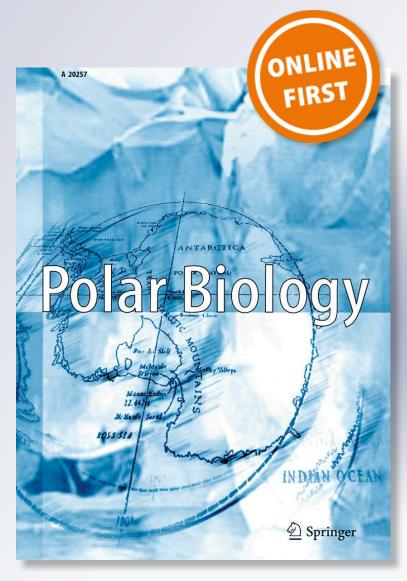# Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations

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SHORT NOTE

Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations

**Luciana Torre · Natalia Servetto · Matias Leonel Eöry ·
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Abstract Glacial retreat and subglacial bedrock erosion
are consequences of rapid regional warming on the West
Antarctic Peninsula. Sedimentation of fine-grained eroded
particles can impact the physiology of filter-feeding
benthic organisms. We investigated the effect of increa-
sing concentrations of sediment on the oxygen con-
sumption of suspension feeding species, the ascidians
Molgula pedunculata, *Cnemidocarpa verrucosa*, *Ascidia
challengeri*, and the pennatulid *Malacobelemnon daytoni*
in Potter Cove (South Shetland Islands, Antarctica). In
A. challengeri and *C. verrucosa,* oxygen consumption
increased gradually up to a critical sediment concentration
(C_{crit}) where species oxygen consumption was maximal
(O_{max} in mg O_2 g^{-1}dm day^{-1}) and further addition of
sediments decreased respiration. C_{crit} was 200 mg L^{-1}
for *A. challengeri* (O_{max} of 0.651 ± 0.238) and between
100 and 200 mg L^{-1} for *C. verrucosa* (O_{max} of $0.898 \pm
0.582$). Oxygen consumption of *M. pedunculata* increa-
sed significantly even at low sediment concentrations
(15–50 mg sediment L^{-1}). Contrary to the ascidians,
sediment exposure did not affect oxygen consumption of
the sea pen. The tiered response to sedimentation in the
four species corroborates recent field observations that
detected a reduction in the abundance of the sensitive
ascidian *M. pedunculata* from areas strongly affected
by glacial sediment discharge, whereas sea pens are
increasing in abundance. Our investigation relates conse-
quences (population shifts in filter-feeder communities) to
causes (glacial retreat) and is of importance for modelling
of climate change effects in Antarctic shallow coastal
areas.

Keywords *Molgula pedunculata* · *Cnemidocarpa
verrucosa* · *Ascidia challengeri* · *Malacobelemnon
daytoni* · Glacier melting · Sedimentation

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Introduction

Studies of the effects of sedimentation on polar coastal
benthos have previously analysed diversity and changes in
the abundance of species on spatial gradients from the glacier
front towards open waters. Benthic filter feeders suffer from
clogging of their filtering organs when exposed to intense
sedimentation (Thrush et al. 2004). Recent rapid glacier
retreat along the West Antarctic Peninsula (WAP) and,

more specifically, around the South Shetland Archipelago (Rückamp et al. 2011) caused a rise in sediment deposition rates over the past 60 years (Monien et al. 2011). In Potter Cove, a tributary inlet of Maxwell Bay, King George/25 de Mayo Island (South Shetlands), high concentrations of sedimentary run-off are produced during the summer melting season (Dominguez and Eraso 2007). The Cove is surrounded by the Fourcade Glacier except for its southern coastline that is already free of ice, still bare of terrestrial vegetation. Here, melt water creeks carrying high amounts of fine-grained sediments discharge into the cove. Retention of the melt water plume within the cove by the predominant north-westerly winds enhances deposition and accumulation of sediments on the sea bed. Significant hydrographical changes were observed in Potter Cove between 1994 and 1998, including a decrease in surface water salinity and an increase of total suspended particulate material (TSPM) (Schloss et al. 2012) as a consequence of glacier retreat. Simultaneously, remarkable changes in benthic macrofaunal community structure were observed, especially for filter-feeding organisms. In a 1994 diving survey, a vertical zonation pattern in the soft bottom benthic community was documented in Potter Cove. Regions shallower than 15–20 m water depth were colonised by a relatively uniform assemblage dominated by the bivalve *Laternula elliptica* and the pennatulid *Malacobelemnon daytoni*. Below 20 m water depth, the ascidian *Molgula pedunculata* was the dominant species, whereas at 30 m, five solitary ascidians species: *M. pedunculata*, *Cnemidocarpa verrucosa*, *Ascidia challengeri*, *Corella eumyota* and *Pyura setosa* constituted the most abundant biomass (Sahade et al. 1998). A second survey 4 years later in 1998 revealed a dramatic reduction in the density of *M. pedunculata,* which was strongly reduced at 30 m from ∼ 16 to < 1 % coverage. At the same time, complanate ascidians (*A. challengeri* and *C. eumyota*) increased slightly in abundance. Furthermore, the pennatulide *M. daytoni* increased in density from 10 to 85 ind m^2 at 20 m and extended its depth distribution to 30 m (Sahade unpub. data). The magnitude and velocity of the observed shifts suggest a possible link to the glacial melting and erosion processes in Potter Cove.

Ascidians are susceptible to high inorganic particle loads and are generally more abundant in clear waters. A reduction in individual growth rate, reproduction and population density has been related to environmental stress in general (Bates 2005). Experiments with high TSPM loads from 600 to 2,000 mg L^{-1} caused a dramatic reduction in growth rate and survival of *Ciona intestinalis* and *Ascidiella scabra,* which was related to their lack of ability to assimilate enough food for metabolic requirements under such conditions (Robbins 1985). This suggests that sediment load may increase the energy expenditure for surface clearance and body maintenance,

possibly at the cost of growth and reproduction. In contrast, pennatulaceans (octocorals, sea pens) are well adapted to inhabit soft sediments. Total or partial withdrawal beneath the sediment surface and full body contraction is common behaviour in response to environmental disturbance (Soong 2005). Colonies of anthozooid external feeding polyps of *M. daytoni* are grouped cylindrically around a main supportive stem (raquis) (López-González et al. 2009). The polyps can also passively tolerate sediment coverage in some parts of the colony, which are usually rapidly cleaned by bottom currents (Best and Best 1988). Antarctic octocorals have been observed to preferentially ingest the fine fraction of seston (<5 μm) instead of larger zooplankton (Orejas et al. 2003). If this holds true for *M. daytoni*, suspended sediments might indeed affect its food absorbance rate. In this study, we measured the oxygen consumption of solitary ascidians *M. pedunculata*, *C. verrucosa*, *A. challengeri* and of the sea pen *M. daytoni* exposed to increasing concentrations of natural sediments. After observing the rapid shifts in the composition of the Potter Cove benthic communities, we wanted to understand how the different species react at the level of metabolism when facing high loads of inorganic matter.

Materials and methods

Study area and sampling

Experimental work was carried out at the Argentinian-German Dallmann laboratory on A. Carlini (Jubany) station at Potter Cove, South Shetland Islands (S 62°14′, W 58°40′). Specimens were collected by divers at 20–30 m depth from the cove (S 62°14′06,799, W 58°40′18,199), at a site fronting Potter Creek, a major tributary stream. All animals were carefully cleaned from debris and attached organisms and placed into tanks containing aerated sea water at 0 ± 1 °C for an acclimation period of 1 week before starting the experiments. Tanks were maintained under dim light conditions and the water exchanged daily during acclimation and experimental phase.

Sediment exposure and respiration measurements

After acclimation, the ascidians were individually placed in 3-L jars that functioned as individual respiratory chambers. Open chambers containing the experimental specimens were placed into a 140-L tank with natural, unfiltered sea water. Overall, five experimental chambers and a reference chamber without animals were placed in each tank. The reference chamber was used to correct for microbial and chemical oxygen consumption in the system. A number of different

individuals of similar size were available for each species: *A. challengeri* ($n = 5$ ind.), *C. verrucosa* ($n = 9$ ind.) and *M. pedunculata* ($n = 13$ ind.). An aerating system and water pumps were used to maintain water flow within the aquarium tanks and keep added sediment in suspension. Due to the difference in body mass and size, a different experimental set-up was used for *M. daytoni*. Experimental chambers of 0.7 L volume were set-up with four sea pens in each. Three experimental respiration chambers and a reference chamber were placed into 50-L tanks. Sea water was pumped through the tank and the chambers. The flow was equally divided between chambers by inserting flow restrictors in each delivery line. Animals were acclimated in the experimental system for 1 week before chambers were closed, to avoid recording stress effects (see Online Resource 1).

Surface sediment was taken with a grab sampler at 20 m depth close to the sampling station, dried at 70 °C and sieved through a 50-μm mesh sediment sieve. This size fraction of natural sediment was chosen because it could be easily suspended in water. The organic fraction was 2.36 ± 0.07 %. Different starting concentrations of TSPM from 0 (without sediment) to 5, 15, 50, 100, 200 and 400 mg L^{-1} were consecutively set-up in the holding tank, in order to cover the whole range of in situ concentrations (from 10 to 200 mg recorded in good weather conditions in Potter Cove (Pakhomov et al. 2003)). Only for *M. daytoni*, further concentration of 600 mg L^{-1} was tested. After 6 h of exposure to an experimental TSPM concentration, the chambers were sealed for 18 h and the change in oxygen concentration measured. After closing the respiration chambers, the water in the tanks was exchanged and the next concentration of sediment applied, according to the TSPM protocol, before the chambers were opened again.

Added sediments did not remain in permanent suspension within the closed chambers. Rather, our set-up mimics a natural situation of temporarily changing sediment deposition in Potter Cove according to wind speed and stratification (see Schloss et al. 2012). Especially, near the coastline, peaks of glacier sediment discharge during high temperature intervals around noon alternate with colder periods of reduced sediment run-off at night (Dominguez and Eraso 2007). Sedimentation in the closed chambers occurred more rapidly at the highest concentrations (see Online Resource 2). Thus, although the concentrations could not be maintained stable in our experimental set-up, we applied a stress gradient of increasing sediment load within the natural range of concentrations.

Oxygen measurement

Eighteen hours after closing the chamber, a 10-mL water sample was taken from each respiration chamber. The minimum value recorded including all measurements was 4.6 mg L^{-1} and thus above the mean oxygen sub-lethal threshold for hypoxia of benthic organisms of 2.05 ± 0.09 mg L^{-1} (Vaquer-Sunyer and Duarte 2008) and the critical concentration obtained with temperate ascidians 3.9 ml L^{-1} (Fiala-Médioni 1979). Water samples were measured by the spectrophotometric Winkler method, optimised after Labasque et al. (2004) with turbidity correction at 466 nm according to Roland et al. (1999), on a Pharmacia Ultrospec 3,000 photometer. Oxygen consumption rates were calculated as the difference between the oxygen concentration in the experimental jars and the respective reference chamber. At the end of the experiment, dry mass (ascidians without tunic) was determined by drying at 70 °C for 72 h. Data are expressed in mg O_2 consumed per g of dry mass per day (mg O_2 g^{-1}dm day^{-1}).

Data analyses

Basal oxygen consumption (O_{bas}) was determined in unfiltered sea water containing 1.19 ± 0.24 mg L^{-1} naturally dissolved TSPM. Differences between O_{bas} and each sediment concentration (O_{sed}) were assessed by non-parametric Kruskal–Wallis test (K–W).

For a better comparison between species, the oxygen consumed at every sediment concentration (O_{sed}) was related to O_{bas} and the relative oxygen consumption O_{rel} calculated as:

$$O_{rel} = (O_{sed} - O_{bas})/O_{bas}.$$

To determine species-specific responses to increasing sediment concentration, a Friedman ANOVA for repeated measurements was performed between O_{rel} at every concentration over all tested individuals of each species. A one-way ANOVA with Tukey′s HSD analysis was performed to compare the response between species at each sediment concentration. Data were Log_2data^2 transformed to satisfy the ANOVA assumptions.

We also calculated the energetic costs (E_{Inv}) during TSPM exposure as J gdm^{-1} from the oxygen consumption during the treatments with up to 400 mg L^{-1} TSPM for each species as:

$$E_{Inv} = \sum_{i=1}^{n} (O_{sed_i} - O_{bas}) \cdot C_f.$$

C_f represents the conversion factor from mg of O_2 to Joules (J) (Gnaiger 1983). Note that if oxygen consumption decreases ($O_{sed} < O_{bas}$), E_{Inv} takes on negative values. A K–W test was used to compare species E_{Inv}. In order to compare species-specific sensitivities to sediment exposure, an arbitrary ranking was performed based on E_{Inv} and O_{max}, where O_{max} is the maximal oxygen consumption at the critical TSPM concentration (C_{crit}). C_{crit} is the sediment concentration at which the highest

oxygen consumption is measured (significantly elevated over control level without sediment) and above which the oxygen consumption starts to decline at higher sediment loads.

Results

Ascidia challengeri and *C. verrucosa* showed increased oxygen uptake with increasing sediment concentration with a significant O_{max} at medium concentrations up to the C_{crit}, beyond which oxygen consumption declined at higher sediment loads (Fig. 1a). Contrary, *M. pedunculata* and *M. daytoni* showed no significant difference in O_{rel} and no O_{max} and hence, C_{crit} could not be determined (Fig. 1b). However, *M. pedunculata* showed a significant increase in oxygen consumption (O_{sed}) even at very low sediment concentrations (15 mg L^{-1} K–W test, $H_{12} = 4.1$, $P = 0.02$) over O_{bas} (Fig. 1a). In the inter-species analysis, *M. pedunculata* showed significantly higher values of O_{rel} than the other species investigated at low (5 mg L^{-1} ANOVA, $F_{(3, 27)} = 4.77$, $P = 0.0085$; 15 mg L^{-1} ANOVA, $F_{(3, 27)} = 3.35$, $P = 0.0338$) and very high sediment concentrations (400 mg L^{-1} ANOVA, $F_{(3, 21)} = 3.19$, $P = 0.0448$). No difference was detected at intermediate TSPM concentrations at which *A. challengeri* and *C. verrucosa* reached their respective O_{max}. Contrary to the effect on ascidians, sediment exposure had no significant effect on oxygen consumption in the pennatulid irrespective of the added sediment amount. In fact, the oxygen consumption of the sea pen declined by approximately 20 % under sediment exposure compared to the sediment-free treatment, but the difference was not significant (Fig. 1b).

There are evidences that some ascidian species can be oxyregulators above 3.9 mL L^{-1} (Fiala-Médioni 1979). None of our oxygen measurements were below that limit. However, we do not certainly know whether the analysed species are oxyregulators or oxyconformers; the results were compared with and without measurements below 70 % oxygen saturation; and there were no major differences except for the O_{max} for *C. verrucosa* that taking into account just measurements above 70 % was 200 mg L^{-1} instead of being between 100 and 200 mg L^{-1}. This difference can be more related to the effect of eliminating the highest oxygen consumption measurements than to a physiological effect and then, in the figures and analyses, all measurements were taken into account.

Overall, ascidians invest significantly more energy into dealing with sediment coverage than the pennatulid (K–W test, $H_3 = 8.39$, $P = 0.0387$). The only exception is the complanate *A. challengeri*, which increased the energy expenditure only marginally when exposed to elevated TSPM loads compared with the other two ascidians (Fig. 2). The ranking of sensitivity from most sensitive to most tolerant response to sedimentation based on C_{crit}, O_{max} and E_{Inv} was: *M. pedunculata* ≪ *C. verrucosa* < *A. challengeri* ≪ *M. daytoni*.

Discussion

According to our measurements, the ascidians in Potter Cove are more sensitive to sediment exposure than the pennatulid. *M. pedunculata*, which diminished most dramatically in abundance over the last 15 years, was by far the most sensitive of all investigated species. Its oxygen consumption increased even at very low sediment
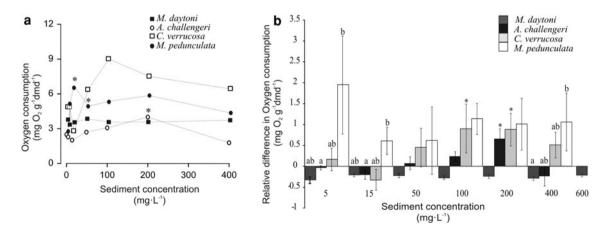

Fig. 1 Mean oxygen consumption (**a**) and O_{rel} (**b**) (mean ± SEM) of *M. pedunculata* ($n = 13$), *C. verrucosa* ($n = 9$), *A. challengeri* ($n = 5$) and *M. daytoni* ($n = 6$) at increasing concentrations of sediment. * Significant difference ($P < 0.05$) of species-specific oxygen consumption during sediment exposure compared to sediment-free control treatments (**a**) and O_{max} (**b**). *Different letters* indicate differences in species-specific response to sediment treatment at each concentration ($P < 0.05$ for the post hoc analyses)
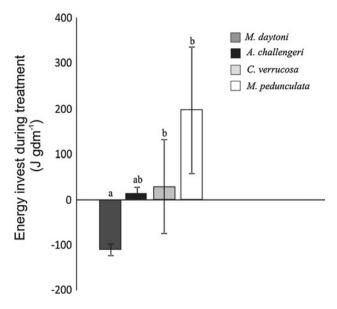
Fig. 2 Energy investment (E_{Inv}) during the whole time of exposure to the full range of sediment concentration from 5 to 400 mg L^{-1} (J gdm^{-1}) of *M. pedunculata* ($n = 13$), *C. verrucosa* ($n = 9$), *A. challengeri* ($n = 5$) and *M. daytoni* ($n = 6$). Data as mean ± SEM. *Different letters* indicate significant differences between species ($P < 0.05$)

concentrations (5–50 mg L^{-1}), well within the range of sediment concentrations presently observed in the inner Potter Cove of 5–25 mg L^{-1} (Philipp et al. 2011). Although considerable quantities of sediment were needed to reach maximum respiration in *C. verrucosa* (100 mg L^{-1}) and *A. challengeri* (200 mg L^{-1}), both species started to respond with increased respiration rates already at much lower sediment concentrations. Extra costs arise presumably from enhanced ciliary activity during ingestion, mucus production and squirting during excretion of non-digestible particles. The decline in oxygen consumption above C_{crit} probably indicates a reduction of filtering activity at high particle concentration in ascidians (Petersen 2007). Obstructions of the respiratory structures might further curtail oxygen uptake, hence reducing aerobic metabolism and, in the extreme case, even suffocating the animals (Modig and Ólafsson 1998). Indeed, ascidians represent a major filter-feeder group mostly in areas where mineral suspension contributes only a small fraction of the overall suspended particle content in the water column (Petersen 2007).

Antarctic soft bottom communities are considered unique with respect to the dominance of sessile suspension feeders and the three-dimensional assemblages they create on soft bottoms (Gili et al. 2006). Our present data document the diversity of experimentally determinable threshold limits of different ascidians to cope with sediment coverage, an important factor needed to model their response to changes in summer glacier melting.

The stalked species *M. pedunculata* and *C. verrucosa* have uncoupled their reproductive cycle from the summer bloom season, energetically most favourable but also compromised by frequent sedimentary run-off events (Sahade et al. 2004). These sensitive species moreover keep their siphons between 10 and 30 cm above the sediment where the amount of TSPM from re-suspension is lower than in the sediment–water interface. Contrary, flat form species as *A. challengeri* and *C. eumyota* lift their siphons less than 5 cm above the sediment and filter directly in the layer carrying the highest amount of re-suspended inorganic particles. Stomach content analysis has revealed high amounts of inorganic material (sand) in *C. eumyota*, whereas in *C. verrucosa* grains were almost absent from stomach contents even during summer (Tatián pers. obs.). Lower filtration rates and lower particle retention efficiency in *A. challengeri* and *C. eumyota* compared to erect species have previously been related to the higher sediment loads these species are exposed to (Kowalke 1999), and the flat species are certainly better adapted to deal with increased sedimentation during summer. However, present annual sedimentary deposit rates are three times higher than the rates recorded between 1940 and 1980 in Maxwell Bay (Monien et al. 2011) and inside Potter Cove mean TSPM values have increased from 5–10 to 20–30 mg L^{-1} in surface water run-off layers in the last 20 years (Schloss et al. 2012). This may be one reason why flat form ascidians are more successful under the present conditions. Contrary to the ascidian response, sediment exposed sea pen did not increase oxygen consumption during sediment exposure. If anything, their oxygen uptake was mildly decreased. This was attributed to the reduced ectodermic respiration upon contraction of the sensitive filtering apparatus in some of the experimental sea pens (Brafield and Chapman 1967). This behaviour parallels the response of large, old *L. elliptica* to similar sediment concentrations (Philipp et al. 2011). The authors suggested that shell closure and reduced oxygen consumption mitigate the ingestion of inorganic particles by the bivalves.

Our results provide a first explanation for the benthic population shifts recently observed in Potter Cove, based on animal response to sedimentation stress. They underline the differences in the tolerance levels of different groups and species with the *M. daytoni* and the bivalve *L. elliptica* being the least sensitive species, which can behaviourally adapt and protect their filtering apparatus in times of high sedimentation. These species exhibit habitat expansion and increased population density in the glacial effluent zone of the inner cove. Complanate ascidians tolerate sediment better than stalked ones, with the latter being most dramatically reduced in numbers within the area affected by sedimentary run-off. Species with intermediate sensitivity such as *C. verrucosa* may be able to remove sediment from

their body by squirting and pumping behaviour, but at higher energy costs, which may reduce their survival and success if the situation worsens. This strongly suggests that sedimentation caused by glacier retreat can play a major role in restructuring benthic filter-feeder communities fronting melting glaciers in the Western Antarctica.

Conflict of interest The authors declare that they have no conflict of interest.

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