



Growth in a Modular Colonial Marine Invertebrate

R. Coma^a, M. Ribes^a, M. Zabala^b and J.-M. Gili^a

^aInstitut de Ciències del Mar (CSIC), Passeig Joan de Borbó s/n, 08039 Barcelona, Spain

^bDepartment d'Ecologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain

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Growth rate, temporal variability and secondary production were quantified for the Mediterranean gorgonian *Paramuricea clavata* off Medes Islands, NW Mediterranean. Fifty-four colonies ranging in size between 5 and 860 cm in total length (3–55 cm maximum height) were monitored photographically for 2 years. Growth varied between and within years. Primary branches accounted for 91% of production, though their growth rates were highly variable (on average 23% of branches displayed zero growth). The gross growth rate of primary branches in colonies <20 cm was higher (0.8 cm year⁻¹) than that of colonies >20 cm (0.5 cm years⁻¹). On average, net growth of primary branches (0.4 cm year⁻¹) was approximately 60% of positive growth. There was a significant size-specific negative growth effect in which smaller colonies displayed higher rates of loss. Mean growth in colony height was 1.8 cm year⁻¹ (range: 0.2–6.4 cm year⁻¹). Based on growth rate data, the largest colonies in the population (55 cm) were around 31 years old. On average, net production for all colonies was 75% of gross production. Gross production was 4.4 g AFDW m⁻² year⁻¹, the production/biomass value was 0.11, and the turnover time was 9 years. Growth rate and its variation with colony size are discussed within the framework of the life history traits of the species. © 1998 Academic Press

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Introduction

For modular colonial organisms, size is the best descriptor of life history features (Jackson, 1985; Hughes, 1989). However, most colonial species exhibit complex patterns of growth in which different sections of the colony grow at widely variable rates (e.g. Lasker, 1990; Yoshioka & Yoshioka, 1991). The sum of these rates determines colony size which in turn affects all aspects of a colony's fitness (Hughes, 1984; Jackson, 1985).

Growth in modular organisms is partially or completely 'indeterminate' (Jackson *et al.*, 1985; Sebens, 1987). The ability to grow asexually through the production of new, energetically self-sufficient modules, combined with the fact that excess energy expendable on growth or reproduction increases proportionally with colony mass, makes unlimited growth possible (i.e. even the largest individuals continue to grow; Buddemeier & Kinzie, 1976; Hughes & Jackson, 1985; Hughes *et al.*, 1992). However, empirical evidence in support of the prediction of unlimited growth is lacking, and in most studied species growth has been observed to attenuate, thus placing a limit on maximum size (Sebens, 1987). Growth will probably be conditioned by the position of branches on the colony, colony size and

environment, due to energetically determined limits (Sebens, 1982) and/or biological interactions (Jackson, 1977). Therefore, although the growth of modular organisms can be indeterminate, in many species it can be limited by interactions with the environment.

Gorgonians (Cnidaria, Octocorallia) are among the most conspicuous components of rocky subtidal communities both in tropical and temperate seas (Péres & Picard, 1964; Kinzie, 1973). They play an important ecological role, providing habitats for epifauna composed of small species and increasing the biomass and diversity of the community (Wendt *et al.*, 1985; Mitchell *et al.*, 1992). Gorgonians are an appropriate group to study growth in modular organisms since colony size is the major determinant of their life history such as: onset of reproduction (Brazeau & Lasker, 1989; Coma *et al.*, 1995a), reproductive output (Grigg, 1977; Coma *et al.*, 1995a), and survival (Harvell & Suchanek, 1987; Yoshioka, 1994). Studies of gorgonian growth share some of the considerations associated with growth in all modular colonial organisms (Jackson *et al.*, 1985). Among the most important features to consider are: (1) unlimited growth (Buddemeier & Kinzie, 1976; Hughes & Jackson, 1985); (2) resorption and translocation of biomass (Sebens, 1987); (3) architectural constraints (Harper, 1985) and; (4) seasonal and interannual variation in

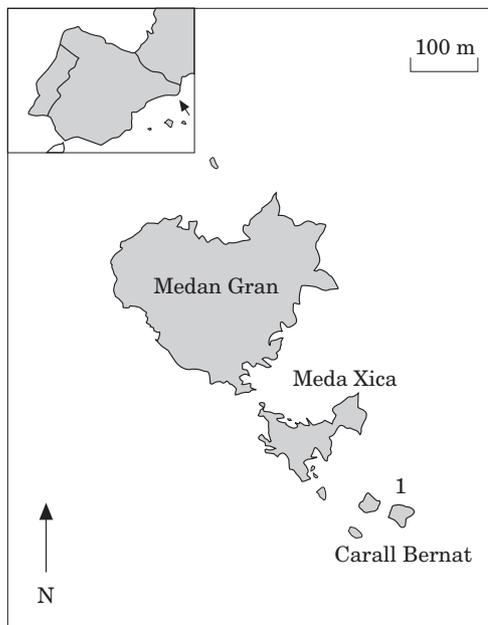


FIGURE 1. Geographical location of the study area and the study site (number 1) at Medes Islands (NW Mediterranean).

secondary productivity (Kinzie, 1973; Velimirov, 1975).

Some of these general features for benthic modular colonial organisms have been analysed while studying growth and secondary production in a population of the gorgonian *Paramuricea clavata*. The present paper endeavours to quantify growth in a population of *P. clavata*, a common species in the north-western Mediterranean, in the framework of a study designed to establish an overall metabolic budget for the species. The aims were to examine variation in growth rate: (1) within the colony; (2) with colony size; and (3) with time (seasonal and interannual variation) in order to assess production for the species.

Materials and methods

The research was carried out on the population of *Paramuricea clavata* off Medes Islands (42°N 3°13'E; NW Mediterranean, Figure 1). *Paramuricea clavata* is common along the east side of Medes Islands. The study was carried out on the *P. clavata* population on the northern face of the Carall Bernat (location 1 in Figure 1). At this site the rock face is nearly vertical (20 m), dropping to a gently sloping bottom of 1 to 10 m³ rocks. The study was conducted in a 1000 m² area between 15 and 27 m. The area is subjected to an average current speed of 10.4 ± 6.4 cm s⁻¹ (unpubl. data) produced by the frequent north winds.

Growth

A total of 54 colonies were randomly selected along three 50 m transects. Height of the colonies ranged between 3 and 55 cm. Colonies smaller than 15 cm were photographed nine times, every 3 months for 2 years (from September 1990 to November 1992) to study seasonal and interannual variation in growth. All the other colonies were photographed twice, in September 1990 and September 1991.

The silhouette of each colony was digitized using an I.B.A.S. image processor, and both the colony height and the length of all branches between bifurcations were measured. Three replicate photos of four colonies were digitized to assess the accuracy of measurement (=1.4 mm). Measurement error comes from photo obtention (mainly parallax and variations in distances between the object and the camera), and to a lesser extent repeatability in using the image processor. The branches were mapped and classified according to their positions in the colony using the model for stream drainage basins (Strahler, 1952), as previously used for gorgonians (e.g. Brazeau & Lasker, 1988; Mitchell *et al.*, 1993). In this ordering scheme, terminal branches are defined as first order branches. A second order branch arises when two first branches join. Higher order branches arise only when two branches of equal lower order join. A minimum of 20 primary branches per colony were randomly chosen and measured for colonies taller than 25 cm.

The data from two consecutive photographs of the same colony were compared to establish: (1) increase in colony height; (2) increase and decrease in the length of all branches; and (3) the emergence of new branches and disappearance of branches over each time interval. Net growth, gross growth (disregarding losses), positive growth (only branches that grew), and losses were estimated for: (a) individual branches; (b) each branch order (mean value); and (c) the colony as a whole (mean value). Hereafter when referring to growth we are referring to gross growth. The studied population was divided into the five size classes (10 cm each) in which standing stock and reproductive output of the population have been previously studied (Coma, 1994; Coma *et al.* 1995a) to estimate production of the species (see below). Then, mean growth values for each size class and mean values for the entire population were also determined. Production of new branches was very low, therefore, where new branches developed on an existing terminal branch, the growth rate was estimated from the change in length of the original branch plus the length of the new branch. Negative growth at a colony level was estimated as the sum of losses of each branch

TABLE 1. Regression in log base e—log base e of different pairs of biometric parameters with the 95% confidence limit for the slope and the r^2 s for the regression

Biometric parameters	Intercept	Slope	95% confidence limits for slope		r^2	P
			Lower	Upper		
Colonies						
Height—total length (cm—cm)	0.060	1.688	1.545	1.831	0.983	<0.001
Height—dry weight (cm—g)	-6.192	2.607	2.340	2.874	0.948	<0.001
Diameter—dry weight (cm—g)	3.133	2.620	2.375	2.865	0.927	<0.001
Diameter—surface (cm—cm ²)	6.711	2.083	1.871	2.295	0.949	<0.001
Surface—dry weight (cm ² —g)	-5.184	1.252	1.179	1.324	0.983	<0.001
Segments (1 cm length)						
Diameter—dry weight (cm—g cm ⁻¹)	-0.924	1.857	1.632	2.082	0.919	<0.001

N=22 colonies.

from all orders and related to the total length of the colony. When only a fragment of the colony was studied, it was assumed that the same negative growth rate had been received by the studied and the non-studied part of the colony. In general, growth values were compiled by following changes in the length of 1883 branches on 54 colonies; of these 270 were measured nine times and the other 1613 were measured only twice. The growth rates measured from the analysis of the entire colony were compared with the estimates based on colony height by repeating the growth calculations based on the changes in colony height. Age was estimated by developing an age-size curve derived from iterative calculations of growth as a function of size. The estimated growth rate per each size class was used under the assumption of equal growth at every size-age.

Twenty two colonies spanning the entire size range were collected and measured fresh to prevent possible morphological changes and alterations in weight caused by preservation. They were then cut into pieces, dried in an oven (24 h at 110 °C), and weighed to establish equations for converting colony size to dry weight and to examine allometric growth. Biomass was related to: (1) colony height; (2) total length for each branch order; and (3) colony diameter at the base, using power functions.

The statistical significance of the differences in growth values as a function of branch order, colony size, seasonality and interannual variations was tested using a ANOVA on log-transformed data (Zar, 1984).

Production, production-biomass quotient (P/B), and turnover time

The diameters of 1172 branches from 22 colonies spanning the entire size range were measured with a

caliper to the nearest 0.14 mm. A total of 10 1-cm long sections were cut from each branch order from these colonies. The sections were dried for 24 h in an oven at 110 °C and then weighed. Half of these were reweighed after incineration in a muffle furnace for 5 h at 550 °C to assess the ash weight (attributed to the skeletal material: skeletal axis plus sclerites) and the ash-free dry weight (AFDW). The other half was assayed in a Carlo-Erba model 1500 C:N:H analyser to determine the carbon content. Twenty additional sections were dissected to remove the skeletal tissue from the coenenchyme and the fractions processes as just described above to determine the carbon content of the two portions. Equations were fitted to the relationships between all these parameters and the diameter of the 1 cm long sections.

The population biomass was estimated as the sum of all the contributions of each size class, which were in turn calculated as the product of the mean biomass for each size class multiplied by its frequency in the overall size distribution for the population (Coma, 1994). Total production was calculated as the summation of growth (length and width) increases. The values of the quotients obtained by dividing net and gross production by biomass at the beginning of the interval were used to calculate the renewal rate (P/B, year⁻¹) and its converse, turnover time (B/P, year). The effect of seasonal and interannual factors on growth was established for colonies <20 cm.

Results

Biometric regularities and conversion factors

Paramuricea clavata had distinctly allometric growth (Table 1). Both based diameter and maximum height showed significant fit with total colony weight, but

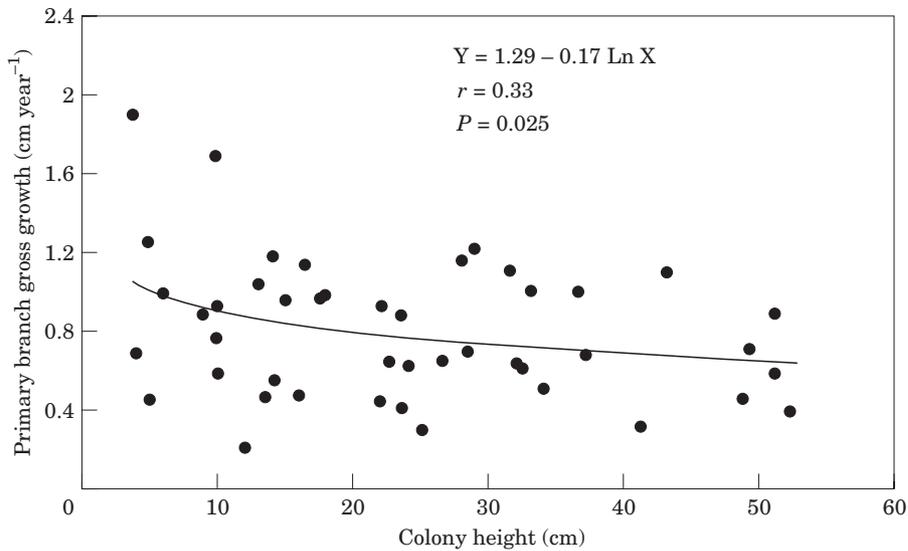


FIGURE 2. Primary branch growth rate per colony (mean; cm year^{-1}) vs colony height (in cm). N , 45 colonies.

since it is easier to take accurate measurements of colony height under water, this feature was the reference measurement of preference. Nevertheless, surface area (fit to an ellipsoid of the same height and width as the colony) yielded the best prediction (Table 1). Branches of higher order than the fifth were not found. Ash-free dry weight of *P. clavata* was $3.8 \pm 0.3 \text{ mg cm}^{-2}$ surface area, which was $17.15 \pm 4.10\%$ of coenenchyme dry weight. Dry weight was significantly related with branch diameter (Table 1), thereby appreciably simplifying biomass estimation by reducing predicted variables to diameter and length. The skeletal axis fraction increased as branch diameter increased.

Growth

Colony increase occurred via increasing branch length and diameter. Only first order branches increased in length. Growth of inner colony branches was achieved through diameter increase. Diameter increased as a function of branch order (diameter = $1.47 + 1.16$ branch order; $r = 0.83$, $N = 1172$, $P < 0.0001$; diameter in mm).

There was great variability in the positive growth rate of primary branches, and considerable unevenness in the distribution of growth (23% of the branches displayed zero growth). Although, highly variable, the percentage of primary branches displaying positive growth (65.3%, average for all colonies) showed a tendency to decrease with colony size ($r = 0.32$, $P = 0.031$, $N = 45$). Variation in primary branch growth rate with colony size was analysed

TABLE 2. Nested analysis of variance for gross growth rate (cm year^{-1}) of primary branches of *Paramuricea clavata* between sizes (<20 cm and >20 cm), and among colonies (colonies nested in size)

Source	d.f.	SS	MS	F	P
Size	1	27.76	27.76	49.97	0.0001
Colony	42	105.20	2.92	5.26	0.0001
Error	610	338.89	0.55		

Degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F ratio (F) and probability (P).

from the difference between the first measurement (September 1990) and September 1991 measurement. Primary branch growth rate also decreased with colony size (Figure 2). However, the relationship between colony size and growth rate was weak for colonies >20 cm (Figure 2). Also, because on average onset of sexual maturity for this species is delayed until colonies attain a size of 20 cm (Coma et al., 1995a), growth rate of colonies <20 cm was compared to growth rate of those >20 cm. The analysis showed that growth rate of colonies <20 cm was significantly higher (0.8 cm year^{-1}) than growth rate of colonies >20 cm (0.5 cm year^{-1} ; Table 2). On average, net growth of primary branches (0.4 cm year^{-1}) was approximately $60 \pm 27\%$ of positive growth.

Colony height growth rate was highly variable, ranging from 0.2 to 6.4 cm year^{-1} . Mean growth in colony height was $1.8 \pm 1.27 \text{ cm year}^{-1}$, and over the size range considered (3–55 cm), colony height did

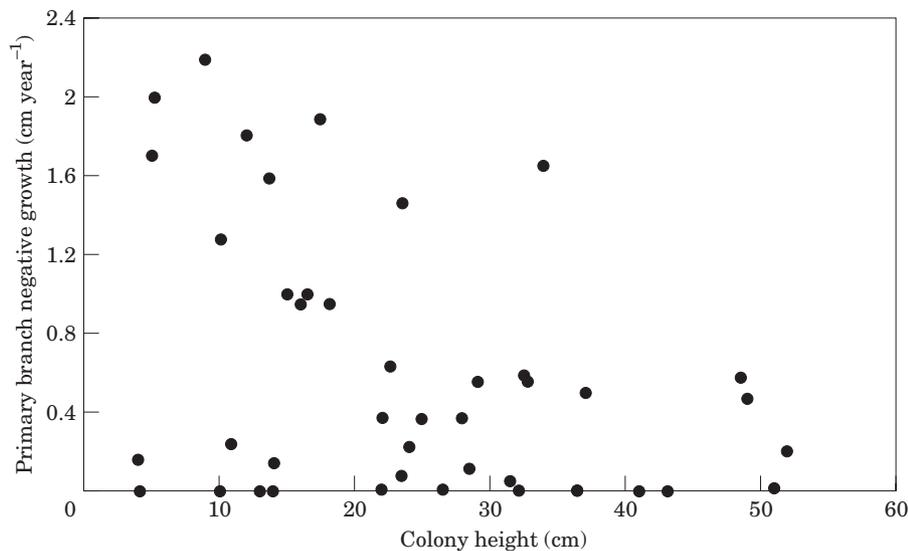


FIGURE 3. Primary branch negative growth rate per colony (mean; cm year^{-1}) vs colony height (in cm). N , 45 colonies.

not exert a significant effect on colony height growth rate ($r=0.25$, $P>0.1$, $N=45$).

Negative growth

Negative growth of the colonies took the form of a reduction in length or loss of branches. Primary branches accounted for 96% of the length loss. The percentage of primary branches displaying negative growth (12.4%, average for all colonies) did not vary significantly with colony size ($r=0.03$, $P=0.84$, $N=45$). Mean loss rate was 0.9 cm year^{-1} per primary branch for those branches exhibiting negative growth. The rate of loss for branches displaying growth decreases may have been even greater than the rate for branches exhibiting positive growth. Nevertheless, the percentage of branches that decreased in length (12.4%), was much lower than the percentage of branches that grew (65.3%).

The mean negative primary branch growth rate, though highly variable within a colony and between colonies, changed significantly with colony height ($r=-0.38$, $P=0.009$, $N=45$, Figure 3). Therefore, there was a significant size-specific negative growth effect in which smaller colonies displayed a higher rate of loss. At a colony level, there was also a significant size-specific negative growth effect in which smaller colonies displayed a higher percentage of loss rate ($r=-0.35$, $P=0.019$, $N=45$) due to both the previous per branch effect and to the fact that the same amount of tissue of a small colony represents a higher percentage of tissue relative to a large colony. Annual negative growth was highly variable between colonies,

varying between 0 and 33% of the total length. For all colonies, mean annual negative growth was 3% of the total colony length. However, this estimation should be considered as highly conservative because some branches that grew may have also suffered some negative growth

Temporal variability

Seasonal measurements of 21 colonies smaller than 15 cm in height for two annual cycles indicated that growth was not constant either within years or between years [Figure 4; Table 3(a)]. In both years growth was high from April to June. This pattern was consistent from one year to the next. However, although accuracy of the growth period is somewhat conditioned by the sampling sequence, in 1991–1992, there was a high growth period which started earlier and ended later than in 1990–1991. The growth variation during this period was the main source of the interannual difference and of the significant interaction difference (Figure 4). In contrast to the temporal variation in growth, there was no well-defined pattern of negative growth either between years or among seasons [Table 3(b)].

Production

Branch order had the most distinct effect on production. On average the primary branches contributed 90.6% of total colony production, secondary branches 5.9%, and tertiary branches 3.5%. Mean production values ranged from $0.12 \text{ g dry weight colony}^{-1}$

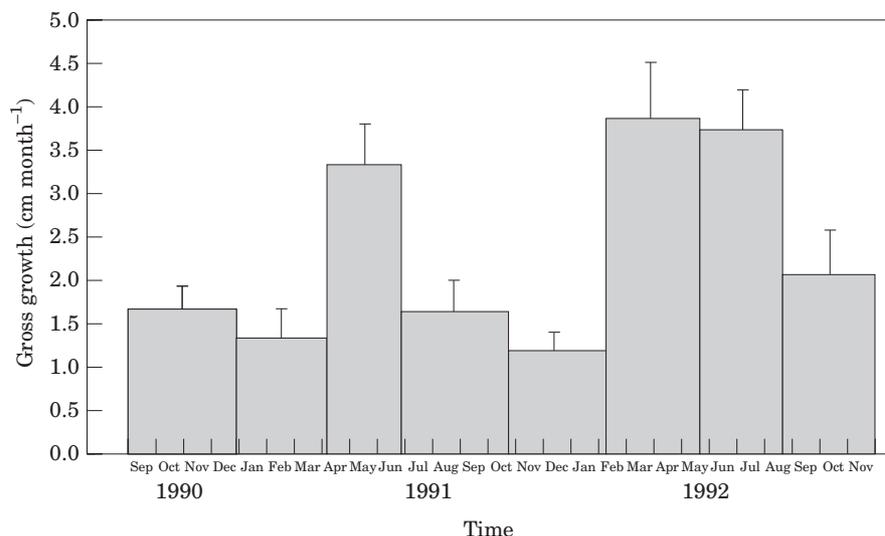


FIGURE 4. Seasonal variations in growth of whole colonies <15 cm over the two annual cycles, 1990–91 and 1991–92. Errors bars show standard error. N , 21 colonies.

TABLE 3. Analysis of variance testing for: (a) whole colony gross growth rate of *Paramuricea clavata* between years (1990–1991 and 1991–1992), and among seasons; (b) whole colony negative growth between years, and among seasons

Source	d.f.	SS	MS	F	P
(a)					
Year	1	21.01	21.01	5.20	0.0238
Season	3	107.41	35.80	8.87	0.0001
Year \times season	3	47.93	15.97	3.96	0.0093
Error	160	641.59	4.03		
(b)					
Year	1	5.14	5.14	2.81	0.0952
Season	3	3.29	1.09	0.60	0.6153
Year \times season	3	10.18	3.39	1.86	0.1383
Error	160	289.96	1.82		

Degrees of freedom (d.f.), sums of squares (SS), mean squares (MS), F ratio (F), and probability (P).

year⁻¹ in the smallest size class (0–10 cm) to 3.11 g dry weight colony⁻¹ year⁻¹ in the largest size class (>41 cm) (Table 4). Gross and net production values for *P. clavata* scaled as a power function of colony size (Figure 5). On average, for all the colonies examined, net production represented 75% (SE=54, $N=45$) of gross production.

Production in a standard plot for the benthic *P. clavata* community at depths between 15 and 25 m off the Medes Islands, with a density of 55.8 colonies m⁻² (average *P. clavata* density and demographic structure for Medes Islands; Coma, 1994), was estimated at 40 g DW m⁻² year⁻¹, the equivalent of

4.4 g AFDW m⁻² year⁻¹ and 6.6 g C m⁻² year⁻¹, of which 2.7 g were organic C (tissues+skeleton) and 3.9 g were inorganic C (sclerites) (Table 4).

Colony age, renewal rate and turnover time

The curves constructed using the values for growth in height or total length were similar (Figure 6). Based on these data, the largest gorgonians recorded in the present study (55 cm) may be 31 years of age.

Production/biomass values were scaled as a power function of colony size (Figure 7). The power function yielded an asymptotic P/B value about 0.1 year⁻¹ (Figure 7). Production/biomass values of the *P. clavata* population off the Medes Islands were weighed according to the population size structure (Table 4). Mean P/B for the population considered was 0.116 and the mean turnover time for population biomass was 9 years.

Discussion

Growth

The observed values of increase in height spanned a broad range from 0.2 to 6.4 cm colony⁻¹ year⁻¹. The values reported by others who have studied this species previously all fall within this broad range (Table 5). Although it is difficult to compare averages, which are dependent upon the size structure of each population, the mean values in this study (1.8 \pm 1.27 cm colony⁻¹ year⁻¹) were closest to the estimates of Weinberg and Weinberg (1979) and Gili

TABLE 4. Biomass (B), production (P) and P/B values per colony and per m² by size class

Size class (cm)	Biomass g D.W. col ⁻¹		Production g D.W. col ⁻¹ year ⁻¹		P/B		Density col m ⁻²	Biomass g D.W. m ⁻²	Production g D.W. m ⁻² year ⁻¹	P/B Weighted	N
	Mean	STD	Mean	STD	Mean	STD					
0-10	0.56	0.30	0.12	0.07	0.27	0.19	20.7	11.58	2.45	0.009	9
11-20	2.58	1.45	0.43	0.35	0.16	0.08	19.6	50.62	8.51	0.023	10
21-30	12.12	4.70	1.32	0.98	0.11	0.07	9.4	113.93	12.41	0.035	11
31-40	24.72	4.87	2.95	1.23	0.12	0.04	4.1	101.35	12.11	0.034	7
>41	47.45	16.67	3.11	1.45	0.07	0.03	1.7	80.66	5.29	0.015	8
Total							55.80	358.14	40.78	0.116	45

(D.W.) dry weight; (Col) colony; (STD) standard deviation; Weighted P/B for the population (N=45 colonies).

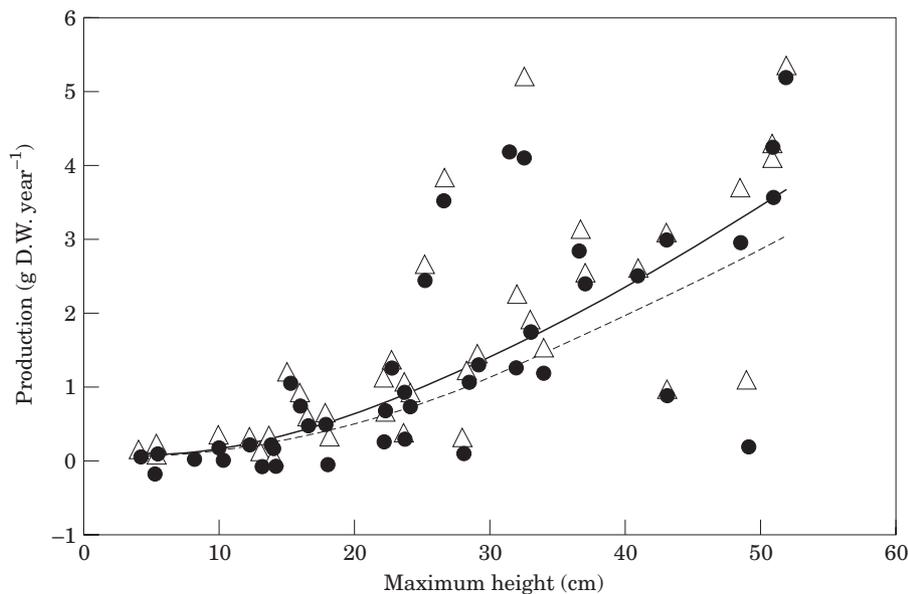


FIGURE 5. Gross and net production (g dry weight) on maximum colony height (cm) based on increases in total length (cm). N 45 colonies. Gross production = $2.59 \times 10^{-3} H^{1.84}$, $r=0.84$, $P<0.001$; net production = $2.67 \times 10^{-3} H^{1.78}$, $r=0.80$, $P<0.001$. —△—, gross; -●-, net.

and García (1985) and were much lower than those reported by Mistri and Ceccherelli (1994a). As the last investigators have pointed out, it is possible that the strong currents in the Strait of Messina are highly conducive to gorgonian growth. The flow speed at the present study area (about 10 cm s^{-1} , unpubl. data), suggests that the population is subjected to a much lower flow regimen than the population from the Strait of Messina ($>50 \text{ cm s}^{-1}$, Mistri & Ceccherelli, 1994a). As several authors have reported water flow has an important influence on octocoral species because it replenishes prey, enhances diffusion of nutrients, oxygen and carbon dioxide, and then increases colony biomass (e.g. Patterson & Sebens, 1989; Fabricius *et al.*, 1995).

Owing to the large standard deviation around the mean *P. clavata* growth rate and to the wide range of growth rates reported for most studied species (Table 5), it appears that there is not a wide range in growth rates among species studied to date, the overall mean rate being less than $3.0 \text{ cm colony}^{-1} \text{ year}^{-1}$ (Table 5).

The decrease in growth rate with colony size is consistent with expectations of competition between growth and reproductive functions for resources remaining after the requirements for maintenance and repair have been fulfilled (Harrison & Wallace, 1990; Brazeau & Lasker, 1992). There are a number of characteristics of the reproductive biology of the species that are consistent with this result. First, there

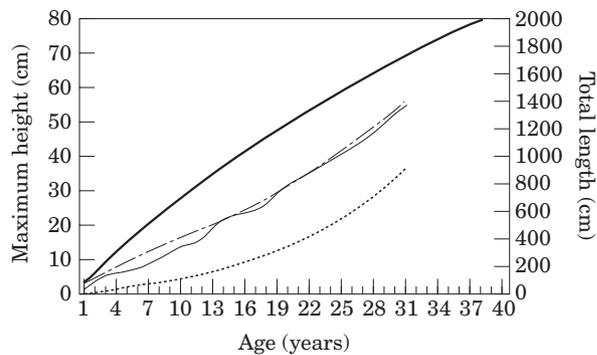


FIGURE 6. Predicted size of colonies using size specific growth rates: (— · — ·) maximum height calculated from the increase in total length (according to the regression given in Table 1); (—), direct measurements of maximum colony height; (—) estimates from Mistri and Ceccherelli (1994a) (· · · ·), total length.

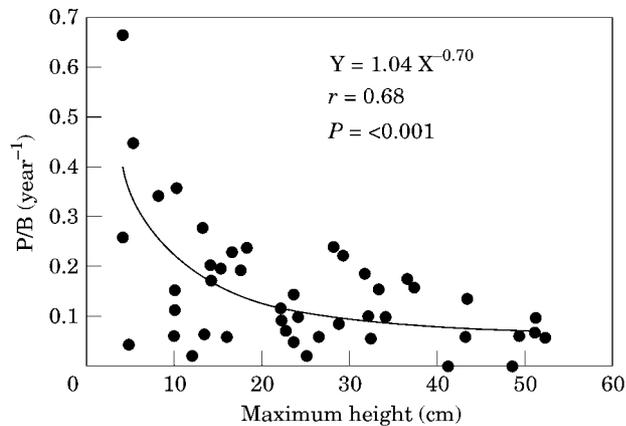


FIGURE 7. Production/biomass (P/B ; year^{-1}) values on colony height (cm). N 45 colonies.

is a delay in reproduction until colonies have attained a size of 20 (11–30) cm (Coma *et al.*, 1995a). Second, reproductive effort increases with colony size due to increases in the percentage of fertile colonies and polyps, and in the number of gonads per polyp (Coma *et al.*, 1995a). This trade-off, through reallocation of energy from growth to reproduction with increasing colony size, may explain the higher growth rate of colonies <20 cm relative to that of colonies >20 cm. However, the relationship between colony size and growth rate was weak for colonies >20 cm (Figure 2), suggesting that growth rate does not decrease after colonies attain sizes >20 cm, but may continue at an undiminished rate for many years. This property would support the prediction for unlimited growth in clonal organisms (Buddemeier & Kinzie, 1976; Hughes & Jackson, 1985). However, the small sample

size (only eight colonies >40 cm) and a large variance in growth among colonies may have prevented the detection of a decrease in growth with increasing colony size. Furthermore, the largest colonies in our study site are not nearly as large as the species at other sites (100 cm at 50 m Port Cross National Parc, MZ pers. observ.). Further research needs to be carried out to address this question.

Negative growth

The net growth of primary branches was 60% of positive growth. This value, while still high, is lower than that for *Briareum asbestinum* reported by Brazeau and Lasker (1992). An important amount of work has been carried out concerning the foraging behaviour of several invertebrates species on gorgonians, and authors which have, directly or indirectly, evaluated negative growth point out that fragmentation and predation appear to be the main sources of negative growth (e.g. Harvell & Suchanek, 1987; Brazeau & Lasker, 1992; Kim, 1996). The authors directly observed epibiosis by filamentous algae and overgrowth by *Parerythropodium coralloides*. Additional losses may be due to predation and/or diseases, because Coma *et al.* (1995b) found that fragmentation is quantitatively negligible in this species. In *P. clavata* and other Mediterranean gorgonians predation by ovulid gastropods (Théodor, 1967) and by polychaetes (Mistri & Ceccherelli, 1994a) has been observed. Areas of necrosis on inner branches have also been reported, which may be due to viral or bacterial infection (Feingold, 1988); such areas are quickly overgrown by epibiotic organisms. Although it would appear that such organisms are not able to overgrow undamaged gorgonian tissues, they might increase resistance to water movements beyond tolerable limits and thus contribute to uprooting of the colony from the substratum (Weinberg & Weinberg, 1979).

There were no measurable cases of resorption of the tissues of 'older' portions. Resorption of incipient buds cannot be ruled out because some buds that were initially visible later disappeared. However, incipient buds were not as quantitatively important as they were within the measurement error. The sample periodicity and the fact that some branches displaying zero or positive growth may have also suffered from some losses, allowed only a minimum estimation of negative growth. However, the low incidence of branch loss and the absence of direct observations of predation, suggest that the observed 13% of primary branches affected by negative growth is accurate.

TABLE 5. Parameters of growth for various gorgonians species

Species	Reg.	Inc Max H		Density		Production	P/B	Turn	Reference
		M (STD)	Min–Max	M (STD)	Min–Max				
<i>Gorgonia flagellum</i>	T	—	0–8.3	—	—	—	—	—	Cary, 1914
<i>Plexaura flexuosa</i>	T	—	0.5–5.5	—	—	—	—	—	Cary, 1914
<i>Plexaura flexuosa</i>	T	—	2.15–1.77	—	—	—	—	—	Cary, 1914
<i>Plexaura homomalla</i>	T	2	0.13–4.2	—	—	—	—	—	Kinzie, 1973
<i>Plexaura homomalla</i>	T	1.99	—	—	—	—	—	—	Kinzie, 1973
<i>Plexaura homomalla t. kukenthalli</i>	T	1.18	—	—	—	—	—	—	Kinzie, 1973
<i>Plexaura A</i>	T	—	3.8–3.9	—	—	—	—	—	Lasker, 1990
<i>Pseudopterogorgia americana</i>	T	—	3.44–4.48	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Pseudopterogorgia acerosa</i>	T	—	2.12–4.03	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Pseudoplexaura wagenari</i>	T	—	2.57–2.13	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Gorgonia ventalina</i>	T	—	1.92–2.34	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Pseudoplexaura porosa</i>	T	—	1.98–2.22	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Eunicea laxispica</i>	T	2.21	—	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Eunicea tourneforti</i>	T	2.06	—	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Muriceopsis flavida</i>	T	1.85	—	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Eunicea succinea</i>	T	1.36	—	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Plexaurella dichotoma</i>	T	0.80	—	—	—	—	—	—	Yoshioka & Yoshioka, 1991
<i>Brlareum asbestinum</i>	T	9.25	—	—	—	—	—	—	Brazeau & Lasker, 1992
<i>Leptogorgia hebes</i>	T	—	—	—	1.6–1.7	2.3–6.8	0.44–0.37	2.3–2.7	Mitchell <i>et al.</i> , 1992
<i>Leptogorgia virgulata</i>	T	—	—	4.0	—	10.54	0.45	2.22	Mitchell <i>et al.</i> , 1992
<i>Muricea californica</i>	TS	—	0–6	—	—	—	—	—	Grigg, 1974
<i>Eunicella cavolini</i>	M	—	0.52–2.15	—	—	—	—	—	Vellmirov, 1975
<i>Eunicella singularis</i>	M	2.24	0–3.3	—	—	—	—	—	Weinberg & Weinberg, 1979
<i>Lophogorgia ceratophyta</i>	M	—	0–2.4	—	—	—	—	—	Weinberg & Weinberg, 1979
<i>Lophogorgia ceratophyta</i>	M	2.57 (0.5)	1.5–3	—	—	—	—	—	Mistri & Ceccherelli, 1994b
<i>Paramuricea clavata</i>	M	—	0.3–3.3	—	—	—	—	—	Gill & Garcia, 1985
<i>Paramuricea clavata</i>	M	1.8	1.6–3.7	—	—	—	—	—	Weinberg & Weinberg, 1979
<i>Paramuricea clavata</i>	M	2.7 (1.6)	0.7–6.3	19.36 (9.2)	—	3.0	0.13	7.5	Mistri & Ceccherelli, 1994a
<i>Eunicella cavolini</i>	M	1.14 (0.44)	—	—	—	—	—	—	Vellmirov, 1973
<i>Eunicella cavolini</i>	M	0.85 (0.46)	—	—	—	—	—	—	Weinbauer & Vellmirov, 1995a
<i>Eunicella cavolini</i>	M	—	—	10.2–180	—	0.3–7.4	0.24–0.32	3.1–4.1	Weinbauer & Vellmirov, 1995b
<i>Paramuricea clavata</i>	M	1.8	0.2–6.4	55.8 (23.8)	—	4.4	0.11	9	This study

Abbreviations and units: (Inc Max H) increase in maximum height (cm year⁻¹); (M) mean; (STD) standard deviation; Density (colonies m⁻²); Production (AFDW m⁻² year⁻¹), P/B (year⁻¹); (Turn) turnover rate (year). Regions (Reg): Tropical (T), Temperate Sea (TS) and Mediterranean (M).

Temporal variability

Seasonal fluctuation in growth rates was studied in colonies <20 cm (non-reproductive; Coma *et al.*, 1995a) because differences in growth should be particularly high for them since all resources are devoted to growth (Coma *et al.*, 1998). More years of monitoring are required to accurately determine the seasonality of growth, however, in both years there was a high growth period in spring. The seasonal differences in growth rates of the species were consistent with seasonal fluctuations in food sources, because the north-western Mediterranean is characterized by a regular annual planktonic production cycle with two peaks, one in spring and one in autumn. The main planktonic production peak occurs in spring and is dominated by bacteria and phytoplankton, followed by an increase in the number of zooplankton (Estrada *et al.*, 1985). Also, flow speed during winter and spring is over two fold that in summer and autumn (Pasqual, unpubl. data). Most of those planktonic groups constitute the diet of *P. clavata* (Coma *et al.*, 1994), therefore food availability, which directly depends on food concentration and flow speed, is at its highest during spring. The increase in the duration of the high growth period in 1992 is consistent with the extraordinary fact that, in that year, spring conditions lasted until the beginning of August (Pasqual, unpubl. data).

Production, renewal time and turnover time

Estimated secondary production in *P. clavata* included only somatic production, because investment in reproductive tissue was not measured. Mitchell *et al.* (1992) estimated the secondary production in two Caribbean gorgonian species (Table 5); their estimates ranged from 2.3 to 10.5 g AFDW m⁻² year⁻¹. Mistri and Ceccherelli (1994a) recently assessed secondary production in *P. clavata* in the Strait of Messina (Italy) at around 3.0 g AFDW m⁻² year⁻¹ (Table 5). Despite higher growth rates, production in the Strait of Messina population was lower than in the Medes Islands population (4.4 g AFDW m⁻² year⁻¹) because population density was much lower (19.4 colonies m⁻² as opposed to 55.8 colonies m⁻²; Coma, 1994). This is a good example of the limited usefulness of comparing production values for different geographical localities occupied by populations with differing densities and demographic structures. Comparisons between production/biomass (P/B) values and turnover times would appear to be much more appropriate in this respect.

Production/biomass values for *P. clavata* were lower than those reported for other gorgonians (Table 5).

The P/B values varied with colony size, but were only slightly less than the estimates made by Mistri and Ceccherelli (1944a). Accordingly, turnover times for *P. clavata* (2–15 years) were the longest reported for gorgonians, and the turnover time weighted by biomass for the Medes Islands population (9 years) was somewhat higher than the value estimated for the population in the Strait of Messina. The age-size curves for the two populations clearly point out these discrepancies, and our results suggest a much higher longevity in the colonies in the Medes Islands population of *P. clavata* than in the population considered by Mistri and Ceccherelli (1994a). According to our results, colonies, which in some localities may exceed 100 cm in height, may attain the age of 50 years proposed as the upper limit to the life-span of this gorgonian (Weinberg & Weinberg, 1979; Weinberg, 1991). The higher longevity of the *Paramuricea clavata* Medes Islands population compared with that of the Messina strait population may be due to the higher growth rate of the Messina strait colonies (2.7–3.0 cm year⁻¹). The faster growing Messina strait colonies will reach the environmental maximum size limit earlier (Weinberg & Weinberg, 1979; Yoshioka & Yoshioka, 1991), and therefore their longevity will be lower than that of the Medes Islands population because detachment by weakening of substratum depends mainly on colony size and is the main source of gorgonian mortality (Kinzie, 1973; Yoshioka & Yoshioka, 1991).

In conclusion, the great variability in growth rate within and between colonies was the most characteristic feature of the growth pattern of these organisms. Growth estimates calculated from increases in total length were more precise than estimates calculated from increases in height and showed that: (1) length increase was restricted to primary branches; (2) branch growth rate was higher in small colonies; (3) 91% of production was accounted for by growth of primary branches; (4) net growth of primary branches was about 60% of positive growth; (5) negative growth was greater for small colonies; and (6) average net production was 75% of gross production. This work contributes to the knowledge of the ecological energetics of modular colonial invertebrates, which are important members of the benthos on hard substrata world-wide, yet apart from corals, have been little studied hitherto.

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