

# Stiffness of Caribbean gorgonians (Coelenterata, Octocorallia) and Ca/Mg content of their axes

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**ABSTRACT:** Fourteen species of gorgonians characteristic of a range of water-movement regimes were examined. Young's modulus was used as a measure of comparative stiffness. Determinations were made separately on whole colony segments and axial skeleton from those segments. Calcium and magnesium content of the axial skeleton segments was determined by atomic absorption spectrophotometry. Whole colony Young's modulus varied widely but increased from colony tip to base in most species. Axial skeleton stiffness was generally highest in tips and mid-colony and lowest at bases. Stiffness often correlated with calcium/magnesium content. Calculation of a theoretical Young's modulus suggested that the cortex contributed significantly to colony stiffness. A tensor muscle system associated with the cortex and activated on compression is postulated to account for the unexpectedly low (in some cases apparently negative) stiffness of some cortices. No simple relationship emerged relating calcium/magnesium content with whole colony and axial skeleton stiffness or with water movement regime.

## INTRODUCTION

In the Caribbean, gorgonians are very successful shallow-water organisms over a wide range of physical habitats from high energy, breaking-wave zones, through the surge zone into the depths where current and tide move water. A relatively large number of species with different morphologies inhabit similar water movement zones (Bayer 1961, Yoshioka & Yoshioka 1989). How similar or different are their biomechanical systems and properties? Basic to answering the question is a determination of the stiffness of the materials that comprise the colonies. There are 2 major components of the biomechanical system in gorgonians; the axis or axial skeleton and the cortex which includes coenenchyme (mesogleal gel and sclerites, formerly known as spicules) plus polyps and gastrovascular canals (Bayer et al. 1983).

Although no investigations have been carried out on the mechanical properties of gorgonian cortex alone, work by Koehl (1982), Wainwright et al. (1982) and Alexander (1983) on related organisms is relevant. Wainwright et al. (1982) characterized mesoglea as an

example of a highly viscous, compliant composite material of randomly-oriented fibres in a hydrated polymeric matrix. Alexander (1983) demonstrated the time-dependent characteristic of this material, which initially opposes sudden force, then complies to it, and Koehl (1977, 1982) outlined the stiffening effect of sclerites, especially in concentrations above 20 % by volume, on mesogleal gel.

Colony segments which included axis and cortex were examined by Lasker (1984) in relation to breaking strain and asexual reproduction in 2 *Plexaurella* species.

Axis Young's modulus was measured in *Pseudoplexaura* sp. by Goldberg et al. (1984) in relation to the weakening of the axis by pathogenic algae for the asexual reproduction of the algae. Jeyasuria & Lewis (1987) determined Young's and torsion moduli for 13 species of gorgonians and noted a relationship between stiffness and water-movement based zonation. Stiffest axes occurred in deep water, the least stiff in regions of surge and moderately stiff axes occurred in the high energy zone. The composition of the axis has received more attention. Marks et al. (1949) first identified collagen as a component of the gorgonian which composes most axiferous holaxonian gorgonian axes. Roche & Eysseric-Lafon (1951), Picken (1960),

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Leversee (1969) and Goldberg (1974) confirmed and extended the information on collagen as a major structural element of gorgonin and Goldberg (1976) further chemically characterized the gorgonins of several species. The sclerotization that stiffens gorgonin has been shown to be associated with high tyrosine (Goldberg 1974, 1976, 1978, Tidball 1982, 1985), aromatic cross-linking (Szmant-Froelich 1974) and DOPA quinone (Tidball 1982). Since Cook (1904) estimated the inorganic fraction of the axes of 12 gorgonian species by weighing ash left after incineration, mineralization has been assumed to be another method of stiffening axes. Jeyasuria & Lewis (1987) correlated high axis stiffness with high calcium and magnesium content but did not characterize the mineral. In several species, Lowenstam (1964) identified either calcite or aragonite mineral as a component of the axis. Wainwright et al. (1982) observed polycrystalline bodies composed of calcite in *Plexaurella nutans* axis and correlated differential deposition of the bodies with directional stiffness. Goldberg (1976) investigated biochemical composition of similar bodies in *Nicella schmitti*. Muzik & Wainwright (1977) also found calcite in several species of Pacific gorgonians. Because both young and older sections of *Leptogorgia virgulata* axis had almost 35 % inorganic component, Tidball (1985) concluded that even if the inorganic content stiffened the axis, it was modification of the organic phase that altered the mechanical properties. More complete characterization of mineralization has been done in the Pennatulacea (Ledger & Franc 1978), some of which are similar to gorgonians.

Koehl (1984) notes that the overall structure of an organism such as a gorgonian should represent the outcome of a design conflict between maximizing surface area for feeding and minimizing hydrodynamic forces on the colony. Organisms can modify the drag forces they encounter by altering their structure or their orientation (Koehl 1984). According to Wainwright et al. (1982), biomechanical systems must possess 4 important characteristics: (1) they must not break or deform to a great degree during stress equilibration; (2) they must be able to carry the applied force over a distance; (3) they must possess reserve strength to survive occasional extremes in stress; and (4) they must be metabolically cost-efficient. That gorgonians demonstrate these principles is evident from a number of studies. Velimirov (1976) and Leversee (1984) correlated differential morphologies with different physical environmental conditions and Sebens (1984) recorded increased growth rates with higher water velocities. The use of flexibility to control local water velocity was shown by Harvell & Barbera (1985) in hydroid colonies and Patterson (1984) described the utilization of different regions of the colony for prey capture at certain

flow speeds. Using transplant experiments, Kinzie (1973) and Goldberg (1976) confirmed that various species of gorgonians are adapted to specific depths and/or water-movement regime. The cumulative work of Wainwright & Dillon (1969), Rees (1972), and Muzik & Wainwright (1977) has shown that orientation of sea fans is a result of hydrodynamic factors.

The present study was undertaken to provide a systematic examination in gorgonians of Young's modulus and calcium and magnesium content of branch orders (Brazeau & Lasker 1988) from tip to base. It was thought that determinations done on both axes and segments of colonies that included both axis and cortex might provide a better understanding of mechanics of gorgonians relative to their habitats.

## MATERIALS AND METHODS

Fourteen species of gorgonians within 11 genera were collected during summer 1987 in north Tobago, West Indies. Mechanical tests required for the determination of Young's modulus were conducted in Tobago on live specimens. Segments of the whole colony including branch tip, mid-branch and base were selected for testing. The outer diameter of the segment, as well as the core diameter, were measured using a Starrett Micrometer Gauge (accuracy 0.01 mm). For each species, the segments selected to be tested were obtained from a single colony. One end of the branch was clamped in a drill chuck so the branch was positioned horizontally. Ten equal weights were hung successively and cumulatively on the distal end of the branch. The vertical deflection at the distal end of the branch was measured with a Starrett micrometer (0.01 mm accuracy) after each weight was hung. Weights were selected so that deflections were not large since large deflections nullify the equations used for the determination of Young's modulus through the method of bending beams (Stephenson 1969). The number of branch orders (Brazeau & Lasker 1988) used per species varied from 2 to 5.

Each of the specimens was air dried on location after testing, packed in boxes, transported to Brock University and stored. Dry axial skeleton segments 1 to 7 cm in length were mechanically cleaned of all coenenchyme and rehydrated in Instant Ocean (Aquarium Systems, Ohio) for about 4 d. From Young's modulus determinations done in the field both prior and subsequent to the current work, it was evident that moduli derived from rehydrated axes approximated those derived from live specimens. A small amount of thymol in crystalline form was added to the rehydrating fluid to minimize bacterial decay (Koehl 1982). Once rehydrated, the radii of the cores (circular cross sections)

and semi-axes of cores (elliptical cross sections) were measured. Specimens with hollow centres or specimens that were difficult to measure with the micrometer were measured using a micrometer scale in a dissecting microscope. The same method as above was used in the determination of Young's modulus of the axis. To prevent dehydration, axial skeletons were sprayed with Instant Ocean from an atomizer throughout the testing procedure.

The general formula for determination of Young's modulus by the method of bending beams is

$$E = mg l^3 / 3\pi A K^2 d \quad (1)$$

where  $m$  = mass attached at the distal end of the specimen;  $g$  = acceleration due to gravity;  $l$  = length of the specimen;  $A$  = area of cross section;  $K$  = radius of gyration about the neutral axis; and  $d$  = deflection at the distal end due to mass attachment. Because cross sections of axes could be either solid or hollow circles or solid or hollow ellipses, 4 forms of this equation were used to fit these specific geometric variations (Stephenson 1969).

Calcium and magnesium content of axes were determined using the Video 11 Atomic Absorption Spectrometer. The same samples of the axes used in the determination of Young's modulus were cleaned carefully, powdered using a mortar and pestle, weighed dry and placed in acid-washed test tubes. Three ml of concentrated  $\text{HNO}_3$  and 2 ml of concentrated  $\text{HCl}$  were added slowly to the powdered core samples. Acid digestion was carried out in a water bath at about  $90^\circ\text{C}$  for about 6 h. Before testing, the test tubes containing specimens were centrifuged and the supernatant poured into a suitably-sized, acid-washed volumetric flask. The dry weights of the specimens varied; thus, samples were decanted into appropriate volumetric flasks and made up to appropriate volumes with a solution containing 0.1 %  $\text{KCl}$  and  $7.0607 \text{ g l}^{-1} \text{ SrCl}_2$ . Dilutions were adjusted until values fell within the range of standards.

Standards for calcium and magnesium were made up with 5 standards of known concentration for each. The standard contained 0.1 %  $\text{KCl}$ ,  $7.607 \text{ g l}^{-1} \text{ SrCl}_2$ , 3 ml of concentrated  $\text{HNO}_3$  and 2 ml of concentrated  $\text{HCl}$ . A blank for zeroing was made containing 0.1 %  $\text{KCl}$ ,  $8.607 \text{ g l}^{-1} \text{ SrCl}_2$  with 3 ml of concentrated  $\text{HNO}_3$  and 2 ml concentrated  $\text{HCl}$ . Calibration curves were generated for standard concentrations of calcium and magnesium against absorption units. These curves were then used to read calcium and magnesium values found in axial skeletons of the 14 species. Concentrations were then calculated as a function of dry skeletal weight. Each analysis was performed in triplicate.

## RESULTS

Raw data for Young's modulus derived from the tests done on each branch sample of the whole colony (cortex plus axial skeleton) for the 14 species of gorgonians were averaged to derive means. Standard deviations for these means were also calculated (Table 1). There was a wide range of whole colony Young's modulus from  $0.0237$  to  $15.7 \text{ Gdyn cm}^{-2}$ , which represents a 700-fold difference in material stiffness. (The 2 lowest readings from Table 1 were disregarded in the foregoing range since they were considered erroneous due to specimen damage.) In most species Young's modulus increased from tip to base in this 2-phase system of cortex and axis with the base usually about 10 times stiffer than the tip. Interspecifically though, the degree of increase was quite variable and ranged from 100 times in *Lophogorgia cardinalis* through 0 in *Eunicea tourneforti* to  $-3$  times in *Muricea muricata*.

Means and standard deviations were also derived from the raw data for Young's modulus test done on the axes (Table 2). There was also a wide range in Young's modulus from  $11.11$  to  $93.1 \text{ Gdyn cm}^{-2}$  in the axis: nearly a 100-fold difference in stiffness. (The single highest and lowest readings from Table 2 were disregarded here. The very high value is due to an experimenter's error and the low value due to a kink or crimp in the very small axis.) For this single-phase, composite material, Young's modulus decreased from tip to base in most species. Interspecifically the amount of decrease was variable and ranged from an extreme of 40 times in *Pterogorgia citrina* through no change in *Eunicea tourneforti* to  $-5$  times in *Lophogorgia cardinalis*. In most species there was about a 4-fold decrease in stiffness from tip to base.

Stiffness of the cortex alone (Table 3) was calculated using a Parent-Coulomb method (Shanley 1957) for composite (heterogeneous) beams. The formula used was

$$E_c = \frac{E_w - E_a \left(\frac{r_a}{r_w}\right)^4}{1 - \left(\frac{r_a}{r_w}\right)^4} \quad (2)$$

where  $E$  = Young's modulus;  $r$  = radius;  $w$  = whole colony;  $c$  = cortex; and  $a$  = axis. Composite beam theory assumes homogeneity of the materials tested. For the cortex of gorgonians, this may not be the case. The calculated, theoretical Young's moduli of 13 of 41 branch orders were negative. No material can have a negative Young's modulus and they could not be used for the calculation of percent cortical contribution to whole colony stiffness (Table 3). The theoretical cortical stiffness covered a wide range from  $0.0020$  to  $10.13 \text{ Gdyn cm}^{-2}$ . Most values were around  $0.05 \text{ Gdyn cm}^{-2}$  which is the range of sponge tissue (Koehl 1982)

Table 1. Young's modulus (means and standard deviations) in Gdyn cm<sup>-2</sup> for the various branch orders of whole colonies (cortex and axis)

Species	Tip			Primary			Secondary			Tertiary		
	$\bar{X}$	$\pm$ SD	(n)									
<i>Ellisella barbadensis</i>	0.364	0.0776	(10)	1.55	0.381	(10)	5.02	0.970	(10)	3.72	0.489	(10)
<i>Lophogorgia cardinalis</i>	0.139	0.00777	(5)	7.92	0.462	(10)	5.50	1.89	(10)	15.7	0.944	(10)
<i>Muricea atlantica</i>				0.00923	0.000706	(10)	0.0513	0.00201	(10)	0.239	0.0231	(10)
<i>Plexaurella nutans</i>	0.0237	0.00812	(11)	0.0515	0.0261	(13)	0.128	0.04	(11)			
<i>Gorgonia ventalina</i>	1.13	0.0144	(10)	1.92	0.0846	(10)	13.1	0.520	(10)	4.88	0.361	(10)
<i>Plexaura homomalla</i>	0.0734	0.00385	(10)				0.148	0.0247	(10)	0.927	0.0679	(10)
<i>Pterogorgia citrina</i>	0.0678	0.00244	(4)	0.158	0.00977	(4)				1.28	0.0664	(9)
<i>Plexaurella fusifera</i>	0.049	0.0061	(10)	0.0651	0.0326	(10)	0.103	0.00845	(10)			
<i>Pseudoplexaura porosa</i>	0.0357	0.00723	(6)	0.0283	0.00799	(7)	0.410	0.0641	(10)			
<i>Muriceopsis flavida</i>	0.168	0.0026	(8)	2.54	0.410	(10)	3.70	0.505	(10)			
<i>Plexaura flexuosa</i>	0.185	0.00728	(7)									
	0.0211	0.00134	(10)				0.0753	0.00830	(10)	0.506	0.0132	(10)
<i>Eunicea tourneforti</i>	0.0872	0.0172	(9)				0.0728	0.0115	(11)			
<i>Iciligorgia schrammi</i>	0.250	0.00778	(10)	1.33	0.0486	(10)	1.26	0.672	(10)			
	0.259	0.0134	(20)	5.14	6.64	(20)	2.6	3.6	(20)			
<i>Muricea muricata</i>	0.599	0.00245	(10)				0.181	0.00397	(10)			

and unspiculated sea anemone mesoglea (Alexander 1962, Gosline 1971b, Koehl 1977). In 7 of 9 cases, stiffness of the cortex increased from tip to base.

The % cortex contribution to the whole colony Young's modulus was calculated from:

$$E_w = \left(\frac{r_a}{r_w}\right)^4 E_a + \left[1 - \left(\frac{r_a}{r_w}\right)^4\right] E_c \quad (3)$$

Where a contribution could be calculated, the cortex often contributed substantially to whole colony stiffness. In 7 of 41 cases it was over 80%. Overall, contributions ranged from 0.8 to 96.9% and were quite variable between and within species. In tips for instance, contributions ranged from a low of 21% in *Ellisella barbadensis* to a high of 97% in *Eunicea*

Table 2. Young's modulus (means and standard deviations) in Gdyn cm<sup>-2</sup> for the various branch orders of axial skeletons

Species	Tip			Primary			Secondary			Tertiary		
	$\bar{X}$	$\pm$ SD	(n)									
<i>E. barbadensis</i>	93.1	4.92	(20)	92.7	5.58	(20)	67.9	4.13	(20)	47.1	2.48	(20)
<i>L. cardinalis</i>	5.09	0.482	(20)	149.9	22.8	(20)	55.5	2.93	(20)	26.0	2.94	(20)
<i>M. atlantica</i>				8.49	0.502	(20)	17.4	1.43	(20)	5.62	0.287	(20)
<i>P. nutans</i>	37.5	1.20	(20)	27.0	2.80	(20)	19.7	2.35	(20)			
<i>G. ventalina</i>	26.0	1.51	(20)	19.3	1.22	(20)	38.2	3.31	(20)	5.95	0.329	(20)
<i>P. homomalla</i>	34.8	2.30	(20)				18.4	2.67	(20)	8.88	0.919	(20)
<i>P. citrina</i>	39.4	6.23	(12)	9.51	2.40	(18)				1.11	0.0740	(20)
<i>P. fusifera</i>	15.4	2.39	(10)	19.8	1.46	(20)	2.69	0.167	(20)			
<i>P. porosa</i>	14.3	0.460	(20)	20.3	0.552	(20)	4.00	0.238	(20)			
<i>M. flavida</i>	11.8	1.29	(20)	52.6	6.001	(20)	12.9	0.469	(20)			
	2.15	0.171	(16)									
<i>P. flexuosa</i>	3.78	0.206	(20)				12.1	0.323	(20)	2.48	0.0636	(20)
<i>E. tourneforti</i>	1.50	0.0218	(20)				1.89	0.156	(20)			
<i>M. muricata</i>	0.541	0.0408	(20)				1.42	0.169	(20)			

Table 3. Theoretical Young's modulus ( $\text{Gdyn cm}^{-2}$ ) of the cortex. Also given are percent contribution of cortex to the Young's modulus of the whole colony; radius of the cortex (cm); ratio of the cross sectional area of the whole colony to the cross-sectional area of the axis

Species	Branch order	Cortex E (theoretical)	Percent cortex contribution	Radius of cortex	Ratio colony to axis
<i>E. barbadensis</i>	Tip	0.077	21.10	0.0845	19.3 :1
	Primary	- 2.66		0.0778	4.61:1
	Secondary	- 2.18		0.0738	3.10:1
	Tertiary	- 2.09		0.109	2.83:1
<i>L. cardinalis</i>	Tip	- 0.045	42.82	0.0415	6.31:1
	Primary	- 6.94		0.04	3.24:1
	Secondary	- 6.55		0.035	2.19:1
	Tertiary	10.13		0.0375	1.75:1
<i>M. atlantica</i>	Primary	0.0089	94.82	0.198	38.5 :1
	Secondary	0.0043	8.36	0.185	24.3 :1
	Tertiary	0.0020	0.82	0.174	5.29:1
<i>P. nutans</i>	Tip	0.016	68.14	0.828	72.8 :1
	Primary	0.034	65.09	0.825	27.7 :1
	Secondary	0.051	30.17	0.608	12.3 :1
<i>G. ventalina</i>	Tip	- 1.31	14.42	0.031	4.05:1
	Primary	- 2.51		0.035	2.47:1
	Secondary	- 11.13		0.033	1.54:1
	Tertiary	2.36		0.028	1.22:1
<i>P. homomalla</i>	Tip	0.043	58.62	0.142	35.7 :1
	Secondary	- 0.061	14.64	0.155	9.41:1
	Tertiary	0.15		0.128	3.28:1
<i>P. citrina</i>	Tip	0.051	75.60	0.0833	38.4 :1
	Primary	0.14	87.52	0.0618	17.5 :1
	Tertiary	1.36	73.46	0.0368	2.49:1
<i>P. fusifera</i>	Tip	0.047	95.84	0.327	90.8 :1
	Primary	0.047	72.47	0.353	34.4 :1
	Secondary	0.094	90.53	0.413	16.9 :1
<i>P. porosa</i>	Tip	0.022	61.22	0.1003	38.0 :1
	Primary	0.014	49.11	0.111	38.0 :1
	Secondary	0.28	65.81	0.148	6.04:1
<i>M. flavida</i>	Tip	- 0.035	84.84	0.0559	6.58:1
	Tip	0.16		0.0668	12.2 :1
	Primary	- 0.24		0.0775	4.57:1
	Secondary	- 0.22		0.0625	2.06:1
<i>P. flexuosa</i>	Tip	0.013	60.60	0.154	22.1 :1
	Secondary	0.0205	27.06	0.168	14.4 :1
	Tertiary	0.15	25.23	0.128	2.79:1
<i>E. tourneforti</i>	Tip	0.085	96.91	0.423	26.6 :1
	Secondary	0.055	74.11	0.42	11.3 :1
<i>M. muricata</i>	Tip	0.050	81.12	0.18	8.25:1
	Secondary	0.12	62.53	0.222	5.48:1

*tourneforti* but in most species were between 60 and 90 %.

The % cortex contribution to the Young's modulus of whole colony stiffness remained approximately constant in 3 of 9 cases and decreased from tip to base in 6 of 9 cases. The radius of the cortex (Table 3) remained nearly constant while the ratio of colony to axis (Table 3) decreased in the 6 species. In 2 of the 3 species where the % contribution remained constant, the radius of the

cortex (Table 3) increased slightly from tip to base. In all species the ratio of the cross-sectional area of the colony to the axis was larger at the tip than at the base. The magnitude of the difference varied between species. With the exception of *Pterogorgia citrina* the radius of the cortex was approximately the same for all branch orders of any single species. Generally, low cortical stiffness corresponded with high colony to axis ratios for those with positive values.

Mean values were obtained for calcium and magnesium respectively for dry masses of the axes tested in 3 atomic absorption spectrum determinations. Values for these proportions used the average concentration of 3 to 9 readings for 3 trials. The ion mass to dry mass for the 2 dilutions completed for each axis sample were averaged. Table 4 shows concentration of  $\text{Ca}^{2+}$  and concentration of  $\text{Mg}^{2+}$  in  $\text{mmol g}^{-1}$  dry wt for 14 species as well as the mole percent  $\text{MgCO}_3$  in  $\text{CaMg}(\text{CO}_3)_2$ . If the readings truly indicate mineralization, there is considerable interspecific variation. *Ellisella barbadensis*, *Plexaurella nutans* and *P. fusifera* are particularly

heavily mineralized. *Lophogorgia cardinalis*, *Gorgonia ventalina*, *Pseudoplexaura porosa*, *Plexaura flexuosa* and *Pterogorgia citrina* are moderately mineralized while the remaining 5 species show very low concentrations of calcium and magnesium. *Iciligorgia schrammi* with its very high degree of mineralization is a special case where the axis is composed almost entirely of sclerites so the mineralization indicates primarily calcium and magnesium content of the calcitic spicules. Especially evident in the heavily and moderately mineralized species is low degree of mineralization of tips relative to higher branch orders.

Table 4. Proportions of calcium and magnesium ( $\text{mmol g}^{-1}$  dry wt) and mole percent  $\text{MgCO}_3$  in  $\text{CaMg}(\text{CO}_3)_2$  in the axial skeleton branch orders

Species	Tip			Primary			Secondary			Tertiary		
	$\text{Ca}^{2+}$	$\text{Mg}^{2+}$	Mole %									
<i>E. barbadensis</i>	3.522	0.2226	5.9	5.587	0.8905	13.8	5.678	1.011	15.1	6.187	1.150	15.7
<i>L. cardinalis</i>				0.7467	0.4657	38.4	0.9232	0.4560	33.1	2.343	1.182	33.5
<i>M. atlantica</i>				0.01085	0.01395	56.3	0.00399	0.01221	75.4	0.003799	0.01088	74.0
<i>P. nutans</i>	1.910	0.5123	21.1	4.037	1.181	22.6	4.345	1.2439	22.3			
<i>G. ventalina</i>	0.1422	0.07080	33.2	0.3307	0.1746	34.6	1.751	0.8965	33.9	0.1759	0.1213	40.8
<i>P. homomalla</i>	0.01149	0.0149	56.5	0.01389	0.02070	59.8	0.008326	0.02043	71.0	0.0203	0.03851	64.5
<i>P. citrina</i>	0.02321	0.02712	53.9	0.01414	0.01120	47.6				0.006064	0.01993	76.7
<i>P. fusifera</i>	1.200	0.4012	25.1	1.794	0.4636	20.5	5.389	1.459	21.3			
<i>P. porosa</i>	0.08701	0.06739	43.7	0.04628	0.06834	59.6	0.08882	0.03208	26.5			
<i>M. flavida</i>	0.004549	0.0264	85.3	0.00616	0.0110	64.1	0.04382	0.05573	56.7			
	0.01678	0.01798	51.7									
<i>P. flexuosa</i>	0.2018	0.0482	19.3				0.1115	0.0260	18.9	0.01832	0.02386	56.6
<i>E. tourneforti</i>	0.009960	0.02442	71.0				0.00662	0.01169	63.8			
<i>I. schrammi</i>	2.407	0.3608	13.0	6.562	0.9729	12.9	5.536	0.09087	14.1			
<i>M. muricata</i>	0.009780	0.01790	64.7				0.01241	0.03894	75.8			

Table 5. Total calcium and magnesium content of axes as a proportion of dry weight for various branch orders. Probable level of mineralization. Average Young's modulus ( $\text{Gdyn cm}^{-2}$ ) exclusive of tip

Species	Tip	Primary	Secondary	Tertiary	$\bar{X}$	$\pm$ SD	(n)	Probable level of mineralization	Average axis E
<i>E. barbadensis</i>	0.146	0.246	0.253	0.276	0.230	0.0576	(4)	High	68
<i>P. nutans</i>	0.0891	0.191	0.204		0.161	0.0627	(3)	High	23
<i>P. fusifera</i>	0.0578	0.0832	0.252		0.131	0.106	(3)	High	11
<i>L. cardinalis</i>	0.0412	0.0481	0.123		0.0708	0.0454	(3)	Moderate	77
<i>G. ventalina</i>	0.00742	0.0175	0.092	0.0366	0.0384	0.0377	(4)	Moderate	21
<i>P. porosa</i>	0.00513	0.00351	0.0114		0.00668	0.00417	(3)	Low	12
<i>P. flexuosa</i>	0.00926		0.00510	0.00131	0.00522	0.00398	(3)	Low	7
<i>P. citrina</i>	0.009969	0.000839		0.00072	0.00384	0.000531	(3)	Low	5
<i>M. flavida</i>	0.000824	0.000513	0.00915		0.00290	0.00417	(4)	Low	33
	0.00111								
<i>M. atlantica</i>		0.000774	0.000458	0.000416	0.000550	0.000195	(3)	None	10
<i>M. muricata</i>	0.000827		0.00144		0.000113	0.00433	(2)	None	1
<i>E. tourneforti</i>	0.000993		0.000549		0.000771	0.000314	(2)	None	2
<i>P. homomalla</i>	0.000876	0.00117	0.00102	0.00210	0.00129	0.000552	(4)	None	14
<i>I. schrammi</i>	0.105	0.287	0.244		0.212	0.0951	(3)		
$\bar{X}$	0.0340	0.0800	0.0921	0.0529					
$\pm$ SD	0.0476	0.0109	0.109	0.110					
(n)	14	11	13	6					

Table 5 shows proportional total calcium and magnesium content of axes and Young's modulus of intermediate branch orders. Generally, high calcium/magnesium content is indicative of high stiffness but there are notable exceptions. Axis Young's modulus was regressed against total  $\text{Ca}^{2+}$  plus  $\text{Mg}^{2+}$  content for tips and for mid sections and yielded correlation coefficients of 0.774 ( $p < 0.01$ ) and 0.854 ( $p < 0.001$ ) respectively.

## DISCUSSION

### Whole colony

As expected from the literature (Goldberg 1976, Wainwright et al. 1982), there was generally a progressive increase in Young's modulus from tip to base. Since regions of colonies approaching the base are also usually much thicker than tips in gorgonians, the effective stiffness of bases is increased where stresses are highest (Koehl 1984). The wide range of Young's modulus, from 0.097 to 17 Gdyn  $\text{cm}^{-2}$ , illustrates that some colonies are much stiffer than others. Since tips vary interspecifically in diameter from 3 to 20 mm and bases may be 60 mm thick, the values alone will not provide much information on how the colonies will react to water movement. For comparison, the lower value is lower than that of vertebrate tendon (Elliot 1965), the higher about the stiffness of bone (Vogel 1988).

### Axis

Young's modulus readings from axial skeletons provided a few surprises. It has been generally assumed that there is an increase in sclerotization (evident from darker colouration) as well as increased mineralization (in those species where it occurs) and therefore increased stiffness of the gorgonin over time (Goldberg 1976, Wainwright et al. 1982). The bases are the oldest part of the colony and also must withstand the highest stress loads. However, in all 11 species where there were adequate samples to compare basal and medial levels, the basal samples had lower Young's moduli. Higher basal stresses may cause more disruption of collagen bonds and of crystal structure in mineralized forms in bases, and, despite greater sclerotization (Tidball 1982) and in some cases mineralization, the Young's moduli are comparatively low.

Axes in tips had unexpectedly high Young's moduli. Four were higher than the highest moduli from other branch orders, 5 about the same as the highest readings from other branch orders and 4 lower. This does not correspond with the assumption of increased sclerotization and mineralization producing stiffer gor-

gonin. Tips are generally lighter in colour (yellowish) and translucent. One possible agent that could account for the unexpected stiffness of these tips could be the lipid noted by Tidball (1981, 1982).

There was a general decrease in stiffness of the axis as the thickness increases with tips (8 of 12) being stiffer than bases. This average 4-fold decrease is probably of little functional consequence because it is usually offset or overridden by an increase in axis diameter and therefore mass of material as the base is approached.

### Mineralization

Jeyasuria & Lewis (1987) found a correlation between calcium and magnesium content and Young's modulus. No such correlation could be derived in this study from pooled data but there was a significant relationship between high Young's modulus and high calcium and magnesium content for primary and secondary branch axes ( $r = 0.854$ ) in concurrence with previous work. For tips, the relationship was of lower significance ( $r = 0.774$ ).

If the calcium and magnesium form mineral crystals in the axes, mole percent  $\text{MgCO}_3$  in  $\text{CaMg}(\text{CO}_3)_2$  may indicate the form of the mineral (Bathurst 1983). The 15 to 20% range of 5 species may represent high magnesium calcite, the 50% range of 4 species may represent dolomite and the ranges around 75% of the remaining 4 species may be magnesite (Table 4). Crystal structure would have to be determined by X-ray diffraction to identify the mineral form. There appear to be 4 groups based on calcium plus magnesium content as a percentage of dry weight (Table 5). In species with high levels of mineralization, there is little doubt that the calcium and magnesium form mineral crystals since all those species exhibit polycrystalline bodies similar to those identified by Wainwright et al. (1982) as calcitic. In species that show moderate mineralization of 7.5 to 11% calcium plus magnesium, there is a high probability of crystallization. In the low level of mineralization group where calcium and magnesium comprise between 0.15 and 1.0% the question of mineralization of the axis is open. In those species with very low calcium and magnesium content in the core, there is probably no mineralization.

In the heavily calcified species there is a trend in 5 of the 7 species toward an increase in calcification from tip to base. Young's modulus does not follow this trend and in all 5 cases is lower closer to the base. This supports the contention that there may have been crystal breakage nearer the bases, because an increase in intact mineral content should increase stiffness since crystalline calcium carbonate has a higher Young's modulus than collagen. There may also be disruption of

the gorgonin since a similar trend toward lower Young's modulus as the base is approached is also evident in the non-mineralized species.

### Theoretical cortical Young's modulus

In terms of gross morphology, the cortex is highly variable interspecifically: thick, thin, hard, soft, tough, friable, gritty, slimy, mushy. Nor is it possible to remove it from the axis without destroying its integrity. Because of this, direct determination of Young's modulus could not be done. Calculation of a theoretical cortex Young's modulus using the method for composite beams assumes homogeneity of material phases. While this condition probably applies for the axis, it almost certainly does not for the cortex. The uniformity of the cortex is interrupted by polyp cavities, gastrovascular and axial canals, differential layering and articulation of sclerites of various types and it is living tissue (Bayer 1961). For this reason, both whole colony and hypothetical cortex stiffness values must be interpreted with caution. The 13 negative Young's modulus values indicate that. The 2 major experimental errors that might result in negatives are axis stiffening between the time colony and axial Young's moduli were determined and unnoticed damage to the integrity of the cortex. Rehydration of axes probably does not return them completely to their original condition because of differential cross-linkage and breakage of both protein and glycosaminoglycan bonds (Muscatine & Lenhoff 1974) during both dehydration and rehydration. Because axis composition differs between genera (Goldberg 1976), extent of return to the original condition may differ from genus to genus. Disruption of the integrity of the coenenchyme can also easily go undetected. Overflexion during collection or transport can readily disarticulate sclerites, interrupt layering by displacement of sclerites and possibly break tubercles on sclerites.

Evidence from 3 sources leads us to believe that the negative Young's moduli are valid and have little to do with either dehydration/rehydration or tissue damage. First, Young's modulus values for both whole colony and theoretical cortex appear to be generally too low. Theoretical cortex stiffness ranges from 0.0020 to 10.13 Gdyn cm<sup>-2</sup>. The lower values are less than those for non-spiculated *Metridium senile* mesoglea (Gosline 1971a, b, Koehl 1982). Most fall in the range of values for spiculated sponge tissues and experimental, gelatin-containing systems with a 15% volume fraction of spicules (Koehl 1982). These are much lower than the stiffness values of several alcyonacean species with spicule volumes of 20% tested by Koehl (1982). When rigid particles (sclerites) are embedded in a deformable

material (mesoglea), the composite is stiffer than the deformable material (Ferry 1970, Deanin et al. 1974, Koehl 1982, Chang et al. 1984). Stiffness is directly related with volume fraction of filler particles and their surface area and inversely related to particle size (Koehl 1982). Though the volume fraction of sclerites was not determined for these specimens, it is high; probably in excess of 50%. Even if the gorgonian mesoglea has only the strength of the Maid Marian, raspberry gelatin used by Koehl (1982) in her experimental model systems, cortical Young's moduli at least 2 times in excess of most of those calculated should be expected.

Second, negative results are consistently from specimens with thin cortices and very small sclerites (0.1 mm) (Bayer 1961). Koehl (1982) has shown that small sclerites with high surface-area-to-volume ratios stiffen more than large sclerites. Positive theoretical cortical Young's moduli are consistently from specimens with thick cortices, larger sclerites and estimated lower volume fractions of sclerites. These results are the reverse of what should be expected from Koehl's (1982) work with both living and experimental systems.

Third, whole colony and axis Young's moduli were done on several living species in the field (unpubl. results). Stiffnesses were generally comparable to those from this study. In *Ellisella barbadensis*, the only one of the species tested live with the thin cortex and small sclerites, theoretical cortical Young's moduli for branches below the tip were negative. All other species were positive. Axis stiffness was determined immediately following whole colony stiffness determination without dehydration or rehydration. There is probably little artefact effect on the axis from dehydration and rehydration.

Because it is impossible for a passive mechanical system to have a negative Young's modulus, one is led to the conclusion that there is some active, living factor affecting the cortex. We propose that this is a muscular system. Muscle systems of gorgonians have not been well documented (Muscatine & Lenhoff 1974) though they have been described for other coelenterates. Usually myoepithelial cells of a variety of types are associated with gut and epidermis, and mesogleal musculature is well developed in some alcyonarians (Hyman 1940). To produce the negative Young's moduli, the muscular system must work in an unexpected fashion. Instead of resisting extension, it must reinforce compression. This would have a marked effect on the stiffness of both cortex and whole colony since the contractile force of striated muscle is 200 kPa for most species (Alexander 1988). The muscle system may be an automatic tensor/relaxer system associated with gastrovascular canals. Longitudinal muscles occur peripheral to the canals in alcyonarians (Hyman 1940).

Contraction of these muscles may shorten the canals and prevent loose folds produced by buckling from being pinched by sclerites moved during compression. Relaxation of the muscles on extension of the coenenchyme would allow the canals to stretch. The magnitude of the reduction in cortical Young's modulus appears to be greater than that required solely to shorten gastrovascular canals. There may be an epidermal and/or coenenchymal muscular system that tenses the mesoglea. This might pre-position sclerites and/or stress soften the mesoglea (Gosline 1971b, Koehl 1982) prior to the application of the full force of the water-movement-induced bending. The unexpectedly low Young's moduli for both cortex and whole colony indicate that all species probably have similar systems.

The cortex is responsible for a surprisingly large proportion of the whole colony stiffness. It substantially modifies the properties of the axis. In tips, especially where cortex to axis ratios were high, the stiffness of the cortex approaches that of the whole colony. Unfortunately, many of the specimens where colony to axis ratios were lower produced negative theoretical stiffness. But, assuming somewhere near a zero cortical contribution, the colony stiffness is that of the axis. Generally, species with thicker cortices had lower whole colony and theoretical cortical stiffness. This may indicate a lower volume fraction of sclerites or larger sclerites (Koehl 1982).

In several species, cortex stiffness increased basally while its thickness remained constant. This may indicate an increase in volume fraction of sclerites (Koehl 1982), a decrease in the numbers of cavities (gastrovascular and axial) per unit area, a decrease in polyp density, a change in consistency of mesogleal gel or fewer muscles per unit area. Unfortunately, these were not investigated.

### Ecological and functional considerations

Jeyasuria & Lewis (1987) noted that axial Young's modulus could be related to water-movement based zonation with stiffest axes occurring in deeper water subject to current only, the least stiff in moderate surge, and relatively stiff forms occurring in shallow, high energy, breaking-wave zones. Measurements of Young's moduli of whole colonies support those premises.

*Lophogorgia cardinalis*, *Ellisella barbadensis* and *Iciligorgia schrammi* are characteristically found in areas of low surge and strong current. They illustrate 3 different modes of producing stiffness that can be used under conditions of steady, unidirectional water flow. Mineralization in these species is high, and they are comparatively brittle. Heavy surge would probably

break them. *L. cardinalis*, a small, planar, finely branched form, has the highest whole colony Young's modulus. The cortex is thin and contains a large number of tiny sclerites so most of the stiffness is attributable to the axial skeleton. Moderately high calcium and magnesium content and dense gorgonin combine to produce the stiff, current-resistant colony. *E. barbadensis*, a sea whip (the one tested was 2 m long) also has a high colony Young's modulus. Whips by definition are flexible and as Denny (1988) notes, flexibility is dependent on length since a piece of material twice the length of another piece compositionally similar in all respects will deflect 8 times further. The heavily calcified, stiff axis is probably necessary to resist the considerable forces generated by tidal current and distributed along the length of the colony. *L. schrammi* is planar-parabolic in form and about 50 cm in height and is one of the stiffer colonies. It is normally found in regions of considerable current. Its leathery cortex and axial skeleton of long, slender, unfused sclerites makes it very different from the other gorgonians examined and because of its unconsolidated axis, no tests of Young's modulus could be performed on the axis. The high degree of mineralization of the axis is a measure of the sclerite content. Again, where sudden, back and forth motion is encountered, long slender sclerites (0.75 mm long by 0.02 mm thick) would readily break but they can be utilized to produce stiffness that counters steady water flow that changes gradually. Sudden stress applied to crystalline substances may cause fracture at stresses lower than will normally cause fracture (Vogel 1988). These 3 species have crystalline calcium carbonate in their axes (unpubl. results).

The 2 species that occur in the high energy zone illustrate 2 different ways of dealing with the harsh conditions. *Gorgonia ventalina*, the sea fan, uses large size with relatively high stiffness in basal regions and increased flexibility around the edges of the fan that permits compliance with the high forces. It occurs in the high energy, shallow, breaker zone and has the second highest colony Young's modulus. The edges and outer regions of the fan are less stiff than the central region and is evident from the response of the fan during a wave cycle with edges flexing much more than the centre of the fan. The cortex is thin and contains large numbers of tiny sclerites so most of the stiffness is attributable to the axis. Calcium/magnesium content is lowest in the most flexible regions and highest in the stiffer central region of the fan. *Pterogorgia citrina* is the other species that often occurs in high energy surge conditions but where flow is less turbulent than that which can be tolerated by *G. ventalina*. The small colonies have flattened, blade-like terminal branches planar in organization and relatively stiff but

certainly not stiff enough to withstand high energy surge without complying. The relatively short, flat, hydrofoil-like blades of the branches in combination with the stiffness of the axial skeleton probably produce the lift required to keep the cortex from being flayed on the substratum.

The remaining 9 species and the majority of the gorgonians examined in this work are characteristic of the moderate-energy surge zone encountered in moderate depths of 5 to 25 m. The species show a great variety of mechanical properties and morphology. The first 3 species, *Muriceopsis flavida*, *Eunicea tourneforti*, and *Plexaura flexuosa*, are often encountered (pers. obs.) in areas of heavy surge. *M. flavida*, the bottle brush with short and long bristles and its usually single, long, main stem, is one of the stiffer gorgonians. Both terminal branches and the main stem are stiff without having high calcium/magnesium content; the gorgonin is very dense. This species often intrudes into the high energy zone and apparently uses its rigidity to tolerate short duration, violent, water movement. Its cortex is thin, hard, and quite abrasion-resistant. In areas of violent water movement these tough colonies often appear stunted and battered. *E. tourneforti*, candelabra-shaped (about 30 cm in height) with finger-thick terminal branches, is also relatively stiff. With low calcium/magnesium content in the axis, whose Young's modulus is also low, its rubbery stiffness must be produced by the cortex. This is one of the species with relatively large sclerites in a thick cortex. Probably because of its springy stiffness this species is also tolerant of relatively harsh water movement. *P. flexuosa* is extremely variable morphologically with a moderately stiff base but, as the name implies, flexible

branches. Its common intrusion into the high energy zone cannot be accounted for by mineralization or cortical stiffness which is also relatively low so there must be some property of sclerite organization that makes this species one of the few tolerant of rough conditions.

The remaining species are more characteristic of the less turbulent middle water zone where relatively gentle surge is encountered (Goldberg 1973, Yoshioka & Yoshioka 1989). All sway gracefully. A wide range of mineralization and morphology in this group result in similar mechanical properties. *Plexaura homomalla* with many thin branches ascending from a few flared-out thicker branches is quite stiff despite its lack of mineralization. These colonies also tolerate considerable turbulence possibly because of the dense, stiff axial skeleton. *Plexaurella fusifera* and *P. nutans* can both form large colonies up to 2 m in height and though branches of *P. nutans* are usually about twice as thick, both have similar colony Young's moduli. Both are also heavily calcified (Wainwright et al. 1982) and have thick, relatively stiff cortices which contribute largely to the stiffness of terminal branches. Very long, seemingly flexible branches belie the actual high stiffness of the axial skeleton. *Pseudoplexaura porosa* with its long, straggly, somewhat tapered branches is quite willowy and flexible. It has low calcium/magnesium content and moderately high axial moduli. *Muricea muricata* and *M. atlantica* are most flexible despite hard, spiny exteriors. Colonies are relatively small at around 30 cm in height with low calcium/magnesium and low Young's moduli.

An hierarchical cluster analysis using Ward's method was performed on the means of 22 attributes for each of

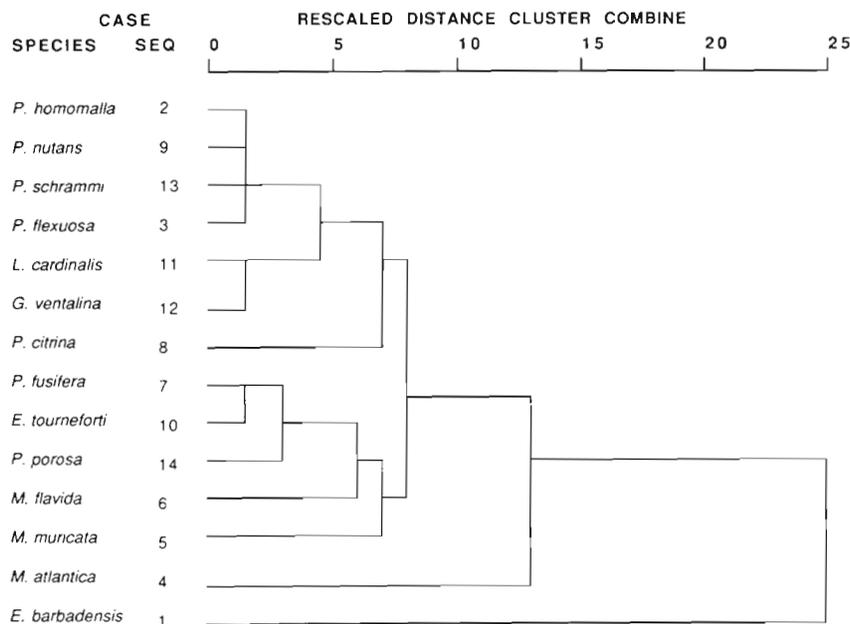


Fig. 1. Hierarchical cluster analysis dendrogram using average linkage (between groups)

the 14 species (Fig. 1). The program used was SPSS-X release 2.1 for Burroughs large systems. Attributes included, for each of 4 branch orders, Young's modulus of the axis, Young's modulus of the colony, axis calcium, axis magnesium, total calcium and magnesium, and, singly for each species, length and branching pattern. All attributes were weighted equally. The dendrogram shows 3 major clusters. The largest, a 7-species cluster, generally contains specimens of high stiffness and high calcium/magnesium. There are representatives from all 3 water movement zones in this cluster. This large cluster illustrates the difficulty of categorizing species attributes with habitat. Though attributes of each species are individually different, they are combined to produce similar properties. These in turn are utilized in all 3 water-movement categories though individual species are generally limited to only one water-movement zone. That species with similar overall properties are found in each zone is not surprising since the water-movement generated forces are not dissimilar and range from 1000 to 10 000 dyn cm<sup>-2</sup> (Roberts et al. 1975). The highest forces are usually encountered in the shallow water of the breaker zone, the lowest in the surge zone, and high, current-generated forces below the surge zone. The 6-species cluster of specimens with generally lower stiffness and lower calcium/magnesium content are representative of the middle surge-only zone. The single species cluster contains the outlier *Ellisella barbadensis*. This sea whip is very different; very long, very stiff, very heavily mineralized and usually occurring below the surge zone. It is evident from the dendrogram that combined physical attributes correspond crudely with niche as defined by water movement regime. Better correlation awaits more refined and detailed information on both.

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