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Received: 24 January 2001
Amended: 10 October 2001
Accepted: 23 October 2001

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Acknowledgments

We thank C. S. Fellows, P. J. Mulholland, R. T. Venterea, E. Wright, and three anonymous reviewers for their valuable contributions during the preparation of this paper. This project was supported by a grant from the National Science Foundation (DEB 9318205) to the University of Colorado, a grant from the Andrew W. Mellon Foundation to Gene E. Likens, and a fellowship from the Cooperative Institute for Research in Environmental Sciences.

Limnol. Oceanogr., 47(1), 2002, 324–331
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Seasonality of in situ respiration rate in three temperate benthic suspension feeders

Abstract—Natural respiration rates of suspension feeders in temperate ecosystems are still poorly known. This lack of information constrains our understanding of the functioning and dynamics of benthic marine ecosystems in temperate areas. We examined the in situ seasonal variation in respiration rate of three benthic suspension feeders (a sponge, an ascidian, and a gorgonian) in northwestern Mediterranean sublittoral communities using a recirculating flow respirometry system. The in situ technique is shown to be highly applicable to seasonal studies of the physiological energetics of benthic suspension feeders. Respiration rates of the three species varied two- to threefold through the annual cycle, exhibiting a marked seasonal pattern but showing no daily cycle or significant day-to-day variability within months. The respiration rate of the sponge and ascidian, active suspension feeders, increased with temperature. The respiration rate of the gorgonian, a passive suspension feeder, did not correlate with temperature. We estimated a Q_{10} of 1.1, which indicates that respiration rate in this species is not highly dependent on temperature. Synthesis of new tissue of some Mediterranean benthic suspension feeders, such as gorgonians, does not correlate with temperature, which allowed us to isolate the effects of temperature and synthesis of new tissue on respiration rate. Synthesis of new tissue increased respiration rate of the gorgonian by ~40%. The low rate of synthesis of new tissue during summer, together with the contraction of polyps and the low Q_{10}, explains the low respiration rates of the gorgonian observed during the period of highest temperature. These low respiration rates support the hypothesis that energy limitations may underlie summer dormancy in some benthic suspension-feeding taxa in the Mediterranean.

Respiration is the metabolic process by which organic substances are broken down to simpler products with the release of energy (Lucas 1996). Oxygen consumption is a

measure of respiration rate that can be converted into energy equivalents. It represents a measure of that part of the food intake that is required to provide energy to support life processes (Clarke 1991). Suspension-feeding invertebrates are one of the most abundant groups in benthic communities (Gili and Coma 1998). The energetics of suspension feeders in coral reef ecosystems is particularly complex because many are symbiotic with algae. Symbiotic suspension feeders have been the focus of several studies, both in the laboratory and in the field, which have contributed important data on respiration and oxygen production (e.g., Sebens 1987; Patterson et al. 1991; Fabricius and Klumpp 1995). However, the natural respiration rates of most suspension feeders in temperate and cold ecosystems are still poorly known, which constrains our understanding of the physiological responses of organisms to their natural environments and of the flow of energy and matter in temperate and cold benthic ecosystems.

Physical factors—including temperature, salinity, ambient oxygen concentration, and water flow—and trophic effects—including particle size, filtration activity, and food concentration—have all been suggested as important factors that affect respiration of benthic filter feeders (Jørgensen et al. 1986; Sebens 1987; Patterson et al. 1991; Lucas 1996; Riisgård and Larsen 2001). Any measured respiration rate is composed of several processes that may include the costs of (1) basal metabolism, (2) locomotion activity, and (3) secondary production (i.e., synthesis of somatic and reproductive tissue). These components are likely to differ in their response to both temperature and season (Clarke 1987*a*).

The respiratory cost of secondary production has been determined under laboratory conditions (*see* Riisgård and Larsen 2001 for a review), but to measure this cost in the field has proved difficult. In most cold temperate and polar invertebrates, growth and reproduction are seasonal and usually occur during the summer period (Coma et al. 2000). The overlap of the period of synthesis of new tissue with that of higher temperatures makes it difficult to distinguish respiration due to secondary production from that due to increased metabolic rate in higher temperatures. In the Mediterranean, synthesis of new tissue of many invertebrates does not correlate with temperature (Coma et al. 2000), making this region a convenient system to distinguish the effect of temperature from that of synthesis of new tissue.

We evaluated annual cycles in respiration rate in nature, to contribute to the understanding of the physiological responses of organisms in their natural environments. This goal required in situ measurements, because the laboratory cannot simulate all environmental and biological factors that affect respiration rate of the organisms under natural conditions. We studied invertebrates from three phyla that occur in the same community: the asymbiotic gorgonian *Paramuricea clavata,* the ascidian *Halocynthia papillosa,* and the sponge *Dysidea avara.* These three species are characteristic and ubiquitous members of Mediterranean sublittoral benthic communities (True 1970). An important data set is already available for the gorgonian (Coma et al. 1994, 1995, 1998*a,* 2001; Ribes et al. 1999*a*), and a preliminary energy budget has already been constructed for this species (Coma et al. 1998*b*). We concluded that basal metabolism accounts for a large fraction of the total energy expenditure, but a detailed seasonal study of respiration was needed to better understand the energetics of this species. Some data are also available for the ascidian (Becerro and Turon 1992; Ribes et al. 1998*a*) and the sponge (Ribes et al. 1999*b*). We focused on two main goals: (1) to examine the seasonal variation of in situ respiration rate and (2) to distinguish and quantify the main factors that affect respiration rate through the annual cycle.

Study site and experimental organisms—The study was conducted at the Medes Islands Marine Protected Area (northwestern Mediterranean Sea, 42°3′N, 3°13′E) from October 1995 to October 1996. Specimens of the sponge *D. avara,* the ascidian *H. papillosa,* and the asymbiotic gorgonian *P. clavata* were selected to have a similar biomass (*D. avara,* 0.20 ± 0.03 standard deviation [SD] g ash free dry mass [AFDM]; *H. papillosa,* 0.51 ± 0.14 SD g AFDM; and *P. clavata,* 0.95 ± 0.19 SD g AFDM), to reduce variation due to the effect of biomass on respiration rate (Lucas 1996).

Respiration rate measurements—About 1 month before each sampling date, several specimens of the three species were collected attached to pieces of natural substrate. Animals were cleaned of macroepibionts and attached to artificial supports by use of PVC posts (for the ascidian and the gorgonian) or an inert mastic compound (Scotch-Calk for the sponge). These specimens were then returned to their natural environment, close to conspecifics, to acclimate to the conditions. This approach greatly reduced disturbance to the organism during subsequent experimental work. For each date, new specimens were collected. Respiration experiments were conducted in hemispherical ultraviolet-transparent Plexiglas chambers ~3 liters in volume at 15-m depth. The chambers had inlet and outlet apertures, allowing the system to be operated in an open or close mode (*see* Ribes et al. 2000 for a detailed description of the system). An electric pump at the outlet aperture forced water through the system at a speed of 0.024 L s^{-1}. At this rate, the water velocity inside the chamber was ~1.2 cm s^{-1} creating turbulent flow around the test animal. At the beginning of each experiment, one specimen was placed on the base of the experimental chamber with the second chamber serving as a control. Specimens were allowed to expand fully. If the incubated specimen did not expand fully within a few minutes, it was eliminated from the experiment. During the acclimation period, the inlet and outlet apertures of the both experimental and control chambers were not connected, so the system was open. After a 1-h acclimation period, inlet and outlet apertures were connected, and the system was closed. In both chambers, oxygen concentration and temperature were recorded every 2 min continuously by use of Wissenschaftlich-Technische Werkstäten oxygen electrodes model EOT 196. Respiration was estimated from 24-h cycles, except when the 24-h cycle could not be completed because of bad weather. The water inside both chambers was totally flushed when oxygen depletion was ~15% of the initial value. Because initial oxygen concentrations were always saturated or supersaturated, flushing always occurred before oxygen con-

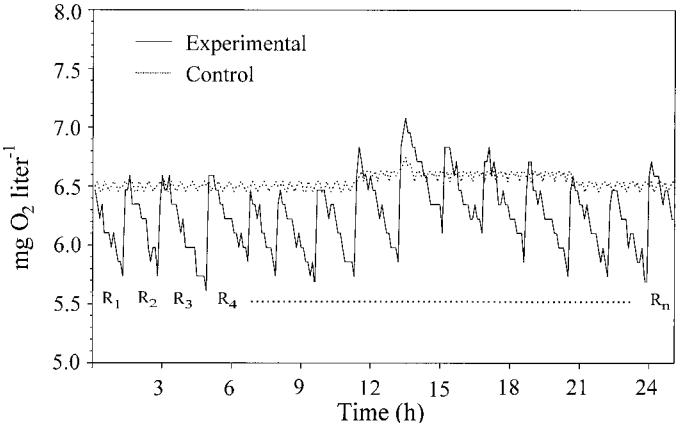

Fig. 1. *Dysidea avara.* Oxygen concentration (mg O_2 L^{-1}) inside the chambers during a daily cycle. Oxygen values were recorded every 2 min in both chambers, and the water inside both chambers was renewed when oxygen concentration changed 15% from its initial value. $R_1 \ldots R_n$ refers to each complete renewal of the water inside the chamber. Experimental, chamber with organism; control, chamber without organisms. Respiration was determined from decrease in oxygen concentration over time.

centration had dropped to 85% saturation. Preliminary experiments demonstrated that a 15% decrease in oxygen concentration did not significantly affect species behavior or respiration rate (Ribes et al. 2000). The control chamber was used to detect ambient oxygen and temperature variations. The behavior of the incubated specimens, as well as that of conspecifics in the area, was monitored by direct observation at 2–3 h intervals during the day and twice at night for every experiment. For the gorgonian, individual polyps were scored as expanded (i.e., polyps with any degree of expanded tentacles) or contracted, and colony expansion was estimated as the proportion of expanded polyps occurring on a colony. The respiration rate of the three species was examined at ~2-month intervals throughout an annual cycle. Three replicate experiments were carried out on each sampling date, giving a total of 18 measurements throughout the annual cycle conducted on 18 different specimens for each species. The effect of expansion and contraction of the polyps on respiration rate of the gorgonian *P. clavata* was examined in two occasions (late June and late August 1996).

Water residence time was determined for each replicate experiment. Mean water residence time in the chambers differed among species: 45 ± 20 SD min for the sponge *D. avara,* 90 ± 30 min for the ascidian *H. papillosa,* and 135 ± 39 SD min for the gorgonian *P. clavata.* Although the specific growth rate of the incubated organisms was not examined, water residence times were shorter than those required to detect significant decrease in food sources (Ribes et al. 2000).

For the three species, daily cycle respiration experiments included several renewals of the water inside the chamber (see Fig. 1 as an example). Respiration rates (mg O_2 $mass^{-1}$ h^{-1}) were estimated from each decrease in oxygen concentration in the organism chamber of 0.4 mg O_2 L^{-1} during each experiment; several respiration rate values within each renewal were thereby obtained (Fig. 1).

Table 1. Analysis of variance of respiration rates between days and months. Days nested in months.

Species	df	SS	MS	*F*	*P*
D. avara					
Day	17	0.20	0.17	0.29	0.990
Month	5	10.18	3.39	58.03	<0.001
Error	452	7.37	0.06		
H. papillosa					
Day	17	0.06	0.03	0.22	0.800
Month	5	2.49	0.62	5.10	<0.001
Error	321	14.28	0.12		
P. clavata					
Day	17	0.24	0.12	0.18	0.830
Month	5	13.41	1.12	5.72	0.040
Error	254	115.08	0.65		

df, degrees of freedom; SS, sums of squares; MS, mean square; *F*, *F* ratio; *P*, probability.

Variation in respiration rate was examined at three levels: within a daily cycle, between days within a month, and between months. Variation within a daily cycle was examined by comparing measurements within renewals with those from other renewals within the same daily cycle by use of a one-way repeated measures ANOVA (e.g., $R_1 \ldots R_n$ in Fig. 1). Variation between days within a month and between months was tested by use of data from all daily cycles with two-way nested ANOVA (days nested in months). The amount of variance in respiration rate through the year that could be explained by water temperature was estimated by use of a one-way ANOVA with temperature as the independent variable and mass-specific respiration as the dependent variable.

When temperatures differed by <10°C, Q_{10} values—i.e., the rate at $(T + 10)$/rate at T—were estimated by applying Van't Hoff's formula (Clarke 1983):

$$Q_{10} = [R_{T2}/R_{T1}][10/(T_2 - T_1)] \quad (1)$$

where R_{T1} and R_{T2} are the respiration rates (mg O_2 $mass^{-1}$ h^{-1}) at temperatures T_1 and T_2.

Biomass and energy calculations—D. avara dry mass (DM) was determined by drying at 100°C for 24 h, and AFDM was determined by combustion at 500°C for 6 h. *H. papillosa* and *P. clavata* DM was determined by drying at 90°C for 24 h and AFDM by combustion at 450°C for 5 h. A general Q_{ox} value of 3,380 cal g^{-1} oxygen consumed (Elliot and Davison 1975) was used to convert oxygen consumption into energy equivalents (1 J = 4.1868 cal).

Results—Respiration rate was estimated from the decrease in oxygen concentration in the experimental chamber (with organism), because oxygen concentration in the control chamber never changed significantly over time (e.g., Fig. 1). Several respiration rate values were obtained along the decrease in oxygen concentration within each renewal (Fig. 1). This allowed us to further test within these experiments whether or not a 15% drop in initial oxygen concentration affected respiration rates. The test was carried out by comparing, for each renewal within a daily cycle, the first res-

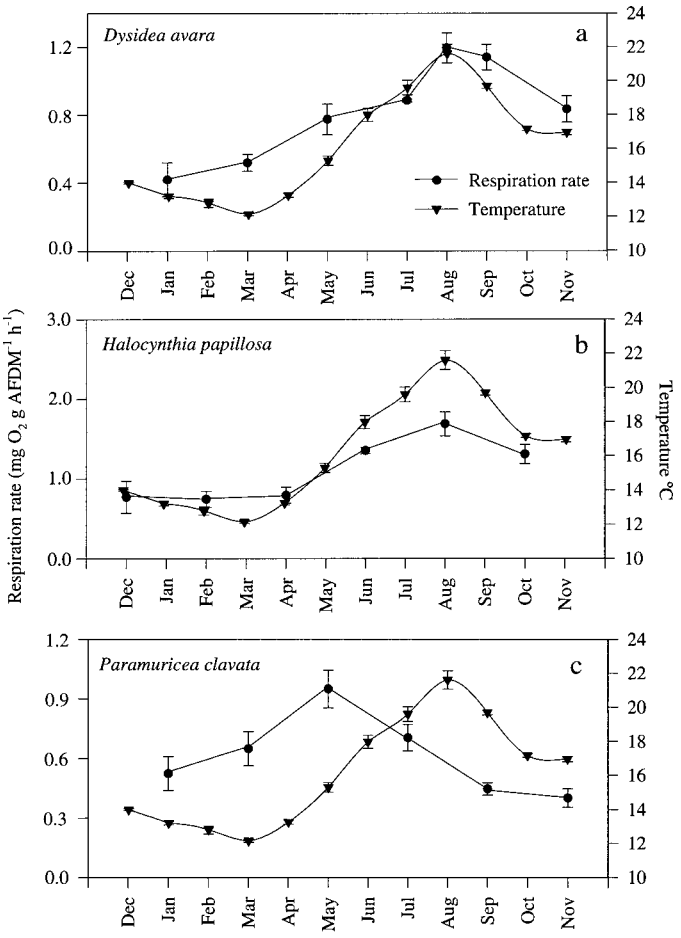

Fig. 2. Variation of respiration rate (mg O_2 g $AFDM^{-1}$ h^{-1}) throughout the year. (a) *D. avara,* (b) *H. papillosa,* and (c) *P. clavata.* The temperature variation over the annual cycle at the study site is included in each species graph. Data expressed as mean ± SE.

piration rate estimate (when the organism was subjected to the initial oxygen concentration) with the last one (when the organism was subjected to an almost 15% drop in oxygen concentration). In none of the three species, was respiration rate significantly affected by the 15% drop of the initial oxygen concentration (Student's *t* test for dependent samples: *D. avara,* $t = 1.1139$, df = 28, $P = 0.265$; *H. papillosa,* $t = 0.995$, df = 19, $P = 0.3322$; and *P. clavata,* $t = -0.56$, df = 13, $P = 0.5829$).

For all species, respiration rate did not significantly vary over the daily cycle (*D. avara:* one-way repeated measures ANOVA, $F_{28,28} = 0.396$, $P = 0.991$; *H. papillosa:* one-way repeated measures ANOVA, $F_{21,21} = 0.930$, $P = 0.568$; and *P. clavata:* one-way repeated measures ANOVA, $F_{9,9} = 0.760$, $P = 0.652$). From this, we concluded that none of the three species exhibited a daily pattern of respiration rate. Respiration rate did not vary among days within months for any of these species (two-way nested ANOVA, Table 1). However, it did show a significant variation between months for the three species (Table 1). The three species showed marked differences in the seasonal patterns of response. Maximum respiration rate values for *D. avara* and *H. papillosa* were observed during late summer, whereas maximum respiration rate values for *P. clavata* were observed during late spring (Fig. 2).

The percentage of AFDM of total DM did not vary through the annual cycle for the three species (*D. avara,* mean value: 33.7 ± 4.6 SD, one-way ANOVA, $F_{6,15} = 0.847$, $P = 0.5185$; *H. papillosa,* mean value: 83.4 ± 7.6 SD, one-way ANOVA, $F_{5,12} = 0.470$, $P = 0.722$; and *P. clavata,* mean value: 32.2 ± 1.4 SD, one-way ANOVA, $F_{5,12} = 0.050$, $P = 0.984$). This suggests that the seasonal pattern of mass-specific respiration rates was determined by changes in oxygen use rather than by changes in tissue composition.

Examination of the effect of temperature on respiration rate for the sponge and the ascidian species showed that respiration rate significantly varied with temperature for *D. avara* (one-way ANOVA, $F_{5,12} = 4.37$, $P < 0.019$) and for *H. papillosa* (one-way ANOVA, $F_{5,12} = 4.84$, $P < 0.01$). Respiration rate of both the sponge and the ascidian increased linearly with temperature within the temperature range at the study site (Fig. 2a,b). From 12°C to 21°C, a Q_{10} of 2.3 was estimated for the sponge, and a Q_{10} of 2.4 was estimated for the ascidian. In contrast, the respiration rates of the gorgonian *P. clavata* did not vary significantly with temperature (one-way ANOVA, $F_{5,12} = 1.62$, $P = 0.2345$). This indicates that factors other than temperature were responsible for the pattern of respiration of this species, the most obvious of which is synthesis of new tissue (*see* Discussion).

The oscula in the sponge species and the siphons in the ascidian species were always open throughout the experiments. However, the gorgonian species exhibited expansion and contraction of the polyps. All experiments were initiated with colonies with expanded polyps. Polyps remained expanded >80% of the time in all experiments except for those conducted in August, when they were only expanded ~20% of the time. This pattern is similar to that observed in conspecifics and to that described elsewhere from natural populations in the field (Coma et al. 1994 and unpubl. data).

The effect of expansion and contraction of the polyps of the gorgonian species on respiration rate of the colony was examined in late June and late August. The respiration rate of colonies with expanded polyps was significantly different from that of colonies with contracted polyps (two-way ANOVA $F_{1,46} = 4.03$, $P < 0.05$). On average, the respiration rate of colonies with contracted polyps was 50% lower than that of colonies with expanded polyps.

The three species exhibited different annual cumulative amounts of metabolic energy expenditure. The ascidian species exhibited the highest metabolic energy expenditure, with an annual cumulative value of 137.8 ± 14.7 standard error (SE) kJ g $AFDM^{-1}$ yr^{-1}. The ascidian annual cumulative metabolic energy expenditure was 43% higher than that of the sponge species (96.5 ± 8.8 SE kJ g $AFDM^{-1}$ yr^{-1}) and 81% higher than that of the gorgonian species (76.0 ± 8.5 SE kJ g $AFDM^{-1}$ yr^{-1}).

Discussion—Much of our understanding of respiration in temperate benthic suspension feeders has come from laboratory studies in which one factor is varied while the others are held constant (e.g., Riisgård and Larsen 2001). These

Table 2. Respiration rates for various marine sponges, ascidians and octocorals species, mean ± SD.

	mgO_2 g DM^{-1} h^{-1}	mg O_2 g $AFDM^{-1}$ h^{-1}	References
Sponges			
Suberites carnosus	1.13		Cotter (1978)
Spongilla lacustris	0.97		Karchenko and Lyashenko (1986)
Halichondria panicea		0.97	Barthel (1988)
H. panicea	0.90	2.63	Thomassen and Riisgård (1995)
Mycale sp.		2.13	Reiswig (1974)
Verongia gigantea		1.54	Reiswig (1974)
Tethya crypta		0.63	Reiswig (1974)
Thenea abyssorum		0.71±0.23	Witte and Graf (1996)
Thenea muricata		0.60±0.36	Witte and Graf (1996)
Tetilla cranium		0.60±0.10	Witte and Graf (1996)
Dysidea avara	0.31 ± 0.13	0.93±0.36	This study
Ascidians			
Ciona intestinalis	1.71		Markus and Lambert (1983)
Phallusia mammillata	0.57–1.00		Fiala-Medioni (1979)
Styela clava	0.83		Markus and Lambert (1983)
S. clava	0.60±0.37		Riisgård (1988)
Styela plicata	1.39		Markus and Lambert (1983)
Halocynthia papillosa	1.39±0.93		This study
Octocorals			
Without symbionts			
Cavernularia obesa		0.81	Mori (1968)
Pennatula rubra		0.42–0.95	Brafield and Chapman (1965)
Veretillium cynomorium		0.42–1.00	Brafield and Chapman (1965)
Pteroides griseum		0.42	Brafield and Chapman (1965)
Alcyonium siderium		0.21–0.27	Sebens (1987)
		0.17–0.34	Patterson and Sebens (1989)
Paramuricea clavata		0.67±0.47	This study
With symbionts			
Plexaura flexuosa		1.40±0.15	Ribes et al. 1998*b*)
Eunicella tourneforti		0.30	Lewis and Post (1982)
Muriceopsis flavida		0.75	Lewis and Post (1982)
Gorgonia ventalina		0.76	Lewis and Post (1982)
Briareum asbestinum		0.15	Lewis and Post (1982)
Eunicella stricta		0.21–0.27	Chapman and Théodor (1969)
Dendronepthya dollfussi		1.30	Svoboda and Ott (1978)
Lithophyton arboreum		2.30–3.80	Svoboda and Ott (1978)
Heteroxenia spp.		2.10–3.20	Svoboda and Ott (1978)
Xenia perauensis		2.20–2.80	Svoboda and Ott (1978)
Several species		0.50–1.20	Fabricius and Klumpp 1995

DM, dry mass; DM_{wt}, dry mass without tunic; AFDM, ash-free dry mass.

studies have provided an understanding of the physical and biological factors that affect respiration rate in benthic suspension feeders. However, the combined action of several factors typically produces a different effect than that caused by any single factor. In their natural environments, organisms are subjected to the combined effect of several factors. Temperature, salinity, ambient oxygen concentration, water flow, size, investment in secondary production, state of expansion and contraction, filtration activity, and food concentration have been suggested as important factors that affect respiration (e.g., Jørgensen et al. 1986; Sebens 1987; Patterson et al. 1991; Lucas 1996; Riisgård and Larsen 2001). By obtaining measurements in the natural environment as well as repeating them throughout the year, we examined respiration rate within the natural range of conditions to which organisms are subjected. Oxygen concentration in ambient water was always fully saturated or slightly supersaturated, and oxygen concentration during the incubations never decreased by >15%, a decrease in magnitude that does not affect respiration of these three species. During the experiments at a constant depth, salinity ranged between 36.5‰ and 38.0‰ (Pascual 1996), a narrow spectrum that does not affect respiration rate (Kinne 1971). The use of specimens of a similar size reduced variability in respiration rate associated with body mass. Flow has been shown to have an important effect on respiration rate of cnidarian species (Patterson et al. 1991). However, we could not examine the effect of flow on respiration rate because of logistic constraints, as well as the lack of knowledge of the range of flows that the organisms are subjected to through the annual cycle. Any patterns in respiration we recorded should be correlated with temperature, feeding, polyp behavior, and

synthesis of new tissue. The in situ technique has been shown to be highly applicable to seasonal studies of the physiological energetics of benthic suspension feeders.

The mean respiration rates values reported in this study for the three benthic suspension feeders were within the range of values reported in the literature for each taxa (Table 2). Data are not available for many octocoral species. However, there is a trend of higher respiration rates in octocoral species with symbionts in comparison to octocoral species without symbionts (Table 2). This trend could be related to the fact that respiration rate in symbiotic species usually includes both symbiont and octocoral oxygen consumption. The respiration rates values reported for the gorgonian species *P. clavata* were within the values reported for other octocoral species without symbionts (Table 2).

The ascidian, an active suspension feeder, exhibited the highest annual cumulative metabolic energy expenditure, 43% higher than that of the sponge, also an active suspension feeder, and 81% higher than that of the gorgonian, a passive suspension feeder. However, these differences were smaller than those expected on the basis of the large differences in filtration capacity (Ribes et al. 1998*a*, 1999*a*,*b*). This fact may be related to the low cost of pumping in benthic filter feeders (Riisgård and Larsen 2001).

The respiration rates of the three species showed a marked seasonal pattern. The respiratory rates of the two active suspension feeders closely follow the annual pattern of the water temperature, rising during summer as temperature increases. The Q_{10} values of 2.3 for the sponge and 2.4 for the ascidian were within the range accepted for unstressed organisms (1–5; Clarke 1991) and close to the range reported for most biological processes (2–3; Clarke 1991).

Parry (1983) observed that many studies of the seasonal pattern of respiration in benthic invertebrates, interpreted as a response to temperature, could also be explained by the pattern of secondary production. There is a respiratory cost associated to the synthesis of new tissue that, for suspension feeders in laboratory conditions, has been estimated to be between 12% and 26% of the actual synthesis of new tissue (Nielsen et al. 1995; Petersen et al. 1995; Clausen and Riisgård 1996). The only sponge species that has been examined had an extremely high cost (139%; Thomassen and Riisgård 1995). The overlap of the period of higher temperature with that of synthesis of new tissue of the ascidian species (Becerro and Turon 1992; Ribes et al. 1998*a*) makes it difficult to distinguish the effects of temperature and secondary production when respiration is recorded in the field. Given the high cost of synthesis observed in one sponge species (Thomassen and Riisgård 1995), we cannot conclude that temperature is the main factor affecting the seasonal pattern in respiration rate in *D. avara*.

In contrast to the temperature-dependent pattern observed in the respiration rate of the two active suspension feeder species, which makes separation of temperature and growth factors difficult to distinguish, the respiration rate of the passive suspension feeder (the gorgonian *P. clavata*) did not exhibit a significant response to temperature. Two main features distinguished the pattern of respiration rate of this species through the annual cycle: (1) the high respiratory demand in spring when temperature had not peaked and (2) the low respiration rate values observed in summer. The high spring respiration rate appears to be related to the seasonal pattern of secondary production in the species, because gonadal development (Coma et al. 1995) and growth (Coma et al. 1998*a*) are highest in spring, and it overlaps with the period of highest food uptake (Ribes et al. 1999*a*). A comparison of the monthly energy investment in gonadal development (data from Coma et al. 1995) for the gorgonian with the mean monthly values of respiration rate showed that reproductive cost explained 65% of the variance in respiration rate ($r^2 = 0.65$, $n = 6$, $P = 0.03$). Respiration rate in late May (15°C and high reproductive investment) was 41% higher than that in late October (16°C and low reproductive investment) (one-way ANOVA, $F_{1,55} = 12.98$, $P < 0.0007$), which suggests that the synthesis of new tissue increased respiration rate by ~40%. These results point to the important role of the synthesis of new tissue in determining the seasonal pattern of respiration.

The low respiration rate of the gorgonian observed in summer, the period of highest temperature, is the most surprising feature of this study, because it seems to contradict the widespread pattern of increase with temperature. The low respiration rate values in summer are related to three main factors: (1) the synthesis of new tissue is at its lowest rates during summer (Coma et al. 1998*b*), (2) the behavioral effect associated with the expansion-contraction pattern of the gorgonian polyps, and (3) the weak temperature dependence of oxygen consumption.

Polyps exhibited a pattern of activity similar to that described elsewhere for natural populations in the field (Coma et al. 1994), expanded ~80% of the time, except during August, when they were expanded only 20% of the time. Polyp contraction produces a 50% reduction in respiration rate of the colonies, within the range of values (10%–60%) observed in other cnidarian species (e.g., Sebens 1987; Fabricius and Klumpp 1995). This reduction appears to be related to the decrease in surface to volume ratio and diminished diffusion of oxygen through the epidermal tissue. The following calculation compares estimated versus observed respiration rates to demonstrate the effect of polyp expansion and contraction on respiration rate. We compared 2 months (late June and late August) with similar temperature (19.5°C and 20°C, respectively) and low secondary production investment (Coma et al. 1998*b*) but different activity rhythms (i.e., percentage of time that polyps are expanded, 80% and 20% expansion, respectively). Observed respiration rate in late June (0.70 ± 0.07 mg O_2 g $AFDM^{-1}$ h^{-1}) includes respiration rate of expanded polyps, 80% of the time, plus respiration rate of contracted polyps, 20% of the time. Because contracted respiration rate is half of the expanded rate, we calculated an expanded respiration rate of 0.78 mg O_2 g $AFDM^{-1}$ h^{-1} and a contracted respiration rate of 0.39 mg O_2 g $AFDM^{-1}$ h^{-1}. When these values are used, respiration rate in late August would be estimated to be 0.47 mg O_2 g $AFDM^{-1}$ h^{-1}, which is close to the observed value (0.45 ± 0.03 mg O_2 g $AFDM^{-1}$ h^{-1}). This calculation indicates that the rhythm of activity of the species, together with the effect of reduction in respiration due to polyp contraction, are among the main effects that produce the low respiration rate values estimated for the gorgonian *P. clavata* during the

summer period. A 2-yr monitoring of the rhythm of activity of several benthic suspension feeders suggests that the pattern observed in *P. clavata* may be a common feature of gorgonacea, alcyonacea, and zoanthidea species in the Mediterranean (Coma unpubl. data).

The third factor is a physiological one related to the temperature dependence of oxygen consumption. The comparison between months with similar secondary production investment and rhythm of activity, such as January and late June (*see* Coma et al. 1998*b*), but subjected to different temperature (January 13°C and late June 19.5°C), allowed a rough Q_{10} estimate of 1.1—i.e., respiration is not highly dependent on temperature. Patterns of reduced temperature dependence on respiration have been reported for other invertebrates (e.g., Griffiths 1979) and fit the hypothesis that there has been a general evolutionary trend of compensation for temperature in basal metabolism (Clarke 1987*b*). A reduction in the temperature dependence of oxygen consumption has an important ecological significance in maintaining the energy budget under conditions of thermal and nutritive stress (Newell and Branch 1980).

The three factors contribute to understanding why the respiration rate during the summer period is not much higher than that of the winter period. The expansion-contraction behavior and probably the low summer rate of synthesis of new tissues of the gorgonian colonies are related to low food capture rates of the species in summer (Coma et al. 1994, 2001; Ribes et al. 1999*a*). The low rate of synthesis of new tissue during summer, together with the contraction of polyps and the low Q_{10}, explains the low respiration rates observed during the period of highest temperature. These low respiration rates support the hypothesis that energy limitations (Coma et al. 1998*b*, 2000) may underlie summer dormancy in some benthic suspension feeder taxa in the Mediterranean.

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Acknowledgments

The comments of H. U. Riisgård, A. Clarke, E. Cox, R. A. Kinzie III, J. D. Ros, and two anonymous reviewers improved the manuscript. Our thanks to A. Svoboda, A. Julià, and J. Parera for their help to develop the recirculating flow respirometry system. The authors gratefully acknowledge the helpful assistance of J. M. Llenas, E. Pola, D. Diaz, and S. Rossi. Thanks to the people of the Point lab (Hawaii Institute of Marine Biology) for a pleasant working environment and valuable discussions. Support for this work was provided by a research contract from the ''Ministerio de Educación y Cultura'' (MEC) to R.C., by a postdoctoral fellowship from the MEC to M.R., by PETRI grant PTR94-0119, by DGICYT grant REN2000-0633-C03-01/MAR, and by a LEA project.

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Received: 1 December 2000
Accepted: 18 September 2001
Amended: 4 October 2001