Comparative morphometry of fan-like colonies of three mediterranean gorgonians (Cnidaria: Gorgonacea)

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Abstract: The aim of the present study was to quantify the variation of the colony structure of the three abundant mediterranean gorgonians *Eunicella singularis*, *E. cavolini* and *Lophogorgia ceratophyta* (Coelenterata: Octocorallia). Only one growth form, i.e. fan-like colonies, was chosen, as this facilitated the comparison between species. Moreover, fan-like colonies are abundant at the study sites and a method is available for the precise determination of colony size. Comparing branching and growth patterns by the correlation between architectural features and fan size, both *Eunicella* species were different from *L. ceratophyta* probably as a result of the taxonomic differences between the two genera. On comparison of the mean values of architectural features, *E. cavolini* showed more similarity with *L. ceratophyta* than with *E. singularis* indicating functional similarity between *E. cavolini* and *L. ceratophyta*. Architectural features as defined in this study might be useful for studying inter- and intraspecific variations of colony structure in gorgonian corals.

Résumé : *Morphométrie comparée des colonies de trois gorgones méditerranéennes (Cnidaria: Gorgonacea)*
Le but de cette étude était de quantifier la variation dans la structure des colonies de trois espèces de gorgones méditer-ranéennes abondantes, *Eunicella singularis*, *E. cavolini* et *Lophogorgia ceratophyta* (Coelenterata : Octocorallia). Pour faci-liter la comparaison entre les espèces, un seul morphotype, la forme en éventail, fut choisi étant donné que ces formes domi-nent dans le site étudié et qu´une méthode est disponible pour la détermination précise de la taille des colonies. Une comparaison de la ramification et de la structure de croissance, i.e. la corrélation entre les traits architecturaux et la taille de l´éventail, montre que les deux espèces d´*Eunicella* se distinguent de *L. ceratophyta*, ce qui est interprété comme une diffé-rence taxonomique entre les deux genres. Cependant, l´étude des structures coloniales, basée sur la comparaison des valeurs moyennes des traits architecturaux, montre que *E. cavolini* est plus proche de *L. ceratophyta* que de *E. singularis*, ce qui indique une similitude fonctionnelle entre *E. cavolini* et *L. ceratophyta*. Les traits architecturaux, tels que nous les avons définis, sont considérés comme utiles pour étudier les variations inter et intraspécifique des structures coloniales chez les gorgones.

Keywords : Gorgonians, Colony structure, Mediterranean Sea.

Introduction

During the course of evolution many different supporting structures that maintain colonies upright in currents have developed in sessile cnidarians. Hydroskeletons, massive skeletons composed of calcium carbonate, free calcium carbonate sclerites and flexible protein skeletons with a varying amount of mineral inclusions are present. These structures produce a wide variety of growth forms, e.g. trees, bushes, whips, dishes and fans. In general, the overall colony structure of an aquatic, arborescent organism is a

compromise between increasing the surface area to maximize particle and nutrient uptake and simultaneously decreasing the surface area to minimize hydrodynamic forces (Koehl, 1984).

In gorgonian corals, it is well known that many species with different morphological features may be found in similar water movement zones (Goldberg, 1973, Kinzie, 1973, Lasker & Coffroth, 1983, Muzik & Wainwright, 1977, Opresko, 1973, Yoshioka & Yoshioka, 1989). However, it is not known how colonies with different morphologies are adapted to similar hydrodynamic forces. In gorgonians, factors such as flexibility or stiffness of colonies (Esford & Lewis, 1990, Jeyasuria & Lewis, 1987, Sponaugle, 1991) and architectural features such as porosity and different growth and branching patterns (Velimirov, 1976, Weinbauer & Velimirov, 1995) were shown to be adaptations to the water flow. Moreover, architectural features change with branch order (Brazeau & Lasker, 1988), colony region and size of colonies (Weinbauer & Velimirov, 1995). However, investigations on the interspecific variation of colony morphology and growth form of corals are sparse (Chamberlain & Graus, 1975, Muzik & Wainwright, 1977). Recently, methods were developed to quantify the branching pattern of gorgonians (Brazeau & Lasker, 1988) and to distinguish growth forms in stony corals (Dauget, 1991). Architectural features may regulate the water flow through colonies, thereby sustaining maximum feeding efficiencies (Harvell & LaBarbera, 1985, Sponaugle, 1991, Sponaugle & LaBarbera, 1991). Also, some information is available on biomechanical properties of octocorals (Esford & Lewis, 1990, Jeyasuria & Lewis, 1987, Wainwright, et al. 1976).

The mediterranean gorgonians Eunicella singularis Esper, E. cavolini Koch and Lophogorgia ceratophyta Linné occasionally grow in the same environment and thus tolerate similar hydrodynamic conditions (Velimirov 1976, Weinberg 1979). Though the colony structure of these species comprises intraspecific variability that is related to colony region or size of colonies and water flow (Mistri & Ceccherelli, 1993, Velimirov 1976, Weinbauer & Velimirov, 1995), their overall structure differs substantially (Weinberg, 1976). Yet, how species that differ in colony structure can coexist under the same hydrodynamic conditions is poorly understood. Fan-like growth forms of E. singularis, E. cavolini and L. ceratophyta develop frequently in oscillating water bodies (Riedl, 1964, Velimirov, 1973). We used fan-like colonies in our investigation because 1) fan-like colonies are the most abundant growth form in the environment investigated, 2) this comparatively simple growth form facilitates the comparison between species and 3) a method developed by Weinbauer and Velimirov (1995) for the precise determination of colony size is available and allows the

investigation of possible variations of architectural features with the colony size. It was the aim of this study to assess the variability of the colony structure of these species in relation to colony region and size by measuring detailed architectural features already used in another study (Weinbauer and Velimirov 1995) such as porosity, interbranch distances, branch thickness, branch lengths, ramification densities and height to width ratios. Porosity is here defined as the amount of free space within the branching network of a colony. Quantifying the intraspecific variability of the colony structure in co-occurring species may be a first step towards understanding how gorgonians can coexist in the same environment.

Material and methods

Sampling site and sampling strategy. Eunicella singularis and E. cavolini were collected in the Bay of Calvi (northwest Corsica, France), whereas Lophogorgia ceratophyta was collected in Cinque Terre (Italy) because the species is only occasionally found in the Bay of Calvi and so we decided against destructive sampling. Since branch thickness, end branch length, and height to width ratio (for a definition of these parameters see below) of the few observed colonies were not different from the colonies from Cinque Terra (data not shown), we used the colonies from Cinque Terra for a comparison with the genus Eunicella. White, yellow and purple colonies of L. ceratophyta were collected in about 30 m. E. singularis colonies were collected at two depth ranges (19 - 23 m and 30 - 34 m). In these depths we found the highest population density of E. singularis. E. cavolini was collected in similar depth ranges (17 - 23 m and 30 - 35 m). Colonies were considered fan-like when a minimum of 3 tips formed a single plane of ramification. For a given species, we collected approximately the same number of colonies for each size class in each depth range. Colonies were dried at 80 °C, cleaned of overgrowth (mainly algae, sponges and encrusting octocorals) and dry weight was determined.

Architectural features. Dried fans were photocopied and total branch length was measured using a planimeter. Height was considered the distance between the holdfast and the most distant branch tip of the colony (Fig. 1). A compass was used to draw 3 arcs across a photocopied colony at equal distances along the height axis by using the holdfast as central point. Along the arcs the distance between neighbouring branches (interbranch distance) and the thickness of each branch was determined. Multiplying the mean branch thickness by the total branch length resulted in the projected branch surface area. Measurements of the outline of the fans and subsequently the fan surface area (FSA) was done as described previously by Weinbauer and Velimirov (1995). Basically, a line was drawn between
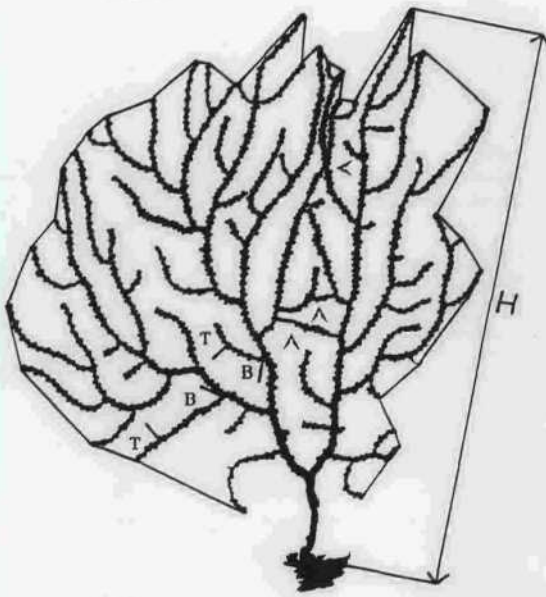
Figure 1. Determination of fan surface area and colony regions. For colony regions only tips (T) and branches (B) are indicated. The basal region is the part without branches and tips. Arrow heads point to anastomoses. H = height axis.

Figure 1. Determination de la surface de l'éventail et régions de la colonie. Seules les pointes des branches (T) et les branches terminales (B) sont indiquées. La région basale est la partie sans branches et sans pointes. Les flèches marquent les anastomoses. H = hauteur de l'axe.

neighbouring branch tips at the periphery of colonies and the area within this outline determined (Fig. 1). We excluded open areas from the FSA, i.e. areas within the outline of the colonies characterized by the absence of branches that do not contribute functionally to the fan (Weinbauer & Velimirov, 1995). End branches along the outline were considered peripheral. The remainders of the end branches were termed central. An end branch extends from a branch tip downwards to the first ramification.

In addition, the following parameters were determined or calculated: 1) peripheral end branch length; 2) central end branch length; 3) ramification density, i.e. the number of ramifications per cm^2 FSA; 4) porosity, i.e. ratio of FSA to branch surface area, 5) height to width ratio where the width is calculated as the mean of three measurements done at equidistant positions at a right angle to the height, and 6) the number of anastomoses, i.e. fusions of branches.

Weight parameters. For determination of weight parameters, the colonies were divided into three colony regions (Fig. 1): branch tips (10 mm length), branches (remainder of the end branches when the tips are clipped off) and the basal region (remainder of the colony). For other species it was shown previously that these colony regions differ with respect to calcium carbonate content and calcification rates (Velimirov & Böhm, 1976). After the

colony regions were weighed the cortex was separated from axial skeletons using tweezers and a mortar. Sclerite content and ash-free dry weight (AFDW) of the cortex were determined by combustion of the cortex at 450 °C for 4 hours (Harvell & Fenical, 1989, Harvell & Suchanek, 1987). This combustion temperature and time avoids losses of sclerite weight due to disruption of water of hydration. Cortex mineralization was calculated as the percent proportion of sclerites on the overall cortex weight.

Results

Weight parameters. The mean values of axis, sclerites and AFDW with respect to total colony weight and the cortex mineralization are shown in Table 1. Sclerite weight and AFDW varied significantly between species, but axis weight did not. The relative proportions of axis, sclerites and AFDW are 1.9 : 3.1 : 1.0 for *E. singularis,* 2.5 : 4.1 : 1.0 for *E. cavolini,* and 2.0 : 2.3 : 1.0 for *L. ceratophyta,* showing that the sclerites are the most prominent weight fraction. Cortex mineralization was highest in *E. cavolini* (80.5%), followed by *E. singularis* (75.7%) and *L. ceratophyta* (70.1%).

Table 1. Weight parameters (± SD) of whole colonies compared (Kuskal-Wallis one-way analysis of variance) between *Eunicella singularis, E. cavolini* and *Lophogorgia ceratophyta.* n = number of colonies. NS = not significant. * P < 0.05, *** P < 0.005.

Tableau 1. Comparaison des paramètres pondéraux (± Écart type) chez *Eunicella singularis, E. cavolini* et *Lophogorgia ceratophyta.* n = nombre de colonies. NS = non significatif. * P < 0.05, *** P <0.005.

species	n	% of total colony weight			cortex mineralization
		axis	sclerites	AFDW	
E. singularis	9	31.7(4.72)	51.8(2.46)	16.4(0.77)	75.7(3.29)
E. cavolini	9	33.1(6.54)	53.9(5.25)	13.0(1.29)	80.5(2.29)
L. ceratophyta	6	37.1(7.28)	44.1(5.01)	18.8(2.28)	70.1(1.94)
H		5.18	12.41	19.78	19.28
Significance		NS	*	***	***

In all species, the axis, sclerite and AFDW proportions and the cortex mineralization varied significantly among colony regions (Table 2). Axis, sclerites and AFDW percentages increased towards the base of the colonies in *E. cavolini* and *L. ceratophyta.* There was also an increase in axis weight of *E. singularis* towards the base, but sclerites and AFDW percentages were highest in the branches and lowest in the tips. In all species the cortex mineralization increased significantly towards the base.

Architectural parameters. In all species, we found a positively skewed frequency distribution of the interbranch distances (Fig. 2). The most frequent interbranch distance

Table 2. Comparison of weight parameters (± SD) of *E. singularis, E. cavolini* and *L. ceratophyta* compared (Friedman two-way analysis of variance) in different colony regions. n = number of investigated colonies. * P < 0.05, ** P < 0.01, *** P < 0.005, **** P < 0.0001.

Tableau 2. Comparaison des paramètres pondéraux (± Écart type), par la méthode d'analyse des variances de Friedman, de différentes régions des colonies de *E. singularis, E. cavolini* et *L. ceratophyta.* NS = non significatif. * P < 0.05, ** P < 0.01, *** P < 0.005, **** P< 0.0001.

| species | n | colony region | % of total colony weight | | | degree of mineralization |
			axis	sclerites	AFDW	
E. singularis	9	tips	1.3(0.80)	4.5(1.52)	1.6(0.55)	73.59(3.10)
		branches	10.0(3.55)	27.0(5.66)	9.6(2.01)	74.10(3.57)
		base	20.3(4.72)	19.7(4.82)	5.2(1.56)	78.39(2.87)
T			16.22	14.00	18.00	14.00
Significance			****	***	****	***
E. cavolini	9	tips	2.5(1.16)	10.7(3.54)	2.8(0.93)	78.91(1.17)
		branches	4.8(1.70)	16.0(3.44)	4.0(0.86)	80.23(3.10)
		base	25.7(6.47)	27.2(4.05)	6.2(0.92)	81.39(2.47)
T			18.20	16.80	15.65	6.20
Significance			****	****	****	*
L. ceratophyta	6	tips	1.8(0.75)	6.1(2.08)	3.1(1.04)	66.60(1.91)
		branches	6.6(7.37)	11.2(2.02)	5.5(1.01)	67.01(2.92)
		base	28.7(5.62)	26.8(2.87)	10.2(1.10)	72.38(2.00)
T			14.00	14.00	14.00	10.33
Significance			***	***	***	**

within the fans (irrespective of fan size) was > 0.4 - 0.6 cm in *E. singularis* and *E. cavolini* comprising 39.0 and 24.4%, respectively, of all size classes, whereas the most abundant branch distance of *L. ceratophyta* was > 0 - 0.2 cm (39.9% of all size classes). The first size class with zero frequency is encountered at approximately 3 cm distance in all species and all following distance frequencies between branches were low, with a maximum of 0.35%. We used this frequency distribution to exclude open areas from the FSA. In case the open areas in a colony were larger than a 3 x 3 cm square, we inserted as many squares as possible in the open areas (Weinbauer and Velimirov 1995). The FSA was corrected for the open areas by subtraction of the sum of all these squares. This correction of FSA had to be performed in 31 % of *E. singularis* colonies compared to 8% in *E. cavolini* and *L. ceratophyta.* The resulting FSAs ranged from 13.5 to 254 cm^2 in *E. singularis,* from 4.0 to 267 cm^2 in *E. cavolini* and from 10.3 to 825 cm^2 in *L. ceratophyta.*

Mean architectural features for all species and the significance of interspecific variations of architectural features are shown in Tables 3 and 4. Porosity values were highest in *E. cavolini* (3.4), followed by *L. ceratophyta* (3.0)

and *E. singularis* (2.8). Expressed as a percentage, porosity was 72.5%, 66.4% and 64.6% of the FSA for *E. cavolini, E. singularis* and *L. ceratophyta,* respectively. The porosity values in *E. cavolini* were significantly different from that of *E. singularis* and *L. ceratophyta. E. singularis* had the thickest branches (2.4 mm); branch thickness of *L. ceratophyta* was the lowest (1.6 mm) and that of *E. cavolini* were intermediate (2.0 mm). The end branch length of *E. singularis* (7.3 cm) was significantly higher than of both *E. cavolini* (2.3 cm) and *L. ceratophyta* (2.0 cm). The ramification density showed significant differences among all species: values were highest in *L. ceratophyta* (0.86 cm), followed by *E. cavolini* (0.45 cm) and *E. singularis* (0.12 cm). The length to width ratio of *E. singularis* (7.6) was significantly higher than that of *E. cavolini* (2.6) and *L. ceratophyta* (2.2). We found no anastomoses in *E. singularis,* whereas 34.4% of *E. cavolini* colonies and 42.3% of *L. ceratophyta* colonies showed anastomoses.

To investigate potential differences of morphological features of *Eunicella* between the two investigated depth ranges, colonies were divided into the size ranges <100 cm^2 FSA, ≥100 <200 cm^2 FSA and ≥200 cm^2 FSA. With the
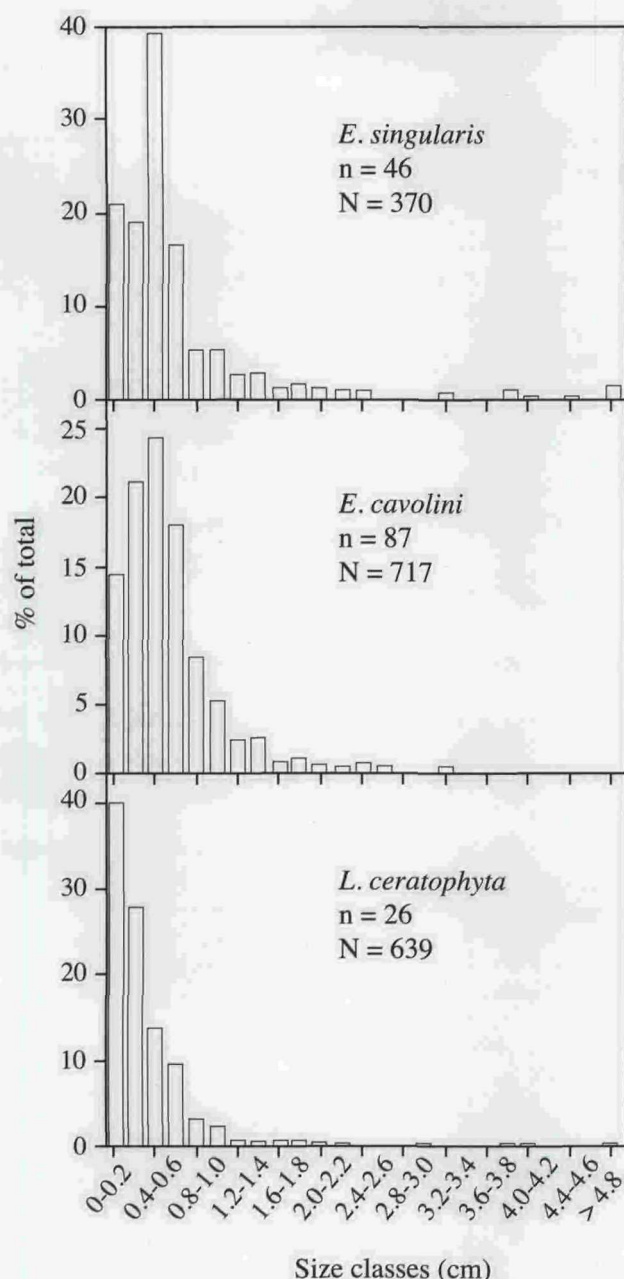
Figure 2. Frequency distribution of interbranch distances of *Eunicella singularis*, *E. cavolini* and *Lophogorgia ceratophyta*. n = number of colonies, N = number of interbranch distances

Figure 2. Distribution des fréquences des distances inter-branches de *Eunicella singularis*, *E. cavolini* et *Lophogorgia ceratophyta*. n = nombre de colonies, N = nombre de distances inter-branches.

exception of branch thickness, architectural parameters did not vary significantly between depths (Mann-Whitney U-test: P always > 0.19). Branch thickness of *E. singularis* in the size class ≥100 <200 cm² FSA and of *E. cavolini* <100 cm² FSA was slightly, but significantly higher in

deeper water (P < 0.05). In the other size classes branch thickness did not vary significantly with depth (P > 0.13).

Since colony morphology generally did not vary with depth, correlations between single architectural features and fan size were calculated for all colonies sampled (Table 5). In no species did the porosity values vary with the size of the colony. However, this parameter showed a high degree of variation in all species, ranging from 1.9 to 6.8 in *E. singularis*, from 2.2 to 8.5 in *E. cavolini* and from 1.9 to 4.4 in *L. ceratophyta*. Only in the genus *Eunicella* did the branch thickness increase significantly with colony size. End branch length showed a significant increase with fan size in all species, whereas the height to width ratio decreased significantly with fan size. *E. singularis* and *E. cavolini* showed a significantly negative correlation of ramification density with fan size, whereas in case of *L. ceratophyta*, ramification density did not vary significantly with fan size. Although we found some significant relationships between architectural features and fan size, the correlation coefficients were generally low. The percentage of colonies with anastomoses increased with colony size in *E. cavolini* and *L. ceratophyta* (Fig. 3). Ca. 17% of colonies ≤100 cm² FSA showed anastomoses compared to ca. 70 - 80% in colonies >300 cm² FSA.

In all species end branch length was significantly greater in the periphery than in the center of colonies (Wilcoxon signed rank test; P < 0.01 for all species; Fig. 4). In the periphery and the center, mean values were 10.4 and 7.0 cm in *E. singularis*, 2.7 and 1.8 cm in *E. cavolini* and 2.3 and 1.6 cm in *L. ceratophyta*.

In *L. ceratophyta*, the architectural parameters did not vary significantly with the color of the colonies (Kruskal-Wallis test: P > 0.15).

Discussion

Pore space is a major parameter determining water flow through a filter such as the branching network of a fan-like gorgonian colony. Since porosity is 66.6% in *E. singularis*, 72.5% in *E. cavolini* and 64.7% in *L. ceratophyta*, approximately one third of the surface area of the fans is occupied by branches. From data reported for Fijian gorgonians (Muzik & Wainwright, 1977) we calculated porosity values in the range of 67 - 91%. Porosity values for the species in the present study are in the lower third of this spectrum indicating that the branching network of *E. singularis*, *E. cavolini* and *L. ceratophyta* is comparatively tight. In species such as *Gorgonia ventalina*, porosity is even considerably lower.

The stiffness of supporting structures, i.e. axis and the extent to which it is mineralized, as well as the cortex and sclerite content influence the ability of gorgonians to withstand hydrodynamic forces. The cortex contributes

Table 3. Measurements of compared architectural features (ANOVA) of *E. singularis*, *E. cavolini* and *L. ceratophyta*. n = number of investigated colonies.
Tableau 3. Mesures des caractères architecturaux comparés (ANOVA) de *E. singularis*, *E. cavolini* et *L. ceratophyta*. n = nombre de colonies étudiées.

parameter	n	E. singularis	n	E. cavolini	n	L. ceratophyta	significance
				species			
porosity	46	2.8(1.01)	49	3.4(1.30)	26	3.0(1.46)	F = 2.374 P < 0.1
branch thickness (mm)	46	2.4(0.34)	87	2.0(0.32)	26	1.6(0.19)	F = 56.921 P < 0.001
end branch length (cm)	46	7.3(5.52)	87	2.3(0.76)	26	2.0(0.34)	F = 114.058 P < 0.001
ramification density	46	0.12(0.053)	87	0.45(0.206)	26	0.86(0.281)	F = 112.585 P < 0.001
Height/width	46	7.6(4.96)	87	2.6(0.66)	26	2.2(0.90)	F = 36.414 P < 0.001

Table 4. A posteriori test (Fischer's PLSD) of the results from table 3 comparing architectural features for groups of two species. NS = not significant. * P < 0.05, *** P < 0.005.
Tableau 4. Test a posteriori (PLSD de Fisher) des résultats du tableau 3, comparant les caractères architecturaux par groupes de deux espèces, NS = non significatif.

source of variation	E. singularis x E. cavolini		E. singularis x L. ceratophyta		E. cavolini x L. ceratophyta	
	F	significance	F	significance	F	significance
porosity	5.056	*	0.352	NS	1.592	NS
branch thickness	33.383	***	113.424	***	49.446	***
end branch length	207.580	***	116.592	***	0.264	NS
ramification density	93.308	***	219.533	***	83.187	***
height/width	86.112	***	52.608	***	0.432	NS

from 0.8 to 96.9% to the stiffness of the colonies (Esford & Lewis, 1990, Jeyasuria & Lewis, 1987). Cortex mineralization in different colony regions of gorgonians ranges from 35% to ca. 95% (Harvell & Fenical, 1989, Harvell & Suchanek, 1987, Velimirov & Böhm, 1976). The investigated gorgonians have mineral contents in the upper half of this spectrum (Table 2). Moreover, sclerite + AFDW content (cortex) is the most important weight fraction in all species (Table 1). Thus, it is conceivable that the cortex contributes significantly to the colony stiffness of the investigated gorgonians. The differences of weight parameters between species indicate that stiffness and flexibility and thus the

resistance of colonies against hydrodynamic forces differed between the investigated species.

In our analysis two methods for interspecific comparison of colony morphology were used. The first compares growth and branching patterns between species estimated from the variation of architectural features with fan size; the second compares the colony structure of individual species using the mean values of architectural features.

In contrast to the *Eunicella* species, branch thickness did not change with fan size in *L. ceratophyta* (Table 5). *L. ceratophyta* has two types of branches: 1) a few thick branches which serve mainly as supporting structures and 2)

Table 5. Correlation between fan surface area and different architectural features of *E. singularis*, *E. cavolini* and *L. ceratophyta*. NS = not significant. * P < 0.05, *** P < 0.005, **** P 0.001, ***** P < 0.0005.

Tableau 5. Corrélation entre surface d'éventail et différents caractères architecturaux de *E. singularis*, *E. cavolini* et *L. ceratophyta*. NS = non significatif. * P < 0.05, *** P < 0.005, **** P 0.001, ***** P < 0.0005.

	E. singularis		*E. cavolini*		*L. ceratophyta*	
	r	P	r	P	r	P
porosity	0.13	NS	0.22	NS	0.28	NS
branch thickness	0.33	*	0.31	***	0.23	NS
endbranch length	0.31	*	0.32	***	0.46	*
ramification density	- 0.36	***	- 0.42	*****	0.09	NS
height/width	- 0.39	*	- 0.34	****	- 0.65	****

Figure 4. End branch length in the center and the periphery of the investigated species. n = number of investigated colonies. Wilcoxon signed rank test showed significant differences between the colony regions for all species (*E. singularis*: P < 0.01: *E. cavolini*: P < 0.0001; *L. ceratophyta*: P < 0.005).

Figure 4. Longueur de la branche terminale au centre et à la périphérie pour chacque espèce. n = nombre de colonies étudiées. Le test de rang de Wilcoxon montre des différences significatives entre ces deux régions de la colonie pour toutes les espèces étudiées.
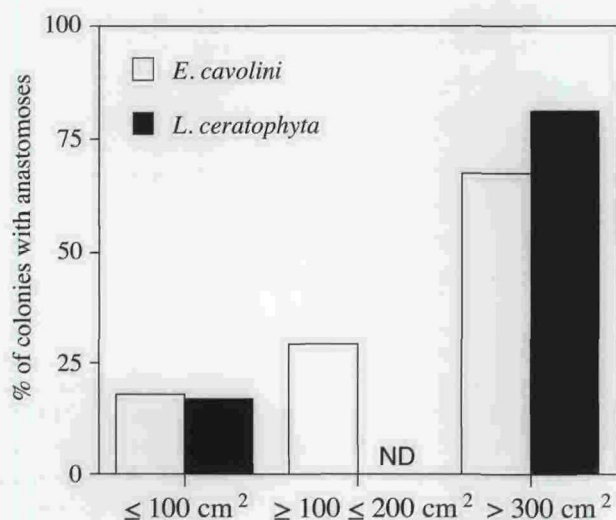

Figure 3. Percentage of colonies with anastomoses in different colony size classes. ND = not determined, because in this size class only one colony was collected.

Figure 3. Pourcentage de colonies avec anastomoses dans les différentes classes de tailles. ND = non déterminé, car une seule colonie a été récoltée dans cette classe de taille.

many fine branches which fill the remaining space. Only the main branches increase significantly in diameter with age. In *Eunicell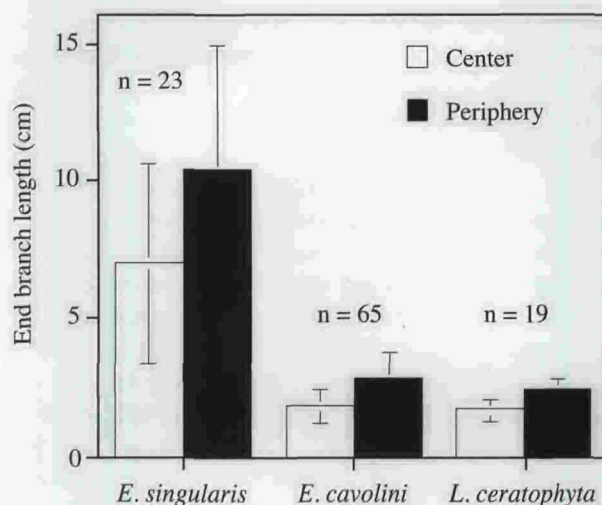a* species there are no main branches and all branches thicken with age. Moreover, large *Eunicella* colonies have a lower ramification density than smaller colonies, whereas ramification density does not change with colony size in *L. ceratophyta*. Using fractal dimensions, Mistri & Ceccherelli (1993) found that colonies of *L. ceratophyta* older than 1.5 - 2.5 years do not change the complexity of their branching pattern. These differences between *Eunicella* species and *L. ceratophyta* correspond to growth and branching pattern differences between the families Plexauridae and Gorgoniidae.

Comparing mean values of the architectural features (Tables 3 and 4) illuminated a different pattern of interspecific variation. *E. singularis* can be described as the species with the longest and thickest branches, the lowest ramification density and the greatest height to width ratio. *L. ceratophyta* is characterized by fine, short and highly ramified branches with a low fan height to width ratio. Colonies of *E. cavolini* were similar to *L. ceratophyta*, but with slightly thicker and less ramified branches. Also, the percentage of colonies with anastomoses was similar in *E. cavolini* and *L. ceratophyta* (Fig. 3), whereas *E. singularis* colonies lacked anastomoses. Overall, the structure of *E. cavolini* is quite similar to that of *L. ceratophyta* indicating similar functional features. Moreover, the importance of all weight parameters decreased from the base towards the tips in *E. cavolini* and

L. ceratophyta, whereas in *E. singularis* the sclerites and AFDW were most prominent in the intermediate colony region. This supports the view that *E. cavolini* and *L. ceratophyta* are more similar to each other than to *E. singularis*.

As *E. singularis* is the only zooxanthellate gorgonian investigated, its different colony structure could be a functional adaptation to this symbiosis with zooxanthellae. The long end branches and the low ramification density of this species may lessen self-shading of branches, and a high surface area for photosynthesis could be provided by the thick branches. Morphological adaptations to different light intensities are well known for stony corals (Barnes, 1973, Dustan, 1975, Jaubert, 1977, Yonge, 1973), and morphological variations of colonies with depth and therefore light intensity have been found in Caribbean gorgonians (Brazeau & Lasker, 1988, West, *et al.* 1993). However, in the present study architectural parameters of *E. singularis* generally did not vary with water depth and thus presumably with light intensity. Whereas the species-specific morphology of *E. singularis* may be related to the symbiosis, light intensity did not seem to affect the architectural parameters at the two depths investigated.

Colony morphology of gorgonians and antipatharians (including parameters investigated in the present study) varies with the intensity of water movement (Velimirov, 1976, Warner, 1981, Weinbauer & Velimirov, 1995). Surprisingly, architectural parameters of the genus *Eunicella* generally did not vary significantly between the depths in the present study. In about 20 m depth, colonies are found in comparatively protected areas, such as small crevices or overhanging walls but not on horizontal subtratum. In 30 - 35 m colonies are also found on horizontal rock faces. Colonization of different habitats in the two depths could indicate a similar exposure to water movement. This is supported by the finding that branch thickness, an indicator of intensity of water movement (Velimirov, 1976, Weinbauer & Velimirov, 1995), showed only minor differences between the two depths investigated. Consequently, the differences of water movement between the two depths might be too small to cause significant differences in architectural features.

Although we did not find variations of colony morphology with depth, some morphological features varied with colony region and fan size. Weinbauer & Velimirov (1995) showed that for each colony size class of *E. cavolini* there exists a balance between low central and high peripheral porosity that leads to mean values that do not change with colony size. This may also be true for *E. singularis* and *L. ceratophyta* and may explain the constant porosity. Since in all species the end branches were longer in the periphery than in the center (Fig. 4) and the end branch length generally increased with fan size (Table 5), a common adaptive function of these morphological features might be expected. Longer end branches, especially at the periphery of the colonies, are more readily bent and thus reduce hydrodynamic forces. In addition, because the mass of structural element (axis and sclerite) is lowest in the branch tips of the colonies (Table 2), branches are easily deflected. This will reduce drag forces. Moreover, in larger colonies of all species, growth by width increases as is indicated by the decrease of the height to width ratios with fan size (Table 5). This is a strategy that slows down the elongation of colonies into water layers with higher current velocities (Russo, 1985, Warner, 1981). The higher percentage of colonies with anastomoses in large than in small colonies may help to keep large colonies upright in currents. The increasing intensity of water movement with distance from the substratum may be an important factor influencing the variation of weight and architectural features noted in colony regions and with fan size. The flexibility of branches and bending of polyps regulate the feeding current through colonies (Harvell & LaBarbera, 1985, Sponaugle, 1991, Sponaugle & LaBarbera, 1991). Thus, the variability of weight and architectural parameters with colony size might not only reduce hydrodynamic forces, but also control the feeding currents in gorgonian colonies.

Overall, our findings indicate that the branching patterns is related to the taxonomic position of the investigated gorgonians, whereas the mean values of architectural features could be used for identifying functional groups. Moreover, the architectural features investigated in this study can be used to determine the intraspecific variation of colony morphology of gorgonians and other fan-shaped organisms. The method applied in this study may also be a useful tool in palaeontological studies to define species and to identify ecophenotypes.

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