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Organic content in gorgonian axis: structural function and implications for energy budget estimates

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ABSTRACT

The organic content of the proteinaceous portion of the skeleton of two Mediterranean gorgonian corals was estimated by means of two different methods: a gravimetric one (combustion and incineration) and by elemental analysis. *Paramuricea clavata* was investigated at a granitic shoal at the northern entrance to the Strait of Messina (Tyrrhenian Sea); *Lophogorgia ceratophyta* at a rocky station located off Tinetto Rock (Ligurian Sea). Both gorgonians were the visually dominant macrobenthic species in their habitat. Twenty colonies per species were collected in 1993, ages were estimated by counting axial annual growth increments, and the total content of the organic matrix of the skeleton was determined. The degree of axis mineralization was found to be different in the two species, suggesting different stiffening strategies to withstand water velocities. Annual weight increment of *P. clavata* due to skeletal organics was estimated in 12.72 g AFDW (ash free dry weight) m^{-2}, while the total resident amount was 78.93 g AFDW m^{-2}. *L. ceratophyta* yielded, respectively, 47.84 g AFDW m^{-2} yr^{-1} and 268.45 g AFDW m^{-2}. Gorgonian corals can be thought of as 'energy storer' organisms, since only a minor part of the organic matter of the colony (*i.e.*, coenenchymal tissue) is immediately available to consumers, while most of it is sequestered in the axial structures, and becomes available to decomposers only after the death of the colony.

KEY WORDS: Cnidaria - *Paramuricea clavata* - *Lophogorgia ceratophyta* - Energy flow.

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INTRODUCTION

Gorgonian corals are conspicuous members of the benthic macrofauna of coralligenous biocoenoses of the western Mediterranean (Pérès & Picard, 1964). Moreover, with their fan-shaped colonies, gorgonians contribute to an increase in abundance and diversity of associated organisms (Sarà, 1986). Because of their suspension-feeding habit, they may play a significant role in the energy transfer process between planktonic and benthic communities. An assessment of the energy budget of such organisms will probably give relevant information about functional relationships in those ecosystems. Secondary production has recently been estimated in some gorgonian species, *Leptogorgia hebes* and *L. virgulata* (Mitchell *et al.*, 1992), *Paramuricea clavata* (Mistri & Ceccherelli, 1994), *Eunicella cavolinii* (Weinbauer & Velimirov, 1996a) and *Lophogorgia ceratophyta* (Mistri, in press), from different geographic areas (northern Gulf of Mexico and the Mediterranean Sea). Considering secondary production as the amount of tissue that is almost immediately available for higher trophic levels (i.e., coenenchymal biomass), gorgonian production estimates were similar for all the species investigated.

The coenenchyme, however, is not the only colony tissue rich in proteinaceous matrix. With the exception of *Corallium rubrum* whose skeleton is almost entirely composed of calcium carbonate, gorgonians, as well as antipatharians (Goldberg, 1991), possess protein-rich axial skeletons (Goldberg, 1974). Gorgonian proteinaceous skeletons have been utilized in growth studies for age backcalculation (Grigg, 1974; Abbiati *et al.*, 1991; Mistri & Ceccherelli, 1993, 1994), but, to date, no study has addressed their organic content. The major component of their skeleton is a protein called gorgonin (Leversee, 1969), which contains a modified collagen more or less sclerotized and/or calcified (Kingsley & Watabe, 1987), and which is deposited in concentric layers. Even if not immediately available to predators, energetic content of the proteinaceous matrix is likely to be not of secondary importance because the skeleton constitutes the major component of the whole colony.

In the present paper the organic content of the skeleton is quantified and an estimate of the protein accumulation due to axial skeletal portions of two Mediterranean gorgonian species, *Paramuricea clavata* (Risso, 1826) and *Lophogorgia ceratophyta* (Linnaeus, 1758) is given, to provide a more precise insight into the energetic content of the taxon.

MATERIALS AND METHODS

Paramuricea clavata was investigated at «La Montagna» (38°15'00" N, 15°43'18" E), a granitic shoal located at the northern entrance to the Strait of Messina (Tyrrhenian Sea). *Lophogorgia ceratophyta* was studied at a station (44°01'04" N, 09°51'01" E) located on a shoal off Tinetto Rock, Ligurian Sea. Detailed infor-

mation about the two study sites can be found in Mistri & Ceccherelli (1993, 1994) and Mistri (1994, in press).

Twenty colonies of different size were haphazardly collected by SCUBA diving between October and November 1993 at each station for each species. In the laboratory, collected gorgonians were aged by counting annual growth rings in cross sections taken at the base of each colony. Whole colonies were gently oven dried at 30° C for 8 h to facilitate removal of the coenenchyme layer. Once dried, colonies were rehydrated by immersion in distilled water for a few hours. Coenenchymal tissues were then easily removed upon etching a few longitudinal tracks with a lancet on branches.

Colony total skeletal volumes were obtained by water displacement in graduated cylinders of appropriate size. Volumes were taken with an Eppendorf pipette at 50 µL accuracy. As an independent test, the volume of five colonies per species was recalculated considering each colony as the summation of the volume ($V = \pi r^2 h$) of n cylinders, each with radius r_i and height h_i (with i from 1 to n). All measurements were taken with a caliper at 0.01 mm accuracy. One large *Paramuricea clavata* colony was elliptical in its basal part, and the volume of this basal cylinder was calculated separately. No statistical difference was observed (*t*-test: *P. clavata*: $t = 0.163$, df = 4, *Lophogorgia ceratophyta*: $t = 0.261$, df = 4) on comparison of volumes obtained by water displacement with the more precise but much more time-consuming method of measuring cylinders.

For biomass measurements, 14 skeleton cylinders of different size per species were measured for volume and oven dried at 103° C to constant weight (48 h). A more precise estimate of gorgonian dry weight would have been obtained by drying in vacuo at 60° C (Crisp, 1984), but, because a vacuum apparatus was not available at our laboratory, the traditional procedure of drying at 103° C was adopted. Ash free dry weight (AFDW) of the skeletal proteinaceous matrix was obtained after incineration in a mouffle furnace. It is reported (Paine, 1964) that above 500° C, water of hydration may be separated from the calcium carbonate embedded in some tissues, causing a generalized loss of weight. For this reason two sets of incineration tests were performed: at 450° C for 4 h (Harvell & Suchanek, 1987), and at 500° C for 3 h (Mitchell *et al.*, 1992). Not statistically significant weight decrement (*P. clavata*: $t = 0.035$ df = 26; *L. ceratophyta*: $t = 0.047$, df = 26) was assessed on comparison of ash weights obtained at the two different temperatures of incineration. To test the procedure, inorganic reagent-grade calcium carbonate (Analytical Carlo Erba) was also processed with the gorgonian samples. A negligible loss of weight (0.624%) in three replicate samples processed was observed.

As an independent test of the reliability of the method adopted to estimate gorgonian organic content, the skeleton of *P. clavata* and *L. ceratophyta* was measured in terms of nitrogen content. Because there are no published reports indicating the presence of nitrite or nitrate in octocoral hard parts, the assumption was made that all nitrogen content was due to the proteinaceous skeletal matrix. Analyses were performed with a Leco CHN-600 (Carbon-Hydrogen-Nitrogen Determinator) on six replicated samples per species. The determination of nitrogen was made by burning a weighed quantity of sample (0.2 g) in pure oxygen at 950° C. Possible products of combustion of the skeletal organic matrix were carbon dioxide, water vapour, oxides of nitrogen, elemental nitrogen and oxides of sulfurs. The latter oxides were removed with calcium oxide so that the water vapour could not combine to form sulfuric acid, while the remaining gases of combustion were collected in a ballast volume and allowed to mix thoroughly. For nitrogen determination, a 10-mL aliquot was taken. The aliquot was carried by helium into a reagent train consisting of hot copper and N-catalyst for the removal of O_2 and the reduction of NO_x to N_2, sodium hydroxide for the removal of CO_2, and magnesium perchlorate for the removal of H_2O. The remaining elemental nitrogen was measured by a thermal conductivity cell. The cell consisted of two pairs of matched filaments used in four legs of a Wheatstone bridge. Output was multiplied by the appropriate calibration factor and K factor, which is a composite factor that corrects for barometric pressure, ballast volume pressure, and chemical interferences. Next, adjustments were made for blank and weight compensation.

Because in previous papers (Mistri & Ceccherelli, 1994; Mistri, in press) secondary production of the soft parts of both *P. clavata* and *L. ceratophyta* were calculated by combustion of tissues at 500° C, AFDWs obtained from the set at 500° C were used in this paper. Weights were determined with a Mettler AE163 electrobalance to the nearest 0.01 mg. AFDWs were then related to initial volumes to obtain the mean weight of the skeletal volume unit (1 cm^3) of each species. Organic content of the skeletal tissues of each colony collected was estimated by multiplying the mean skeletal unitary volume weight by the volume of each colony. Organic content was regressed against colony age to determine the mean skeletal organic content of each age class of each species and tested for significance (ANOVA).

Population density of *P. clavata* and of *L. ceratophyta* was estimated, respectively, in August 1992 and November 1993 by means of quadrat counts along transects. At «La Montagna», three vertical, 8-m long, depth-transects were considered: 213 *P. clavata* colonies were counted and measured for total height. At Tinetto Rock, sampling was done for *L. ceratophyta*, and 123 colonies were censused along two parallel, 20-m long, horizontal-transects. Height classes were converted into age classes by means of specific growth curves previously calculated for both populations (Mistri & Ceccherelli, 1993, 1994).

Total skeletal organic content was estimated as the sum of the mean skeletal organic content for all age classes of each species. The annual mass increment due to skeletal organics was calculated by means of an increment-summation method (Crisp, 1984).

RESULTS

By means of a gravimetric method (combustion and incineration), the mean skeletal unitary AFDW of *Paramuricea clavata* was determined to be 0.69 (± 0.15 SD) g cm^{-3}; the percentage of AFDW of the skeletal dry weight was 89.61 (± 14.46 SD). For *Lophogorgia ceratophyta* the mean skeletal unitary AFDW was 0.56 (± 0.11 SD) g cm^{-3}, and its percentage of the skeletal dry weight was 50.91 (± 6.08 SD).

By means of element analysis, total nitrogen content in the skeleton of *P. clavata* was determined as 13.21% (± 2.58 SD), while in *L. ceratophyta* it was 7.71% (± 1.25 SD). Nitrogen total content was converted into protein content by means of an appropriate ratio (protein/nitrogen = 6.25; Crisp, 1984): axial proteinaceous content in *P. clavata* was 82.56%, while in *L. ceratophyta* was 48.19%. The absence of significant difference between these data and those obtained with the gravimetric method (*t*-test for not paired data: *P. clavata*: $t = 0.968$, df = 18, NS; *L. ceratophyta*: $t = 0.848$, df = 18, NS) confirmed the reliability of the method.

Skeletal organic content of *P. clavata* was regressed on age (Fig. 1) to provide estimates of colony organic content for each age class. The regression was highly significant ($F = 120.96$; df = 1,18; $P < 0.001$), while population density in the studied area was 19.36 (± 9.20 SD) colonies m^{-2}. In Table I, parameters for the increment-summation method for calculating the population's increment in weight of skeletal organic content are given. Resident skeletal organic content of the *P. clavata* population was 78.93 g AFDW m^{-2}, with a 95% confidence limit (CL) from 68.67 to 88.01 g AFDW m^{-2}. The annual increment of organic matter was estimated at 12.72 g AF-

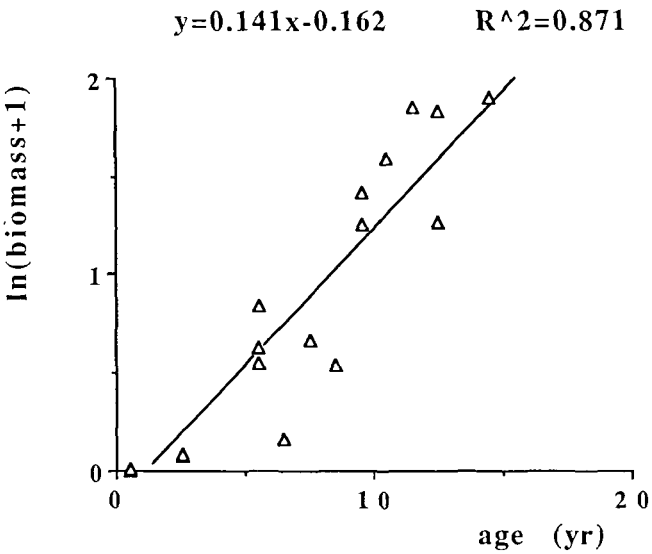

Fig. 1 - *Paramuricea clavata*. Log-transformed organic content (g AFDW) estimates regressed on age classes.

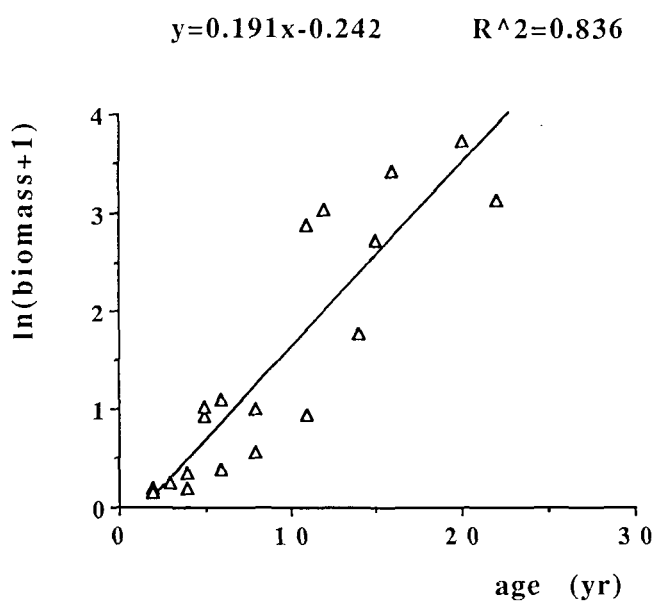

Fig. 2 - *Lophogorgia ceratophyta*. Log-transformed organic content (g AFDW) estimates regressed on age classes.

DW m^{-2}, with a 95% CL from 11.07 to 14.19 g AFDW m^{-2} yr^{-1}.

The regression between skeletal organic content and age for *L. ceratophyta* (Fig. 2) was highly significant (F = 91.44; df = 1,18; P < 0.001). Population density at Tinetto Rock was 6.8 (± 3.0 SD) colonies m^{-2}. Table II reports parameters for the increment-summation method for calculating the increment in weight of skeletal organic matter of the species. Resident skeletal organic content of the *L. ceratophyta* population was 268.45 g AFDW m^{-2}, with a 95% CL from 239.72 to 294.49 g AFDW m^{-2}. Annual increment was estimated at 47.84 g AFDW m^{-2}, with a 95% CL from 42.72 to 52.48 g AFDW m^{-2} yr^{-1}.

TABLE I - Paramuricea clavata. *Skeletal organic content and organic increment estimates.*

Age class (yr)	Density (ind. m^{-2})	Organic content (g AFDW m^{-2})	Organic increment (g AFDW m^{-2} yr^{-1})
0-1	0.46	–	–
1-2	0.64	0.69	0.03
2-3	1.18	0.25	0.19
3-4	2.18	0.86	0.40
4-5	1.09	0.67	0.23
5-6	0.82	0.69	0.20
6-7	1.18	1.33	0.33
7-8	0.91	1.32	0.29
8-9	1.45	2.65	0.54
9-10	0.82	1.84	0.35
10-11	1.37	3.73	0.67
11-12	1.18	3.90	0.67
12-13	1.45	5.75	0.95
13-14	0.64	2.99	0.48
14-15	0.73	4.05	0.63
15-16	0.09	0.60	0.09
16-17	0.36	2.80	0.42
17.18	0.91	8.21	1.20
18-19	0.27	2.88	0.41
19-20	0.27	3.35	0.48
20-21	0.18	2.60	0.37
21-22	0.18	3.02	0.42
22-23	0.55	10.53	1.46
23-24	0.00	–	–
24-25	0.18	4.71	0.64
25-26	0.09	2.73	0.37
26-27	0.09	3.15	0.43
27-28	0.09	3.63	0.47
Total	19.36	78.93	12.72

DISCUSSION

Gorgonian corals possess inner axial skeletons which are mainly composed by an organic matrix. The two species investigated showed quite a different proportion of skeletal proteinaceous matrix. The skeleton of *Paramuricea clavata* has an organic weight content of about 89.6%, while about 50.9% of the skeleton dry weight of *Lophogorgia ceratophyta* is due to organic matter. Because of the loss of water of hydration, these values have probably been underestimated: the difference between ash weights obtained at 450° and 500° C was 1.45% for the former species, and 1.79% for the latter. It is reported (Crisp, 1984) that incineration at temperatures higher than 500-600° C can cause a loss of ash weight through the removal of carbon dioxide of up to 44%. Harvell & Suchanek (1987) warned about incineration above 500° C in determining AFDW of gorgonian soft tissues. Nevertheless, the AFDWs utilized in the present study to estimate production seem to be quite acceptable. Skeletal nitrogen content determined by elemental

TABLE II - Lophogorgia ceratophyta. *Skeletal organic content and organic increment estimates.*

Age class (yr)	Density (ind. m^{-2})	Organic content (g AFDW m^{-2})	Organic increment (g AFDW m^{-2} yr^{-1})
0-1	–	–	–
1-2	0.17	0.01	0.01
2-3	0.28	0.07	0.06
3-4	0.28	0.15	0.07
4-5	0.28	0.24	0.09
5-6	0.44	0.55	0.17
6-7	0.56	0.96	0.26
7-8	0.33	0.76	0.19
8-9	0.44	1.32	0.31
9-10	0.56	2.12	0.47
10-11	0.33	1.61	0.34
11-12	0.22	1.35	0.27
12-13	0.11	0.84	0.17
13-14	0.33	3.11	0.60
14-15	0.50	5.76	1.09
15-16	0.33	4.72	0.88
16-17	0.22	3.85	0.71
17.18	0.22	4.71	0.86
18-19	0.00	–	–
19-20	0.06	1.77	0.32
20-21	0.00	–	–
21-22	0.17	7.80	1.38
22-23	0.06	3.18	0.56
23-24	0.00	–	–
24-25	0.06	4.68	0.82
25-26	0/22	22.50	3.95
26-27	0.06	6.88	1.21
27-28	0.17	24.88	4.36
28-29	0.06	10.11	1.77
29-30	0.17	36.53	6.38
30-31	0.11	29.42	5.13
31-32	0.00	–	–
32-33	0.00	–	–
33-34	0.00	–	–
34-35	0.06	31.92	5.56
35-36	0.00	–	–
36-37	0.00	–	–
37-38	0.06	56.65	9.85
Total	6.84	268.45	47.84

analysis produced a similar estimate of skeletal protein content, which confirmed the correctness of the data gathered.

In gorgonians, the function of the skeleton as a mechanical support system is related to colony need to carry on metabolic exchanges (food capture, catabolite release, oxygen uptake etc.) with the flowing water. The axial skeleton must be rigid enough to hold the colony erect, and must be able to withstand the water velocities of that particular habitat (Muzik & Wainwright, 1977). A method of stiffening axes in gorgonians is deposition of carbonates within the collagen interstitial spaces (Jeyasuria & Lewis, 1987): stiffness roughly correlates with the broad water movement regimes within which various gorgonian species occur (Yoshioka & Yoshioka, 1989). Both *P. clavata* and *L. ceratophyta* populations under study thrive in areas of strong currents. Colony habitat does not include surge or surf zone and the different extent of mineralization of gorgonian axes may reflect different ways of producing stiffness under conditions of unidirectional water flow. It must be said that resistance to currents is not only determined by the mechanical properties of the skeleton but also by the strength of the basis attachment on the substrate. *P. clavata* develops its fan most generally on one plane and has thick terminal branches. Its coenechymal layer is thick (Mistri & Ceccherelli, 1994) and is reinforced by a huge amount of sclerites (mean cortex mineralization = 72.3%; Weinbauer & Velimirov, 1995b). An axis with low mineral content (10.4% in weight) is likely to produce a sort of 'rubbery' stiffness which may allow colonies to resist initially and then comply with the strong tidal currents which flow through the Strait of Messina. *L. ceratophyta* is usually planar, although bushy forms can be the dominant growth-form in particular microhabitats (Mistri, pers. obs.) and is finely branched. The coenenchyme is thin (Mistri, in press), and contains quite a large amount of sclerites (mean cortex mineralization: 68.7%; Weinbauer & Velimirov, 1995b). Stiffness is probably attributable to the relatively heavily mineralized axial skeleton (49.1% in weight); in fact, a similar conclusion was drawn for the Caribbean gorgonian *Lophogorgia cardinalis* (Esford & Lewis, 1990). Sclerites increase the stiffness of colony tissues (Lewis & Von Wallis, 1991), but also play an important role in deterring predation (Van Alstyne & Paul, 1992): how cortex sclerites and the degree of axis mineralization interact to determine the stiffness of Mediterranean gorgonians is not yet quantifiable on the basis of the data given in the present paper.

Skeletal organic content of the colony of the two species of Mediterranean gorgonians investigated is quite high when compared to the organic content of the coenenchyme (Mistri & Ceccherelli, 1994; Mistri in press). This is a trivial finding, since most of the colony is skeletal matrix which is, in turn, mainly composed of organic matrix. Coenenchyme constitutes only a thin layer surrounding the supporting structure. In both populations, most skeletal organic content is due to older age. Of interest is the difference between the amount of skeletal organic content due to older colonies in the two species. In fact, splitting both populations into only two age classes (< and > 15 yr), older age classes of *P. clavata* account for 61.1% of the entire skeltal organic content, while *L. ceratophyta* colonies older than 15 yr account for 93.0% of the total resident organic content. This finding most likely reflects the different age structure of the two populations, since the *L. ceratophyta* population contains more older colonies: colonies with an age > 15 yr constitute 16.9% and 20.0% of population densities respectively. It may also reflect the different branching pattern strategy of the two species. The fan of larger *P.*

clavata colonies is almost a flat, fluffy surface: a relatively low number of branches constitute the colony and interbranch spaces of this 'filtering dish' are reduced by the extension of large polyps. On the contrary, the trunk of *L. ceratophyta* larger colonies carries quite a dense canopy made up by a huge number of more or less thin branchlets. Comparing two colonies of almost the same age (15-16 yr) and of similar rectangular area (*P. clavata*: about 750 cm^2; *L. ceratophyta*: about 600 cm^2), total branch development of *L. ceratophyta* was 5-fold that of *P. clavata*.

The coenenchymal production of both *P. clavata* and *L. ceratophyta* has recently been estimated. At the densely populated (19.4 colonies m^{-2}) station of «La Montagna» (Tyrrhenian Sea), the secondary production of *P. clavata* was 3.0 g AFDW m^{-2} yr^{-1}, with a standing stock biomass of 22.5 g AFDW m^{-2} (Mistri & Ceccherelli, 1994). At the less densely populated (6.8 colonies m^{-2}) Tinetto Rock (Ligurian Sea), the production of *L. ceratophyta* was estimated at 0.54 g AFDW m^{-2} yr^{-1}, with a resident biomass of 5.44 g AFDW m^{-2} (Mistri, in press). If one sums coenenchymal and skeletal estimates of organic content, *P. clavata* shows an increment of colony organic content of 15.72 g AFDW m^{-2} yr^{-1}, and a resident amount of organics of 101.43 g AFDW m^{-2}, *L. ceratophyta*, instead, exhibits an increment of colony organic content of 48.38 g AFDW m^{-2} yr^{-1}, and a resident amount of organics of 273.89 g AFDW m^{-2}. Skeletal increment accounts for 81% (*P. clavata*), and 99% (*L. ceratophyta*) of the population total increment of colony organic content, respectively. From these data, it would seem that investment is higher in skeleton than in coenenchyme. This may probably be not true, because the skeleton is laid down once and remains almost intact for 20 years or more, while the coenenchyme must constantly be reworked metabolically. On the other hand, unequivocally a large amount of organic matter is 'stored' in gorgonian inner skeletal parts. Notwithstanding that, the collagen/protein inner portion of the colonial anthozoan skeleton must be considered non-living, since it is completely acellular except for a sleeve of secretory cells on the outside that produce the axial material (Goldberg, 1991). Because skeletal organics cost energy to be laid down, this huge amount of organic matter should be taken into account when estimating gorgonian energy budget. That of the symbiotic scleractinian *Cladocora caespitosa* has recently been estimated (Schiller, 1993), and only about 3.5% of the daily animal carbon budget was found to be diverted into skeletogenesis. The energetic cost of laying down an inorganic skeleton is lower than that for a proteinaceous one, so the amount of energy devoted to skeletogenesis is probably much higher in gorgonian than in scleractinian corals. Once a hermatypic coral has died, its calcareous skeleton is simply eroded by environmental agents and boring organisms, or becomes substrate for algae or other corals (Warner, 1984). Contrastingly, the high energetic content sequestered in gorgonian skeletal structural proteins is then available to decomposers, and a flow of energy will occur along detrimental pathways. The importance to the energetics of benthic communities of organic matter from breakdown of gorgonian axes has not yet been recognized.

Gorgonian corals may be thought analogous to plants in a variety of ecologically significant ways. As sessile, modular, clonal organisms, they are architecturally and functionally (those that are zooxanthellate) similar to trees. As with terrestrial plants, their gross shape is a supporting trunk bearing a canopy of modular units functioning to capture energy. Instead of modular units composed of leaves, the units are composed of polyps, and instead of investing a great amount of the energetic budget into the building of an almost perennial supporting structure, a wooden trunk, considerable organic content of the colony is allocated to proteinaceous skeleton. As with trees, consumer attacks are centred on modular units and on the external cortex (Harvell & Suchanek, 1987; Vreeland & Lasker, 1989; Mistri, pers. obs.). Gorgonian corals can be thought of as 'conservative' producers from the way they sequester organic matter. The energetic content of the cortex is immediately available, since the coenenchyme is directly cropped by grazers, but it probably constitutes only a minor part of the whole colony organic content. Energy allocated in skeletal structures is likely to be utilized almost only by decomposers after the colony has died, and thus it is recycled into the ecosystem with times that may probably even differ in orders of magnitude. To date, no paper has dealt with the skeleton decomposition time of such organisms, and this sort of retarded loss of available food source is not yet quantifiable.

REFERENCES

Abbiati M., Buffoni G., Di Cola G., Santangelo G., 1991 - Red coral population dynamics: stability analysis and numerical simulation of time evolution of perturbed states. *In*: O. Ravera (ed.), Terrestrial and aquatic ecosystems: perturbation and recovery. Hellis Horwood Ltd, London, pp. 219-228.

Crisp D. J., 1984 - Energy flow measurements. *In*: N. A. Holme & A. D. McIntyre (eds), Methods for the study of marine benthos. I.B.P. Handbook No. *16*, Blackwell Scientific Publications, Oxford, pp. 284-372.

Esford L. E., Lewis J. C., 1990 - Stiffness of Caribbean gorgonians (Coelenterata, Octocorallia) and Ca/Mg content of their axes. Mar. Ecol. prog. Ser., *67*: 189-200.

Goldberg W. M., 1974 - Evidence of a sclerotized collagen from the skeleton of a gorgonian coral. Comp. Biochem. Physiol., *49B*: 525-529.

Goldberg W. M., 1991 - Chemistry and structure of skeletal growth rings in the black coral *Antipathes fiordensis* (Cnidaria, Antipatharia). Hydrobiologia, *216/217*: 403-409.

Grigg R. W., 1974 - Growth rings: annual periodicity in two gorgonian corals. Ecology, *55*: 876-881.

Harvell C. D., Suchanek T. H., 1987 - Partial predation on tropical gorgonians by *Ciphoma gibbosum* (Gastropoda). Mar. Ecol. prog. Ser., *38*: 37-44.

Jeyasuria P., Lewis J. C., 1987 - Mechanical properties of the axial skeleton in gorgonian. Coral Reefs, *5*: 213-219.

Kingsley R. J., Watabe N., 1987 - Role of carbonic anhydrase in calcification in the gorgonian *Leptogorgia virgulata*. J. exp. Zool., *241*: 171-180.

Leversee G. J., 1969 - Composition and function of the axial skeleton in the gorgonian coral *Leptogorgia virgulata*. Am. Zool., *9*: 1115.

Lewis J. C., Von Wallis E., 1991 - The function of surface sclerites in gorgonians (Coelenterata, Octocorallia). Biol. Bull., *181*: 275-288.

Mistri M., 1994 - Ecological observations on a population of the Mediterranean gorgonian *Paramuricea clavata* (Risso, 1826). Boll. Zool., *61*: 163-166.

Mistri M., (in press) - Population structure and secondary production of the Mediterranean Octocoral *Lophogorgia ceratophyta* (L. 1758). P.S.Z.N.I.: Mar. Ecol.

Mistri M., Ceccherelli V. U., 1993 - Growth of the Mediterranean gorgonian *Lophogorgia ceratophyta* (L. 1758). P.S.Z.N.I: Mar. Ecol., *14*: 329-340.

Mistri M., Ceccherelli V. U., 1994 - Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. Mar. Ecol. prog. Ser., *103*: 291-296.

Mitchell N. D., Dardeau M. R., Schroeder W. W., Benke A. C., 1992 - Secondary production of gorgonian corals in the northern Gulf of Mexico. Mar. Ecol. prog. Ser., *87*: 275-281.

Muzik K., Wainwright S. A., 1977 - Morphology and habitat of five Fijian fans. Bull. mar. Sci., *27*: 308-337.

Paine R. T., 1964 - Ash and caloric determinations of sponge and opisthobranch tissues. Ecology, *60*: 384-387.

Pérès J. M., Picard J., 1964 - Nouveau Manuel de Bionomie Benthique de la Mer Méditerranée. Rec. Trav. Stn. mar. Endoume, *31*: 1-137.

Sarà M., 1986 - Sessile macrofauna and marine ecosystem. Boll. Zool., *53*: 329-337.

Schiller C., 1993 - Ecology of the symbiotic coral *Cladocora caespitosa* (L.) (Faviidae, Scleractinia) in the Bay of Piran (Adriatic Sea): II. Energy budget. P.S.Z.N.I: Mar. Ecol., *14*: 221-238.

Van Alstyne K. L., Paul V. J., 1992 - Chemical and structural defenses in the sea fan *Gorgonia ventalina*: effects against generalist and specialist predators. Coral Reefs, *11*: 155-159.

Vreeland H. V., Lasker H. R., 1989 - Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. J. exp. mar. Biol. Ecol., *129*: 265-277.

Warner G. F., 1984 - Diving and marine biology. Cambridge University Press, Cambridge, 210 pp.

Weinbauer M., Velimirov B., 1955a - Biomass and secondary production of the temperate gorgonian coral *Eunicella cavolinii* (Coelenterata: Octocorallia). Mar. Ecol. prog. Ser., *121*: 211-216.

Weinbauer M., Velimirov B., 1995b - Calcium, magnesium and strontium concentrations in the calcite sclerites of Mediterranean gorgonians (Coelenterata: Octocorallia). Estuarine Coastal Shelf Sci., *40*: 87-104.

Yoshioka P. M., Yoshioka B. B., 1989 - Effects of wave energy, topographic relief and sediment transport on the distribution of shallow-water gorgonians of Puerto Rico. Coral Reefs, *8*: 145-152.