Ecology and energetics of two Antarctic sponges

Jens Kowalke*

Alfred Wegener Institute of Polar and Marine Research, Columbusstrasse, 27515 Bremerhaven, Germany

Received 8 October 1999; received in revised form 2 December 1999; accepted 20 December 1999

Abstract

Retention efficiencies, pumping and respiration rates of the two Antarctic sponge species Mycale acerata and Isodictya kerguelensis from Potter Cove, King George Island, were measured. None of the species reached a 100% retention efficiency at any given particle size. This is probably due to the sediment-laden environment in which the animals were dwelling. A less efficient retention decreases the risk of the filtering structures being clogged. Both species filter down into the bacterial size range. Pumping rates of the species were 180 ml h⁻¹ (M. acerata) and 220 ml h⁻¹ (I. kerguelensis) per g ash free dry mass (T = 1°C), being lower than measured in temperate water species. Oxygen consumption was 0.088 ml O₂ h⁻¹ (M. acerata; T = 1.8°C) and 0.035 ml O₂ h⁻¹ (I. kerguelensis; T = 1°C) per g ash free dry mass. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Antarctica; Sponges; Retention efficiency; Pumping rate; Respiration rate

1. Introduction

Sponges account for a major proportion of Antarctic soft and hard bottom dwellers (Voss, 1988; Barthel and Gutt, 1992; Starmans, 1997) and more than 300 species have been described for the Southern Ocean of which 50% are endemic (Koltun, 1970). Six species of hexactinellids dominate the Weddell Sea shelves (Barthel and Tendal, 1994). These animals structure the shelf habitats forming 'multi-storied assemblages' (Gutt and Schickan, 1998) which form important secondary substrata for holothurians, crinoids, crustaceans and fishes (Dearborn, 1977; Wägele, 1988; Barthel et al., 1991; Kunzmann, 1996; Barthel, 1997). Sponges have described as important benthos constituents from
shallow waters around the Antarctic Peninsula (King George Island: Sahade et al., 1998; Livingston Island: Saiz-Salinas et al., 1997; Signy Island: Barnes, 1995) and the McMurdo Sound (Dayton, 1978), but are, with the exception of McMurdo Sound, less numerous.

Sponges can be considered as a singular filter system, as the whole body functions as a filter. The water flows via numerous ostia (formed by porocytes) into branching channels, which end in choanocyte chambers generating the water flow. From these chambers the water is discharged into outflowing channels into one or several osculae. Particle uptake takes place at three different levels (Johnston and Hildemann, 1982). The maximum size of filterable particles, around 50 μm, is determined by the diameter of the ostia. Food particles as small as 1 μm are taken up through more or less specialised cells (archaeocytes) in the transmitting channels. Particles around 1 μm are filtered by the bases of the choanocytes and particles down to 0.1 μm from microvilli, which form the choanocyte collar. Sponges are obviously unable to filter selectively and take up particles regardless of their nutritive value (Kilian, 1952; Reiswig, 1971; Wolfrath and Barthel, 1989).

Schmidt (1970) and Reiswig (1990) have shown that assimilation of dissolved organic material by choanocytes may also take place.

The food spectrum of Antarctic sponges is little known through a paucity of studies. Gaino et al. (1994) found diatoms, both of pelagic and benthic origin, in the cortex of two Antarctic species, which shall act as an additional skeleton and, during the nutrient poor Antarctic winter, as a food reserve. Klöser (personal communication) found up to 70% of benthic diatoms in different sponges of nearby Maxwell Bay, King George Island.

Potter Cove is not a favourable habitat for sponges, as inorganic particles are abundant in the water column throughout the year (Kowalke, 1998, 1999). The same could be stated for the entire Antarctic Peninsula region, as glacial melting during spring and summer bring sediments into the water column. Sponges, which are not able to close their inflowing channels, suffocate more easily than ascidians or bivalves, which can better manage these concentrations of inorganic suspended material. Sponges thus play a major role in habitats without heavy sedimentation — the shelf areas and high Antarctic sites like McMurdo Sound (Dayton and Oliver, 1977; Barry, 1988).

Nevertheless six species of sponges were found to dwell on the soft bottoms of Potter Cove (Kowalke, 1998). Mycale acerata, an important and fast growing species in Antarctic shallow waters (Dayton et al., 1974), occurs in densities of 0.02 individuals m⁻² and has a biomass of 5.83 g m⁻² ash free dry mass (unpublished data). It grows sporadically, but in colonies up to 1.5 m in height (Kowalke, 1998). Although M. acerata contains secondary metabolites, which are at least highly toxic for fishes, it is predated by asteroids (McClintock, 1987). Isodictya kerguelensis occurs in densities of 0.10 individuals m⁻² and its ash free dry mass is 0.69 g m⁻² in 30 m depth (unpublished data).

In this investigation, retention efficiency, pumping rate and oxygen consumption of the two species Mycale acerata and Isodictya kerguelensis of Potter Cove (King George Island) were measured to helping explain the differences in abundance and biomass.
2. Material and methods

The investigation was conducted at the Dallmann Laboratory, Potter Cove, King George Island, Antarctica (Fig. 1). Potter Cove is an inlet of the larger Maxwell Bay system and stretches over 2 km². Maximum water depth is 50 m and the bottom is mainly composed of fine sediments imported by glacial meltwater. Hard substrata, such as rocky shores, cobbles and pebbles border the mouth of the cove. The soft bottom communities are characterised by a wide variety of suspension and deposit feeding animals (Kowalke and Abele, 1998; Sahade et al., 1998). The hydrography of the cove

Fig. 1. Geographic location of Potter Cove, the × indicates the sampling station; shaded area is free of ice and snow during summer.
is governed by strong, mostly westerly winds, which block the water circulation inside the cove and hamper the outflow of sediment-laden water (Klöser et al., 1994).

Between December 1995 and February 1996 divers collected the experimental animals which were immediately placed in aerated flow-through aquaria of 25 l volume. The sponges were individually kept for several days in order to acclimate before starting the experiments. The water was drawn directly from the cove from 10 m depth.

2.1. Filtration

At the beginning of the experiment, the water supply was cut off for 40 h, however, aeration provided sufficient turbulence for stirring and thus keeping particles in suspension. At 8-h intervals, in the vicinity of each animal, 20 ml of water were siphoned off and immediately analysed on a Elzone Particle Counter 280 equipped with a 60-μm aperture tube. The time-span of 40 h was used to allow for maximum retention. To determine pumping rates the indirect method was employed because low pumping rates rendered flow through methods unsuccessful. For further discussion, see Kowalke (1999).

The aquaria were artificially cooled to maintain a temperature of 1°C. Size spectra analysis took place between 1 and 15 μm. The abundance of particles above 9 μm was too small to allow for any statistical calculation and, therefore, excluded. Two aquaria without animals were used as blanks for the calculation of cell sedimentation and fission rates. After the correction for blanks, the retention efficiency and the standard deviation was calculated as the percentage of particles remaining in suspension.

The often used simple exponential model for the calculation of pumping rates requires a complete filtration of all particles after a given time for a correct evaluation of rates. Thus, the Williams (1982) formula, which allows for correction for unfiltered particles in each size group, was used:

\[
C_t = y_0^{(-k \cdot t)} + z_0
\]

\[PR = k \cdot V\]

where \(k\) = filtration constant, \(C_t\) = particle concentration of a given size at time \(t\), \(y_0\) = particle concentration of a given filterable size at time 0, \(z_0\) = particle concentration of a given unfilterable size (constant) at time 0, \(PR\) = pumping rate, \(V\) = volume of water in aquaria.

2.2. Respiration

Four hours prior to the experiment the tube shaped \(M. \text{acerata}\) were cut in rings, halved and maintained at 1.8°C in aerated 0.2-μm filtered flowing seawater to clean off debris and sediment, which fill the cavities of the animals. These sediments are out-washed prior to the measurements and cannot influence the results.

The parts did not show any negative reaction following the procedure like rotting etc. After ending the procedure the animal parts showed still enormous quantities of mucus secretion which also indicated a good condition. Branches of \(I. \text{kerguelensis}\) were cut off.
and maintained at 1.0°C in aerated 0.2-µm filtered seawater. The use of halved rings and branches made it possible to operate with small experimental chambers, which were accommodated in a cooling system. The use of sponge parts is common in methods in order to make very large individuals manageable (Cotter, 1978; Burlando et al., 1992). This handling did not seem to have any negative influence on the status of the animals.

A one-electrode open flow system was used. A permanently aerated reservoir contained the water, to which a membrane electrode was calibrated to 100% oxygen saturation. This water passed through a 175-ml experimental chamber. The O₂-depletion in the outflowing water was continuously recorded by an oxygen electrode (Eschweiler, Kiel) and plotted on a Linseis printer in % against the 100% saturation of the inflowing water. The consumption in ml h⁻¹ was calculated by using an oxygen solubility table (Grasshoff, 1983) for a salinity of 3.7% and a temperature of 1.8/1.0°C, respectively.

The difference in the O₂-concentration is dependent on the metabolic rate of the animal and the flow speed of the water but not on the experimental chamber size. Animals reduce the oxygen content in the chamber until a steady state concentration is reached. As bacterial-free seawater was used, a correction for background respiration was not necessary.

Here the curves showed an acclimatisation of the animals to the experimental conditions after 3 h and analysis readings were done after this time.

For the experiments the animals were inserted into the cooled experimental chambers and recleaned with a continuous stream of 0.2-µm filtered seawater. The measurements were done in darkness at a flow speed of 108 ml h⁻¹ at 1.8°C (M. acerata) and 1.0°C (I. kerguelensis) for 8–10 h.

### 2.3. Computations

After the experiments, dry mass and ash free dry mass of each animal was determined by drying at 60°C for 48 h and burning at 500°C for 5 h, respectively.

The metabolic rates (MR; pumping and respiration rates) are expressed as a function of body mass using the allometric equation, which was fitted using a least-squares regression with ln-transformed values:

\[
\ln MR = a + b \cdot M
\]

where \( M \) is the body mass and \( b \) the linear regression coefficient.

### 3. Results

Fig. 2 shows the retention efficiencies for the two species. No species reached 100% efficiency for particles in the range between 1 and 9 µm, even taking the S.D. into account. For particles bigger than 5 µm maximum retention reaches 70% in both species. Maximal retention for particles smaller than 1 µm, which are mainly bacteria, differed between species; \( M. acerata \) filtered particles around 0.4 µm with an efficiency of 75%, whereas \( I. kerguelensis \) retained particles around 0.8 µm with 55%, the
efficiency for smaller particles drops to 30%. A sharp decline can be observed around 1 μm and a depression between 2 and 4 μm in both species.

Pumping rates are shown in a double-log plot (Fig. 3). *M. acerata* pumps 180 ml h\(^{-1}\) and *I. kerguelensis* 220 ml h\(^{-1}\) (standardised to an animal of 1 g ash free dry mass). The regression coefficients are below the theoretical value of 0.75.

Fig. 4 shows the respiration rates in a double-log plot. *M. acerata* consumes 0.088 ml O\(_2\) h\(^{-1}\) at 1.8°C and *I. kerguelensis* 0.035 ml O\(_2\) h\(^{-1}\) at 1°C (standardised to an animal of 1 g ash free dry mass).

4. Discussion

Sponges are known to filter down into the bacterial range (e.g. Reiswig, 1971, 1975; Stuart and Klumpp, 1984) using their effective, microvilli-based particle capture system.
Fig. 3. Pumping rates (ml h$^{-1}$) in relation to ash free dry mass, ln-transformed. (A) Mycale acerata, $Y = 0.439X + 5.194$ ($n = 7$; $r = 0.69$; $F = 4.564$; $P = 0.857$); (B) Isodictya kerguelensis, $Y = 0.305X + 5.398$ ($n = 16$; $r = 0.84$; $F = 34.622$; $P = 0.0001$).
Fig. 4. Respiration rates (ml h⁻¹) in relation to ash free dry mass, ln-transformed. (A) *Mycale acerata*, \( Y = 0.609X - 2.426 \) (\( n = 8; r = 0.62; F = 4.015; P = 0.0919 \)); (B) *Isodictya kerguelensis*, \( Y = 0.678X - 3.357 \) (\( n = 18; r = 0.74; F = 19.414; P = 0.0004 \)).
Reiswig (1971) and Pile et al. (1996) showed for different demosponges that this capture system supplied up to 80% of the total carbon diet. Antarctic sponges as well are able to take a part of their food from minute particles such as bacteria. So far, nothing is known, whether other Antarctic suspension feeding taxa are able to exploit this size range, but this might explain why sponges dominate vast areas of the Antarctic shelves (e.g. Dayton, 1978; Gutt and Starmans, 1998).

The decline of efficiency around 1 μm, which was measured in all experiments, is a result of either a negative selection of this particle size range or a production of faeces which lowers the apparent efficiency. Stuart and Klumpp (1984), who observed the same phenomena between 2 and 4 μm in the species Haliclona anomyca, showed a particle production in this size range, but this can not be validated for these Antarctic species as data are still lacking.

Retention efficiencies are important when considering the food availability, especially during times of food limitation. Antarctic winter is believed to be such a food-limited period due to ice coverage and unfavourable light conditions (e.g. Gruzov, 1977). Yet at least in the Antarctic Peninsula region food in the nano and picoplankton size ranges may be abundant for a considerable period of the year (Barnes and Clarke, 1994; Leakey et al., 1996). Barnes and Clarke (1995) observed various taxa ceasing feeding only for a short time in winter. In McMurdo Sound, Berkman et al. (1986) observed viable benthic micro-algae during winter and argued that resuspension of these particles make them available for suspension feeding animals in near-shore environments of the Southern Ocean. Another food source during winter might be decaying algae debris, which fuels the growth of bacteria populations (Delille, 1993). No data on bacteria dynamics are available for Potter Cove, but debris of the brown algae Desmarestia sp. is abundant at least in autumn (personal observations). As M. acerata exploits the bacterial size range more efficiently as I. kerguelensis does, there might be more food available for the former species during winter.

The pumping rates of the sponges M. acerata and I. kerguelensis are below those of animals of boreal waters (for a compilation of rates, see Thomassen and Riisgård, 1995). This was shown for ascidians and a bivalve as well and is not only correlated with the low temperatures but also with inorganic sediment concentrations, which prevail in Potter Cove during spring and summer (Kowalke, 1998, 1999). Gerrodette and Flechsig (1979) showed a negative influence of rising sediment concentration on the pumping rate of the tropical sponge Verongia lacunosa. Even the small concentration of 11 mg l⁻¹ reduced the pumping performance significantly, an addition of 95.4 mg l⁻¹ by 41%.

The pumping rate of M. acerata was lower. It thus lowers the threat of clogging its ostia in comparison to I. kerguelensis. Additionally, a high mucus secretion allows the former species to clean its surface after strong sedimentation events fast and efficiently. Own observations showed that only few hours after storms, M. acerata had cleaned its sediment-covered surface. The mucusless I. kerguelensis pumps more rapidly, consequently clogs its ostia faster and needs longer to clean itself (by pumping) after sedimentation events. It might even be forced to cease pumping to avoid suffocating. This favours M. acerata in Potter Cove and probably in other places too, as M. acerata is the so far only Antarctic sponge species, in which growth could be measured (10–67% per year; Dayton et al., 1974).
The regression coefficients are below the postulated value of 0.75 (Hemmingsen, 1960). This could be due to the suppression of water transport in bigger animals, which might be more sensitive to experimental conditions (Jørgensen, 1996). Riisgård et al. (1993) and Thomassen and Riisgård (1995) doubted the applicability of the allometric equation for sponges due to their singular morphology: they grow simply by increasing their number of water-pumping choanocytes. But the uptake of particles is not limited to the chambers. The numerous channels, which as well phagocytise particles, are subject to allometric growth. Another rejection of this view might be the increase of dead choanocyte chambers in older (and thus larger) animals, which possess in relation to smaller individuals fewer ‘engines’ of water processing.

The standard metabolism, which is defined as metabolisms without food intake, growth and reproduction, could be measured by the use of bacteria-free filtered seawater. The only published data of polar sponges concern stem from three deep-sea species from the Greenland Sea (Witte and Graf, 1996). Consumption was between 0.407 and 0.478 ml O₂ per h and g ash free dry mass, at a temperature of −0.5°C. These values are tenfold higher than the respiration data of I. kerguelensis and fivefold higher than those of M. acerata. An explanation of this difference might be a depression-related artifact concerning the deep-sea species, as those values seem to be too high. Highly mobile Antarctic amphipods consumed less oxygen than the Greenland sponges (Rakusa-Suszczewski and Klekowski, 1973; Rakusa-Suszczewski, 1980). Respiration data of sessile Antarctic benthos showed values between 0.07 ml and 0.144 ml O₂ h⁻¹ (ascidians, unpublished data; bivalve Laternula elliptica: Ahn and Shim, 1998; gorgonian Ainigmaptilon antarcticus: Gili et al., 1999), which are in the same range as are the Antarctic sponges.

The filtration effectiveness (amount of water pumped per ml O₂ consumed) of both species lies within the range of sponges from warmer waters and is even higher than the effectiveness of the bivalve L. elliptica (Table 1). This confirms the findings of Thomassen and Riisgård (1995) who stressed the importance of the habitat, which dominates biological factors. As 0.46 mg C correspond to 1 ml O₂, a minimum of 0.22

| Table 1 |
|-----------------|-----------------|
| **Species**     | **F/R (1 ml⁻¹ O₂)** | **Source** |
| Porifera        |                  |            |
| Mycale sp.      | 19.6             | Reiswig (1974) |
| Verongia gigantea | 4.1             | Reiswig (1974) |
| Verongia fistularis | 9.7             | Reiswig (1974) |
| Tethya crypta   | 22.8             | Reiswig (1974) |
| Halichondria panicea | 2.7           | Thomassen and Riisgård (1995) |
| Mycale acerata  | 2.1              | this study |
| Isodictya kerguelensis | 6.3         | this study |
| Antarctic invertebrates |        |            |
| Cnemidocarpa verrucosa (Asciacea) | 15.1 | Kowalke, unpublished data |
| Molgula pedunculata (Asciacea) | 6.0 | Kowalke, unpublished data |
| Laternula elliptica (Bivalvia) | 1.2 | Kowalke, unpublished data |
mg C l⁻¹ must be available for \textit{M. acerata} and 0.07 mg C l⁻¹ for \textit{I. kerguelensis} to fulfill the maintenance requirements. These values are easily reached in Potter Cove during this time of the year (Kowalke, 1998).

5. Conclusions

The success of \textit{M. acerata} (the biomass is tenfold higher) compared to \textit{I. kerguelensis} has a number of possible explanations. The ability of \textit{M. acerata} to exploit the bacterial size range more efficiently may be vital in periods of low availability of nano and microplankton. If the members of the microbial food chain are important nutritive sources during winter, as Barnes and Clarke (1995) have suggested, \textit{M. acerata} simply gets more food. The second reason is the production of mucus by \textit{M. acerata}. A sediment-covered surface can be cleaned with great efficiency and does not hamper filtration and respiration for long times. Slattery and Bockus (1997) suggested the success of the soft coral \textit{Alcyonium paessleri} in McMurdo Sound to be due to the production of mucus. This seems advantageous even taking the metabolic costs into account. Furthermore, a lower pumping rate reduces the intake of particulate material and the risk of subsequent suffocation of the animal.

However, species like \textit{I. kerguelensis} are able to dwell in environments like Potter Cove due to their low metabolic costs, even if the sediment-laden habitat does not favour species without proper cleaning mechanisms. Their biomass is consequently lower.

Acknowledgements

I would like to thank the Alfred Wegener Institute for Polar and Marine Research and the staff of the Dallmann Laboratory for logistical support. Dr V. Koltun (St. Petersburg) helped with identification of species. Professor W. Arntz, Dr T. Brey and two anonymous referees gave valuable comments on the manuscript. This work was partially financed from the Deutsche Forschungsgemeinschaft. This is AWI publication no. 1721. [RW]

References


