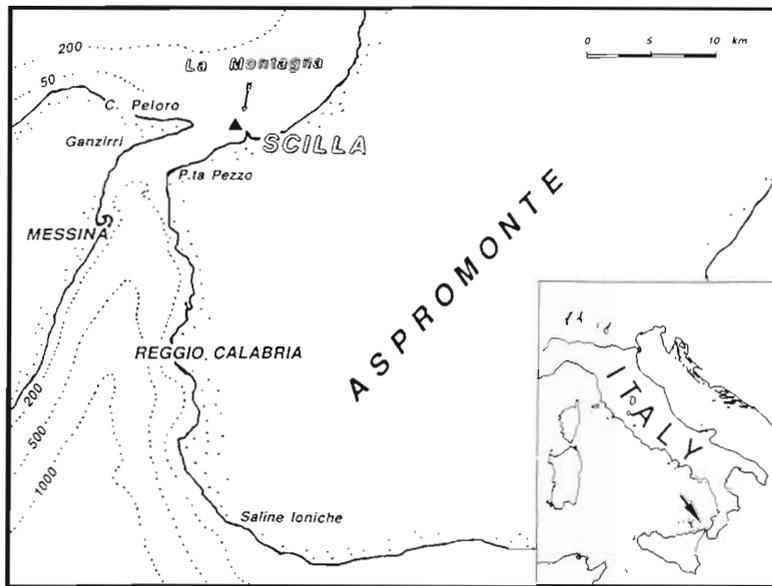


Fig. 1. Study site location of *Paramuricea clavata* population. Arrow indicates position of the described site

Paramuricea clavata were randomly chosen along a depth transect (28 to 38 m) and tagged in April 1991. Plastic markers were applied to the major growth branch of each colony. Maximum height (i.e. the distance between colony base and the furthest point of the tagged endbranch) was measured to the nearest mm. Measurements were repeated in October 1991 and April 1992.

Along the same transect, at 30 and 36 m depths, a stratified random sample collection was carried out in August 1992. A minimum number of colonies (28) was collected by means of a hammer and chisel. In the laboratory, collected colonies were aged under the microscope by counting apparent growth rings in cross sections cut 1 cm from the base (Grigg 1974). Following cutting and grinding of the sections, age was determined from the mean of 5 replicated cross sections per colony. Maximum colony height was measured on each colony to the nearest mm. A *t*-test was then performed to assess the differences between the means of colony height of gorgonians collected at different depths. Since no statistical difference was found ($t = 0.71$; $df = 26$), all data from the 28 colonies were pooled before calculating the growth curve. The relationship between age and colony height was then determined by fitting the Bertalanffy growth model.

Biomass measurement. Colony biomass for each age class was estimated in August 1992. The external surface area of the 28 collected colonies was measured by cutting each colony into segments and then summing

the (A) area of these cylinders from height (h) and diameter (d) ($A = \pi dh$) with adjustments for branchlet apices [$\pi(d/2)^2$] (Mitchell et al. 1992). On a stratified subsample of 7 colonies, coenenchyme thickness was measured from each of 3 regions: base, middle and tips. A total of 21 coenenchyme layers were removed from the skeleton and measured both for thickness (to the nearest 0.05 mm) and area. Differences among coenenchyme thicknesses of the 3 regions were tested (1-way ANOVA) for significance. Since no statistical difference was observed ($F = 2.48$; $df = 2,18$), weight estimates were made on the unitary 'coenenchymal brick' (1 cm² wide), whose thickness was assumed to be almost equal in the 3 colony regions. Coenenchymal bricks, scraped from each of the 3 regions of the above subsample, were weighed to determine ash-free dry weight (AFDW). Tissue AFDW was obtained by subtracting ash weight

(obtained after exposure to 500 °C for 3 h) from the dry weight of coenenchyme dried at 103 °C for 24 h. Weights were determined to the nearest 0.1 mg. Because it could not be assumed that the ratio between living tissue and embedded spicules in the 3 regions is identical, a 1-way ANOVA was then performed in order to assess differences among base, middle and tip coenenchymal weights. Because no significant differences were observed ($F = 2.63$; $df = 2,18$), the 3 regions were pooled and the mean weight of the 1 cm² coenenchymal brick was calculated. Biomass of the living tissue of each of the 28 colonies collected was then estimated by multiplying the mean coenenchymal brick weight times the external surface area of each colony. Biomass was regressed on colony age to determine the mean biomass of each age class.

Density estimates. *Paramuricea clavata* population density was estimated from the number of colonies per 1 m² quadrat along 3 depth transects in August 1992. Along each transect, 4 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. Height classes were converted into age classes from the calculated Bertalanffy growth equation. Density (colonies m⁻²) of each age class was determined by the fraction of each age class of the 213 colonies times total density.

Standing stock biomass was estimated as the sum of mean biomass for all age classes. Total production was calculated by means of the increment-summation method (Crisp 1984).



Fig. 2. *Paramuricea clavata*. Thin basal cross section of the axis of a gorgonian. Each annual ring is made up of 2 alternating growth bands, light and dark (15 \times , fluorescent ring illuminator)

RESULTS

Growth

Out of 30 tagged branchlets of *Paramuricea clavata* from different colonies, 24 tags remained at the end of 1 yr. Linear growth ranged between 0.7 and 6.3 cm yr⁻¹. One branchlet showed negative growth (-2.2 cm), possibly due to predation (the polychaete *Hermodice carunculata* was often observed feeding on polyps). Mean linear growth was calculated by averaging growth increments, and yielded an estimate of 2.7 (± 1.6 SD) cm yr⁻¹.

Table 1. *Paramuricea clavata*. Age classes and height of the collected colonies

Age class (yr)	Height (cm)	Age class (yr)	Height (cm)
0-1	1.2	5-6	14.0
0-1	1.8	6-7	15.6
0-1	0.9	7-8	30.1
0-1	1.9	8-9	18.3
0-1	4.0	8-9	25.0
0-1	3.1	9-10	33.3
0-1	4.2	9-10	35.0
2-3	9.0	10-11	27.7
2-3	8.8	10-11	42.4
2-3	10.2	10-11	24.8
2-3	15.0	11-12	35.1
4-5	12.3	12-13	36.1
5-6	18.1	12-13	58.6
5-6	20.2	14-15	31.9

Table 2. Sigmoidal regression relating age to height for *Paramuricea clavata*. Regression coefficients (L_{∞} , K , t_0), standard errors (in brackets), index of determination (r^2) and regression ANOVA significance are also given

Coefficient	Bertalanffy curve [$L = L_{\infty}(1 - e^{-(Kx - t_0)})$]	r^2	Significance
L_{∞}	149.09 (276.15)	0.830	$p < 0.001$
K	0.02 (0.01)		
t_0	-0.07 (0.08)		

In Fig. 2, a thin basal cross section of the proteinaeous axis of *Paramuricea clavata* is shown. Each annual ring is made up of 2 alternating growth bands, light and dark. Colonies collected in August 1992 regularly showed a light outer band corresponding to the faster period of growth, whereas dark bands are usually indicative of slower growth (Grigg 1974). Age classes of the sampled colonies ranged between 0-1 and 14-15 yr. In Table 1, ages and colony heights are reported. Parameters of the Bertalanffy equation, fitted to the vectors of age and height, are reported in Table 2. A sigmoidal growth curve calculated for height is shown in Fig. 3. Yearly growth rates were calculated by fitting the Bertalanffy equation: the youngest colonies (age class 0-1 yr) exhibited a growth rate of about 3.4 cm yr⁻¹; this value decreases to about 2.5 cm yr⁻¹ for the oldest colonies. Mean growth rate of *P. clavata* was estimated by averaging the values of each yearly growth interval. In the sampled age interval, we calculated a mean height growth rate of 3.0 (± 0.3 SD) cm yr⁻¹.

Production

The mean coenenchyme thickness was 0.06 (± 0.02 SD) cm. AFDW of *Paramuricea clavata* was 15.13% (± 3.82 SD) of dry weight. The mean coenenchymal

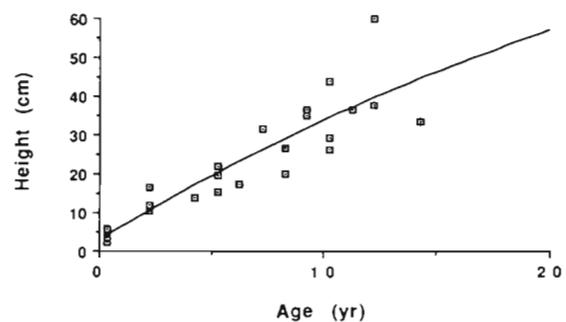


Fig. 3. Bertalanffy growth curve according to height; actual height measurements are also shown

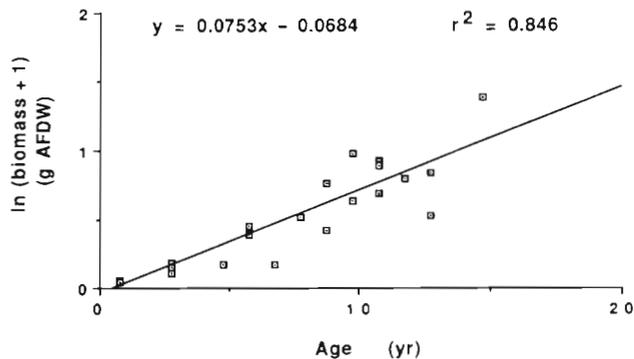


Fig. 4. Log-transformed biomass (g AFDW) estimates regressed on age classes

brick weight was $0.0047 (\pm 0.0020 \text{ SD}) \text{ g cm}^{-2}$ surface area. Living tissue biomasses of colonies were regressed on age (Fig. 4) in order to provide better estimates of colony biomass for each age class. The regression was highly significant ($F = 142.51$; $df = 1,26$; $p < 0.001$). Colony density, determined by quadrat sampling, was $19.36 (\pm 9.20 \text{ SD}) \text{ colonies m}^{-2}$. In Table 3, parameters for secondary production calculation are given. Standing stock of *P. clavata* was $22.5 \text{ g AFDW m}^{-2}$, with 95% CL from 16.8 to $26.2 \text{ g AFDW m}^{-2}$. Production was estimated at $3.0 \text{ g AFDW m}^{-2} \text{ yr}^{-1}$, with 95% CL from 2.2 to $3.5 \text{ g AFDW m}^{-2} \text{ yr}^{-1}$. The corresponding annual production/biomass ratio (P/B) was 0.13; its reciprocal, the turnover time, was estimated as 7.5 yr.

DISCUSSION

By means of 2 different methods (tagging and fitting of a growth curve), we estimated similar mean annual growth rates for *Paramuricea clavata* (2.7 and 3.0 cm yr^{-1} respectively). Our values are higher than those observed at Banyuls-sur-Mer (southern France) by Weinberg & Weinberg (1979), who tagged 26 colonies of *P. clavata* at 24 m depth and reported an average growth rate of 1.8 cm yr^{-1} (range: 0.2 to 3.7 cm yr^{-1}).

It was reported previously (Velimirov 1976) that octocoral colony size increases with increased water velocity. This is likely due to both the beneficial role of water movement in carrying prey (Sebens 1984) and increasing respiration by reduction of the boundary layer thickness which promotes oxygen diffusion into the colony tissues (Sebens 1987). Since the colonies of *Paramuricea clavata* measured in the Banyuls area live in a moderate to strong water flow regime (100 to 350 m h^{-1}) (Weinberg 1979), the higher annual growth rates exhibited by the Scilla population may be due to the stronger tidal currents characterizing the Strait of Messina area. In addition, in the north entry zone of

Table 3. *Paramuricea clavata*. Secondary production estimates

Age class (yr)	Density (ind. m^{-2})	Biomass (g AFDW m^{-2})	Production (g AFDW $\text{m}^{-2} \text{ yr}^{-1}$)
0-1	0.46	—	—
1-2	0.64	0.03	0.03
2-3	1.18	0.15	0.10
3-4	2.18	0.47	0.19
4-5	1.09	0.34	0.10
5-6	0.82	0.34	0.08
6-7	1.18	0.62	0.13
7-8	0.91	0.58	0.11
8-9	1.45	1.12	0.19
9-10	0.82	0.74	0.11
10-11	1.37	1.45	0.20
11-12	1.18	1.44	0.19
12-13	1.45	2.03	0.25
13-14	0.64	1.01	0.12
14-15	0.73	1.30	0.15
15-16	0.09	0.18	0.02
16-17	0.36	0.81	0.09
17-18	0.91	2.26	0.23
18-19	0.27	0.75	0.07
19-20	0.27	0.83	0.08
20-21	0.18	0.61	0.06
21-22	0.18	0.68	0.06
22-23	0.55	2.23	0.20
23-24	0.00	—	—
24-25	0.18	0.89	0.08
25-26	0.09	0.49	0.04
26-27	0.09	0.53	0.05
27-28	0.09	0.58	0.05
Total	19.36	22.46	2.98

the Strait the nutrients increase in intermediate Ionian waters, pushed to the Lower Tyrrhenian Basin by the tidal currents (Magazzù et al. 1981). Reed (1983) and Sebens (1984) reported that both hard and soft corals grow larger in areas exposed to upwelling of nutrient-rich water compared with those in non-upwelling areas.

Growth rates estimated in this study are comparable to values reported from the few other Mediterranean species whose annual linear growth increments were measured. Weinberg & Weinberg (1979) found that *Lophogorgia ceratophyta* grows 2.4 cm yr^{-1} in the Banyuls area, compared to the 2.6 cm yr^{-1} estimated by Mistri & Ceccherelli (in press) in a station near La Spezia (Ligurian Sea). Since the species is characterized by very thin branch tips, one would expect *L. ceratophyta* to be a faster-growing species than *Paramuricea clavata*, which has the thickest branches among Mediterranean gorgonians (Weinberg 1976). Yoshioka & Yoshioka (1991) measured growth rates of 13 Caribbean gorgonians, and reported that the fastest-growing species (*Pseudopterogorgia americana*, 4 cm yr^{-1}) was characterized by thin branch tips, while the slowest-growing one (*Plexaurella dichotoma*,

0.8 cm yr⁻¹) had the thickest branches of the gorgonians examined. The Mediterranean *Eunicella singularis*, which bears branches of intermediate thickness between *L. ceratophyta* and *Paramuricea clavata*, grew at a mean annual rate of 2.3 cm yr⁻¹ (Weinberg & Weinberg 1979). These observations seem to exclude a relationship between linear growth rate and thickening of branches, suggesting that interspecific variations in growth rates among Mediterranean gorgonians are not as wide as those exhibited by Caribbean gorgonians.

The percentage of AFDW on the total tissue dry weight is relatively low (15.13 ± 3.82 SD) when compared to the values reported by Widbom (1984) and Wacasey & Atkinson (1987) for marine meio- and macrobenthic invertebrates, because of the mass of calcareous spicules embedded in the coenenchyme. The percentage of AFDW on blotted dry weight (8.41 ± 1.56 SD) is, however, very close to those reported by Mitchell et al. (1992) for 2 species of tropical gorgonians (8.94 and 9.27% respectively).

Unlike stony corals (Buchsbaum & Muscatine 1971) and other gorgonian species (Ciereszko 1962, Brafield et al. 1965), tissues of *Paramuricea clavata* do not host symbiotic zooxanthellae, and biomass accumulation is only due to heterotrophic nutrition.

In determining *Paramuricea clavata* secondary production, we focused only on somatic production; gonad output was not taken into consideration. Moreover, predation by Ovulidae gastropods (Theodor 1967) and *Hermodice carunculata* (Vreeland & Lasker 1989) is likely to play a primary role in gorgonian tissue losses. We also observed several *H. carunculata* specimens feeding on *P. clavata* branches. On the basis of the above considerations, we have estimated total production conservatively. Mitchell et al. (1992) estimated the secondary production of 2 gorgonian species (*Leptogorgia hebes* and *L. virgulata*) in 3 sites facing the Alabama and Florida coasts (Gulf of Mexico); their estimates ranged between 2.3 and 10.5 g AFDW m⁻² yr⁻¹ for the different sites. Measured production of the Mediterranean *P. clavata* (3.0 g AFDW m⁻² yr⁻¹) is consistent with these estimates. Different *P/B* values (0.13 for *P. clavata*; 0.44 and 0.37 for *L. hebes*; 0.45 for *L. virgulata*) and, consequently, turnover times (7.5 yr for *P. clavata*; 2.3 and 2.7 yr for *L. hebes* and 2.2 yr for *L. virgulata*) reflect the different age structure of the gorgonian populations investigated. *P. clavata* colonies had a mean age of 9.6 yr and were older than *L. hebes* (2.6 and 5.5 yr) and *L. virgulata* (3.1 yr) (Mitchell et al. 1993). The *P/B* ratio has been shown to decrease with the age of an organism (Waters 1977).

A *P/B* ratio of 0.13 suggests a low metabolism and slow turnover in *Paramuricea clavata*. Therefore occasional mass mortality may have prolonged effects on *P.*

clavata populations. Indeed, in recent years (summer 1990 and 1991), large scale occurrences of mucus masses caused by macroalgae *Ectocarpales* sp. and *Xantophyceae* sp. (M. C. Buia pers. comm.) in the central Tyrrhenian Sea sank to the bottom, and covered the sessile fauna. Entire gorgonian populations, and particularly *P. clavata*, have been dramatically reduced in the Monte Argentario Promontory and Giannutri Isle (Tuscany) (M. Mistri & M. Bergamini pers. obs.). Stachowitsch et al. (1990) reported about mucus clouds entangled in projecting gorgonians (*Eunicella* sp.) in the northern Adriatic, but, to date, no study has addressed the ecological consequences of such events on gorgonians. Studies are needed to investigate the recovery of Mediterranean gorgonian populations from occasional mass mortality.

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