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Oxygen consumption by a coral reef sponge

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SUMMARY

Oxygen consumption of the Red Sea coral reef sponge *Negombata magnifica* was measured using both incubation and steady-state methods. The latter method was found to be the more reliable because sponge activity remained stable over time. Oxygen consumption rate was measured during three levels of sponge activity: full activity, reduced activity and basal activity (starved). It was found that the active oxygen consumption rate of *N. magnifica* averaged 37.3±4.6 nmol O_2 min^{-1} g^{-1} wet mass, which is within the upper range reported for other tropical marine sponges. Fully active *N. magnifica* individuals consumed an average of 41.8±3.2 nmol O_2 min^{-1} g^{-1} wet mass. The mean basal respiration rate was 20.2±1.2 nmol O_2 min^{-1} g^{-1} wet mass, which is 51.6±2.5% of the active respiration rate. Therefore, the oxygen used for water pumping was calculated to be at most 10.6±1.8 nmol O_2 min^{-1} g^{-1} wet mass, which is 25.1±3.6% of the total respiration. Combined oxygen used for maintenance and water pumping activity was calculated to be 30.8 nmol O_2 min^{-1} g^{-1} wet mass, which is approximately 74% of the sponge's total oxygen requirement. The remaining oxygen is directed to other physiological activities, mainly the energy requirement of growth. These findings suggest that only a relatively minor amount of energy is potentially available for growth, and thus might be a factor in controlling the growth rate of *N. magnifica* in oligotrophic coral reefs.

Key words: sponges, oxygen consumption, energy budget, Red Sea, *Negombata magnifica*.

INTRODUCTION

Sponges can be found in all aquatic benthic habitats, in which they may constitute a significant part of the biomass in the food chain (Barthel and Gutt, 1992; Barnes and Bell, 2002). In some marine habitats sponges are disappearing rapidly, and the lack of knowledge of their basic physiology impedes detection of the detrimental factors responsible (Wulff, 2006). In addition to their ecological significance, sponges are known as producers of bioactive products. The culture of sponges offers one option for obtaining a reliable supply source for such active metabolites (Osinga et al., 1999; Donia and Hamann, 2003). Therefore, understanding the energetic needs and constraints that might influence sponge growth, whether in nature or in culture systems, is of the high interest, particularly in oligotrophic waters such as those of the Red Sea.

In aerobic organisms oxygen is required for all energetic processes in the body, and thus its consumption can indicate the total energy expenditure of an organism (Kleiber, 1975). Oxygen can also be used as a measure of the energy requirements for defined physiological activities, such as digestion, assimilation activity and growth (McCue, 2006). In mussels, for example, a reduction in feed elicited a downregulation of their water pumping rate, resulting in a lower oxygen consumption rate (Bayne et al., 1985).

Oxygen consumption, calculated on the basis of respiration rates, has been measured in different species of sponges, such as *Mycale* sp., *Tethya cripta*, *Verongia gigantea* (Reiswig, 1974), *Halichondria panicea* (Barthel and Theede, 1986), *Mycale acerata*, *Isodictya kerguelensis* (Kowalke, 2000) and *Dysidea avara* (Reiswig, 1974; Barthel and Theede, 1986; Kowalke, 2000; Coma et al., 2002).

Several studies have estimated the energy costs of the various physiological activities in the sponge. Using a theoretical calculation, Riisgård et al. (Riisgård et al., 1993) estimated that the energy expenditure for a sponge's water-pumping activity constitutes less than 1% of its energy loss through respiration, thus exemplifying the low energy requirements for the sponge's basic activities. Thomassen and Riisgård (Thomassen and Riisgård, 1995), showed, in *Halichondria panicea,* an exceptionally (in comparison to other invertebrates) high specific dynamic activity (SDA), defined as an increase in specific respiration rate in response to growth, that amounted to 139% of the biomass production. They concluded that, for this sponge, energy for maintenance constitutes only a small fraction of the energy required for growth, as was suggested for unicellular organisms (Fenchel, 1982). Here we provide experimental data that may challenge these theoretical concepts.

The aim of the present research was to determine oxygen consumption of a coral reef sponge, under conditions of full activity, at a reduced activity and while starved (basal rate) to estimate how much of the sponge's total energy expenditure is used for its basal activity, and how much for propelling the water through its body; and ultimately to posit a primary evaluation of sponge growth potential based on the remainder oxygen. For this purpose we employed a new method that we developed based on previous (unpublished) observations. A secondary objective was to validate the accuracy of the experimental methodology used by comparing flow-through with closed-chamber incubations.

The studied sponge, *Negombata magnifica* (Keller 1889), is distributed from the Gulf of Aqaba in the north, along the Red Sea, to Djibuti in the Gulf of Aden in the south (Ilan, 1995). *N. magnifica* has been found to be a source of the two bioactive metabolites, latrunculin A and latrunculin B (Groweiss et al., 1983).

Several experimental methods have been used to measure oxygen consumption rate in sponges, but the most frequently used is the incubation method (Cotter, 1978; Thomassen and Riisgård, 1995; Kowalke, 2000). However, it was noted that incubation in a metabolic chamber lowered sponge activity, consequently affecting its oxygen consumption rate (Simpson, 1984). The flow-through and steady-state systems partially overcome the problem of water re-filtration by the sponge (reviewed by Riisgård, 2001). In this system the organism is kept in an almost unaltered environment by the continuous supply of fresh seawater. Several studies such as that by Cotter (Cotter, 1978), have employed this method to measure oxygen consumption in sponges.

Various sensors have also been employed in studies of oxygen consumption. The most commonly used methods for oxygen-sensing are polarographic electrodes, a chemical procedure developed from the Winkler method (Winkler, 1888), couloximetry, and the relatively novel method of optrodes (Gatti et al., 2002). The main advantage of the latter method is that, unlike the polarographic electrodes, the optrode does not consume oxygen, its drift over time is expected to be low, and it is not stirring dependent, thus enabling oxygen measurements in changing flow regimes (Gatti et al., 2002).

MATERIALS AND METHODS

Influence of water exchange rate on sponge clearance rate

Preliminary observations indicated that reduction of water exchange rate through the aquaria caused the contraction of the sponge oscula (exhalant openings), thus changing its filtration rate and consequently its activity level. Sponge filtration rate (ml water min^{-1} g^{-1} sponge) could not be measured directly because this would require simultaneous recording of the outflow current velocity and the diameter of all oscula [*N. magnifica* has on average 4.6±0.94 oscula per 10 g (wet mass) sponge (this study)]. The removal efficiency of the cyanobacterium *Synechococcus* sp. was found to be practically 100% [99.3±1.2 (s.d.), N=28] in all natural concentrations that ranged between 15 000 and 60 000 cells ml^{-1} (E.H., unpublished data). Therefore, the clearance rate (CR) of this prevalent cyanobacterium was used as an indicator of the sponge filtration rate (FR) since under such conditions the sponge CR equals its FR (Riisgård, 2001).

The FR of *N. magnifica* was measured under high, medium and low water exchange rates (635±6 ml min^{-1}, 355±1 ml min^{-1} and 165±2 ml min^{-1}, respectively). The experimental system consisted of eight identical plastic 3.5 l containers supplied with a small water pump to mix the water and maintain a constant water flow over the sponge at all inflow water rates, and thereby avoid any effect of this factor on sponge activity (Vogel, 1978). Seven containers were each stocked with a single individual sponge and the eighth was left empty and used as a control. Fresh seawater was supplied to each container from a 20 l header tank at an initial high flow rate. The water inside the header tank and the sponge aquaria was continuously mixed at a rate of 100 l min^{-1} and 10 l min^{-1}, respectively. After 2 h of acclimatization, water samples were collected from the containers' outflow and from the header tank (representing the containers' inflow water). The header tank was sampled twice, before and after sample collection from the containers; the second sample was needed to compensate for possible changes in plankton/particle concentrations during a sampling period that was shorter than 4 min. All water samples were collected in duplicates of 1.5 ml and were fixed in glutaraldehyde (G-5882; Sigma, Rehorot, Israel) at a final concentration of 6%. The same experimental procedure was applied when testing the other two exchange rates, measured consecutively on the same sponge individuals. The amount of *Synechococcus* sp. in the water samples was counted in a flow cytometer (FACScan, Becton Dickinson, Franklin Lakes, NJ, USA) using standard procedures (Marie et al., 2000).

Sponge CR was determined using the following formula (Riisgård, 2001):

$$\mathrm{CR} = \mathrm{FR} = \mathrm{Fl} \times \frac{C_1 - C_2}{C_2}, \quad (1)$$

where Fl is the flow rate through the container (ml min^{-1}) and C_1 and C_2 are the concentration (cells ml^{-1}) of *Synechococcus* cells in inflow and outflow water, respectively.

Sponges and seawater

Individuals of *Negombata magnifica* were taken randomly from a stock of sponges cultured at the northern end of the Gulf of Aqaba (Hadas et al., 2005). These sponge individuals were already attached to PVC plates. This provided complete intact individual sponges for all measurements, thus reducing to a minimum stress related to sponge translocation and positioning in the experimental systems. The laboratory work was conducted at the Interuniversity Institute (IUI), Eilat, Israel. For all the experiments non-filtered, ambient water was pumped directly from the sea. The experiments were conducted in winter when water temperature was 22.5±1°C. Sponges were brought into the laboratory 24 h prior to the beginning of the experiment to acclimatize them to the experimental set-up. During acclimatization, sponges were kept in individual 3.5 l tanks with a constant supply of flow-through seawater at a rate of about 1 l min^{-1}.

Measurement of respiration at three activity levels

Three respiration rates were defined, following those measured by Thompson and Bayne (Thompson and Bayne, 1972) for *Mytilus edulis*: (1) when the sponge is fully active and pumping water; (2) when the sponge is at basal (routine) activity; and (3) when the pumping activity has ceased but the sponge still maintains a high level of activity. Measurement of the three respiration rates (*sensu* Thompson and Bayn, 1972) was carried out in a three-step experiment in which values were recorded repeatedly in seven sponges, using the steady-state system (each sponge was measured once). In the first step, water flow was set to 600 ml min^{-1} to measure the respiration rate of an active sponge. Active oxygen consumption was defined as the amount of oxygen consumed when the oscula are wide open and both filtration and digestion processes are active.

After this measurement, the water flow was reduced to 100 ml min^{-1}, thus causing the sponge to stop its filtration activity. Oxygen measurement was carried out within 30 min after most of the sponge's oscula had contracted, indicating significant decrease in pumping activity, defined as reduced activity state.

The final measurement was performed 14 h later, during which the sponges were supplied with seawater filtered online by a 0.2 μm mesh size filter (Suporlife 200, PALL, Biopharmaceuticals, East Hills, NY, USA), at a constant rate of 100 ml min^{-1}. In each activity level, water samples were collected simultaneously from the inflow and outflow currents directly into 50 ml calibrated glass bottles (three consecutive replicates for each measurement at 5 min intervals).

Oxygen concentration in each sampling bottle was determined using a Winkler automatic titrator (702 SM Titrino, Metrohm, Switzerland). The oxygen concentrations in the inflow and outflow water were determined as the mean value of the three replicates.

The sponge respiration rate in the steady-state system was calculated using the following equation:

$$\dot{M}_{O_2} = \mathrm{Fl} \times \frac{C_1 - C_2}{\text{wet mass}}, \quad (2)$$

where $\dot{M}_{O_2}$ is the respiration rate in a steady-state system (nmol O_2 min^{-1} g^{-1} wet mass), Fl is the water flow rate (ml min^{-1}) and C_1 and C_2 are the oxygen concentration in inflow and outflow water, respectively. The average respiration rate of all sponges was determined as the linear regression coefficient between the individual respiration rates and the sponge size.

Respiration in a steady-state system

The methodology of the steady-state oxygen measurement was adapted from the system described by Riisgård (Riisgård, 2001) and oxygen concentration was determined using Winkler's method (Winkler, 1888).

Respiration rate of 17 individual sponges in full activity was measured in a 1 l Perspex respiration chamber constantly supplied with unfiltered seawater (each sponge was measured once). A single pre-weighed sponge individual was placed in a respiration chamber that was sealed and mounted on top of a magnetic stirrer, to guarantee mixing of the water. The water flow rate to the chamber was adjusted to the desired value, maintaining a measurable oxygen gradient between the inflow and outflow water, while also keeping the sponge active. The oxygen concentrations in this experiment were determined by the Winkler method and all measurement procedures and calculations were identical to those performed in the former experiment in the steady-state system.

Each day, prior to measurements, the respiration chamber was sealed without a sponge inside, water exchange rate was set to 100 ml min^{-1}, inflowing and outflowing water were sampled, and the oxygen concentration was measured to estimate non-specific oxygen consumption that could potentially result from respiration of planktonic organisms and from oxidation of organic compounds in the water (chemical oxygen demand).

Respiration in an incubation system

The oxygen measurements were carried out in a Perspex respiration chamber with an effective volume of 4740 ml, equipped with a water pump to ensure water mixing. The respiration rate of nine different sponges in the incubation system was measured; each was measured once. Sponges were acclimatized to the experimental chamber for 2 h prior to measurements, during which fresh seawater was constantly supplied. The metabolic chamber was then sealed and the oxygen concentration was recorded each second for 40 min using an optrode. Because of the low ratio between sponge respiration rate and chamber volume, the oxygen concentration inside the chamber never decreased below 95% of the initial concentration. Measurement started only when the sponge oscula were wide open, indicating that the sponge was actively pumping water. Concomitantly, a control oxygen measurement without a sponge was conducted in the same manner to estimate the electrode drift and the rate of biological oxygen demand (BOD). The changes in oxygen concentration detected in the control measurements were used to correct the sponge's measured oxygen consumption rate.

Oxygen concentration was measured using a single optrode (Ocean Optics Inc., Dunedin, FL, USA) connected *via* fiber optics to a light source (LS-450) and to a spectrometer (USB2000; Ocean Optics Inc.). The operation software OOIBase32^{TM} (Ocean Optics) controlled the system and the data were logged automatically into a computer. The optrode was calibrated at the beginning of each working day according to the Ocean Optics operation manual (Klimant et al., 1995). The reference for the calibrations was determined using the Winkler method.

The rate of change in oxygen concentration in the respiration chamber was determined as the linear regression coefficient. The respiration rate was analyzed during two phases of the measurement. The first was throughout the initial 6 min of the measurement, and the second started 15 min after sealing the chamber and lasted 10 min. The sponge respiration rate ($\dot{M}_{O_2}$) in the incubation system was calculated by the following equation:

$$\dot{M}_{O_2\mathrm{in}} = \frac{(R_2 - R_1) \times C \times 1000}{32 \times 1440 \times \text{wet mass}}, \quad (3)$$

where $\dot{M}_{O_2\mathrm{in}}$ is the oxygen consumption rate in the incubation chamber, expressed in nmol O_2 min^{-1} g^{-1} wet mass sponge; R_1 and R_2 are the regression coefficients for sponge respiration and control (each expressed as p.p.m. O_2 day^{-1}; respiration rate had a negative value and the control always had a positive value); and C is the net chamber volume (i.e. excluding sponge volume). The units obtained from the regression were in mg O_2 24 h^{-1}. By dividing the numerator by 32 the oxygen consumption rate is converted to mmol O_2 and by further dividing by 1440 it is converted to minutes.

Statistical analysis

Statistical analyses were performed using JMPIN (v 5.0.1a, SAS Institute Inc., Cary, NC, USA). Variance homogeneity was assessed by Bartlett's test, and the Shapiro–Wilk test was used to check for normality. Data sets were log transformed when necessary to meet the requirements of normality and homogeneity of variance. Difference between the respiration rates at the three activity levels was tested by applying a one-way ANOVA model with random effect (the difference between the seven sponges), analyzed using the residual maximum likelihood (REML) method.

RESULTS

Water flow rate effect on filtration

The filtration rate of *Negombata magnifica* was correlated to water flow rate through the container (Fig. 1). When sponges were supplied with water flow rate of about 600 ml min^{-1}, they filtered on average 10.5±1.4 ml min^{-1} g^{-1} wet mass. When water exchange rate was reduced to 300 ml min^{-1}, sponge filtration rate significantly decreased (one way ANOVA, $F_{2,18}$=14.5, P<0.001) to 8.1±0.9 ml min^{-1} g^{-1} wet mass, a drop of 23% relative to the filtration rate at the higher water flow rate. Further reduction in water flow rate to 100 ml min^{-1} resulted in a considerable fall in filtration rate to only 2.52±0.58 ml min^{-1} g^{-1} wet mass, which is 76% less than the maximal filtration rate recorded in this experiment. In the control container without sponges, differences of up to 5% in concentration of *Synechococcus* sp. cells were recorded between the inflow and the outflow water (compared to a decrease of more than 20% in the sponge containers).

Oxygen consumption rate in a steady-state system

The oxygen consumption of *N. magnifica* measured in a steady-state system indicated a significant linear fit between the sponge respiration rate and its wet mass (Fig. 2, regression model I, y=37.3x+56, r^2=0.8, N=17, P<0.01). By using the regression coefficient it was estimated that *N. magnifica* oxygen consumption was 37.3±4.6 (± s.e.m.) nmol O_2 min^{-1} g^{-1} wet mass.

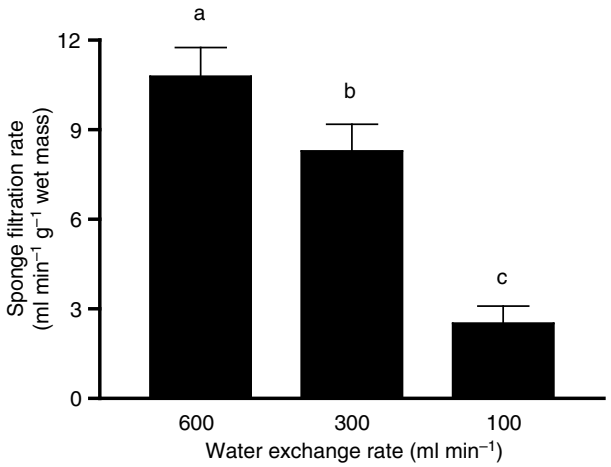

Fig. 1. *Negombata magnifica* mean filtration rates maintained under three different water exchange rates. Error bars indicate standard error of the mean (s.e.m.) and different letters indicate statistically significant differences (P<0.05), N=7.

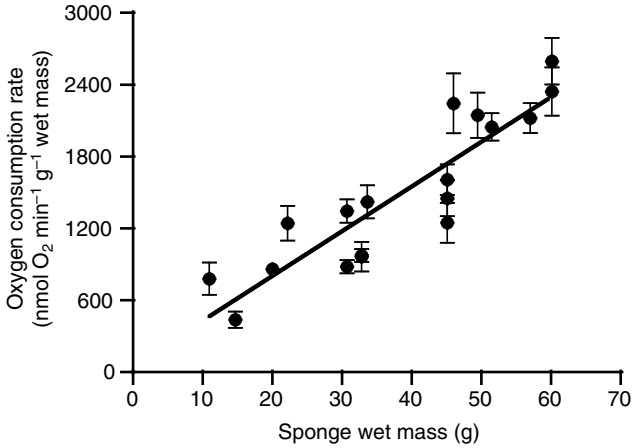

Fig. 2. *Negombata magnifica* oxygen consumption as a function of sponge size, measured in a flow-through system. Bars indicate the s.e.m. (N=3). A linear regression model was fitted to the data: y=37.3x+56.9. r^2=0.8, P<0.001, N=17.

Oxygen consumption rate in the incubation system

The average respiration rate during the first 6 min of the measurement was 29.1±2.8 nmol O_2 min^{-1} g^{-1} wet mass, significantly decreasing to 14.4±1.4 nmol O_2 min^{-1} g^{-1} wet mass during the period 15–25 min post chamber sealing (paired t-test, d.f.=8, t=5.5, P<0.001). No linear regression could be fitted between the oxygen demand for the two time frames and the sponge wet mass (slope≠0, r^2=0.2, N=9, P=0.26 and slope≠0, r^2=0.3, N=9, P=0.1, respectively, Fig. 3).

In all trials the control measurement showed a minor increase in oxygen concentration inside the chamber because of a constant drift of the optrode. Nevertheless, the background noise-to-signal ratio was always less than 0.1.

Respiration at three activity levels

Sponge respiration rates at the various activity levels differed significantly ($F_{8,20}$=17.5, P<0.001; Fig. 4). The mean oxygen consumption of the sponge at the beginning of the experiment (active stage) was 41.8±3.2 nmol O_2 min^{-1} g^{-1} wet mass. Thirty minutes after the water flow rate was reduced (reduced activity stage), average oxygen consumption had significantly decreased to 31.3±1.8 nmol O_2 min^{-1} g^{-1} wet mass, a reduction of 25.1±3.6% relative to the rate at full activity level. At the third measurement (basal stage), the sponges' oxygen consumption had further decreased to 20.2±1.2 nmol O_2 min^{-1} g^{-1} wet mass, a reduction of 51.6±2.5% relative to a fully active sponge.

DISCUSSION

Evaluation of the experimental method

Water pumping rates of *N. magnifica* were manipulated by changing the water flow rates into the chamber in which the sponge was held. It is not clear why the reduction of water flow rate in the experimental set-up affected the sponge. None of the measured water quality parameters (oxygen, nitrate, total nitrogen, ammonia and silica) were significantly changed by the alteration of the water flow rate. Moreover, it was shown that the number of planktonic cells in the water had no effect on sponge activity (E.H., data not shown). The advantage of manipulating the sponge activity by decreasing the water flow rate through the respiration chamber lies in the immediate response of the sponge. In this case the sponges remained in good physiological condition and thus unbiased oxygen measurements were more likely. Because of the constant water exchange in a flow-through system, it is reasonable to assume that no deleterious compounds that might affect sponge activity could accumulate in the aquaria.

The influence of water flow rate on sponge activity has a direct bearing on the particular experimental system to be deployed. Whereas in a steady-state system it can be controlled, in the commonly used incubation system water exchange does not take place. Thus the latter system might not be suitable for measurement of oxygen consumption rates of a sponge, including *N. magnifica*. Indeed, comparison of the mean active respiration rate of *N. magnifica* between the two tested systems revealed that oxygen consumption measured in the steady-state system was 22% higher than the mean value measured during the first 6 min, using the incubation method

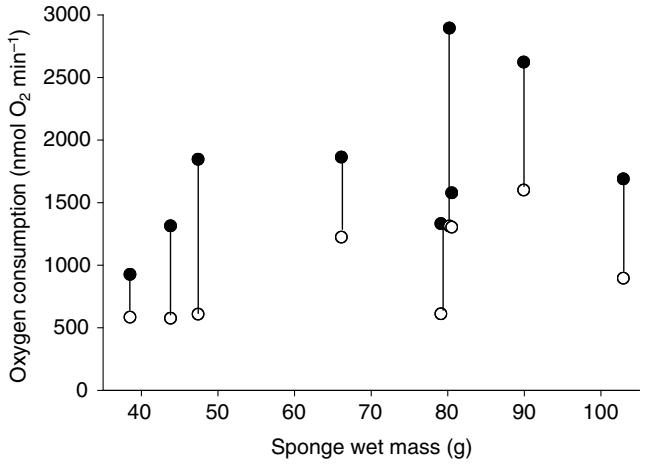

Fig. 3. *Negombata magnifica* respiration rates measured in an incubation chamber. Filled circles indicate measurements during the first 6 min when sponges were fully active; open circles indicate oxygen consumption rate after 15–25 min of incubation. Pairs of open and filled circles are connected with lines to emphasize that they represent consecutive measurements on the same sponge. N=9.

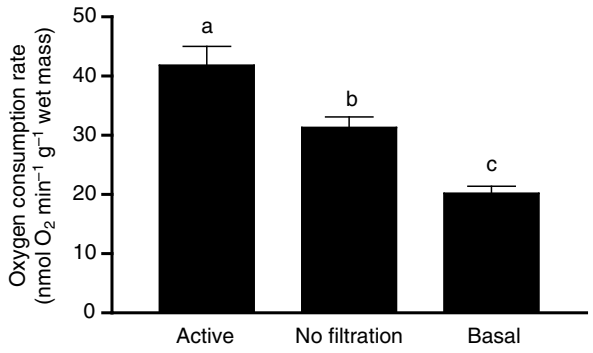

Fig. 4. *Negombata magnifica* oxygen consumption rate at three activity levels (see text). The bars represent s.e.m. and different letters indicate significant difference (P<0.05) between the means of the treatments. N=7.

(37.3±4.6 and 29.1±2.8 nmol O_2 min^{-1} g^{-1} wet mass, respectively), although the latter is within the confidence limits (95%) of the former. Moreover, sponge mean oxygen consumption in the incubation system was not stable over time and within 15–25 min it had decreased to 14.4±1.4 nmol O_2 min^{-1} g^{-1} wet mass, which is only 40% of the level found in the steady-state system. This oxygen consumption level is similar to that found in the present study for the sponge basal activity.

It was hypothesized that the manipulation carried out in the present experiment would result in a lower than normal metabolic rate in the sponge (Ortmann and Grieshaber, 2003). If so, this would mean that the estimated amount of energy is a minimal value, and that under 'better' experimental conditions the energy expenditure for maintenance would be higher, with a consequent reduction in the estimated proportion of energy spent on water filtration. As a consequence, the proportion between the various activities might change, but this would not change the fact that most of the *N. magnifica* energy is used for maintenance and water propulsion.

Sponge energy expenditure

The oxygen consumption of *N. magnifica* in the active state was found to be within the range of other tropical marine sponges (Table 1), higher than the respiration rate of Antarctic sponges but lower than that, of, for example, temperate calcareous sponge *Syconciliatum* (Cotter, 1978). Great interspecies variability in oxygen consumption rate of sponges obviously exists within the same habitat (Table 1).

The oxygen consumption and filtration rates that were found for *H. panicea* (Thomassen and Riisgård, 1995) were 0.6 ml O_2 h^{-1} g^{-1} (dry mass) and 28.35 ml min^{-1} g^{-1} (dry mass). It was found here that *N. magnifica* consumed 0.33 ml O_2 h^{-1} g^{-1} (dry mass) and filtered water at a rate of 70 ml min^{-1} g^{-1} (dry mass). These results show that the latter species is more efficient in terms of water pumping, possibly as an adaptation to the oligotrophic conditions at the northern end of the Red Sea.

Realizing the existence of a positive correlation between sponge filtration rate and water flow rate through the respiration chamber allowed reduction of the sponge FR to about 25% of the maximal rate (Fig. 1). The instantaneous reaction of a sponge to such manipulation enabled measurement of filtration rate within 30 min after reduction in water exchange rate, which should minimize the effect of other physiological processes (e.g. digestion) on sponge oxygen consumption.

The amount of oxygen required for water pumping activity (maximally 10.6±1.8 nmol O_2 min^{-1} g^{-1} wet mass) was about 25% of the sponge's total oxygen consumption. This empirical result is much higher than that estimated for *Halichondria panicea* [<1% (Riisgård et al., 1993)], but it is lower than the level of about 50% reported for other filter feeders, such as the bivalves *Mytilus edulis* and *Cardium edule* (reviewed by Newell and Branch, 1980). It is also in accordance with the model proposed by Willows (Willows, 1992), who demonstrated that under low food concentrations (as in the oligotrophic coral reefs of the Red Sea) the energy expenditure for water filtration of suspension feeders is high (the animal has to filter more water in such environments) and probably sets the upper limit for the filtration rate.

The basal energetic needs of *N. magnifica*, defined as the amount of energy consumed by a starved organism (Bayne, 1976), were estimated using a method similar to that used to measure the energetic cost of pumping, but this time the sponges were maintained for 14 h in 0.2 μm-filtered seawater. The data (Fig. 1) show that a complete cessation of water pumping was not achieved (sponge oscula remained partially open), probably because continuous water flow, at a minimal rate, is essential to prevent total depletion of oxygen in the sponge body (Hoffmann et al., 2005); as such, this minimal pumping can be considered as part of the basal energetic needs. Demonstrating that this minimal activity is not a transient state that could lead to the sponge's death, sponges that were maintained for 27 days under similar conditions lost 22.5% of their organic dry matter during this period, but suffered no mortality (E.H., unpublished data). The *N. magnifica* basal respiration rate was

Table 1. Oxygen consumption rates of marine sponges from various habitats

Species	Habitat	Oxygen consumption (nmol min^{-1} g^{-1} sponge)*	Oxygen consumption (nmol min^{-1} g^{-1} dry mass sponge)**	Oxygen consumption (nmol min^{-1} g^{-1} ash free dry mass sponge)**	Source
Negombata magnifica	Tropical sea	37.3±4.6	248	310	Present work
Theonella swinhoei	Tropical sea	23±13			(Yahel et al., 2003)
Mycale sp.	Tropical sea	34			(Reiswig, 1974)
Verongia gigantean	Tropical sea	50			(Reiswig, 1974)
Tethya crypta	Tropical sea	15			(Reiswig, 1974)
Sycon ciliatum	Temperate sea		410		(Cotter, 1978)
Dysidea avara	Temperate sea		161		(Coma et al., 2002)
Cinachyra antarctica	Antarctic sea			67–282	(Gatti et al., 2002)
Isodictia kerguelensis	Antarctic sea			20–30	(Kowalke, 2000)

In the present research, sponge size was determined by wet weighing the sponges. To compare these data with other measurements from the literature, proximate biochemical composition of *N. magnifica* was used (Hadas et al., 2005).

*Assuming that 1 ml sponge has a mass of approximately 1 g (wet mass).

***Negombata magnifica* dry mass and ash free dry mass is 15% and 12%, respectively, of the sponge wet mass.

20.2±1.2 nmol O_2 min^{-1} g^{-1} wet mass, which was approximately 50% of its respiration rate during the active state.

Approximately 75% of the oxygen consumed by *N. magnifica* was used for the energy-demanding processes of sponge maintenance and water propulsion. This implies that no more than 25% of total oxygen remains for energy allocated to growth. In comparison, the energy cost per unit of growth in the polychaete *Nereis diversicolor* was 26% (Nielsen et al., 1995). A growth rate of 0.55% per day of this polychaete, which is comparable to that of *N. magnifica* (Hadas et al., 2005), increases the specific respiration rate of *N. diversicolor* by 0.14 mg O_2 mg^{-1} day^{-1}, an increase of total respiration (over maintenance) by 9%. This value is lower than that found in our work for *N. magnifica* (25%), but closer than the value of 139% found for *Halichondria panicea* (Thomassen and Riisgård, 1995). The relatively low level of energy that is potentially available for growth of *N. magnifica* might imply that energetic constraints play a significant role in the growth potential of this sponge. Further studies might reveal whether the sponge growth rate is restricted by energetic constraints (e.g. if increased food availability would correlate to faster growth rate) or by other physiological parameters, such as the rate of diffusion of nutrients between the sponge cells.

The specific respiration rate of *N. magnifica* was constant for sponges along the entire tested size range of 10–60 g wet mass. This finding is in agreement with other studies of sponge respiration (Cotter, 1978; Thomassen and Riisgård, 1995) and may distinguish the sponges from other multicellular organisms, in which the relationship between an organism's age (which is positively correlated to size) and respiration rate [$M=aW^b$; where M is total respiration, a is a parameter (metabolism for unit of weight), W is weight unit and b is a constant indicating at what speed and in which direction respiration changes as size increases] is well documented. This difference between sponges and other metazoans might be explained by the homogeneous structure of a sponge (Reiswig, 1975), which maintains a constant ratio between body volume and its gas exchange surface area (Ultsch, 1973); or be due to the experimental use of different sized sponge fragments rather than individuals of different ages.

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