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Biomass and secondary production of the temperate gorgonian coral *Eunicella cavolini* (Coelenterata: Octocorallia)

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ABSTRACT: Secondary production and standing stock biomass of *Eunicella cavolini*, one of the most abundant shallow-water gorgonians in the Mediterranean Sea, were estimated between 1989 and 1991 at 3 study sites: shallow boulders, a deep channel, and a deep wall. Secondary production was derived from colony densities, age structure, ash-free dry weight (AFDW) per age class, and the increase of AFDW between age classes. Estimation of secondary production ranged from 4.9 to 7.4 g AFDW m⁻² yr⁻¹ in the channel, from 1.3 to 1.6 g AFDW m⁻² yr⁻¹ at the wall, and from 0.26 to 0.38 g AFDW m⁻² yr⁻¹ at the boulders. Population turnover times were lowest in the channel (3.1 to 3.6 yr), intermediate at the wall (3.3 to 3.7 yr), and highest at the boulders (3.6 to 4.1 yr). Secondary production and turnover were intermediate compared to gorgonian species investigated so far. Standing stock of total biomass of *E. cavolini* of the present study (up to 584.6 g m⁻²) is comparable to reported standing stock biomass of tropical gorgonian communities. We assume that sclerite production of gorgonians can be an important contribution of calcium carbonate to the sediments in the investigated environment.

KEY WORDS: Production · Gorgonians · Biomass · Calcium carbonate · Sclerites · Mediterranean Sea

INTRODUCTION

Abundance, distribution and species composition of gorgonians have been intensively studied (Goldberg 1973, Kinzie 1973, Opresko 1973, Preston & Preston 1975, Yoshioka & Yoshioka 1989), and some information is also available on growth rates (Velimirov 1975, Yoshioka & Yoshioka 1991, Brazeau & Lasker 1992, Mistri & Ceccherelli 1993, Mitchell et al. 1993). However, there is only little information on the secondary production of gorgonian corals. Secondary production has been estimated in 3 gorgonian species and annual production/biomass (P/B) ratios between 0.13 and 0.45 were reported (Mitchell et al. 1992, Mistri & Ceccherelli 1994). Although estimations of standing stock biomass of gorgonians are rare (Goldberg 1973, Kinzie 1973), it was suggested (Cary 1918, cited in Milliman 1974) that gorgonian sclerites might contribute significantly to sediment calcium carbonate.

Gorgonians were observed to dominate the benthic shallow-water communities on rock faces in the Mediterranean Sea (Weinberg 1978, Gili & Ros 1985). For *Eunicella cavolini*, one of the most abundant Mediterranean gorgonian species (Weinberg 1978), data on population structure are available (Velimirov & Weinbauer 1992), but, in the Mediterranean Sea, secondary production was only investigated in the species *Paramuricea clavata* (Mistri & Ceccherelli 1994).

In this paper, we estimated secondary production and standing stock biomass of *Eunicella cavolini* colonies at 3 sites on the rock faces in the Ligurian Sea on the northwestern coast of Corsica, and we tried to evaluate the contribution of sclerites, i.e. calcium carbonate, to the sediments.

MATERIALS AND METHODS

Colonies of *Eunicella cavolini* were counted and measured at 3 sites on the west coast of Corsica near Calvi at Stareso: (1) a slightly overhanging wall in a

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large underwater channel at about 25 m depth, (2) a steep wall from 16 to 28 m depth and (3) a group of large boulders between 10 and 15 m depth. Here, these sites are termed 'channel', 'wall' and 'boulders'. In the channel and at the wall, 2 transects 25 cm wide and between 3.5 and 10 m long were set up on each rock face. At the boulders we surveyed 8 areas of about 0.5 m² each. Mean colony density was determined from the transects and surveyed areas, respectively. *In situ* measurements were made with rulers by using SCUBA. In the channel and at the wall, measurements were made in August 1989, August 1990, and August 1991. At the boulders, measurements were initiated in 1990 and repeated the year after. Total colony numbers at the start of the study were 316 in the channel, 289 at the wall and 52 at the boulders.

Age structure was determined as follows. Total branch length (TBL) was calculated using 2 methods. TBL of any fan was obtained by using a regression equation developed for *Eunicella cavolini* (Velimirov & Weinbauer 1992): $TBL \text{ (cm)} = -2.30 + 1.52 \text{ RFSA (cm}^2\text{)} - 0.0017 \text{ RFSA}^2 \text{ (cm}^2\text{)}$, where rectangularized fan surface area (RFSA) of such colonies is defined as length \times mean width. Length was determined as the distance between the 2 most distant points of the colony and mean width as the average of 3 measurements done at a right angle to the length. For small colonies or where no fan had developed, TBL was determined by measuring each branch length separately. TBL of each colony was then converted to age by using the hypothetical growth equation developed for *E. cavolini* (Velimirov 1975)

$$N_t = \frac{N_{\max}}{1 + e^{-0.608(t-9)}}$$

where N_t is the colony size at age t and N_{\max} is the TBL of the largest colony observed at the study sites (278 cm). To test this growth equation on colonies at our study sites, the TBL of several colonies was measured and the growth increments were monitored for 1 yr. Since the observed growth of the surviving 28 colonies was well within the range of the expected growth for the estimated specific age classes (Velimirov & Weinbauer 1992, Weinbauer & Velimirov in press), we used the hypothetical growth equation for estimating the age of colonies. Total densities were converted into age-specific densities by using the age distributions.

Gorgonian production was calculated by slightly modifying the method described in Mitchell et al. (1992). In the channel and at the boulders 45 colonies were collected for the determination of colony biomass. Colonies were cleaned of epibionts and care was taken to remove non-axial material from the holdfast. Colonies were dried to constant weight at 80°C, and after determination of the total colony weight, the cortex

was separated from the axial skeleton. In small colonies, cortex weight and ash-free dry weight (AFDW) was determined for the whole cortex. AFDW was measured by combusting the cortex at 450°C for 4 h (Harvell & Suchanek 1987, Harvell & Fenical 1989). This combustion temperature and time avoids a loss of sclerite weight due to disruption of water of hydration. Since AFDW varies in different growth regions of *Eunicella cavolini* (Weinbauer & Velimirov 1995b) the whole cortex of large colonies was pooled and grinded. The homogenized cortex was mixed and AFDW was determined from triplicate samples. AFDW was then calculated for the whole colony by multiplying the cortex weight by the proportion of measured AFDW. Sclerite weight was determined as the fraction remaining after combustion of the cortex. The dry weight of the axis was determined by subtracting cortex dry weight from the total biomass. A regression between colony age and AFDW, sclerite dry weight as well as axis dry weight was calculated in order to determine the mean AFDW, sclerite dry weight, and axis dry weight of each age class.

Standing stock AFDW, sclerite dry weight and axis dry weight was calculated as the sum of mean dry weight for all age classes. Total standing stock biomass is the sum of AFDW, sclerite weight and axis dry weight. Total production of AFDW, i.e. secondary production, was calculated by using the increment-summation method (Crisp 1984).

RESULTS

AFDW varied strongly within size classes. Nonetheless, the regression of AFDW on age showed a significant relationship (Fig. 1; $R^2 = 0.65$; $p < 0.0005$). Since AFDW of the age classes did not differ between the two most different study sites of the present study, i.e. between the boulders and the channel (paired t -test, $p > 0.5$), the regression was used to estimate age-specific AFDW at all study sites. A logarithmic transformation of data improved the relationship between AFDW and age (cf. Mitchell et al. 1992, Mistri & Ceccherelli 1994). Significant relationships were also established between sclerite weight and age as well as between axis weight and age (Table 1). Paired t -tests showed that age-specific weights of sclerites as well as axis did not differ between the channel and the boulders (sclerites: $p > 0.3$; axis: $p > 0.2$). Therefore, the regressions of both sclerites and axis on age were used to determine the age-specific weight of these skeleton types at all study sites.

From 1989 to 1991, AFDW production ranged from 1.3 to 1.6 g m⁻² yr⁻¹ at the wall (Table 2) and from 4.9 to 7.4 g m⁻² yr⁻¹ in the channel (Table 3). From 1990 to 1991, variability of AFDW production at the boulders

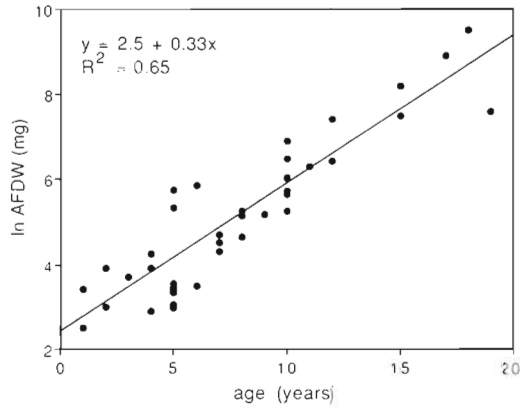


Fig. 1. *Eunicella cavolini*. Relationship between AFDW and age

was between 0.26 to 0.38 g m⁻² yr⁻¹ (Table 4). AFDW production varied only slightly between years at each of the study sites.

P/B ratios of AFDW were highest in the channel (0.28 to 0.32), intermediate at the wall (0.27 to 0.30) and lowest at the boulders (0.24 to 0.28) (Table 5). The time it takes to replace the biomass of the population, i.e. the turnover time, ranged from 3.1 to 3.6 yr in the channel, from 3.3 to 3.7 at the wall and from 3.6 to 4.1 at the boulders (Table 5).

AFDW standing stock, given as range of the investigated years, was highest in the channel (16.4 to 23.2 g m⁻²), intermediate at the wall (4.9 to 5.5 g m⁻²) and lowest at the boulders (0.9 to 1.6 g m⁻²; Table 6). Sclerite standing stock ranged from 121.3 to 260.2 g m⁻² in the channel, from 12.8 to 44.8 g m⁻² at the wall, and from 1.5 to 2.0 g m⁻² at the boulders. Total biomass, i.e. the sum of AFDW, sclerites and axis, was highest in the channel (260.9 to 584.6 g m⁻²), intermediate at the wall (27.9 to 102.2 g m⁻²), and lowest at the boulders (3.4 to 4.6 g m⁻²).

DISCUSSION

Recalculating data from Opresko (1973), total biomass of gorgonian communities derived from 3 shallow-water sites off Florida ranged from 557.7 to 1250.3 g m⁻².

Table 1. *Eunicella cavolini*. Relationship of sclerite and axis dry weight with age. The regression equation is expressed as $y = a + bx$. Age is given in years and axis as well as sclerites in mg. n: number of colonies investigated

Variables	a	b	n	R ²	p	
x	y					
Age	ln (Axis)	1.25	0.583	45	0.73	<0.0005
Age	ln (Sclerites)	1.75	0.546	45	0.69	<0.0005

Table 2. *Eunicella cavolini*. Estimation of secondary production per m² at the wall site. Biomass for each age class estimated from Fig. 1

Age class (yr)	Density (colonies m ⁻²)			Production (g AFDW m ⁻² yr ⁻¹)		
	1989	1990	1991	1989	1990	1991
0-1	6.67	7.50	4.00	0.03	0.04	0.02
1-2	13.99	7.75	8.64	0.09	0.05	0.06
2-3	12.61	12.85	11.93	0.12	0.12	0.11
3-4	9.64	13.48	10.21	0.12	0.17	0.13
4-5	9.17	4.85	5.08	0.16	0.09	0.09
5-6	4.16	6.87	5.29	0.10	0.17	0.13
6-7	4.55	4.66	4.64	0.16	0.16	0.16
7-8	3.23	3.09	2.86	0.16	0.16	0.14
8-9	1.12	0.44	0.44	0.07	0.03	0.03
9-10	0.46	0.44	0.44	0.04	0.04	0.04
10-11	0.23	0.22	-	0.03	0.03	-
11-12	0.23	0.22	0.22	0.04	0.04	0.04
12-13	-	-	-	-	-	-
13-14	-	-	-	-	-	-
14-15	0.23	-	-	0.11	-	-
15-16	-	-	-	-	-	-
16-17	-	-	-	-	-	-
17-18	-	-	-	-	-	-
18-19	-	-	-	-	-	-
19-20	-	0.22	0.22	-	0.53	0.53
Total	66	63	54	1.3	1.6	1.5

Table 3. *Eunicella cavolini*. Estimation of secondary production per m² at the channel site. Biomass for each age class estimated from Fig. 1

Age class (yr)	Density (colonies m ⁻²)			Production (g AFDW m ⁻² yr ⁻¹)		
	1989	1990	1991	1989	1990	1991
0-1	21.31	50.04	17.43	0.10	0.24	0.08
1-2	19.24	23.04	18.03	0.13	0.15	0.12
2-3	25.76	19.62	23.99	0.24	0.18	0.22
3-4	15.74	19.62	22.95	0.20	0.25	0.29
4-5	12.08	15.12	12.52	0.22	0.27	0.22
5-6	14.15	16.56	15.50	0.35	0.41	0.38
6-7	14.63	14.04	15.50	0.50	0.48	0.53
7-8	14.63	16.56	11.03	0.74	0.84	0.56
8-9	9.70	10.44	5.51	0.62	0.67	0.35
9-10	3.50	3.96	3.43	0.32	0.37	0.32
10-11	2.54	1.51	0.25	0.33	0.20	0.03
11-12	2.54	1.98	-	0.46	0.36	-
12-13	1.02	0.50	-	0.25	0.12	-
13-14	0.51	-	-	0.18	-	-
13-15	-	-	-	-	-	-
15-16	-	-	-	-	-	-
16-17	-	0.50	-	-	0.47	-
17-18	-	-	-	-	-	-
18-19	0.51	0.50	-	0.92	0.91	-
19-20	-	-	-	-	-	-
20-21	0.51	-	0.51	1.79	-	1.79
Total	159	180	149	7.4	5.9	4.9

Table 4. *Eunicella cavolini*. Estimation of secondary production per m^2 at the boulders site. Biomass for each age class estimated from Fig. 1

Age class (yr)	Density (colonies m^{-2})		Production (g AFDW $m^{-2} yr^{-1}$)	
	1990	1991	1990	1991
0–1	0.83	1.39	0.004	0.006
1–2	–	1.11	–	0.017
2–3	1.94	1.11	0.018	0.010
3–4	1.11	1.39	0.014	0.018
4–5	2.78	1.94	0.050	0.035
5–6	2.78	2.50	0.069	0.062
6–7	2.22	1.11	0.077	0.038
7–8	2.5	1.67	0.126	0.084
8–9	0.28	–	0.018	–
Total	11.1	10.2	0.38	0.26

In different geomorphological zones of a reef, Goldberg (1973) found a gorgonian biomass in the range of about 100 to 600 $g m^{-2}$. In the present study, estimations of the standing stock of gorgonians ranged from 3.4 to 584.6 $g m^{-2}$. At the investigated study sites in the Bay of Calvi, other gorgonians, i.e. *Eunicella singularis* and *Paramuricea clavata* colonies, were rare or not present. In deeper water, *P. clavata*, a species larger than *Eunicella cavolini*, becomes abundant, and the size of *E. cavolini* as well as *P. clavata* generally increases with depth (pers. obs.; cf. Russo 1985). Thus it is possible that total gorgonian biomass may be higher in greater depths than at our study sites.

Interestingly, the maximum standing stock of AFDW is very similar in all species investigated so far, ranging from 18.3 to 23.2 $g m^{-2}$ (Table 6; Mitchell et al. 1992, Mistri & Ceccherelli 1994), although maximum age, size and abundance of colonies differ strongly between species. Thus it might well be that the carrying capacity for AFDW is similar in the 4 gorgonian species investigated in the northern Gulf of Mexico and in the Mediterranean Sea. Less abundant, but large, species might have a similar maximum standing stock of AFDW compared to a very abundant, but small species.

From data given in Lewis & Post (1982) a conversion factor of 6.5 ± 0.21 kcal g^{-1} AFDW for gorgonian tissue (mean of 5 species) can be recalculated. Using this con-

Table 5. *Eunicella cavolini*. Production/biomass (P/B) ratios of AFDW and turnover at the study sites. Values calculated from data in Tables 2 to 4. nd: not determined

Study site	P/B			Turnover time (yr)		
	1989	1990	1991	1989	1990	1991
Channel	0.32	0.28	0.30	3.1	3.6	3.3
Wall	0.27	0.29	0.30	3.7	3.4	3.3
Boulders	nd	0.24	0.28	nd	4.1	3.6

version factor, a production from 1.7 to 48.1 kcal $m^{-2} yr^{-1}$ can be estimated for *Eunicella cavolini* at the study sites of the present study. In other gorgonians, energy values ranged from 14.9 to 68.5 kcal $m^{-2} yr^{-1}$, when using the same conversion factor (Mitchell et al. 1992, Mistri & Ceccherelli 1994). Lewis (1981) reported on a large range of production of stony corals. However, all except 1 species are in the range of 29.2 to 57.0 kcal $m^{-2} yr^{-1}$. Schiller (1993) determined maximum energy values of 105.7 kcal $m^{-2} yr^{-1}$ in the stony coral *Cladocora caespitosa* from the Mediterranean Sea. Thus, energy values of gorgonians are similar to some stony corals.

Lewis (1981) reported P/B ratios of stony corals in the range of 0.94 to 2.67. Other sessile marine invertebrates have P/B ratios between 0.3 and 3.2. P/B ratios of gorgonian corals are lower ranging from 0.13 to 0.45 (Table 5; Mitchell et al. 1992, Mistri & Ceccherelli 1994). This suggests that gorgonians have a low metabolism and a slow turnover. P/B ratios of gorgonian populations of the present study (0.24 to 0.32; Table 5) were between *Paramuricea clavata* (0.13; Mistri & Ceccherelli 1994) and the *Leptogorgia* spp. (0.37 to 0.45; Mitchell et al. 1992). Likewise, maximum colony age from different study sites was highest in *P. clavata* (28 yr), lowest in *Leptogorgia* spp. (6 to 11 yr) and intermediate in *Eunicella cavolini* (9 to 21 yr). This indicates that species with old colonies tend to lower P/B ratios.

We found differences of production and P/B ratios of AFDW between the investigated study sites. The ranking of study sites in terms of production and biomass (from highest to least: channel, wall, and boulders) is predominantly due to the different abundances

Table 6. *Eunicella cavolini*. AFDW, sclerite and total biomass ($g m^{-2}$) at the study sites. Values were calculated from Tables 2 to 4. nd: not determined

Study site	AFDW			Sclerite biomass			Total biomass		
	1989	1990	1991	1989	1990	1991	1989	1990	1991
Channel	23.2	21.4	16.4	260.2	121.3	172.9	584.6	260.9	396.5
Wall	4.9	5.5	5.0	12.8	44.8	44.1	27.9	102.2	100.6
Boulders	nd	1.6	0.9	nd	2.0	1.5	nd	4.6	3.4

between study sites, and to a lesser extent due to the different age structure. Turnover times are lowest in the channel, slightly higher at the wall, and highest at the boulders (Table 5), indicating older colonies at the boulders. Although maximum colony age was much higher in the channel and at the wall than at the boulders, the most abundant age classes are between 1 and 4 yr in the channel and at the wall and between 5 and 8 yr at the boulders. This skewed age structure towards older colonies at the boulders caused the lower turnover.

Eunicella cavolini is an azooxanthellate gorgonian. Thus, primary production did not contribute to the estimation of secondary production of *E. cavolini* as might be the case in the zooxanthellate genus *Leptogorgia* (Mitchell et al. 1992). Moreover, grazing could bias the estimation of production based on AFDW measurements. However, the amphipod *Caprella acanthifera* and grazing spurs of the ovulid snail *Simnia spelta* were only seen occasionally, and other grazers on *E. cavolini* were not observed in the present study. Mitchell et al. (1992) argued that mucus production of gorgonian colonies could result in an underestimation of gorgonian production. However, mucus production seems not to be important in *E. cavolini*.

Overgrowth was observed on many of the colonies (Weinbauer & Velimirov in press). Since repair growth is necessary to compensate for overgrowth, this could have led to an underestimation of production by simply deriving production from AFDW changes between age classes. Since gonad production (compare Mistri & Ceccherelli 1994) and the formation of sclerites and axis is not considered in the method used for measuring production, and the estimation of production is only based on AFDW, data on secondary production should be considered as conservative.

Sclerites of *Eunicella cavolini* are composed of calcium carbonate with only small amounts of Mg (1.6 to 2.2%; Weinbauer & Velimirov 1995a) and organic material. To estimate the amount of calcium carbonate that is set free in terms of sclerites, we used the turnover times given in Table 5. Sclerite turnover ranged from 33.7 to 83.9 g m⁻² yr⁻¹ in the channel, from 3.5 to 13.4 g m⁻² yr⁻¹ at the wall and from 0.5 to 0.9 g m⁻² yr⁻¹ at the boulders. Since age structure is comparatively stable between years in all investigated environments, we can imply that the sclerite turnover is equivalent to calcium carbonate that is set free. Based on the dimensions of the study sites (channel: 4 × 4 m; wall: 10 m high, 7 m wide), we estimated that the amount of calcium carbonate set free ranges from 539 to 1342 g yr⁻¹ in the channel and from 245 to 938 g yr⁻¹ at the wall. It was estimated that gorgonians at Dry Tortugas contribute about 250 g sclerites m⁻² yr⁻¹ to the sediments (Cary 1918, cited in Milliman 1974).

From this citation it is not clear whether the per square meter production of sclerites is based on the whole study site or only on the area where gorgonians grow. Nevertheless, we conclude that gorgonian sclerites can contribute significantly to the sediment calcium carbonate.

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