

A general approach to the *in situ* energy budget of *Eudendrium racemosum* (Cnidaria, Hydrozoa) in the Western Mediterranean

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SUMMARY: An *in situ* energy budget of the hydropolyp *Eudendrium racemosum* (Cavolini, 1785) is presented. Ingestion and respiration rates and ammonium excretion were studied over two 24 h cycles, with two-hour sample intervals. The species ingested as much as 25.9 % of its own biomass per day (minimum rate). Respiration was 1.62 ml O₂ g⁻¹ dw h⁻¹ while excretion was 13.6 μM NH₄ g⁻¹ dw h⁻¹. We estimated that the species increased its biomass at a rate of 9.6 % per day (Growth + Reproduction). This value is higher than those previously reported for other cnidarians. We can assume that the capacity of *E. racemosum* to survive — albeit for a limited period of the year — in the highly-competitive shallow-water communities is based on its high growth rate.

Key words: *Eudendrium racemosum*, energy budget, ecological strategies, Western Mediterranean.

INTRODUCTION

Hydroids are one of the most abundant zoological taxa among hard substrate benthic communities, particularly in temperate areas like the Mediterranean Sea (BOERO, 1984). In spite of this, there have been very few metabolic studies (ingestion rates, energy budgets and ecological energetics) on hydroids. Energy budgets have been studied only in the laboratory for non-marine species (PAFFENHÖFER, 1968; SCHROEDER, 1969). Although the natural diet has been studied (CHRISTENSEN, 1967; SIMKINA, 1980), there are no data on energy intake rates. Respiration has been measured in a few species, both marine (SVOBODA, 1981) and non-marine (LENHOFF & LOOMIS, 1957; ARNDT, 1984).

In this paper we present an *in situ* energy budget for the marine hydroid *Eudendrium racemosum* (Cavolini, 1785). *In situ* energy budgets help to understand better benthic energy fluxes as well as the ecological strategies of some groups where the energetical processes have not been studied. Our aim was to show that the short life-cycles reported for some

hydroids (CROWELL, 1957; HALE, 1973) as well as the seasonality of others (BOERO *et al.*, 1986) is reflected by this budget. We assume that the high competitiveness of the benthic system and the high predatory activity suffered by the polyps (MCLEOD & VALIELA, 1975) are compensated for by a high energy intake rate and relatively low and constant metabolic costs, resulting in high growth efficiencies.

In a previous study we examined the ingestion rates of the hydropolyp *Eudendrium racemosum*, over 24-h cycles, with sample intervals of two hours (BARANGÉ & GILI, 1988): data on energy intake are complemented in this paper by data on respiration and excretion rates from samples with the same periodicity as in the previous study.

It should be noted that this type of study involves various sources of error, such as bacterial influence on metabolic rate and the estimation of ingested organic matter from coelenteric contents analyses. Nevertheless, these data reflect natural situations, thus leading to new hypotheses on how the benthic system works and how it is organized.

MATERIALS & METHODS

E. racemosum forms extensive populations on the SE slope of the Meda Xica I. (Medes Islands, NE of Spain). The population studied lives within a shallow-water algal community, growing over a stony substrate encrusted by calcareous algae (BARANGÉ & GILI, 1988).

The population has been observed in this area for many years and shows a maximum density from May to November, with a minor hydrocauli density during the rest of the year, when the hydroid regress to a dormant stage. Gonophores have been observed from July to October (GILI, 1986).

1. Collection and respiratory requirements

Samples were taken over two 24-h cycles (July, 20th-21st and September, 3rd-4th, 1986), at two-hourly intervals. Collected colonies were completely cleaned of macroepibionts, and then incubated *in situ* and separately for one hour (no more than 20 min elapsed between collection and incubation). Respiration rates at ambient temperature of 21 °C were measured using the Winkler method (STRICKLAND & PARSONS, 1968) with 40 ml dark bottles. Ammonium excretion of hydroids in 80 ml dark bottles was measured by the phenolhypochlorite method (SOLÓRZANO, 1969). The water used for incubation was previously filtered with a 60 µm mesh-size net. Although this mesh-size does not eliminate smallest organisms, control incubations gave negligible values.

2. Daily acquisition of energy

The coelenteric contents of 100 randomly sampled polyps collected every two hours through each day were studied (BARANGÉ & GILI, 1988). Taking into account a maximum prey residence time of five hours (BARANGÉ & GILI, 1988) ingested organic matter was calculated by the following procedure: The first sample (11 h) was considered as without food (all the content was captured before that time). Consequently every prey detected 4 hours later was considered to have been captured within this interval. The same procedure was used for each 4-hour period. This method underestimates ingestion rates since some prey can be digested quickly, but it permits an evaluation of minimum food intake.

Considering that most of the items could only be identified as "crustacean fragments" or "copepod eggs", we counted six fragments or 4 eggs as "one prey item", since only whole prey have known biomass. These biomasses were obtained from SEBENS & KOEHL (1984), after correction for the size of our specimens.

3. Energy budget

By assuming that most of the ration is made up by small crustaceans, average caloric values of food were obtained from COLES (1969) and PAFFENHÖFER (1968) (22.6 J mg dw⁻¹). An assimilation efficiency of 60.7 % of ingestion was used from PAFFENHÖFER (1968; Table II). This is the lowest efficiency obtained for cnidarians, but from the closest species, in terms of size, to *E. racemosum* (SEBENS, 1987).

The scope for growth was obtained by subtracting daily respiratory requirements (Respiration + Excretion) from total assimilated energy. This scope was transformed into hydroid biomass using a value of 23.7 J mg of colony dry weight⁻¹, an accepted value for hydroid-energy conversions (PAFFENHÖFER, 1968; SCHROEDER, 1969).

RESULTS

1. Ingested organic matter

The organic matter ingested in each 24-h cycle is shown in Table I. An average of 22.9 µg dw polyp⁻¹ day⁻¹ was obtained. With a conversion of 13 mg of dry weight for a colony of 147 polyps, a medium-size colony of *E. racemosum* ingests 5.86 KJ g⁻¹ d⁻¹. This value represents 25.91 % of its own organic matter per day, higher than previous values obtained for other cnidarians (Table II), as well as the previous maximum of 10 % known for benthic carnivorous invertebrates (CONOVER, 1978).

2. Respiration

Average respiration rates for each cycle are shown in Table I. Thus, *E. racemosum* consumes 1.62 ml O₂ g dw⁻¹ h⁻¹. Values within cycles are very variable, and daily metabolic rhythms are impossible to detect.

This value is comparable to those obtained for other hydropolyps, specially the only marine species without symbionts already studied (Table II, *Aglaophenia tubiformis*). Hydroids seem to have higher

TABLE I. — Average metabolic rates of *E. racemosum* in the two 24-h cycles performed. Weight unities are on a dry weight basis.

	Ingestion µg polyp ⁻¹ day ⁻¹	Respiration ml O ₂ g ⁻¹ h ⁻¹	Excretion µM NH ₄ g ⁻¹ h ⁻¹
July 1986	19.91	2.19 ± 1.70	13.5 ± 25.5
Sept. 1986	25.91	1.05 ± 1.93	13.7 ± 34.0
Average	22.91	1.62	13.6

values than other cnidarians, as can be expected considering their smaller module size (SEBENS, 1987).

3. Excretion

Table I also shows the ammonium excretion rates calculated for each cycle. A daily cycle could not be observed because of the high variability of the results. The averages of the two cycles were similar, giving an average value of $13.67 \mu\text{M NH}_4 \text{ g dw}^{-1} \text{ h}^{-1}$. No data for hydroid excretion could be obtained from the literature. Although other cnidarians have lower values, this could be due to their lower percentage of nitrogen excreted as ammonium (approx. 50 % for siphonophores; Larson, pers. comm.).

NQ (mol nitrogen excreted per mol oxygen consumed) was 0.189, slightly higher than that obtained for anemones (ZAMER & SHICK, 1987). Higher excretion in relation to respiration would then be expected for hypopolyps. On the other hand, planktonic cnidarians have lower NQ (0.006-0.1; Larson, pers. comm.).

4. Energy budget

An energy budget could be calculated using the equations,

$$I = G + R + \text{Ex} + \text{Rep} + \text{Eg}$$

and

$$A = I - \text{Eg} \text{ (CRISP, 1984)}$$

where I = ingestion; A = assimilation; G = growth; R = respiration; Ex = excretion; Rep = reproductive effort and Eg = egesta.

We used a conversion factor of 20.95 J for each ml of oxygen consumed (CONOVER, 1978). Thus, respiration and excretion were as high as $1.62 \text{ KJ g dw}^{-1} \text{ d}^{-1}$ or 27.78 % of the total ingested organic matter. Nevertheless, the value is lower than those obtained by PAFFENHÖFER (1968: 32.86 % in *C. multicornis*), SCHROEDER (1969: 30-44 % in *H. pseudoligactis*) and ZAMER & SHICK (1987: 41-50 % in *A. elegantissima*). This means that *E. racemosum* must ingest prey amounting to 7.2 % of its own biomass to satisfy its minimum respiratory requirements.

Net growth efficiency (K_2) was then estimated as 58.4 %. Although not very different from other coelenterates (Table II), it is higher than that of other carnivorous invertebrates (average, 27.6 %; HUMPHREYS, 1979). Consequently, the species will theoretically restore its biomass by a factor of 9.6 % per day, which is higher than anemones (1.2-1.8 %; ZAMER & SHICK, 1987), but similar to the value deduced from PAFFENHÖFER (1968). This theoretical production is more similar to that obtained for planktonic organisms than for benthic ones (GREZE, 1978).

TABLE II. — Metabolic parameters for hydroid species from the literature. Average values for some other cnidarian groups are also presented (See SEBENS, 1987, for more information). Weight unities correspond to dry weight.

Group	Ingestion % body wt.	Assimilation % ingestion	Respiration ml $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	Excretion $\mu\text{M NH}_4 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	Growth Efficiency	Source
<i>E. racemosum</i>	25.9 %	—	1.62	13.67	¹ 58.35 %	This study
<i>Perigonimus megas</i>	—	88 %	—	—	—	SIMKINA (1980)
<i>Clava multicornis</i>	2.3-19 %	60.7-74 %	2.24-2.97	—	² 39.3-49.3 %	PAFFENHÖFER (1968)
<i>Hydra littoralis</i>	—	—	10.2	—	—	LENHOFF & LOOMIS (1986)
<i>H. pseudoligactis</i>	50-70 %	67-89 %	—	—	³ 46-55 %	SCHROEDER (1969)
<i>Aglaophenia sp.</i>	—	—	1.19-1.40	—	—	SVOBODA (1981)
<i>A. nubiformis</i>	—	—	3.5-4.9	—	—	SVOBODA (1981)
<i>Cordylophora caspia</i>	—	79-86 %	1.3-2.3	—	—	ARNDT (1984)
<i>Clava multicornis</i>	—	89 %	1.2	—	—	ARNDT (1984)
<i>Pelmatohydia oligactis</i>	—	76 %	4.02	—	—	ARNDT (1984)
Hydromedusae	¹ 20 %	—	0.1-1.4	—	—	IKEDA (1974)
						ARAI (1986)
Siphonophores	17-45 %	74.2-80.4 %	0.25-0.33	0.63-1.48	² 33-48 %	LARSON (1987b)
						NIVAL <i>et al.</i> (1972)
						BIGGS (1977)
						PURCELL (1983)
						PURCELL & KREMER (1983)
Anthozoans	4.5-6 %	70-80 %	0.02-4.01	2.09	³ 28-41 %	IMAFUKU (1973)
						MERGNER & SVOBODA (1977)
						DAVIES (1980)
						CLAYTON JR. (1986)
						ZAMER & SHICK (1987)
Scyphozoans	5-65 %	—	0.14-0.88	—	² 27-37 %	FRASER (1969)
						LARSON (1987a)
						LARSON (1987b)

¹estimated

² K_1

³ K_2

⁴values very variable as a function of weight.

DISCUSSION

Because of the opportunistic, non-selective feeding pattern of suspension-feeders as well as their potentially high feeding rates (BARANGÉ, 1988; BARANGÉ & GILI, 1988), *in situ* ingestion rates are of basic importance. The high and constant ingestion rate, as shown by *E. racemosum*, gives animals an energy maximizing feeding strategy (SCHOENER, 1971). In the case of *E. racemosum* this rate is reached due to its capacity of capturing several prey items at the same time, thus decreasing ingestion time per item, resulting in sudden increases in the ingestion rate when prey concentration is high (CLAYTON Jr., 1986). This high food intake is exemplified by 12 copepods being found in a single polyp and may be still higher if phytoplankton ingestion (CORNELIUS & ÖSTMAN, 1987; pers. obser.) and dissolved organic matter ingestion (SCHLICHTER, 1980) is included. For these reasons and because the method does not detect quickly-digested items, the calculated ingestion rate should be considered as a minimum rate.

A high and constant metabolism could be deduced from the respiration and excretion rates, without changes according to the observed variability of feeding along the day (BARANGÉ & GILI, 1988). This leads us to conclude that the *E. racemosum* metabolism does not depend on the intake rhythm. The NQ value is typical of proteinic catabolism (MAYZAUD, 1973), although physiological parameters are expected to change according to temperature and the metabolic and feeding state (KINNE & PAFFENHÖFER, 1965).

Our data suggest that respiration rates may be higher in hydroids than in hydromedusae (IKEDA, 1974; NIVAL *et al.*, 1981), as well as in siphonophores (PURCELL & KREMER, 1983), because of the shorter life cycle of the hydroid modules and, probably, the higher number of potential prey items found in the benthic environment.

Cnidarians have high assimilation efficiencies (Table II). Although the value used in this work is the lowest reported, we verified that it is as expected by using tables from CONOVER (1978). In this paper the author expects assimilation efficiencies to be of 64 % (66.7 % in our work) for net growth efficiencies of 58.5 % (58.3 % in our work).

Our K_2 efficiencies are one of the highest reported for benthic invertebrates, due mainly to lack of movement of the hydroid and the very low energy spent in finding prey items. Our conclusion agrees with VERNBERG (1981), that considered that "sit and wait" predators have growth efficiencies as high as 50-80 %.

The daily biomass increase of 9.5 % is high compared to other cnidarians, both planktonic (LARSON, 1987b) and benthic (ZAMER & SHICK, 1987),

but is similar to that reported in the laboratory for other hydroids (PAFFENHÖFER, 1968), supporting that the high renewal rate of the modules of hydroids is coupled with high production rates. High renewal rates are not specific to hydrozoans. HERON (1972) shows that the high renewal rate of Thaliacean species (46h) is based on the regulation of the energy spent in movement and on their high capture rate.

To discuss the factors determining the nearly complete disappearance of the *E. racemosum* population from November-December until May is not possible at this point of time. Recent studies related to seasonal distribution of hydroids in the Western Mediterranean (BOERO & FRESI, 1986; LLOBET *et al.*, in press) suggest competition with macroalgae to be the major factor controlling the Mediterranean hydroid populations. On the other hand, the high concentration of Opisthobranch gastropods on the colonies from August onwards (pers. obs.) could be an important factor. Although the predatory activity of opisthobranchs on cnidarians is well known, very few studies have quantified this activity. No definite conclusion can be drawn, but if we consider that every gastropod can eat between 25 and 200 polyps per day (MCLEOD & VALIELA, 1975) we can expect a reduction of the hydroid population due to this activity. In any case any conclusion must be done with caution, since SUTHERLAND & KARLSON (1977) demonstrated that some hydroids resist predation successfully.

In short, the *E. racemosum* capacity to survive — although for a limited period of the year — in the strong competitive benthic shallow-water communities is based on its high ingestion rate and growth efficiencies. Its nearly complete disappearance from the substratum is ruled by unknown factors, but two of them, the predatory activity of some opisthobranch gastropods and competition with other benthic organisms, mainly algae, must be the most important factor (GILI *et al.*, 1989), at least during certain periods of the hydroid life-cycle.

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