

Growth of Five Species of Gorgonians (Sub-Class *Octocorallia*) in the Sedimented Waters of Singapore

N. K. C. GOH & L. M. CHOU

Department of Zoology, National University of Singapore, Kent Ridge,
Singapore 0511, Republic of Singapore.

With 2 figures and 3 tables

Key words: Gorgonian, growth, sedimentation, time-lapse photography, Singapore.

Abstract. Annual growth rates of gorgonians in the Indo-Pacific region are reported for the first time. A method of measuring gorgonian growth using periodic photographic monitoring that is sensitive to horizontal growth and changes in growth foci but that does not require tedious underwater measurements is applied. Growth parameters of five species of gorgonians from three families (*Plexauridae*, *Melithaeidae*, and *Subergorgiidae*) were monitored over a period of 18 months using this method. Growth rates ranged from $2.30 \text{ cm} \cdot \text{a}^{-1}$ to $7.88 \text{ cm} \cdot \text{a}^{-1}$ in the highly sedimented waters of Singapore. The maximum number of branches added per year ranged from 1.7 to 14.5.

Problem

Growth rates of scleractinian corals have been extensively studied using different techniques, including direct measurements (SHINN, 1966), X-radiography (BUDDEMEIER & MARAGOS, 1974; HIGHSMITH, 1979), alizarin staining (LAMBERTS, 1974; GLADFELTER *et al.*, 1978), use of radioactive tracers (GOREAU, 1959), buoyant weighting (DAVIES, 1989), and time-lapse photography (BARNES & CROSSLAND, 1980; VAGO *et al.*, 1994). These measurements have been made in both long- and short-term experiments. In addition, coral growth has also been related to available light (BAK, 1974), sedimentation and turbidity (DODGE *et al.*, 1974; DODGE & VIASNYS, 1977), and water depth (OLIVER *et al.*, 1983).

Fewer studies have been made on the growth rates of gorgonians, one of the early published works being that of CARY (1914). In all these studies, colonies were measured directly, either with (WEINBERG & WEINBERG, 1979) or without (YOSHIOKA & YOSHIOKA, 1991) tagging of individual colonies. Sectioning of branches to measure growth rings has also been carried out (GRIGG, 1974; MITCHELL *et al.*, 1993). In terms of geographic location, these studies were conducted in the Mediterranean (VELIMIROV, 1975; WEINBERG & WEINBERG, 1979; MISTRI & CECCHERELLI, 1993), eastern Pacific (GRIGG, 1974), and the Caribbean (CARY, 1914; KINZIE, 1970; LASKER, 1991; YOSHIOKA & YOSHIOKA, 1991).

Growth rates of scleractinians have been used as indicators of changes in environmental conditions (BUDDEMEIER, 1974; HIGHSMITH, 1979). Gorgonian growth patterns should also be indicative of the environment in which they grow. Gorgonians generally grow faster than scleractinians, and changes in the environment that affect growth rates may be reflected more rapidly in gorgonian versus scleractinian corals. Since gorgonians are generally planar, their linear growth rates can be easily measured directly using the methods described here.

This paper provides baseline data on the growth rates of gorgonians in sedimented water in Singapore, using retrospective measurements with the aid of periodic photographic monitoring. No known study of this sort has been carried out on gorgonians in the Indo-West Pacific region. Two of the species studied, viz., *Acabaria robusta* and *Subergorgia suberosa*, are unlike previously studied gorgonians in that they are scleraxonians and do not possess a collagenous axial rod. In addition, gorgonians are generally believed to require relatively clear water to grow (BAYER, 1961). This study monitors gorgonian growth in a sedimented water environment. Although the species studied here may be azooxanthellate, extra energy would necessarily have to be expended to remove sediment from the surface, logically leading to growth rates that are lower than in reefs with clear waters. On the other hand, organic matter present in sediment would provide an easily available food source for the animals.

Material and Methods

1. Site description

The study site at Terumbu Pempang Tengah (TPT) is a patch reef (Fig. 1 with a significant (in terms of abundance and diversity) gorgonian community (GOH & CHOU, 1994). Scleractinian coral cover on reefs in Singapore generally ends at about 10 m below the reef crest. Gorgonians at TPT are found deeper than 10 m below the reef crest (actual depth: 12–14 m). The substrate on which the gorgonians are found consist mainly of a sandy bottom interspersed with rocks and boulders of various sizes. Sedimentation around the islands south of Singapore, including TPT, is high, averaging $14.1 \text{ mg cm}^{-2}\text{d}^{-1}$ (LOW & CHOU, 1994). This high sediment load can be attributed to extensive land reclamation around the coastline of the main island since the 1960s.

2. Species studied

Five species from three gorgonian families were studied. From the *Plexauridae*, *Echinogorgia* spp. A, C, and D; from the *Melithaeidae*, *Acabaria robusta*, and from the *Subergorgiidae*, *Subergorgia suberosa* (ESPER). The latter two families are classified in the suborder *Scleraxonia*, whose members lack a proteinaceous (collagenous) central core. Species of the *Plexauridae* are holaxonians, i.e., their 'skeleton' consists of a proteinaceous axial support (BAYER, 1981). Specimens are lodged in the Zoological Reference Collection, Department of Zoology, National University of Singapore. The colonial morphology of each of the five species is illustrated in Fig. 2.

3. Photographic monitoring

Permanent quadrats at about 12 m depth were established at the site. The extent of each quadrat was delineated by angle iron poles joined by nylon string. Compared with individual tagging of colonies,

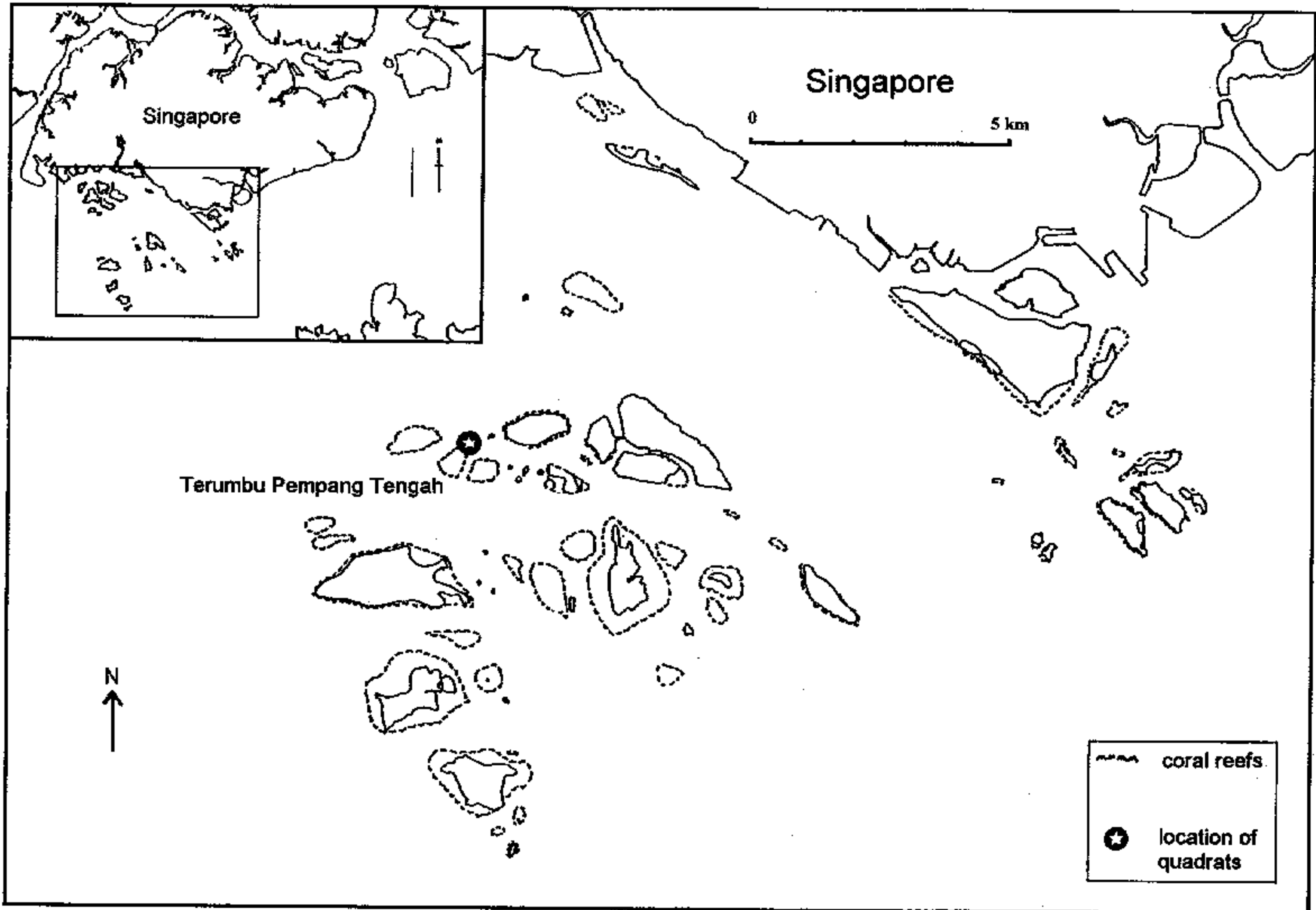


Fig. 1. The islands and reefs off Singapore's south coast, showing the study site at Terumbu Pempang Tengah.

this method does not introduce the unknown effect of the tag on the growth of the animal. Observations began on 10 March 1992 and the last colony was collected on 16 September 1993. All colonies were monitored for at least 12 months. Quadrats were visited at intervals of between 3 and 9 months, with each colony photographed a minimum of three times. Due to time constraints, it was not possible to prolong monitoring, although it would have been ideal to obtain measurements spanning at least 2 years. Colonies within the quadrats were photographed using a Nikonos V underwater camera with a 28 mm close-up unit artificially illuminated with an underwater strobe. The close-up frame ensured equidistance between the lens and the colony for each observation. Whole colonies were photographed where possible; in larger colonies, a series of photographs was used to record growth. Care was taken to ensure that the colony was placed within the same plane as the close-up frame. Since the photographic images were only used for comparison and not for actual measurements, this was not crucial but merely ensured a focussed image.

4. Growth measurements

At the end of the observation period, all colonies within the quadrats were collected, air-dried, and branch lengths measured. Measurements prior to and after drying revealed that shrinkage due to drying was less than 1% and this was subsequently ignored. Growth measurements were made retrospectively, directly on the collected colonies in relation to observable increases in size recorded in the time-lapse photographic slides. Annual growth was estimated by measuring the increase in length of individual branches. These increases in branch length were then used to calculate the average annual growth. Length increases were measured to the nearest tenth of a millimetre directly on the dried colonies using calipers. The establishment of new branches between observations was also recorded from the photographic slides. The branching frequency for each colony is given as the maximum number of branches that developed from a single 'parent' branch in a year. Colony height and colony widths were also measured on the dried colonies. Fan area was estimated by assuming the colony to be circular in shape in its plane of growth. The diameter of the circle was given by the mean of the colony height and

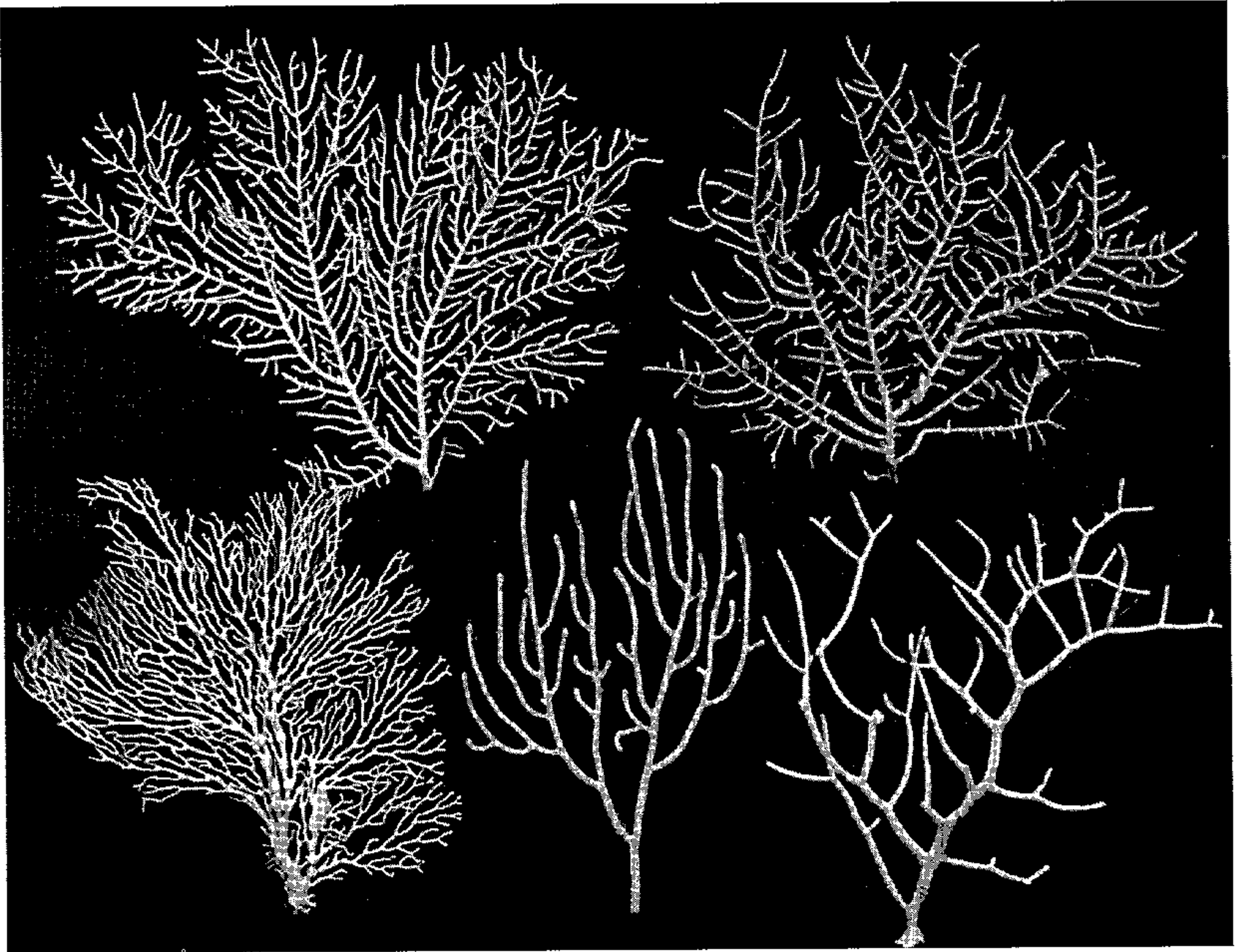


Fig. 2. Colony morphology of the five species studied, showing differences in branching patterns: top, left: *Echinogorgia* sp. C; top, right: *Echinogorgia* sp. A; bottom, left: *A. robusta*; bottom, centre: *Echinogorgia* sp. D; bottom, right: *S. suberosa*.

width. A circle was the most representative shape for which area could be approximated using the measurements obtained.

Results

Table 1 summarizes the growth parameters for each of the five species studied. Growth rates ranged from $7.88 \text{ cm} \cdot \text{a}^{-1}$ to $2.30 \text{ cm} \cdot \text{a}^{-1}$ (expressed in terms of 1 year for comparison with published work). The species, in descending order of growth rate, are: *A. robusta*, *S. suberosa*, *Echinogorgia* sp. D, *Echinogorgia* sp. C, and *Echinogorgia* sp. A. Species also differed in the rates of addition of new branches, with branching frequency ranging from 14.5 to 1.7 per year. *A. robusta* had the highest annual maximum rate of branch additions, followed by *Echinogorgia* sp. A, *Echinogorgia* sp. C, *S. suberosa*, and *Echinogorgia* sp. D. Colony size was expressed as fan area, colony height, and colony width.

The non-conformity of the data to the assumptions of the test for analysis of variance (ANOVA) precluded the use of the parametric test. Instead, the non-parametric KRUSKAL-WALLIS test was employed. Significant ($\alpha = 0.01$) differences were found in growth rate for all pairwise comparisons, except between *Echinogorgia* sp. C and *Echinogorgia* sp. D (Table 2).

The results of correlation analyses between growth rate and fan area, colony

Table 1. Summary of growth parameters for the five gorgonian species studied.

species		fan area (cm ²) ¹	colony height (cm)	colony width (cm)	branching frequency ²	growth rate ³ (cm · a ⁻¹)
family <i>Plexauridae</i>						
<i>Echinogorgia</i> sp. A	mean (n) ⁴	142.2 (9)	13.8 (9)	11.5 (9)	12.4 (9)	2.3 (82)
	SD	102.1	6.4	3.8	6.7	1.6
	min.	33.2	7	6	4	0.4
	max.	306.4	23.5	17.5	22	8.71
<i>Echinogorgia</i> sp. C	mean (n) ⁴	195.7 (5)	14.8 (5)	15.8 (5)	12 (5)	3.09 (41)
	SD	107.1	5.2	3.9	3.5	1.04
	min.	78.6	7.5	12.5	8	0.98
	max.	346.4	21.5	20.5	14	5.63
<i>Echinogorgia</i> sp. D	mean (n) ⁴	246.7 (4)	21.6 (4)	13.4 (4)	1.7 (4)	3.64 (43)
	SD	96.1	5.3	1.8	1.2	1.69
	min.	182.7	18.5	11	1	1.08
	max.	388.9	29.5	15	3	6.82
family <i>Melithaeidae</i>						
<i>Acabaria robusta</i>	mean (n) ⁴	220.7 (8)	17 (8)	14.4 (8)	14.5 (8)	7.88 (47)
	SD	150.2	7.1	6.7	2.9	2.59
	min.	44.2	7.5	4	10	3.96
	max.	424.6	30	24	19	13.74
family <i>Subergorgiidae</i>						
<i>Subergorgia suberosa</i>	mean (n) ⁴	931.3 (5)	29.6 (5)	33.8 (5)	4.3 (5)	5.47 (39)
	SD	774	12.8	17.4	4	2.36
	min.	154	15.5	12.5	1	2.3
	max.	1924.7	43.5	55.5	10	11.53

Notes: 1. Fan area is expressed as π multiplied by $\{(\text{mean of colony height and width})/2\}^2$. (Cross section of fan is assumed to be a circle with diameter given by the mean of the colony height and colony width).

2. Branching frequency denotes the maximum number of branches arising in a year from a single 'parent' branch.

3. Growth rate refers to annual linear increase in length of an individual branch (including 'daughter branches').

4. n refers to number of colonies measured for each species.

Table 2. Comparison of growth rates among the five gorgonian species studied.

	<i>Echinogorgia</i> sp. A	<i>Echinogorgia</i> sp. C	<i>Echinogorgia</i> sp. D	<i>Acabaria robusta</i>
<i>Echinogorgia</i> sp. C	0.0001*** 15.131			
<i>Echinogorgia</i> sp. D	0.0001*** 20.188	0.2576@ 1.2815		
<i>Acabaria robusta</i>	0.0001*** 78.34	0.0001*** 59.744	0.0001*** 46.152	
<i>Subergorgia suberosa</i>	0.0001*** 50.948	0.0001*** 27.979	0.0002*** 13.658	0.0001*** 17.086

*** denotes significant differences at the 0.01 level using the KRUSKAL-WALLIS non-parametric test; @ denotes non-significance at the 0.1 level.

Upper value gives Prob > χ^2 ; lower is the χ^2 value.

height, colony width, and branching frequency as well as between branching frequency and fan area, colony height, and colony width are shown in Table 3. Growth rate was correlated to area in both *Echinogorgia* sp. A ($P = 0.0044$) and *Echinogorgia* sp. D ($P = 0.088$). The correlation between growth rate and colony height was strongly significant ($P = 0.0007$) for *Echinogorgia* sp. A, but not correlated in the other four species. No significant correlation was found between growth rate and colony width except in *Echinogorgia* sp. D, but even then, the correlation was weak ($P = 0.088$).

Branching frequency was significantly ($P < 0.05$) correlated to fan area, colony height, and colony width in *Echinogorgia* sp. C, *A. robusta*, and *S. suberosa*. *Echinogorgia* sp. A had significant correlations between branching frequency and fan area and between branching frequency and colony height ($P = 0.0001$ for both), while *Echinogorgia* sp. D only had a significant correlation between branching frequency and colony height ($P = 0.0001$).

Discussion

Making accurate measurements *in situ*, while possible, requires much time. The constraints of not exceeding SCUBA diving no-decompression limits favours the use of a method that optimises the time spent underwater, *i.e.*, recording from as

Table 3. Correlation between growth rate and branching frequency and other colony morphometric parameters.

species		area	branches	height	width
<i>Echinogorgia</i> sp. A	rate	-0.31143 0.0044	0.81609 0.0001	-0.36696 0.0007	- n.s.
	branches	-0.4106 0.0001	- -	-0.49238 0.0001	- n.s.
<i>Echinogorgia</i> sp. C	rate	- n.s.	- n.s.	- n.s.	- n.s.
	branches	0.83333 0.0001	- -	0.83333 0.0001	0.83333 0.0001
<i>Echinogorgia</i> sp. D	rate	0.26332 0.088	0.69581 0.0001	- n.s.	0.26332 0.088
	branches	- n.s.	- -	-0.89072 0.0001	- n.s.
<i>Acabaria robusta</i>	rate	- n.s.	- n.s.	- n.s.	- n.s.
	branches	0.38327 0.0078	- -	0.31137 0.0331	0.35711 0.0137
<i>Subergorgia suberosa</i>	rate	- n.s.	0.44743 0.0055	- n.s.	- n.s.
	branches	-0.34238 0.0381	- -	-0.34238 0.0381	-0.34238 0.0381

Note: Upper value gives the SPEARMAN correlation coefficient (r), while the lower gives the significance probability that the true correlation in the population is zero (P value). r indicates the relationship between the two parameters; negative values correspond to inverse relationships.

n.s. denotes a P -value greater than 0.1; corresponding value for r is omitted.

many colonies as possible in the shortest possible time. Retrospective measurements aided by time-lapse photography overcomes this constraint. Since measurements are made directly on the colonies and not on the photographic images, the problem of ensuring that every picture in a series is taken from exactly the same orientation and aspect is eliminated. The method has one basic assumption, the growth between established branch points is negligible or zero. From comparisons of time-lapse slides, this assumption appears to be reasonable.

While the method works well for colonies with planar growth forms, it becomes less reliable for colonies with arborescent growth forms, where the orientation of branches in more than one plane makes comparisons of linear increases in length difficult. (This problem was avoided in this study by choosing species with generally planar colonies.) A possible solution is to frame the branches between two sheets of perspex so that they all lie in a single plane. If a grid is marked on one of the sheets, the other problem of detecting and measuring growth in colonies which show little or no branching (*e.g.*, sea whips) is also solved.

It is noteworthy that among the five species studied, the two fastest growing species, *A. robusta* and *S. suberosa*, are scleraxonians, while the genus *Echinogorgia* belongs to the *Holaxonia*. The lack of a proteinaceous axis in *A. robusta* and *S. suberosa* may account for their faster growth rates (Table 1). The growth rates reported in this paper are within the known ranges for gorgonians from other zoogeographical regions. The published rates for the Caribbean are: 0.8–3 cm · a⁻¹ (CARY, 1914) and 0.8–4.5 cm · a⁻¹ (YOSHIOKA & YOSHIOKA, 1991). In the Mediterranean, VELIMIROV (1975) reported growth rates of 0.5–2.2 cm · a⁻¹, WEINBERG & WEINBERG (1979) observed rates ranging from 1.3 cm · a⁻¹ to 3.3 cm · a⁻¹ for various species, while MISTRI & CECCHERELLI (1993) measured the mean annual growth rate for *Lophogorgia ceratophyta* to be 2.57 cm · a⁻¹. GRIGG (1974) reported growth rates of 0.0–6.0 cm · a⁻¹ for *Muricea californica* off the coast of California.

These comparable growth rates are noteworthy because some authors have stated that gorgonians require water of low turbidity for growth (*e.g.*, BAYER, 1961). The waters off Singapore are highly turbid, with SECCHI disc readings of between 1.3 m and 4.7 m, more commonly in the lower range (CHOU, 1986). Light attenuation is 60% in the first 4 m and at 10 m, where the quadrats were located, it increases to 95% (CHUANG, 1977). Besides blocking light, sediment in the water also affects sessile invertebrates by causing them to expend energy to rid themselves of the fine sediment (SALVAT, 1987). Sedimentation rates in local waters average 14.1 mg · cm⁻² · d⁻¹ (LOW & CHOU, 1994). The ability of Singapore gorgonians to grow in these high levels of sedimentation and turbidity could be due to their heterotrophic mode of nutrition (GOH, unpublished data), but they would still have to deal with the physical smothering effects of the sediment. An alternative explanation could be that the species that occur here are sediment-tolerant or sediment-adapted. LANE (1991) found that high sedimentation did not significantly retard hard coral growth in Singapore. An observable effect of the high sedimentation on gorgonians is that they occur at shallower depths than on other reefs in the region with clear water (GOH & CHOU, 1994).

None of the studies on gorgonian growth referred to above used branching frequency as a growth parameter. In some species, growth is mainly by elongation of existing branches (*e.g.*, *Echinogorgia* sp. D), whereas in others, the inter-nodal lengths are relatively short, with overall increase in length also involving the

addition of new branches (*e.g.*, *A. robusta*). Combining branching frequency with growth rates describes growth more fully and reveals differences that would go undetected if only linear growth rate was considered. BRAZEAU & LASKER (1988) observed that the reproductive polyps of many gorgonians are located on second and third order branches. Branching frequency and colony height might then be used to estimate age at onset of sexual maturity.

Colony height increase has been used to express gorgonian growth (*e.g.*, CARY, 1914; GRIGG, 1974; YOSHIOKA & YOSHIOKA, 1991; MISTRI & CECCHERELLI, 1993). WEINBERG & WEINBERG (1979) noted that using this parameter has the disadvantage of not recording horizontal size increases. VELIMIROV (1975) used the sum of the lengths of all the branches of a colony to express growth. While this method accounts for both vertical and horizontal growth, it is tedious and time consuming. WEINBERG & WEINBERG (1979) based their measurements on the increase in length of the longest budding sequence. This procedure addresses the problem of horizontal growth and is also relatively simple. However, it does not take into account changes in growth foci over time: the longest branch may stop growing in deference to the growth of another branch. The method used here (mean growth rates of branches throughout the colony) eliminates the three problems mentioned here, *i.e.*, horizontal growth, tedious measurements, and changes in growth foci. The present study shows that removing the entire colony (and all the colonies studied) is unnecessary. Instead, taking height and width measurements *in situ* and removing only the distal branches (plus some adjoining branches for reference) would suffice.

Many workers also assume colony height to be proportional to colony size. Since some species grow preferentially or equally in the horizontal vs. the vertical direction (*e.g.*, *S. suberosa*), colony size might be underestimated. Using fan area takes both horizontal and vertical growth into account.

The significant differences in annual growth rates between species (Table 2) is tempered by the fact that there was also significant within-species variation (except in *A. robusta*). Annual growth rate was significantly ($P < 0.05$) correlated to size only in *Echinogorgia* sp. A (Table 3). Growth for all colonies was recorded from a small area on the same reef. The prevailing currents, food and light availability, and sedimentation levels experienced by all the colonies would therefore be similar. The different growth rates between and within species point to different levels of efficiency in resource utilisation. This agrees with the high intra-specific variability in growth rates recorded by YOSHIOKA & YOSHIOKA (1991) in the Caribbean. The significant inter-specific differences could be partly accounted for by individual colony fitness in addition to inherent species-specific growth characteristics, *e.g.*, different skeletal composition.

Mixed results were obtained in Table 3 for correlations between growth rate and the other growth parameters. Only one (*Echinogorgia* sp. A) of the five correlations between growth rate and colony height was found to be significant. This contrasts with two significant correlations (*Echinogorgia* sp. A and *Echinogorgia* sp. D) between growth rate and fan area. These results support the use of fan area as a growth parameter (see earlier discussion). Significant correlations ($P < 0.05$) between branching frequency and colony height in all five species lead to the conclusion that, in general, colony height can be used to predict branching frequency for a particular species. Fan area was correlated ($P < 0.05$) to branching frequency in all species (except *Echinogorgia* sp. D), again indicating the usefulness

of this parameter in predicting branching frequency. Colony width was less reliable in predicting branching frequency, with only three out of five species showing significant correlations. Negative SPEARMAN correlation coefficients were obtained between growth rate and fan area, growth rate and colony height, branching frequency and fan area, and branching frequency and colony height in *Echinogorgia* sp. A. This was also the case for branching frequency and colony height in *Echinogorgia* sp. D, and between branching frequency and fan area, and colony height and colony width in *S. suberosa*. This indicates that for these three species, the growth rate or branching frequency (or both) decreases as colony size increases.

Summary

The method described here of using retrospective growth measurements to record temporal increases in branch lengths and branching frequency throughout the colony has the advantages of shorter underwater time (compared with direct measurements) as well as sensitivity to vertical and horizontal growth and to changes in growth foci. The use of fan area to more accurately describe colony size is suggested as an alternative to simple height measurements. The usefulness of this parameter is supported by the larger number of correlations between fan area and growth rate than between colony height and growth rate.

Annual growth rates of the five gorgonian species studied ranged from 2.30 $\text{cm} \cdot \text{a}^{-1}$ to 7.88 $\text{cm} \cdot \text{a}^{-1}$, with relatively high intra-specific variation, and were comparable to published growth rates from non-sedimented environments. The annual colony branching frequency varied according to species from 1.7 to 14.5 branches per year.

Acknowledgements

We would like to thank Dr PHIL ALDERSLADE of the Northern Territory Museum of the Arts and Sciences for help in taxonomy. The Reef Ecology Study Team, Department of Zoology, National University of Singapore was involved in various aspects of the field work. NKCG is supported by a research scholarship from the National University of Singapore and this paper forms part of his dissertation research. This paper was improved by suggestions from two anonymous reviewers.

References

- BAK, R. P. M., 1974: Available light and other factors influencing growth of stony corals through the year in Curacao. Proc. 2nd Int. Coral Reef Symp., Great Barrier Reef Committee, Brisbane, Vol. 2: 229–233.
- BARNES, D. J. & C. J. CROSSLAND, 1980: Diurnal and seasonal variations in the growth of a staghorn coral measured by time-lapse photography. Limnol. Oceanogr., **25**: 1113–1117.
- BAYER, F. M., 1961: The shallow water Octocorallia of the West Indian region. Martinus Nijhoff, The Hague; 373 pp.
- , 1981: Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa) with diagnoses of new taxa. Proc. Biol. Soc. Wash., **94**: 902–947.
- BRAZEAU, D. A. & H. R. LASKER, 1988: Inter- and intraspecific variation in gorgonian colony morphology: quantifying branching patterns in arborescent animals. Coral Reefs, **7**: 139–143.
- BUDDEMEIER, R. W., 1974: Environmental controls over annual and lunar cycles in hermatypic coral

- calcification. Proc. 2nd Int. Coral Reef Symp., Great Barrier Reef Committee, Brisbane, Vol. 2: 259–267.
- & J. E. MARAGOS, 1974: Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. *J. Exp. Mar. Biol. Ecol.*, **14**: 179–200.
- CARY, L. R., 1914: Observations upon the growth-rate and ecology of gorgonians. *Publ. Carnegie Inst. Wash.*, **182**: 79–90.
- CHOU, L. M., 1986: The coral reef environment of Singapore. In: L. S. CHIA, H. C. LEE, A. RAHMAN, P. L. TONG & W. K. WOO (Eds.), *Proceedings, Conference on the biophysical environment of Singapore and its neighbouring countries*. Geography Teachers' Association, Singapore: 93–102.
- CHUANG, S. H., 1977: Ecology of Singapore and Malayan coral reefs: preliminary classification. Proc. 3rd Int. Coral Reef Symp., Miami, Florida, Vol. 1: 55–61.
- DAVIES, P. S., 1989: Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar. Biol.*, **101**: 389–395.
- DODGE, R. E., R. C. ALLER & J. THOMSON, 1974: Coral growth related to resuspension of bottom sediments. *Nature*, **247**: 574–577.
- & J. R. VIASNYS, 1977: Coral populations and growth patterns: Responses to sedimentation and turbidity associated with dredging. *J. Mar. Res.*, **35**: 715–730.
- GLADFELTER, E. H., R. K. MONAHAN, & W. B. GLADFELTER, 1978: Growth rates of five reef-building corals in the northeastern Caribbean. *Bull. Mar. Sci.*, **28**: 728–734.
- GOH, N. K. C. & L. M. CHOU, 1994: Distribution and biodiversity of Singapore gorgonians (sub-class Octocorallia) — a preliminary survey. *Hydrobiologia*, **285**: 101–109.
- GOREAU, T. F., 1959: The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biol. Bull. (Woods Hole)*, **116**: 59–75.
- GRIGG, R. W., 1974: Growth rings: Annual periodicity in two gorgonian corals. *Ecology*, **55**: 876–881.
- HIGHSMITH, R. C., 1979: Coral growth-rates and environmental control of density banding. *J. Exp. Mar. Biol. Ecol.*, **37**: 105–125.
- KINZIE, R. A., 1970: The ecology of the gorgonians (Cnidaria, Octocorallia) of Discovery Bay, Jamaica. Ph. D. dissertation, Yale University, U.S.A.: 107pp.
- LAMBERTS, A. E., 1974: Measurement of alizarin deposited by coral. Proc. 2nd Int. Coral Reef Symp., Great Barrier Reef Committee, Brisbane, Vol. 2: 241–244.
- LANE, D. J. W., 1991: Growth of scleractinian corals on sediment-stressed reefs at Singapore. Proceedings of the Regional Symposium on Living Resources in Coastal Areas, Marine Science Institute, University of the Philippines, Dilliman, Quezon City 1101, Philippines: 97–106.
- LASKER, H. R., 1991: Population growth of a gorgonian coral: equilibrium and non-equilibrium sensitivity to changes in life history variables. *Oecologia*, **86**: 503–509.
- LOW, J. K. Y. & L. M. CHOU, 1994: Sedimentation rates in Singapore waters. Proceedings, ASEAN-Australia Symposium on Living Coastal Resources, Bangkok, May 16–20, 1994: 697–701.
- MISTRI, M. & V. U. CECCHERELLI, 1993: Growth of the Mediterranean gorgonian *Lophogorgia ceratophyta* (L., 1758). *P.S.Z.N.I: Marine Ecology*, **14**: 329–340.
- MITCHELL, N. D., M. R. DARDEAU & W. W. SCHROEDER, 1993: Colony morphology, age structure, and relative growth of two gorgonian corals, *Leptogorgia hebes* (VERRILL) and *Leptogorgia virgulata* (LAMARCK), from the northern Gulf of Mexico. *Coral Reefs*, **12**: 65–70.
- OLIVER, J. K., B. E. CHALKER & W. C. DUNLAP, 1983: Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of *Acropora formosa* (DANA, 1846). *J. Exp. Mar. Biol. Ecol.*, **73**: 11–35.
- SALVAT, B., 1987: Dredging in coral reefs. In: B. SALVAT (Ed.), *Human impacts on coral reefs: facts and recommendations*. Antenne Museum E.P.H.E., French Polynesia: 165–184.
- SHINN, E. A., 1966: Coral growth-rate, an environmental indicator. *J. Paleontol.*, **40**: 233–241.
- VAGO, R., E. VAGO, Y. ACHITUV, M. BEN-ZION & Z. DUBINSKY, 1994: A non-destructive method for monitoring coral growth affected by anthropogenic and natural long term changes. *Bull. Mar. Sci.*, **55**: 126–132.
- VELIMIROV, B., 1975: Wachstum und Altersbestimmung der Gorgonie *Eunicella cavolinii*. *Oecologia*, **19**: 259–272.
- WEINBERG, S. & F. WEINBERG, 1979: The life cycle of a gorgonian: *Eunicella singularis* (ESPER, 1794). *Bijdr. Dierk.*, **48**: 127–140.
- YOSHIOKA, P. M. & B. B. YOSHIOKA, 1991: A comparison of the survivorship and growth of shallow water gorgonian species of Puerto Rico. *Mar. Ecol. Prog. Ser.*, **69**: 253–260.