Filtration in antarctic ascidians – striking a balance

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Abstract

Retention efficiencies and pumping rates of the four Antarctic ascidian species *Ascidia challengeri*, *Cnemidocarpa verrucosa*, *Corella eumyota* and *Molgula pedunculata* from Potter Cove, King George Island, were measured. None of the species reached a 100% retention efficiency at any given particle size. Pumping rates of the four species range between 250 and 349 ml/h per gram of ash free dry mass ($T = 1°C$), being lower than measured in temperate water species. This is connected to the sediment laden environment in which the animals are dwelling. A less efficient retention and low pumping rates decrease the risk of filtering structures being clogged. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Antarctica; Ascidians; Pumping rates; Retention efficiency

1. Introduction

Suspension feeding animals play a significant role in bentho–pelagic coupling throughout the oceans (Hargrave, 1973; Flint and Kamykowski, 1987; Doering et al., 1986; Ahn, 1993). The uptake of phytoplankton and particulate organic matter from the water column followed by the biodeposition of faeces and pseudofaeces is known to be one of the major trophic pathways in marine ecosystems (Doering and Oviatt, 1986; Martin et al., 1991).

Antarctic soft bottoms also reveal a rich and diverse fauna of suspension feeders often dominated by sponges, ascidians, bivalves and bryozoans (Belyaev and Uschakov, 1957; Propp, 1970; Winston and Heimberg, 1988; Kirkwood and Burton, 1988; Galeron et al., 1992; Gerdes et al., 1992; Barnes, 1995; Barnes et al. 1996; Starmans, 1997; Sahade et al., 1998), which thus form a major part in Antarctic bentho–pelagic interactions.

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Despite the importance of these taxa, their ecological role is still poorly investigated in Antarctic waters. Potter Cove, the site of investigation on King George Island, South Shetlands, is dominated by strong north-western winds and, during summer time, by enormous amounts of glacial meltwater which transports terrestrial sediments (Klöser et al., 1994a). Thus, the bottom of the inner cove consists mainly of fine sediments and houses a variety of suspensivores of up to 25 ind/m^2 which are mainly ascidians, the clam *Laternula elliptica* and the sponge *Mycale acerata* (Sahade et al., 1998; Kowalke, 1998).

To establish a basis for the calculation energy budgets of one of these important trophic groups, the dominant ascidians *Ascidia challengeri*, *Cnemidocarpa verrucosa*, *Corella eumyota* and *Molgula pedunculata*, the most abundant solitary ascidian species in Potter Cove, were chosen for further investigation.

The focus of this study was to (i) measure retention efficiencies and pumping rates of the four species and (ii) discuss the results in an ecological context.

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 km^2. Maximum water depth is 50 m and the bottom is mainly composed of fine sediments imported by glacial meltwater. Hard substrates, rocky shores, stones and pebbles border the mouth of the cove. The soft bottom communities display a wide variety of suspension and deposit feeding animals (Sahade et al., 1998; Kowalke and Abele, 1998). The hydrography of the cove 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., 1994a).

Between December 1995 and February 1996 divers collected the experimental animals which were immediately placed in an aerated flow-through aquaria of 8 to 25 l, according to animal size. The ascidians were individually kept for several days in order to acclimatise before starting the experiments. The water was drawn directly from the cove from 10 m depth.

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 animals were continuously pumping as could be concluded from permanently open siphons. The aquaria were artificially cooled to maintain a temperature of 1°C. Size spectra analysis took place between 1 and 15 μm divided into 64 size groups. 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 variation coefficient for each particle size was computed by dividing the standard deviation by the mean.
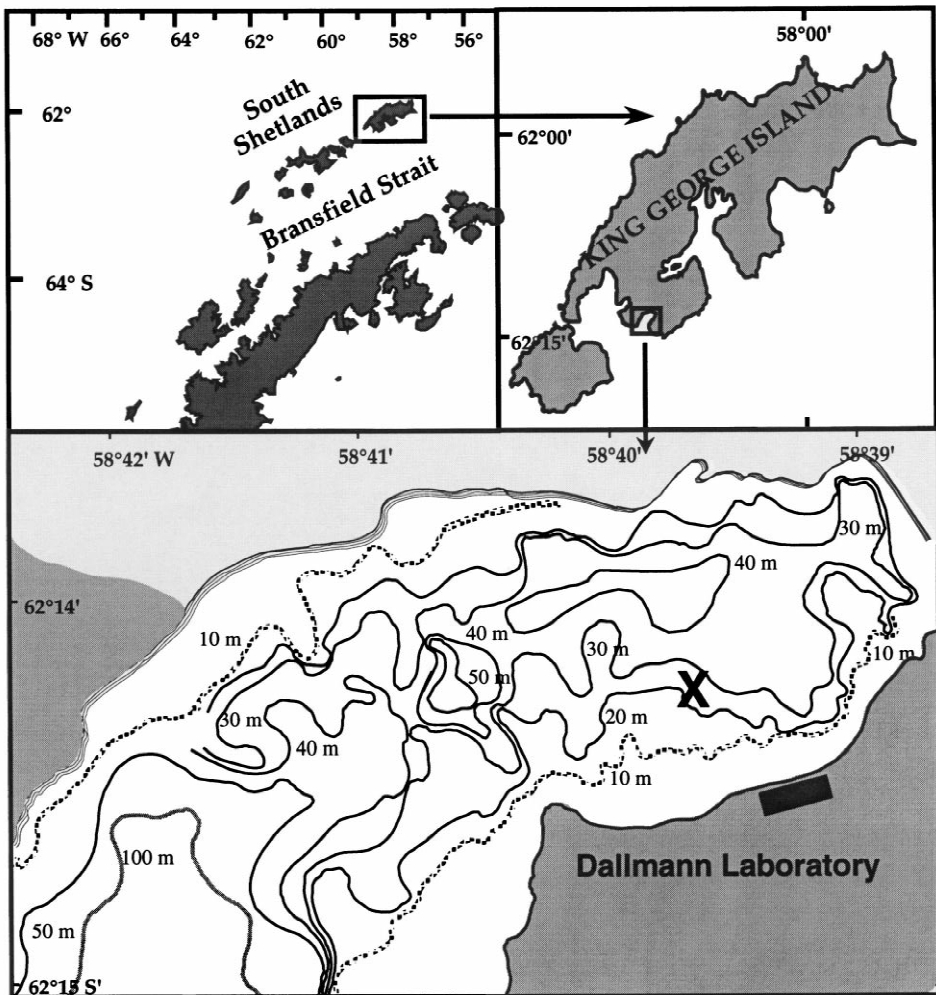
Fig. 1. Geographic location of Potter Cove, the x indicates the sampling station; shaded area is free of ice and snow during summer.

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' formula, which allows for correction for unfiltered particles in each size group, was used (see Williams, 1982).

$$C_t = y_0^{(-PR \cdot t)} + z_0$$

where

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 = unfilterable fraction of a given particle size (constant) at time 0
PR = pumping rate

The pumping rate is expressed as a function of body mass using the allometric equation, which was fitted using a least-squares regression with ln-transformed values:

$$\ln PR = a + b \cdot M,$$

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

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

3. Results

Fig. 2 shows the retention efficiencies for all four species. No species reached 100% efficiency for particles in the range between 1 and 9 μm, even taking the SD into account. The variation coefficients range below 0.5 for particle sizes bigger than 1.5 to 2 μm and show that the experimental data are no artefacts.
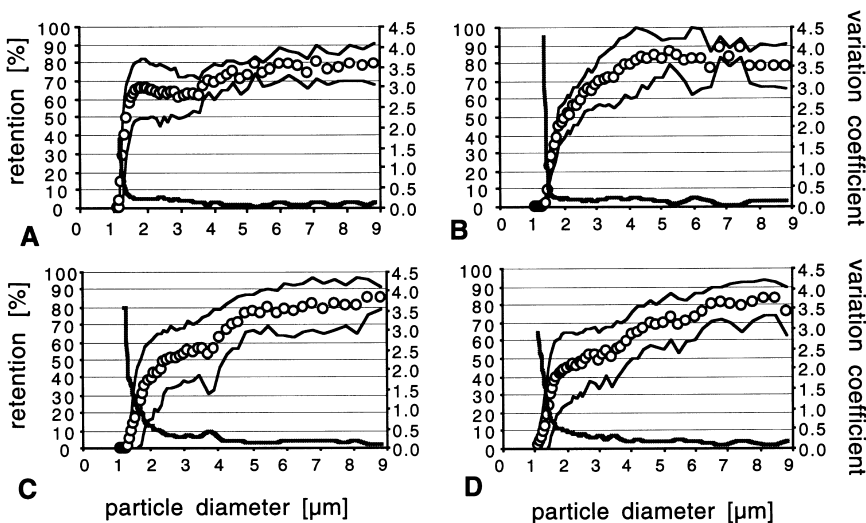

Fig. 2. Retention efficiencies (%) of the four ascidian species, A: *Ascidia challengeri*, B: *Cnemidocarpa verrucosa*, C: *Corella eumyota*, D: *Molgula pedunculata*; points refer to means, solid lines to SD (left *y*-axis); the greyish curve is the variation coefficient (right *y*-axis).
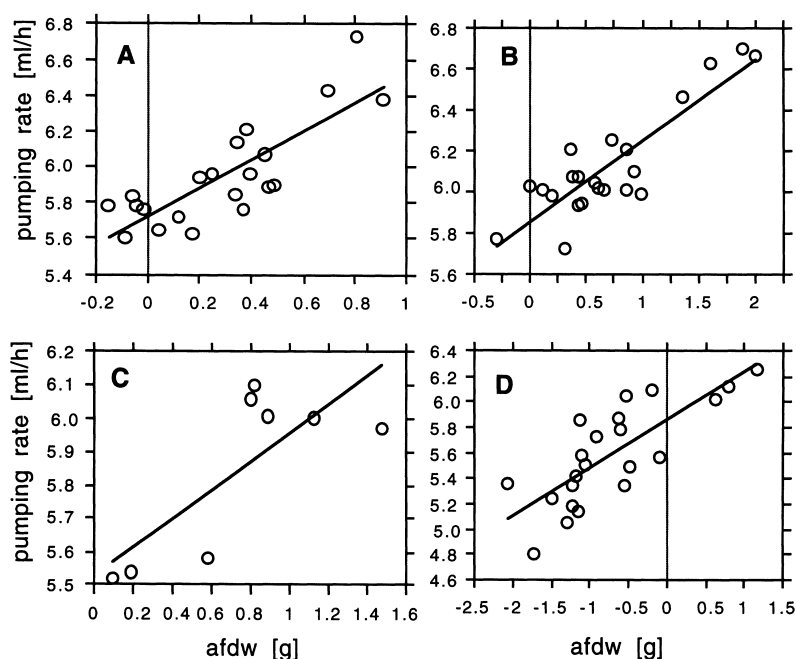
Fig. 3. Pump rates in relation to ash free dry mass, ln-transformed; A: *Ascidia challengeri*, $Y=0.804X+5.717$ ($n=21$; $r=0.82$; $F=38.31$; $P=0.0001$); B: *Cnemidocarpa verrucosa*, $Y=0.395X+5.852$ ($n=22$; $r=0.87$; $F=63.21$; $P=0.0001$); C: *Corella eumyota*, $Y=0.435X+5.524$ ($n=8$; $r=0.78$; $F=9.33$; $P=0.0224$); D: *Molgula pedunculata*, $Y=0.376X+5.855$ ($n=22$; $r=0.78$; $F=30.78$; $P=0.0001$).

A. challengeri, *C. eumyota* and *M. pedunculata* retain particles larger than 1.2 μm, *C. verrucosa* retains particles larger than 1.4 μm. Minimum particle size for maximum retention differs greatly between the species; 2 μm in *A. challengeri*, 4 μm in *C. verrucosa*, 5 μm in *C. eumyota* and even 6.5 μm in *M. pedunculata*.

Pumping rates are shown in ml/h in a double-log plot (Fig. 3). They vary between 250 and 349 for an animal of 1 g ash free dry mass (Table 1). The erect forms of *M.*

Table 1
Regression equations, standard errors and pumping rates in ml/h for the four ascidian species; ash free dry mass (RE_1; SE_1; PR_1) and dry mass (RE_2; SE_2; PR_2)

Species	RE_1	SE_1	PR_1	RE_2	SE_2	PR_2
A. challengeri	$0.804 \cdot \ln_M + 5.717$	0.173	304	$0.793 \cdot \ln_M + 4.704$	0.181	110
C. verrucosa	$0.395 \cdot \ln_M + 5.852$	0.295	348	$0.346 \cdot \ln_M + 5.439$	0.354	230
C. eumyota	$0.435 \cdot \ln_M + 5.524$	0.308	251	$0.575 \cdot \ln_M + 4.684$	0.228	108
M. pedunculata	$0.376 \cdot \ln_M + 5.855$	0.517	349	$0.369 \cdot \ln_M + 5.311$	0.512	203

pedunculata and *C. verrucosa* pump more water per unit time than the flattened forms of *A. challengeri* and *C. eumyota*. Data for dry weight are given in Table 1.

4. Discussion

4.1. Methodology

The indirect method was used to determine retention efficiencies and pumping rates because low pumping rates rendered flow through methods unsuccessful. The indirect method bears the problem that the water sampled does not necessarily pass the animal but floats alongside and thus dilutes the filtered water. This problem can be minimised by taking the samples closest to the exhalant aperture, but cannot be completely overcome. Another reason is the continuous fission of autotrophic and heterotrophic cells, which, due to the long time of experimental exposure and permanent excretion of ammonia by the ascidians must be taken into account (Porter, 1976; Roman and Rublee, 1980). But as excretion rates are very low (between 0.02 and 0.04 μm/day; Kowalke, 1998), this probably does not stimulate planktonic cell growth.

4.2. Retention efficiencies

Retention efficiencies are lower compared to temperate water species, which cleared a natural suspension with a 100% efficiency (Stuart and Klumpp, 1984). Randløv and Riisgård (1979), using algal cells, reported a complete retention for particles bigger than 2 to 3 μm in diameter. An equally low efficiency of 70% calculated by Fiala-Médioni (1978) for Mediterranean species probably reflected an underestimation due to the methodology used (Randløv and Riisgård, 1979; Robbins, 1984) and not a natural behaviour.

The low efficiencies recorded here in Antarctic ascidians might partly be related to the experimental set up. Permanent aeration, holding particles in resuspension, was provided, which diluted the already filtered water. But after 24 h of filtration the concentration of particles remained stable (Kowalke, 1998) and the variation coefficient is below 0.5 for particles bigger than 2 μm (Fig. 2), the low retention efficiencies do not seem to be experimental artefacts: the ascidians probably produce less efficient mucus nets. Robbins (1984) did not detect any regulation of the retention efficiency in the boreal species *Ascidia mentula* using inorganic particle concentrations of up to 300 mg/l. His animals were taken from the river Clyde area in Scotland, where normal particle concentrations in the water column range from 1–10 mg/l (Robbins, 1983), much less than the normal total particulate matter (TPM) content in Potter Cove. Thus, there might be a trend towards less efficient mucus nets in the Potter Cove species. But unless there are no data on these species from other sites, this cannot be confirmed.

Two groups can be separated, *A. challengeri* and *C. verrucosa*, both of which start filtration from ca. 1.3 μm on, but reach their maximum efficiency at a smaller particle size than *M. pedunculata* and *C. eumyota*, which filter from 1 μm on. As *A. challengeri* and *C. eumyota* always occur together as *M. pedunculata* and *C. verrucosa* do (Sahade,
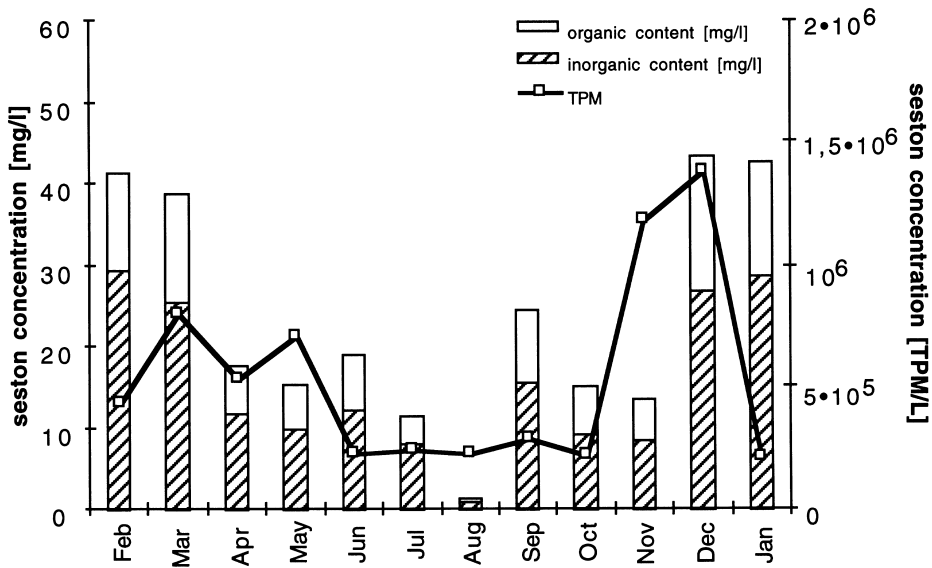
Fig. 4. Seston concentration, organic and inorganic content of the seston in 30 m depth (size class 0.8 to 30 μm diameter) for the period of February 1995 to January 1996 (from Kowalke, 1998, altered; TPM=total particulate matter).

personal communication), they separate nutritional niches by size selectivity and thus reduce competition.

This becomes important in the background of food availability. Particles larger than 8 μm, e.g. most diatom species, are comparatively rare during most of the year. A year round analyses of total particulate matter (TPM) between 8 and 30 μm in diameter shows less than 10^6 particles/l with an inorganic fraction of always more than 50% (Fig. 4; see Kowalke, 1998), which corresponds to 0.3 to 0.5 μg/l chlorophyll a (Schloss, 1997). Particles of smaller sizes like protozoans and bacteria seem to play a significant role in the nutrition of these species. *M. pedunculata* and *Corella eumoyta*, by far the most abundant ascidians of Potter Cove in terms of biomass (Table 2; Kowalke, 1998), obviously benefit from their ability to exploit particles down to the bacterial range.

Table 2
abundance (ind/m^2) and average biomass per individuum (dry mass) and biomass per square meter (dry mass/m^2) of Potter Cove (from Kowalke, 1998, altered)

Species	ind/m^2	dw (g)	dw/m^2 (g)
A. challengeri	2.3	1.6	3.7
C. verrucosa	1.0	5.7	5.7
C. eumyota	2.2	5.2	11.4
M. pedunculata	14.7	0.9	13.2

4.3. Pumping rates

The pumping rates are clearly below those of temperate water animals (Table 3). Holmes (1973) reported a depression of water transportation of animals measured in static water conditions with factors between three and nine for the species *Ascidiella aspersa* and *Styela clavata*, respectively, when compared to flow through methods (Table 3). In general steady state methods diminish the pump rates by CO_2 enrichment. A rough calculation of CO_2 accumulation in the aquaria yielded maximum concentrations of 0.02 mmol/l, which did not impair the measurements.

However, most investigations with temperate water suspension feeding species seem

Table 3
Pumping rates (ml/h) reported for different species in gram dry mass

Species	T (°C)	PR/g dm/h	Method	Source
Ciona intestinalis Mediterranean	15	5880 ml (organ weight)	Indirect static	Fiala-Médioni, 1978
Phallusia mammillata Mediterranean	15	6300 ml (organ weight)	Indirect static	Fiala-Médioni, 1978
Styela plicata Mediterranean	15	10680 ml (organ weight)	Indirect static	Fiala-Médioni, 1978
Ciona intestinalis Clyde	15	3540 ml	Indirect static	Robins, 1983
Ascidia mentula Scotland	15	2500 ml	Flow meter	Robins, 1984
Ciona intestinalis Skagerrak	15	7080 ml	Indirect static green algae	Petersen and Riisgård, 1992
Pyura stolonifera South Africa	13	480–1260 ml	Indirect, flow through	Stuart and Klumpp, 1984
Ascidiella aspersa Engl. Channel	10	960 ml	Indirect static dye	Holmes, 1973
Ascidiella aspersa Engl. Channel	10	3180 ml	Direct flow through dye	Holmes, 1973
Styela clavata Engl. Channel	10	516 ml	Indirect static dye	Holmes, 1973
Styela clavata Engl. Channel	10	4680 ml	Direct flow through dye	Holmes, 1973
Ascidiella aspersa Kattegat	10	2580 ml	Indirect static	Randløv and Riisgård, 1979
Ascidiella aspersa Kattegat	10	3240 ml	Direct, flow through	Randløv and Riisgård, 1979
Ciona intestinalis Kattegat	10	2760 ml	Direct, flow through	Randløv and Riisgård, 1979
Ascidia challengeri Potter Cove	1	110 ml	Indirect static	this work
Corella eumyota Potter Cove	1	230 ml	Indirect static	this work
Molgula pedunculata Potter Cove	1	108 ml	Indirect static	this work
Cnemidocarpa verrucosa Potter Cove	1	203 ml	Indirect static	this work

to overestimate water transportation rates. Doering and Oviatt (1986), working with the clam *Mercenaria mercenaria* in mesocosm tanks using labelled ^{14}C carbon assumed an overestimation of pumping rates in investigations using unnatural suspensions like monoalgal cultures. This was confirmed by MacDonald and Thompson (1986), Grant and Cranford (1991) and Cranford and Gordon (1992) for pectinid clams and Prins et al. (1995) for *Mytilus edulis*. So far the only available publication using natural suspensions as food sources for ascidians states 480–1260 ml/h at 13°C (*Pyura stolonifera*; Stuart and Klumpp, 1984), whereas rates of *Ascidiella aspersa* or *Ciona intestinalis* yielded 2580 and 2760 ml/h, respectively, at 10°C (Randløv and Riisgård, 1979).

Particle loads have an influence on pumping rates. Robbins (1984) found a rate decreased by 50% when *Ascidia mentula* was exposed to 100 mg/l inorganic seston. Petersen and Riisgård (1992) found similar results for *Ciona intestinalis* using green algae as the food source. As ascidians are not able to discriminate between particles of organic or inorganic origin (Robbins, 1984), the Potter Cove species presumably pump less water due to the sediment laden ambient water. Squirting, a rhythmical contraction of the body wall to get rid of surplus particles, was never observed in the Antarctic species. But as the animals were not continuously observed during the long lasting experiments, it cannot be excluded. These events would of course lower the mean pumping rates. Another factor, which is reducing the pumping rates, is the increased water viscosity at low water temperatures. But as Antarctic surface water at 0°C is only 50 to 60% more viscous than water of 20°C, the temperature difference alone cannot account for the observed rates.

4.4. Ecological implications

At first sight Potter Cove seems to be an unfavourable habitat for filter feeding benthos. Primary production is very low (Schloss, 1997) and the benthos has to cope with sinking inorganic sediments of glacial origin that dilutes an already scarce planktonic food supply (Klöser et al., 1994b; Varela, 1998). Benthic material, re-suspended by fierce wind, is of greater nutritional value (Schloss et al., in press) but still contains large amounts of inorganic particles (Kowalke, 1998). Ascidians in Potter Cove are thus forced to handle large quantities of particles of low average nutritional value, but have to prevent the blockage of the filtering apparatus due to an overload of particles. As ascidians are not able to select particles and directly reject unwanted ones, this can only be done by closing the inhalant openings as well as by squirting, both at the cost of energy (Hoyle, 1953; Werner and Werner, 1954). Robbins (1985) demon-strated for *Ciona intestinalis* a high mortality rate due to starving at sediment concentrations higher than 600 mg/l, a reasonable value in certain conditions for Potter Cove (Varela, 1998). The species of Potter Cove present a new strategy minimising the risk of clogging the filtering structures by lowering the retention performance.

The two flat forms with their inhalant openings close to the bottom, *A. challengeri* and *C. eumyota*, pump less water than the erect species *M. pedunculata* and *C. verrucosa* (Table 1). The particulate matter is not distributed evenly above the sea bottom. A few centimetres above ground the TPM is highest, but the particulate organic matter (POM) is considerably lower than 15 to 25 cm above ground (Schloss et al., in

press). After resuspensive events like storms, POM is generally sinking slower than the inorganic fraction (Fabiano et al., 1997) thus raising the level of organic material in higher regions and diluting POM concentrations close to the ground. To get the same amount of energy, the flat species have to pump more water, process more useless inorganic particles and squirt more often than the other two.

These species reduce in comparison to the erect forms the pumping rates to avoid an overload of inorganic particles. However, the strategies, lowering both retention efficiencies and pumping rates, certainly decrease the energy intake.

5. Summary

These investigated Antarctic ascidians have to balance between their energetic demands and the threat of suffocating to optimise production but nevertheless seem to be physiologically well adapted to near shore waters with high turbidity and sediment load and thus dominate benthic communities in these areas (Gallardo et al., 1977; Jazdzewski et al., 1986; Ramos et al., 1987, Saiz-Salinas et al., 1997), whereas zones of low turbidity and high water clarity, in shallow as well as in deeper waters, are mainly populated by sponges (Dayton et al., 1974; Battershill, 1989; Barthel and Gutt, 1992; Starmans, 1997) or bryozoans (Barnes, 1995; Barnes et al., 1996; Starmans, 1997). Nevertheless, it remains unclear to which degree heavy particle loads hamper production. This remains to be investigated in the future.

Acknowledgements

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