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The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 de Mayo)

Synopsis of research performed 1999-2006 at the Dallmann Laboratory and Jubany Station

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# Role of benthic filter feeders in pelagic-benthic coupling: assimilation, biodeposition and particle flux

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#### Introduction

Potter Cove is characterized by two clearly distinct areas, the outer cove with high benthic primary production and the inner cove with low primary but high secondary benthic production. The substrate of the outer cove is comprised of solid rocks and big boulders which support a dense canopy of phaeophyte macroalgae down to 25 m depth (Klöser et al., 1994). The inner cove is dominated by sessile macrofaunal assemblages on a muddy substrate (Sahade et al., 1998). A rich filter-feeding community occupies this area, in spite of what appears to be unfavorable conditions for their their feeding activities. These conditions include high sedimentation and low pelagic primary production. In Phlebobranchiate ascidians, high suspended inorganic particles reduce the amount of food assimilated by limiting the intake of utilizable food by a process of dilution and/or reducing the efficiency of assimilation of such food (Robbins, 1985). In summer, creeks formed by melting ice transport large amounts of inorganic material from the surrounding land into the cove, resulting in high sedimentation rates of about 18-30 g m<sup>-2</sup> day<sup>-1</sup> in the inner cove, (Ferreyra et al., 2003). In Potter Cove, the sediment load in the water column is frequently enhanced in the summer by resuspension of the fine bottom material, when the sea surface is ice-free and winds result in turbulent mixing that affects the bottom to 30 m depth (Schloss et al., 1999). The suspended sediment then affects the penetration of light into the water column which together with the deep vertical mixing explains the low phytoplankton biomass within inner Potter Cove (Schloss and Ferreyra, 2002). Water-column analyses from Potter Cove suggested that some organic material in the deposited sediments is released from the water-bottom interface even during winter (Kowalke, 1999; Tatián et al., 2002). Although scarce, this material seems to be the food source for benthic organisms, especially long-lived species that undergo growth and reproduction during winter (Sahade et al., 2004). The origin and composition of this material is, nevertheless, not completely understood. One of the most reasonable hypotheses is that part of this material may be macroalgal debris that originated in the outer cove, which is then continuously carried into the inner cove by clockwise water currents (Ferreyra et al., 2003). This material is sometimes easy to observe as little brown-greenish particles floating on the sea surface and a thick bed of brown material that is patchily present on the bottom.

Filter feeding animals can play a significant control on phytoplankton biomass, coupling the pelagic and benthic systems. The uptake of phytoplankton and particulate organic matter from the water column, followed by biodeposition by filter feeding animals is known to be one of the major trophic pathways in marine ecosystems (Kowalke, 1999; Ahn, 1993). In phytoplankton-impoverished coastal waters, as Potter Cove, the role of benthic suspension feeders is important, since their fecal depositions can nourish the benthic fauna.

The focus of this study was to measure assimilation efficiencies of natural and provided seston (powdered macroalgae) by a series of experiments performed with one bivalve and two ascidian species. The aim was to reveal insights into the possible response of filter feeders to a food source other than phytoplankton. The mass-specific deposition rate was measured, as well as the C:N composition of deposits (feces) should make it possible to determine the contribution of suspension feeders to the particle flux near muddy bottoms in Potter Cove.

# Material and Methods

Experiments were carried out in aquaria disposed in a cold and wet room, at the Dallmann laboratory. Sea water was first pumped from the cove (1-3 m depth) into 2.500 I tanks were the temperature was maintained at 0° C. Seawater passed through filters to remove coarse suspended material before filling the experimental aquaria. Diets were natural seston (particles suspended in running seawater) and powders made from kelp fragments and inorganic material (precombusted diatomaceous earth) suspended in filtered sea water. The kelps Desmarestia mensiezii and D. anceps were collected prior to the treatments in the intertidal of the outer cove. The kelps were washed in freshwater to remove the salts, and a portion of the material was then lyophilized for 48 hs. The dried material was ground to powder and sieved through 50, 125 and 250 µm mesh. Diatomaceous earth was ashed (5 h 450° C) to eliminate residuals of organic matter and sieved as the kelp material. Different diets were composed by particle size and macroalgae/diatomaceous earth concentrations. These diets were stored at -20° C. Test filter feeders used were the clam Laternula elliptica (King and Broderip, 1831) and the ascidians Cnemidocarpa verrucosa (Lesson, 1830) and Pyura setosa (Sluiter, 1905).

*Laternula elliptica*: experiments were carried out during February and March 2002. Animals were collected at 10 m depth by SCUBA diving and immediately transported to the laboratory. Bivalves were cleaned of fouling organisms and debris and kept for several days in aquaria for acclimatization (open system with running sea water, at  $1 \pm 1^{\circ}$ C). Seven specimens were placed in individual 2 I - PVC aquaria and nourished near the oral siphon using a Pasteur pipette with a solution made by yeast and carmine-red in sea water. The time until the production of red feces (gut residence time, GRT) was recorded. Seven specimens were placed in individual 1 I - PVC flasks and two pebbles instead of bivalves (controls), putted randomly on the bottom of a 90 I aquarium, a close system filled with 0.45 µm filtered sea water. Animals were starved in the experimental aquarium for two days. Water was changed at the beginning of each experiment. During three days, animals were fed on different diets (Table I) with a suspension of 4 mg I<sup>-1</sup> (initial concentration). Water in the

aquarium was stirred using airstones and resuspension pumps to keep particles in suspension. Every 24 h, triplicate water samples and deposits were filtered onto precombusted and preweighed GF/F filters. Suspended particulate matter, particulate organic matter (POM) and particulate inorganic matter were measured gravimetrically. POM was calculated after combustion of filters (5 hs at 450° C). Assimilation efficiency (AE) was calculated using the ratio of Conover (Navarro and Thompson, 1994) which assumes that an animal can digest and absorb the organic component of the food, but not the inorganic fraction. The organic matter is calculated as the percentage of mass loss after combustion of water samples, which is compared with the corresponding percentage of mass loss after combustion of feces. According to Ahn (1993), *L. elliptica* produces feces and pseudofeces. As it was not possible to continuously follow the deposition activity, a parallel experiment was used, collecting pseudofeces by a Pasteur pipette for correction purposes.

*Cnemidocarpa verrucosa* and *Pyura setosa*: experiments were performed from January to March 2004; the animals were collected by SCUBA diving at 20 m depth, cleaned of debris and fouling organisms and washed under flowing seawater. Acclimatization of the animals was allowed in an aquarium system similar to that used with *L. elliptica*. Gut residence time (GRT) experiments were performed accordingly. A total of six specimens of *C. verrucosa* and five specimens of *P. setosa* were placed in individual flasks on the bottom of two 90 I aquaria, as well as two controls. The first experiment was performed by feeding animals with natural seston (running sea water) in an open system. The following experiments were run in a closed system filled with filtered (0.2 µm) sea water. During five days, animals were fed on diets prepared with macroalgae and precombusted diatomaceous earth (aprox. 4 mg  $\Gamma^1$  of seston). Dietary composition for each feeding condition is showed in Table I.

Species	Diet	Composition	Size
		F	narticles
Laternula elliptica	1	Particulate macroalgae (60%), diatomaceous earth (40%)	< 50 µm
	2	Particulate macroalgae (30%), diatomaceous earth (70%)	< 50 µm
	3	Particulate macroalgae (60%), diatomaceous earth (40%)	< 125 µm
	4	Particulate macroalgae (60%), diatomaceous earth (40%)	< 250 µm
Cnemidocarpa verrucosa and Pyura setosa	5	running seawater, natural seston	
	6	Particulate macroalgae (25%), diatomaceous earth (75%)	< 50 µm
	7	Particulate macroalgae (13%), diatomaceous earth (87%)	< 50 µm
	8	Particulate macroalgae (25%), diatomaceous earth (75%)	< 125 µm

**Table I:** Diet composition of the different experiments performed to estimate assimilation efficiency (AE).

To estimate the assimilation efficiency (AE), determinations of total matter (organic and inorganic) were performed from triplicate filtered water and feces samples, dried (60° C, 24 hs), ashed (450° C, 5hs) and weighed filters and deposits. Feces were taken using a Pasteur pipette. Organic carbon and organic nitrogen were both determined from feces deposited after feeding Diet 5 using a Carlo-Erba NA-1500 analyzer, after removing calcium carbonate with CIH, to estimate the quality of the feces (C:N ratio). Once experiments were terminated, animals were sacrificed and the tunic dissected. The rest of the ascidian was dried (60° C, 24 h) before mass determinations (gDM). The biodeposition rate (BR) is calculated as mg DM of feces produced per individual per d<sup>-1</sup>. Mass specific biodeposition rate (MSBR) as mg DM of feces produced per  $gDM^{-1}$  of animals per d<sup>-1</sup>. Data on mean mass (gDM) and density (ind m<sup>-2</sup>) of C. verrucosa and P. setosa at different sites of Potter Cove (E1: southern inner cove, muddy bottoms; E2: outer cove, hard substrates; E3: northern inner cove, moraine deposits) were used (Sahade, 1999; Kowalke, 1999, Fig. 1) to estimate biomass per square metter. This information made it possible to estimate total particle flux, and fluxes of particulate organic carbon (POC) and particulate organic nitrogen (PON) by deposits produced by both ascidians in these areas.



**Fig. 1:** Map of Potter Cove. E1: sampling site. E1, E2, E3: sites with available data on ascidian abundance.

#### **Results**

All *L. elliptica* specimens produced red feces 15-19 h after they were fed with the yeast-carmine solution. On the other hand GRT for the ascidians was difficult to estimate, because specimens commonly rejected the carmine solution or produced red feces through a very wide time range (between 20 to 90 h). Samples taken from the controls not revealed a significant sedimentation of particles during the experimental time. All diets were assimilated from the three test species: mean of the AE varied between 26-50 % in the case of *L. elliptica*, and 26-72% for ascidians, reaching higher AE when natural seston was sup-

plied (Fig 2 A, B). Differences between diets were not significant in *L. elliptica* (ANOVA F = 1,38, n = 28, p = 0.27), *C. verrucosa* (ANOVA F = 2.01, n = 23, p = 0.14) and *P. setosa* (ANOVA F = 2.65, n = 20, p = 0.08). The latter species was the less influenced by the sediment condition: highest AE was calculated under high amounts of inorganic material (Diet 7). This species did not decrease the assimilation efficiency in the presence of large particle sizes (Diet 8), but AE were lowered under these conditions in *L. elliptica* (Diet 4) and *C. verrucosa* (Diet 8).



**Fig. 2A:** Assimilation efficiency (mean ± SD) with different diets: *Laternula elliptica.* 



**Fig. 2B:** Assimilation efficiency (mean ± SD) with different diets: *Cnemidocarpa verrucosa* (black bars) and *Pyura setosa* (white bars).

Estimated BR and MSBR while the organisms were feeding on natural seston was also higher in *C. verrucosa* than in *P. setosa* (Table II). Thus, the particle, POC and PON fluxes vary according to species, density and biomass (Table III).

	<i>Cnemidocarpa verrucosa</i> n = 6	<i>Pyura setosa</i> n = 5
Biodeposition rate (BR) mg specimen <sup>-1</sup> d <sup>-1</sup>	$10.9\pm2.6$	$5.4\pm0.3$
Mass specific biodeposition rate (MSBR) mg gDM <sup>-1</sup> d <sup>-1</sup>	$\textbf{6.4} \pm \textbf{2.7}$	$3.8\pm2.2$

**Table II**: Cnemidocarpa verrucosa and Pyura setosa. Deposition rate and mass specific deposition rate under running seawater (natural seston).

**Table III**: Estimated particle, PON and POC fluxes by *Cnemidocarpa verrucosa* and *Pyura setosa* at different areas in Potter Cove, 30 m.

	Cnemidocarpa verrucosa		Pyura setosa			
	E1	E2	E3	E1	E2	E3
Animal density (ind m <sup>-2</sup> )	1.8	1.9	3.6	0.9	-	0.1
Animal biomass (gDM m <sup>-2</sup> )	3.5	3.7	7	1	-	0.12
Total particle flux (mgDM m <sup>-2</sup> d <sup>-1</sup> )	22.5	23.7	44.9	3.9	-	0.44
POC flux (mg m <sup>-2</sup> d <sup>-1</sup> )	1.03	1.09	2.07	0.09	-	0.01
PON flux (mg m <sup>-2</sup> d <sup>-1</sup> )	0.11	0.12	0.22	0.01	-	0.001

## Discussion

Estimations of GRT depended on animal behavior and stress conditions. Clams fed, however, despite acclimatization time while ascidians did not. Ascidians are generally very sensitive to water movements, closing their siphons when disturbed. To estimate AE, GRT was assumed to be approximately 24 h as was previously stated for other ascidian species (Klumpp, 1984; Robbins, 1985). In the ascidian *Pyura stolonifera*, feeding depends on seston quality: squirting produces rejection of particles under high inorganic loads (25 mg l<sup>-1</sup>, 3 % POM) and large particle size, > 65 µm (Klumpp 1984). According to Armsworthy et al. (2001), AE decreased significantly from 46% to 23 % when adding up to 46 mg l<sup>-1</sup> sediment to the natural seston. High concentrations of particles can lower AE; however, such high concentration were not measured in Potter Cove, where particulate inorganic matter close to the bottom, at 30 m was an average 3 mg l<sup>-1</sup> during a year-round period study (Tatián et al., 2002). Nevertheless, we need to emphasize that water samples analysed in this study were taken under calm weather conditions, higher values are possible during

storms. As an adaptation to inorganic sedimentation, in the case of the species C. verrucosa, Molgula pedunculata, C. eumyota and Ascidia challengeri from Potter Cove, less efficient retention and low pumping rates decrease the risk of filtering structures being clogged. Nevertheless, it remains unclear to which degree heavy particle loads lower production (Kowalke, 1999). The supplied inorganic particles did not decreased significantly the AE in the three species studied. Besides, abundance of these species suggests that impact of sedimentation is still low or present species can cope well with the actual sedimentation rates. Under low seston concentration (approximately 4 mg l<sup>-1</sup> in all diets) our results show that differences in the AE depend on the diet, species and even individuals. In the case of *L. elliptica*, no significant differences in AE was observed owing to inorganic percentage nor in particle size up to 125 µm but, a decrease of the mean AE was measured when food particles in the provided diet were larger than 250 µm in size. Cnemidocarpa verrucosa appeared to be more affected by inorganic particles and particle size, showing a decrease in AE from natural seston (Diet 5) to diets enhanced with inorganic material (Diets 6, 7, 8) and from smaller to higher particle size. This was not the case in P. setosa that showed higher AE under powdered kelp suspensions and higher inorganic percentages in the diet. In the Arctic bivalve Hiatella arctica, AE decreased under increased food levels, from 90% to 32% (Sejr et al., 2004). Similarly L. elliptica produces fecal pellets with higher organic carbon and chlorophyll a/phaeopigment ratios when increased chlorophyll a concentration in the seawater (Ahn, 1997). This indicates an ineffective AE under higher water quality as this bivalve feeds in excess of its needs. AE varies according to diets: monoculture was reported to be efficiently (up to 92%) assimilated by ascidians (Fiala-Médioni, 1974). Other particles, i.e. natural seston were also efficiently assimilated: Tito de Morais and Fiala-Médioni (1985) estimated up to 95%. Although with less efficiency (up to 42%), kelp detritus was also reported to be assimilated by the ascidian P. stolonifera (Klumpp, 1984).

Antarctic sessile suspension-feeders consume a broad spectrum of the seston fraction in an opportunistic strategy, ingesting particles in proportion to their availability (Gili et al., 2001). Since filter-feeders are non selective, the use of macroalgal debris as food depends on their capacity for retention and assimilation of these particles. Minimum particle size for maximal retention efficiencies measured in four solitary ascidian species from Potter Cove, is 2 - 6.5µm (Kowalke, 1999), but no data are available for maximal particle size. Gut content analyses carried out from the ascidians C. verrucosa and Corella eumyota immediately fixed after sampling revealed the presence of recognizable macroalgal debris of up to 500 µm in size (Tatián et al., 2004; this volume). Although with less food value than fresh material, decaying kelp detritus as part of the bacterial loop can be a potential food source (Tenore et al., 1982; Albertelli et al., 1998). Bacteria represent a nitrogen source of comparable importance to phytoplankton (Seiderer and Newell, 1985). Macroalgal diets were assimilated at least at 25% efficiency by the species studied: thus, suspension-feeding communities may use kelp detritus and the associated bacteria as alternative food source in this impoverished phytoplankton environment. Fatty acid studies performed in water column and sediment samples at Potter Cove (Graeve et al., this volume) revealed high amounts of detritus and low contributions of phytoplankton from the water column but in sediment samples, fatty acids were typical for bacteria and their degradation products.

Filter-feeding is successful within inner Potter Cove, as indicated by high abundance of clams and ascidians (Sahade et al., 1998). Abundance and capacity of these species to filter water samples seems to be important in pelagic-benthic coupling. The biodeposits (feces and pseudofeces) enhance particle flux nourishing the associated benthic fauna. BR estimated for *L elliptica* at the close Marian Cove, in King George Island was 0.26 - 2.17 mgDM gWM<sup>-1</sup> d<sup>-1</sup> (Ahn, 1993). BR was higher in *C. verrucosa* than in *P. setosa*. The higher abundance and biomass of the former species at different sites of Potter Cove (Sahade et al., 1998; Kowalke, 1999) suggests that *C. verrucosa* has an important role in the benthic community and in the particle flux. Particularly interesting are the POC and PON percentages measured in the feces of ascidian species: the C:N ratio is higher in comparison to filter-feeding bivalves (Table IV).

		POC (%)	PON (%)	C:N	Reference
Crassostrea virginica	Bivalve	18.1	3.4	5.3	Frankenberg & Smith, 1967 (cit. Ahn, 1993)
Geukensio demissa	Bivalve	2.4	0.35	6.9	Kraeuter, 1976 (cit. Ahn, 1993)
Laternula elliptica	Bivalve	5.68 ± 3.54	1.04 ± 0.72	6.0 ± 1.1 5 - 7	Ahn, 1993 Mercuri et al., this volume
Adamussium colbecki	Bivalve	-	-	5.13	Chiantore et al., 1998
Halocynthia pyriformis	Ascidian	3.7 ± 0.7	0.3 ± 0,05	13.6 ± 1.1	Tatián et al., 2003
Styela rustica	Ascidian	9.1 ± 2.6	1.3 ± 0.4	8 ± 0.7	Tatián et al., 2003
Cnemidocarpa verrucosa	Ascidian	4.6 ± 1.3	0.5 ± 0.1	9.7 ± 1.97	This study
Pyura setosa	Ascidian	2.3 ± 1.2	0.3 ± 0.1	7.9 ± 2.1	This study

**Table IV**: POC, PON and C:N in feces in different suspensivores under running seawater (natural seston).

Taking into account that the bivalve *L* elliptica ceases feeding during the four winter months (Brockington, 2001), the continuous filtering activity of ascidians may be important, because implies the permanent feces production. This continuous particle flux from the animals to the system is especially important during low periods of primary production and when the water column is stable, lowering events that make particles available (i.e. advection, sedimentation and resuspension).

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