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Role of suspension feeders in Antarctic pelagic-benthic coupling: trophic ecology and potential carbon sinks under Climate Change

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This research is an important contribution to previously unquantified aspects of the effects of climate change in species-mediated energy transfer between pelagic and benthic Antarctic coastal areas.

Author Contributions: GA, MT, VLF originally formulated the idea, GA, MT, VF, AO, CO, IRS conceived and designed the experiments, AO, JM developed and constructed experimental setup, GA, TM, JM conducted fieldwork and performed the experiments, GA performed statistical analyses and developed the energy budget, GA wrote the manuscript, all the authors contributed with the interpretation of results and provided editorial advice.

HIGHLIGHTS

- Food processing and energy acquisition was studied on two Antarctic filter-feeder species subjected to different food sources and sediment concentrations.
- A general energy model was developed to assess the energy balance of an ascidian and to evaluate its potential as a carbon sink in coastal Antarctic ecosystems.
- Food characteristics and animal densities modulate the impact of ascidians on pelagic-benthic coupling and on carbon immobilisation.
- Increasing inputs of sediment runoff would be a major constraint in coastal areas.

ABSTRACT

Sea-ice and coastal glacier loss in the Western Antarctic Peninsula open new ice-free areas. They allowing primary production and providing new seabed for colonisation, both acting as a negative feedback of climate change. However, the injection of sediment-laden runoff from the melting of land-terminating glaciers may reduce this feedback. Changes in particulate matter will affect nutrition and excretion (faeces stoichiometry and properties) of suspension feeders, reshaping coastal carbon dynamics and pelagic-benthic coupling. Absorption efficiency and biodeposition of *Euphausia superba* and *Cnemidocarpa verrucosa* were quantified for different food treatments and varying sediment concentrations. Both species showed high overall absorption efficiency for free-sediment diets, but were negatively affected by sediment addition. High sediment conditions increased krill biodeposition, while it decreased in ascidians. Energy balance estimation indicated high carbon sink potential in ascidians, but it is modulated by food characteristics and negatively affected by sediment inputs in the water column.

KEYWORDS Potter Cove, *Euphausia superba*, *Cnemidocarpa verrucosa*, absorption efficiency, faecal production, biodeposition, carbon sink

INTRODUCTION

While the rapid temperature increase in the Antarctic Peninsula seems to be paused since the late 1990s due to a short-term natural climate variability (Turner et al. 2016), evident impact of climate change is observed in the West Antarctic Peninsula (WAP) over the cryosphere (Rückamp et al. 2011, Cook et al. 2014, Gutt et al. 2015), the continental shelf and in particular the coastal area (Meredith and King 2005, Cook et al. 2016). Furthermore, climate model projections indicate that a large anthropogenic regional warming signal is likely to result in substantial warming across the Peninsula over the 21st century (Bracegirdle et al. 2008, Etourneau et al. 2019).

The loss of ice shelves and the retreat of coastal glaciers in Antarctica over recent decades, have created around $2.4 \times 10^4 \text{ km}^2$ of new open water, enhancing planktonic primary production (Peck et al. 2010, Moreau et al. 2015, Jansen et al. 2018a), but also new ice-free seabed areas prone to benthic colonisation (Bowden et al. 2006, Barnes et al. 2018, Jansen et al. 2018b). For instance, in Potter Cove (King George Island/Isla 25 de Mayo), high macroalgae and suspension feeder abundances have been reported in new ice-free areas (Quartino et al. 2013, Lager et al. 2017, 2018). Similarly, in the Mertz Glacier Tongue (East Antarctic), there has been a large increase in suspension feeder abundance after massive ice loss (Jansen et al. 2018b). Such new production (planktonic and benthic) represents an important food source and an increase in energy and biomass for the whole ecosystem (Barnes et al. 2018, Jansen et al. 2018a). Furthermore, a high potential carbon (C) sink (blue carbon storage) could act as negative feedback to climate change due to water column C drawdown (Peck et al. 2010, Quartino et al. 2013, Barnes 2015, Barnes et al. 2018). Indeed, benthic secondary production would be an important C sink, as it involves long-term carbon storage in animal biomass (Rossi et al. 2012, Barnes 2015, Barnes et al. 2016).

Some WAP coastal areas are subjected to seasonal and sporadic injections of fresh water loaded with sediments due to melting of marine-terminating glaciers (Klöser et al. 1994, Monien et al. 2017, Meredith et al. 2018). In these areas phytoplankton and macroalgae growth seem to be arrested via light-limitation (Dierssen et al. 2002, Schloss et

al. 2002, 2012, Quartino et al. 2013, Deregibus et al. 2016). Furthermore, low concentrations of key nutrients and organic particulates occur when inorganic particle loads are high, which constrains food supplies for planktonic and benthic suspension feeding species (Klöser et al. 1994, Pakhomov et al. 2003, Müller-Navarra 2008, Fuentes et al. 2016). A high concentration of suspended sediments can also clog the filtering apparatus of these species, which further constraints physiological performance (Torre et al. 2012, 2014) and can even lead to massive mortality events (Pakhomov et al. 2003, Fuentes et al. 2016).

Suspension feeders are able to feed on a wide spectrum of food particle types and sizes (Riisgård and Larsen 2010). Through their trophic activity (ingestion and faecal production) these animals play a major role in pelagic-benthic coupling (PBC) and in the flow of C through marine shallow ecosystems, modulating the cycling of nutrients and moving C from the pelagic to the benthic realm and vice versa (Gili and Coma 1998). Sediment trap studies in shallow nearshore waters (5-25 m depth) indicate that faecal pellets from krill and other mesozooplanktonic consumers are important components of the organic matter (OM) flux (Schloss et al. 1999, Isla et al 2001, Alurralde 2018). Antarctic krill (*Euphausia superba*) is a key planktonic suspension feeder occurring in the Southern Ocean (Siegel 2016). High densities are frequent in the coastal areas of the WAP (Atkinson et al. 2009, Warren and Demer 2010, Steinberg et al. 2015, Belcher et al. 2016, 2017), where 66.7–96.3% of total particulate organic carbon (POC) flux in shallow waters (20-180 m depth), is represented by krill faeces (Isla et al. 2001, Belcher et al. 2016, 2017). In Potter Cove, krill annual abundances can be as high as $\sim 3.000 \text{ ind.}100 \text{ m}^{-3}$ (Fuentes 2006), which promote high but seasonally variable inputs of faecal pellets ($1.5 \cdot 10^3 - 7.53 \cdot 10^5 \text{ mm}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) sinking to the seafloor (Alurralde 2018). This enable benthic suspension feeders such as hydrozoans, corals, glass sponges and ascidians to feed directly on them and benefit from their organic contents (Orejas et al. 2000, Duineveld et al. 2004, Leys et al. 2004, Tatián et al. 2004). This functional group is the dominant component of the Southern Ocean shelf benthos (Gili et al. 2006, Gutt et al. 2013) and in contrast to the Arctic, nearshore biomass and diversity in fjords is much higher than the offshore sites (Grange and Smith 2013). Suspension feeders not

only enhance PBC in shallow waters (Ahn 1993, Tatián et al. 2004), but also develop complex three-dimensional biogenic structures particularly on soft bottoms (Tatián et al. 1998, Gili et al. 2006), where epibiosis is a common phenomenon especially over solitary ascidians (Rimondino et al. 2015). Solitary and compound ascidians comprise dominant representatives of Antarctic epifaunal macrobenthic communities on the shelf (Gutt et al. 2013, Segelken-Voigt et al. 2016), fjords and coastal areas (Grange and Smith 2013, Moon et al. 2015, Sahade et al. 2015, Lagger et al. 2018). In new ice-free areas of the WAP ascidians reach the higher abundances (Lagger et al. 2017, 2018), which could increase retention of a greater share of the productivity in their living structures for decades (Kowalke et al. 2001). Nevertheless, these organisms of apparently great C sink potential in shallow waters (Petersen and Riisgård 1992, Coppari et al. 2014) are generally neglected in the overall equation of C circulation in our changing world (Rossi et al. 2015).

The abundance and distribution of benthic suspension feeders depend on the quality of available food sources (Gardner 2000, Rossi et al. 2015, Jansen et al. 2018a,b). The degree to which the quantity and composition of accessible food meets the consumer's nutritional needs defines food quality (Müller-Navarra, 2008), while the characteristics of the diet define the way in which the digestion process takes place in suspension feeders (e.g. Jørgensen 1996, Mayer et al. 1997, Hawkins et al. 1998). Only part of the ingested food is absorbed (i.e., transported across the gut wall); the rest is expelled as faeces. A fraction of the absorbed food is diverted to growth and reproduction, while another fraction is used to maintain resting metabolism. If the energy expended in resting metabolism is lower than the energy gained through digestion, organisms are in a position of net energy gain, thus enabling biomass production that immobilises C in somatic tissues. But if absorption is low, a higher proportion of OM would be transferred to the seabed through faeces that will be remineralised by microbial activity and hence released back into the water column later (Claquin et al. 2010, Mermillod-Blondin 2014), buried in the sediments and/or consumed by detritivores, a process known as biodeposition (Ahn et al. 1993, Tatián et al. 2008, Mermillod-Blondin 2014). Consequently, the quantification of uptake efficiency for different

food sources and of biodeposition are essential to assess energy flows through benthic and pelagic ecosystems.

Predicted changes in the properties of suspended particulate matter along the WAP (Montes-Hugo et al. 2009, Schofield et al. 2010) are expected to have profound implications for the trophic processes of suspension feeders, such as energy uptake (Robbins 1985, Wotton and Malmqvist 2001, Atkinson et al. 2012a), which will ultimately impact their net energy balance. The ecological consequences may be dramatic since the WAP supports a high abundance of both planktonic (Atkinson et al. 2012b, Puigcorb et al. 2016) and benthic (Gutt et al. 2013) suspension feeders, and these species are the food supply to the scavengers and carnivores that form the rest of the benthic food web. Furthermore, faecal production may be affected by alterations in the rate, stoichiometry and properties of pellets (Ragueneau et al. 2005, Gergs et al. 2009), with cascade effects on ecosystem functioning (Claquin et al. 2010, Alcaraz et al. 2014, Coello-Camba et al. 2017). In the same way, high sediment inputs in marine coastal areas could drastically impact suspension feeders (Fuentes et al. 2016, Sahade et al. 2015), limiting blue carbon storage ecosystem services as it occurs with ice scour disturbance (Barnes 2017, Barnes et al. 2018).

In the present study, we first examined the absorption efficiency (AE) and biodeposition of *E. superba* and *C. verrucosa* subjected to different food conditions (diet composition and sediment concentrations). These abundant and conspicuous filter feeders are able to sieve particles from the water in a wide range of sizes (0.06 μm to $>100 \mu\text{m}$), overlapping with other suspension feeders (Riisgrd and Larsen 2010, Suh and Nemoto 1987) making them good representatives of the suspension feeder guild. By means of a general energy budget, we assessed the energy balance of *C. verrucosa* under those food conditions to evaluate its potential as a C sink and the consequences of alternative food scenarios (i.e. phytoplankton- or macroalgal detritus-dominated seston, and increased suspended sediment concentration). Finally krill was considered in its role of food provider for benthic communities throughout biodeposition. To this end, we included krill faeces as food source for ascidians.

METHODS

Study area. Experiments were conducted at the Argentinean-German Dallmann Laboratory in the Argentinean Antarctic station Carlini (former Jubany) next to the study area in Potter Cove ($62^{\circ} 14' \text{ S}$, $58^{\circ} 40' \text{ W}$), in King George Island (25 de Mayo), South Shetland Islands. The cove (Fig. 1), which is surrounded by the Fourcade Glacier on its north and east sides, is 4 km long and 2.5 km wide (Al-Handal and Wulff, 2008) with a maximum depth of 100 m. During the summer, melt water creeks carry large amounts of sediment from the land-terminating glacier (average maximum 284 mg L^{-1}), which are discharged into the cove by several creeks (Monien et al. 2017). A comprehensive description of the coastal ecosystem of Potter Cove can be found in Wiencke et al. (2008), and the hydrographical characteristics and environmental conditions for the last two decades are reported by Schloss et al. (2012) and Meredith et al. (2018).

Figure 1. Location of Potter Cove, King George/25 de Mayo Island, South Shetland Islands, Antarctica. Average spatial distribution of total suspended particulate matter (TSPM)

concentration in the surface waters of Potter Cove during summer 2010/2011 (based on Figure 5a, Monien et al. 2017). E1, E2, E3, indicate the sampling stations mentioned by Sahade et al. 1998 and I, the ice-free area (Island) mentioned by Lagger et al. 2018.

Target species and collection. During the summers of 2012/2013 and 2013/2014, we collected juvenile and adult *E. superba* from the outer part of Potter Cove using a 200 μ m mesh Nansen net with a 2 L cod end, towed vertically and obliquely (40 m below the surface). The contents of the cod end were immediately transferred to a 50 L plastic bucket filled with cooled (0°C) filtered seawater and then taken directly to a cool room (0 $\pm$ 1°C), where the animals were placed in a 100 L container (further details in Fuentes et al. (2016)). Specimens of *C. verrucosa* were collected by SCUBA divers between 20 - 30 m depth in the inner part of Potter Cove (Fig. 1). Sampled individuals were immediately transported to the station aquaria in a 50 L plastic bucket filled with cooled (0 $\pm$ 1°C) seawater and subsequently placed in a 100 L container after cleaning their tunics from large epibionts. Both species were kept in an open flow system with natural seawater (0 $\pm$ 1°C) directly pumped from the cove for at least 10 days for acclimation (Torre et al. 2012, 2014). Prior to the experiments, krill specimens were starved for 48 h and ascidians for 5 days in filtered seawater (0.1 μ m) to allow the specimens to empty their stomachs.

Experimental setup. For both species, we used six independent cylindrical 8-L aquaria with individual closed circulation systems, placed in a 90 L running seawater bath for the incubation experiments at constant temperatures (0 $\pm$ 1°C). We fitted a mesh (200 μ m for krill and 1 mm for ascidians) 10 cm above the bottom of each cylindrical aquarium, allowing water to flow and avoiding the disaggregation of the faeces in the circulating system. For each treatment (see below) we used one control and five replicates. For krill incubation, we placed 12 juvenile krill specimens per aquarium (range size: 35-46 mm total length). For ascidian incubation, we placed 1 individual per aquarium (range size: 8-12 cm high).

Test Diets. Two types of diet were used (Table 1). Primary diets consisted of: 1) natural seston (S) present in surface seawater pumped directly from the cove; 2) natural

phytoplankton (P); 3) macroalgal detritus (D). Natural phytoplankton was collected by towing a 70 µm mesh net horizontally in the outer part of the cove to ensure the predominance of phytoplankton in the sample, which was transferred to a 60 L tank of 0.1 µm filtered seawater. Macroalgal detritus was collected by sieving debris directly from the water column on days following storms when there were significant amounts of resuspended detrital deposits. Macroalgal detritus was dried at 60°C, ground and sieved through a 50 µm mesh before being suspended in 0.1 µm filtered seawater at a final concentration of 5 mg L⁻¹. To evaluate the effect of suspended inorganic sediments, we used natural seston and natural seston with the addition of two suspended sediment concentrations: 1) 20 mg L⁻¹ (S and 20 mg of sediment per litre; S20); 2) 40 mg L⁻¹ (natural seston and 40 mg of sediment per litre; S40). These concentrations are within the range of the *in situ* concentrations recorded in Potter Cove (Pakhomov et al. 2003, Phillipps et al. 2011, Schloss et al. 2012, Sahade et al. 2015). The sediment added (<50 µm) in the experiments was obtained from the surface bottom sediments of the inner cove area (around 15 m depth, close to the mouth of the major creek), dried at 70°C and sieved through a 50 µm mesh, following Torre et al. (2012). Sediment OM content was gravimetrically estimated to correct subsequent calculations and to avoid biases in the estimation of trophic parameters.

Table 1: Details of the diet composition (food treatments) used in the feeding experiments and explanation of the abbreviations used. S, S20, S40, P were the primary diets offered to *Euphausia superba* and *Cnemidocarpa verrucosa*. FS, FS20, FS40, FP and FD were the secondary diets offered only to *C. verrucosa*.

Primary diets

S	Natural seston (running seawater pumped directly from the cove at 6 m depth)
S20	Natural seston with 20 mg L ⁻¹ of sediment added
S40	Seston with 40 mg L ⁻¹ of sediment added
P	Microalgae collected by towing of 50 µm net and diluted in GF/F filtered seawater

D Detritus of macroalgae collected with a 1 mm sieve from the sea surface, dried, crushed and sieved through a 50 µm mesh. Concentration: 5 mg L⁻¹ in GF/F filtered seawater

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Secondary diets

FS Faecal pellets of krill fed on seston diet (S). Concentration: 5 mg L⁻¹ of faecal pellets suspended in GF/F filtered seawater

FS20 Faecal pellets of krill fed on S20 diet. Concentration: 5 mg L⁻¹ of faecal pellets suspended in GF/F filtered seawater

FS40 Faecal pellets of krill fed on S40 diet. Concentration: 5 mg L⁻¹ of faecal pellets suspended in GF/F filtered seawater

FP Faecal pellets of krill fed on phytoplankton diet (P). Concentration: 5 mg L⁻¹ of faecal pellets suspended in GF/F filtered seawater

FD Faecal pellets of krill fed on macroalgae detritus diet (D). Concentration: 5 mg L⁻¹ of faecal pellets suspended in GF/F filtered seawater

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Secondary diets (only used to feed *C. verrucosa*) consisted of krill faeces obtained from krill fed on the same primary diets and sediment conditions described above. Hence, a total of five secondary diets were used to feed *C. verrucosa*: 1) faeces of krill obtained after animals fed on S (FS); 2) faeces of krill obtained after animals fed on S20 (FS20); 3) faeces of krill obtained after animals fed on S40 (FS40); 4) faeces of krill obtained after animals fed on P (FP); 5) faeces of krill obtained after animals fed on D (FD). Faeces from each condition were collected, dried and suspended in 0.1 µm filtered seawater at a final concentration of 5 mg L⁻¹.

Absorption Efficiency (AE). We estimated the AE of the organic fraction by means of the Conover ratio (Conover 1966), which assumes that only the organic component of the food is significantly affected by the digestive process. We calculated the AE as the difference of the ratio of mass loss after combustion of food and the corresponding percentage of mass loss after combustion of faeces, as follows:

$$AE = (F - E) / [(1 - E) * F]$$

where F is the organic fraction of the food and E the organic fraction of the faeces. AE values are reported as percentages.

To determine the organic fraction in food, at the beginning of each experiment (i.e.

each diet condition) we measured total suspended particulate matter (TSPM) concentration gravimetrically after filtering 0.25 – 2 L of aquaria seawater through combusted (500°C, 4.5 h) and pre-weighed 25 mm Whatman GF/F filters. After filtration, we rinsed filters twice with distilled water, dried them for 24 h at 60°C, and weighed them again to obtain the dry weight (DW) of the particles in the water samples. Filters were then burned at 500°C for 4.5 h to obtain ash weight of the sample, and by difference with the dry weight, the ash-free dry weight (AFDW). To estimate the organic fraction in the faeces, we used the same process as with the filters. In both cases, we measured the inorganic material directly as ash weight after ignition at 500°C, from which ash-free dry mass was estimated by subtraction from the dry weight values to determine the particulate organic matter (POM) and the particulate inorganic matter (PIM).

Faecal Production and Biodeposition Rates. We calculated the Faecal Production Rate (FPR) as the DW of faeces produced individual⁻¹ day⁻¹, while we also presented the data as the Mass-specific Faecal Production Rate (MSFPR), which was the mass of faeces produced day⁻¹ divided by the animal body mass (not including the tunica in the ascidians), for comparison purposes with previous studies (e.g. Tatián et al. 2008, Torre et al. 2012, 2014). For experiments conducted with krill, faeces were collected every 30 minutes during the first 6 h of incubation and hourly until 24 h incubation, following the protocol reported by Atkinson et al. (2012a). For experiments conducted with ascidians, we collected faeces every 24 h following the protocol of Tatián et al. (2008). After the experiments, we dried the organisms at 60°C, weighed them and then ignited them in a muffle furnace at 500°C for, 4.5 h, when they were weighed again. The organic fraction (AFDW) of each specimen was obtained from the difference between the ash weight after ignition and DW. When FPR was related to animal densities, we called this the Biodeposition Rate (BR).

Carbon Balance. To estimate the potential of *Cnemidocarpa verrucosa* as a C sink and its role in the PBC, we followed the approach of Coppari et al. (2014). Since ammonia excretion was not measured, the estimation of C balance is expected to be slightly elevated. The balanced C equation (without ammonium excretion) was considered as follows:

$$C_i = T + R + F$$

where C_i is the total C ingested (as a function of the filtration rate (FR) and the C content of the food: $FR \cdot C_{\text{food}}$), T is the production of somatic and reproductive tissues, R is the respiratory C loss, and F is the faeces C loss. Because the absorbed fraction (A) is the product of C_i and AE, T can be expressed as the difference between C absorbed from the food and C expenditure due to respiration ($T = A - R$). Hence T reflects the overall C balance and the values represent estimates of C gain or loss. Positive T values reflect the C which is available for biomass production (C sink potential) after meeting routine metabolic demands, whereas negative T values reflect an overall deficit of C.

Specific daily rates of filtration were calculated for each tested diet, based on the measurements of faecal pellet production by using the following relation:

$$FR = PR_{IF} / PIM = [FPR (1/E)] / PIM$$

where PR_{IF} is the inorganic fraction of Faecal Production Rate (FPR) and E is the organic content of faeces, as used in the Conover equation. This calculation (Iglesias et al. 1998) is correct on the only assumption that inorganic matter is a conservative tracer in the gut (no absorption of inorganics would occur). The oxygen consumption of *C. verrucosa* was obtained from published values for standard conditions (Kowalke et al. 2001) and after sediment exposure to increased sediment loads (Torre et al. 2012). All data were standardised to 1 g dry tissue weight. Oxygen consumption was converted to carbon dioxide production using the respiratory quotient ($RQ = CO_2 \text{ evolved} / O_2 \text{ consumed}$). We assumed the respiratory quotient (RQ) of 0.949 recommended for ammonotelic organisms as ascidians (Lampert 1984). In 3 water sample replicates (3 x 250 ml per replicate) collected at the beginning of the experiments for all treatments, we determined the C content of food (after removing calcium carbonate with hydrochloric acid) using a Carlo-Erba EA1108 analyser.

Known densities of *E. superba* (Fuentes 2006) and *C. verrucosa* for Potter Cove (Sahade et al. 1998, Lagger et al. 2017, 2018) and shelf areas of the WAP (Steinberg et al. 2015; Segelken-Voigt et al. 2016) were used to produce local scale estimates of the potential

biodeposition rates and C sinks.

Statistical analysis. We tested the normality of residuals using the Shapiro-Wilks test (Mahibbur Rahman and Govindarajulu 1997) and confirmed homoscedasticity by Levene's tests (Montgomery 1997). One-way ANOVA was employed to test the effects of the independent variables (primary and secondary diets) upon each separate trophic dependent variable (AE, FPR and MSFPR). The concentrations of S and P diets were uncontrolled, since both reflected the natural amounts in the local seawater. Moreover, those values may be related to the variables under study (especially for krill feeding). Thus, we used TSPM as a covariate. In the cases where the covariate was significant, we reported ANCOVA results. Finally, we performed one-way ANOVA to test differences in the carbon balance of *C. verrucosa* related to the different treatments. In all cases, when we encountered significant differences in ANOVA, we used the Tukey–Kramer method (Miller 1981) as a *post-hoc* test. All statistical analyses were performed using InfoStat v. 2016 (Di Rienzo et al. 2016).

RESULTS

Test Diets. The composition and concentration of the different treatments tested are summarized in Table 2. The initial TSPM of each treatment did not differ between experiments with krill or ascidians ($P > 0.05$), with the exception of the P treatment, which was higher in the case of ascidians (Table 2). However, the treatments showed differences between experiments with krill and ascidians in terms of initial PIM, POM and the organic fraction ($P < 0.001$). The organic component (POM) of S did not differ among krill and ascidian experiments ($F = 0.34$; $P = 0.5737$). Secondary diets (krill faeces) showed no difference in terms of initial TSPM nor PIM, but there was difference for the initial POM and for the organic fraction, f ($P < 0.001$). Food C content varied significantly among the different treatments (primary and secondary diets) for both species ($P < 0.0001$ in all cases, Table 2). The carbon to nitrogen ratio in primary diets was significantly higher for D ($P = 0.014$ for krill experiments, $P = 0.027$ for ascidian experiments), but no differences were observed for secondary diets ($F = 2.42$; $P = 0.081$).

Table 2. Composition and concentration of diet used in the feeding experiments conducted with *Euphausia superba* and *Cnemidocarpa verrucosa*. Values are given as mean $\pm$ standard deviation. TSPM: Total Particulate Matter (mg L^{-1}), PIM: particulate inorganic matter (mg L^{-1}), POM: particulate organic matter (mg L^{-1}), f : organic fraction (POM/TSPM), Chl a: chlorophyll a ($\mu\text{g L}^{-1}$), C:N: carbon and nitrogen ratio, POC: particulate organic carbon (mg L^{-1}).

Species	Diet	TSPM (mg L^{-1})	PIM (mg L^{-1})	POM (mg L^{-1})	f (POM/TSPM)	C:N	POC (mg L^{-1})
<i>E. superba</i>	S	2.39 $\pm$ 0.53	0.41 $\pm$ 0.20	1.98 $\pm$ 0.35	0.83 $\pm$ 0.07	6.2	0.26 $\pm$ 0.19
	S20	22.30 $\pm$ 1.60	15.16 $\pm$ 1.11	7.14 $\pm$ 0.48	0.32 $\pm$ 0.03	6.1	1.14 $\pm$ 1.08
	S40	42.80 $\pm$ 2.30	33.38 $\pm$ 1.77	9.42 $\pm$ 0.50	0.22 $\pm$ 0.01	6.4	1.12 $\pm$ 0.56
	P	5.81 $\pm$ 1.27	2.50 $\pm$ 1.05	3.31 $\pm$ 0.58	0.57 $\pm$ 0.02	6.3	1.56 $\pm$ 0.60
	D	4.72 $\pm$ 0.39	1.65 $\pm$ 0.56	3.07 $\pm$ 0.30	0.65 $\pm$ 0.10	7.6	0.94 $\pm$ 0.23
<i>C. verrucosa</i>	S	2.64 $\pm$ 0.94	1.00 $\pm$ 0.55	1.64 $\pm$ 0.65	0.62 $\pm$ 0.12	5.0	0.09 $\pm$ 0.03
	S20	21.44 $\pm$ 1.59	17.37 $\pm$ 1.61	4.07 $\pm$ 0.14	0.19 $\pm$ 0.02	5.7	0.50 $\pm$ 0.05
	S40	39.92 $\pm$ 1.06	32.73 $\pm$ 7.74	7.19 $\pm$ 1.36	0.18 $\pm$ 0.02	6.5	0.63 $\pm$ 0.10
	P	17.73 $\pm$ 3.48	10.29 $\pm$ 3.14	7.44 $\pm$ 0.72	0.42 $\pm$ 0.08	nd	nd
	D	4.93 $\pm$ 0.43	2.91 $\pm$ 0.33	2.02 $\pm$ 0.56	0.41 $\pm$ 0.08	6.8	1.07 $\pm$ 0.38
<i>C. verrucosa</i>	FS	4.93 $\pm$ 0.77	3.50 $\pm$ 0.64	1.430 $\pm$ 0.28	0.29 $\pm$ 0.05	8.8	0.23 $\pm$ 0.05
	FS20	4.69 $\pm$ 0.34	3.80 $\pm$ 0.38	0.891 $\pm$ 0.09	0.19 $\pm$ 0.02	8.0	0.17 $\pm$ 0.04
	FS40	4.67 $\pm$ 0.17	3.92 $\pm$ 0.25	0.75 $\pm$ 0.09	0.16 $\pm$ 0.02	6.7	0.16 $\pm$ 0.04
	FP	4.74 $\pm$ 0.21	3.46 $\pm$ 0.12	1.280 $\pm$ 0.14	0.27 $\pm$ 0.02	7.2	0.11 $\pm$ 0.02
	FD	4.71 $\pm$ 0.26	3.39 $\pm$ 0.20	1.32 $\pm$ 0.13	0.28 $\pm$ 0.02	7.8	0.11 $\pm$ 0.01

Absorption Efficiency (AE). The mean AE was higher for S in both species

(*Euphausia superba*: 88.29% $\pm$ 0.04; *Cnemidocarpa verrucosa*: 86.05% $\pm$ 0.07), reaching about 60% for the sediment-free primary diets (P and D); however, these were not significantly different ($P > 0.05$) (Fig. 2a, b). When S was compared to S20 and S40, the addition of sediment caused a 75% drop in AE in both species. Sediment concentration was inversely related to krill AE and differed significantly among the three tested concentrations (S, S20, S40) ($F = 27.85$, $P < 0.0001$) (Fig. 2a); the fall in AE was greater for S40 than for

S20 ($P < 0.05$; $15.75\% \pm 3.62$ and $21.44\% \pm 15.27$, respectively). The same response was observed for *C. verrucosa* ($F = 9.17$, $P = 0.0045$), where its AE was reduced to $23.83\% \pm 12.44$ and $15.12\% \pm 7.42$ in the S20 and S40 treatments respectively. However, no differences ($P > 0.05$) were detected between these two concentrations (Fig. 2b). For *C. verrucosa* fed on secondary diets, the maximum mean AE ($52.6\% \pm 5.91$) was recorded in the FD diet ($F = 6.60$; $P = 0.0015$), while the lowest mean AE ($21.97\% \pm 16.19$) corresponded to the FS40 diet (Fig. 2c). In the remaining secondary diets (FS, FS20, FP) there were no significant differences.

Faecal Production Rate. The mean FPR of *E. superba* did not differ between diets P ($2.9 \text{ mg.ind}^{-1}.\text{d}^{-1} \pm 1.2$) and D ($3.0 \text{ mg.ind}^{-1}.\text{d}^{-1} \pm 0.9$), but it was lower for S ($1.4 \text{ mg.ind}^{-1}.\text{d}^{-1} \pm 0.6$) ($F = 12.52$, $P < 0.0001$). Sediment concentration in diets S, S20 and S40 was positively related ($F = 82.75$, $P < 0.0001$) to mean FPR, with a higher production ($4.6 \text{ mg.ind}^{-1}.\text{d}^{-1} \pm 0.3$) feeding on S40 (Fig. 3a). The mean MSFPR of krill exhibited a trend similar to FPR (Fig. 3a) although no significant differences were detected among diets ($F = 1.26$, $P = 0.32$). Similarly in krill diets S, S20 and S40 did not produce any differences in MSFPR ($F = 2.45$, $P = 0.1279$).

Faecal Production Rates (FPR and MSFPR) of *C. verrucosa* were variable for both primary and secondary diets (Fig. 3b, c). For primary diets, the highest rates were recorded when animals were feeding on S (FPR: $F = 5.06$, $P = 0.0056$; MSFPR: $F = 4.63$, $P = 0.0082$) (Fig. 3b), while for secondary diets the highest rates were achieved under FP and FD diets (FPR: $F = 13.16$, $P < 0.0001$; MSFPR: $F = 8.73$, $P = 0.0003$) (Fig. 3c). Sediment addition was related negatively with the amount of faeces produced, and there were differences among all diets (S, S20, S40) (FPR: $F = 9.87$, $P = 0.0029$; MSFPR: $F = 7.22$, $P = 0.0088$). Sediment had no detectable effect among secondary diets FS, FS20 and FS40 (FPR: $F = 0.91$, $P = 0.4269$; MSFPR: $F = 0.17$, $P = 0.8463$).

Figure 2. Absorption Efficiency (AE) (expressed in % as mean $\pm$ standard error) under the different treatments (see Table 1 for abbreviations). **a** *Euphausia superba* feeding on primary diets. **b** *Cnemidocarpa verrucosa* feeding on primary diets. **c** *C. verrucosa* feeding on secondary diets (krill faecal pellets). Different letters on the top of the bars indicate significant differences ($P < 0.05$). Data of *E. superba* AE on diets S, S20 and S40 are redrawn from Fuentes et al. (2016).

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389 **Figure 3.** MassSpecific Faecal Production Rate (MSFR) expressed as $\text{mg faeces g} \cdot \text{ind}^{-1} \text{d}^{-1}$ 390 and Faecal Production Rate (FPR) expressed as $\text{mg faeces ind}^{-1} \text{d}^{-1}$. **a** *Euphausia superba*391 feeding on primary diets. **b** *Cnemidocarpa verrucosa* feeding on primary diets. **c** *C.*392 *verrucosa* feeding on secondary diets (krill faeces).

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Carbon Balance. Based on the C content of the experimental diets and the AE determined for *C. verrucosa*, maximum mean C absorption (*A*) was obtained for S ($11.69 \pm 8.75 \text{ mgC g}^{-1} \text{ d}^{-1}$) followed by D ($5.97 \pm 3.46 \text{ mgC g}^{-1} \text{ d}^{-1}$), being higher than the other primary diets ($F = 5.50$, $P = 0.0104$; Table 3). In contrast, for secondary diets, the highest mean *A* ($11.38 \pm 2.82 \text{ mgC g}^{-1} \text{ d}^{-1}$) was estimated for FD ($F = 19.86$, $P < 0.0001$; Table 3). Mean respiratory C loss (*R*) differed among primary diets ($F = 214.01$, $P < 0.0001$), and there was a negative effect of sediment addition. The highest sediment concentration (S40) generated the highest *R* ($67.68 \pm 6.76 \text{ mgC g}^{-1} \text{ d}^{-1}$), followed by the S20 diet where *R* was $55.43 \pm 8.08 \text{ mgC g}^{-1} \text{ d}^{-1}$. The remaining treatments had no detectable on *R* (Table 3), and *R* did not differ among secondary diets ($P = 0.24$).

Table 3. Estimated C ingested (C_i) (as a function of the filtration rate and the C content of the food), C absorbed (*A*) (the product of C_i and AE) and respiratory C loss (*R*) for *Cnemidocarpa verrucosa* ($\text{mgC.g}^{-1} \text{d}^{-1}$), considering the C content of the different diets. Values are expressed as mean $\pm$ standard deviation.

Primary diet	C_i	<i>A</i>	<i>R</i>
S	13.48 ± 9.61	11.69 ± 8.75	0.20 ± 0.03
S20	0.51 ± 0.19	0.12 ± 0.07	55.43 ± 9.78
S40	1.21 ± 0.44	0.16 ± 0.04	67.68 ± 8.18
P	nd	nd	nd
D	10.08 ± 6.34	5.97 ± 3.46	0.25 ± 0.05
Secondary diet	C_i	<i>A</i>	<i>R</i>
FS	2.74 ± 2.07	1.42 ± 1.42	0.21 ± 0.06
FS20	2.43 ± 1.89	0.62 ± 0.55	0.18 ± 0.05
FS40	2.38 ± 2.26	0.34 ± 0.22	0.24 ± 0.05
FP	11.83 ± 11.14	4.75 ± 4.09	0.19 ± 0.07
FD	21.86 ± 6.01	11.38 ± 2.82	0.21 ± 0.04

The overall C balance (*T*) after feeding on primary diets (Fig. 4) was positive for

413 animals feeding on S, and D, but there was a marked deficit under conditions where
 414 sediment was added (S20 and S40) ($F = 158.45$ $P < 0.0001$). The greatest C gain ($11.45 \pm$
 415 $8.76 \text{ mgC g}^{-1} \text{ d}^{-1}$) was estimated for *C. verrucosa* feeding on S while the largest C deficit ($-$
 416 $81.76 \pm 1.05 \text{ mgC g}^{-1} \text{ d}^{-1}$) was for individuals feeding in the highest sediment concentration
 417 (S40), although this was not different ($P > 0.05$) from S20 ($-66.98 \pm 0.39 \text{ mgC g}^{-1} \text{ d}^{-1}$).
 418 Secondary diets lead to positive T (Fig.4), although gains from FS20 and FS40 were almost
 419 negligible (0.41 ± 0.58 and 0.05 ± 0.22 , respectively). FD diet generated a C gain of $11.12 \pm$
 420 $2.79 \text{ mgC g}^{-1} \text{ d}^{-1}$ that was significantly higher than the remaining diets ($F = 20.41$, $P < 0.0001$)

Figure 4. Carbon Balance of *Cnemidocarpa verrucosa* relating absorbed and respired carbon from different diets. Results are expressed as mean and standard deviation.

Biodeposition Rate and ascidian C sink potential. BR for krill and *C. verrucosa*

(Tables 4 and 5 respectively), varied with population density at different sites and depths as well as the potential of ascidians to act as C sink (Fig. 5 and 6). The highest BR for krill identified here was in Potter Cove under a S40 diet ($1226.4 \pm 92.24 \text{ mg.m}^{-3}.\text{d}^{-1}$), and this decreased throughout the offshore sites where lower densities of krill were reported (Table 4). Also for *C. verrucosa*, the highest BR ($4199.47 \pm 2036.26 \text{ mg.m}^{-2}.\text{d}^{-1}$) was calculated to

occur where there were high densities of ascidians, such as those reported for a new ice-free area in the inner part of Potter Cove, but when feeding on the S diet (Table 5). For the same diet, high BR ($2755.9 \text{ mg.m}^{-2}.\text{d}^{-1} \pm 1136.29$) was calculated for Bransfield Strait, where high densities of *C. verrucosa* are also reported (Table 5). For secondary diets, the same trend was observed, but for the FP ($12285 \text{ mg.m}^{-2}.\text{d}^{-1} \pm 5365.17$) and FD ($18067 \text{ mg.m}^{-2}.\text{d}^{-1} \pm 5315.36$) diets (Table 5). Similarly, the potential of ascidians to act as a C sink varied with population density at different sites and depth in Potter Cove (Figure 5) and in Bransfield Strait (Fig. 6). The highest C sink potential was calculated to be in new ice-free areas in the inner part of Potter Cove (Fig. 5) followed by the Bransfield Strait (Fig. 6).

Table 4. Biodeposition Rate (BR, g.d^{-1}) for reported abundances of *Euphausia superba* in Potter Cove and the Western Antarctic Peninsula. BR is expressed as mean $\pm$ standard deviation.

	POTTER COVE			WAP	
	2002	2003	Coast	Shelf	Slope
Abundance (ind.100 m^{-3})	264.1	3000	18.2	10.2	2
DIET					
S	0.37 $\pm$ 0.15	1044.17 $\pm$ 466.06	0.03 $\pm$ 0.01	0.01 $\pm$ 0.01	0.003 $\pm$ 0.00
S20	0.71 $\pm$ 0.06	3396.40 $\pm$ 2645.29	0.05 $\pm$ 0.00	0.03 $\pm$ 0.00	0.01 $\pm$ 0.00
S40	1.23 $\pm$ 0.09	4646.51 $\pm$ 3639.44	0.08 $\pm$ 0.01	0.05 $\pm$ 0.00	0.01 $\pm$ 0.00
P	0.77 $\pm$ 0.31	2140.75 $\pm$ 711.01	0.053 $\pm$ 0.02	0.03 $\pm$ 0.01	0.01 $\pm$ 0.00
D	0.79 $\pm$ 0.24	5189.28 $\pm$ 6145.21	0.05 $\pm$ 0.02	0.03 $\pm$ 0.01	0.01 $\pm$ 0.00

Table 5. Biodeposition Rate (BR, $\text{mg.m}^{-2}.\text{d}^{-1}$) for reported abundances of *Cnemidocarpa verrucosa* at different depths in Potter Cove and Bransfield Strait. BR is expressed as mean $\pm$ standard deviation.

	POTTER COVE																BRANSFIELD STRAIT		
	E1				E2				E3				Island				Station I	Station II	Station III
Depth (m)	15	20	25	30	15	20	25	30	15	20	25	30	15	20	25	30	204	175	117
Abundances (ind.m ⁻²)	0.17	3.33	7.67	0	0	0	0	1.67	0	0	6.33	7.67	160	90	140	70	105	90	60
Primary Diets																			
S	0.004 $\pm$ 0.002	0.09 $\pm$ 0.04	0.20 $\pm$ 0.1	0.0	0.0	0.0	0.0	0.04 $\pm$ 0.02	0.0	0.0	0.17 $\pm$ 0.08	0.20 $\pm$ 0.10	4.20 $\pm$ 2.04	2.36 $\pm$ 1.15	3.67 $\pm$ 1.78	1.84 $\pm$ 0.89	2.76 $\pm$ 1.15	2.36 $\pm$ 0.76	1.57 $\pm$ 0.00
S20	0.001 $\pm$ 0.0002	0.01 $\pm$ 0.003	0.03 $\pm$ 0.01	0.0	0.0	0.0	0.0	0.01 $\pm$ 0.002	0.0	0.0	0.03 $\pm$ 0.01	0.03 $\pm$ 0.01	0.64 $\pm$ 0.15	0.36 $\pm$ 0.09	0.56 $\pm$ 0.13	0.28 $\pm$ 0.07	0.42 $\pm$ 0.10	0.36 $\pm$ 0.09	0.24 $\pm$ 0.06
S40	0.002 $\pm$ 0.001	0.04 $\pm$ 0.01	0.09 $\pm$ 0.03	0.0	0.0	0.0	0.0	0.02 $\pm$ 0.01	0.0	0.0	0.08 $\pm$ 0.03	0.09 $\pm$ 0.03	1.97 $\pm$ 0.72	1.11 $\pm$ 0.40	1.72 $\pm$ 0.63	0.86 $\pm$ 0.31	1.29 $\pm$ 0.47	1.11 $\pm$ 0.40	0.74 $\pm$ 0.27
P	0.002 $\pm$ 0.002	0.04 $\pm$ 0.03	0.10 $\pm$ 0.07	0.0	0.0	0.0	0.0	0.02 $\pm$ 0.02	0.0	0.0	0.08 $\pm$ 0.06	0.10 $\pm$ 0.07	2.02 $\pm$ 1.56	1.14 $\pm$ 0.88	1.77 $\pm$ 1.36	0.89 $\pm$ 0.68	1.33 $\pm$ 1.02	1.14 $\pm$ 0.88	0.76 $\pm$ 0.58
D	0.001 $\pm$ 0.001	0.03 $\pm$ 0.02	0.07 $\pm$ 0.05	0.0	0.0	0.0	0.0	0.02 $\pm$ 0.01	0.0	0.0	0.06 $\pm$ 0.05	0.07 $\pm$ 0.05	1.52 $\pm$ 1.14	0.86 $\pm$ 0.64	1.33 $\pm$ 1.00	0.67 $\pm$ 0.50	1.00 $\pm$ 0.75	0.86 $\pm$ 0.64	0.57 $\pm$ 0.43
Secondary Diets																			
FS	0.002 $\pm$ 0.01	0.04 $\pm$ 0.01	0.09 $\pm$ 0.02	0.0	0.0	0.0	0.0	0.02 $\pm$ 0.01	0.0	0.0	0.07 $\pm$ 0.02	0.09 $\pm$ 0.02	1.82 $\pm$ 0.51	1.02 $\pm$ 0.29	1.59 $\pm$ 0.45	0.80 $\pm$ 0.22	1.20 $\pm$ 0.34	1.02 $\pm$ 0.29	0.68 $\pm$ 0.19
FS20	0.004 $\pm$ 0.004	0.08 $\pm$ 0.08	0.19 $\pm$ 0.18	0.0	0.0	0.0	0.0	0.04 $\pm$ 0.04	0.0	0.0	0.15 $\pm$ 0.15	0.19 $\pm$ 0.18	3.90 $\pm$ 3.70	2.19 $\pm$ 2.08	3.41 $\pm$ 3.24	1.70 $\pm$ 1.62	2.56 $\pm$ 2.43	2.19 $\pm$ 2.08	1.46 $\pm$ 1.39
FS40	0.002 $\pm$ 0.003	0.04 $\pm$ 0.05	0.10 $\pm$ 0.12	0.0	0.0	0.0	0.0	0.02 $\pm$ 0.03	0.0	0.0	0.08 $\pm$ 0.10	0.10 $\pm$ 0.12	2.14 $\pm$ 2.55	1.20 $\pm$ 1.44	1.87 $\pm$ 2.23	0.94 $\pm$ 1.12	1.40 $\pm$ 1.68	1.20 $\pm$ 1.44	0.80 $\pm$ 0.96
FP	0.02 $\pm$ 0.01	0.39 $\pm$ 0.27	0.90 $\pm$ 0.63	0.0	0.0	0.0	0.0	0.20 $\pm$ 0.14	0.0	0.0	0.74 $\pm$ 0.52	0.90 $\pm$ 0.63	18.72 $\pm$ 13.16	10.53 $\pm$ 7.40	16.38 $\pm$ 11.51	8.19 $\pm$ 5.76	12.29 $\pm$ 8.64	10.53 $\pm$ 7.40	7.02 $\pm$ 4.93
FD	0.03 $\pm$ 0.08	0.57 $\pm$ 0.17	1.32 $\pm$ 0.39	0.0	0.0	0.0	0.0	0.29 $\pm$ 0.08	0.0	0.0	1.09 $\pm$ 0.32	1.32 $\pm$ 0.29	27.53 $\pm$ 8.10	15.49 $\pm$ 4.56	24.09 $\pm$ 7.09	12.04 $\pm$ 3.54	18.07 $\pm$ 5.32	15.49 $\pm$ 4.56	10.32 $\pm$ 3.04

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Figure 5. Estimated Carbon Balance of *Cnemidocarpa verrucosa* relating absorbed and respired carbon from different diets. Results based on abundances reported for different stations and depths in Potter Cove, are expressed as $\text{gC.m}^{-2} \text{d}^{-1}$. Sampling stations: E1, E2, E3, Island. 15, 20, 25, 30 indicate the depth in meters.

Figure 6. Estimated Carbon Balance of *Cnemidocarpa verrucosa* relating absorbed and respired carbon from different diets. Results based on abundances reported for selected stations (I, II, III) in Bransfield Strait, are expressed as gC.m⁻² d⁻¹. Sampling stations: I (204 m), II (175 m), III (117 m).

DISCUSSION

PBC intensity is directly linked to depth (Buesseler et al. 2007), hence PBC plays a major role in shallow coastal areas, determining the production and biological structure of these ecosystems (Sañe et al. 2012, Smith et al. 2012). Biodeposition, mediated by pelagic and benthic suspension feeders (especially active filter feeders) is the most recognized biological process promoting PBC in shallow waters (Gili and Coma 1998, Turner et al. 2015), since it can result in local downward flux of OM exceeding that of passive physical sedimentation (Ahn 1993, Tatián et al. 2008). Our results show that this process is dependent not only on animal densities, but on its interplay with species-specific AE and faecal production. For instance, a high AE leads to low OM in faeces, but this could be compensated by a high production of faeces due either to high animal specific production or high biodeposition, just because of high animal density.

Both studied species feed on POM that varies with shifts in coastal Antarctic environmental conditions. Because the direction of such change is unknown, we selected the most likely particles based on gut content observations performed in previous studies (for

krill: Schmidt et al. 2012, Fuentes et al. 2016; for ascidians: Tatián et al. 2004) and the composition of particulate matter collected in sediment traps (Alurralde 2018). Furthermore, we considered similar potential food sources for *E. superba* and *C. verrucosa*, since Potter Cove is a shallow fjord where the water column is generally well mixed (Schloss et al. 2002). Both target species displayed the expected high AE when fed primary diets free of sediment (Clarke et al. 1988, Tatián et al. 2008), in accordance with their omnivore or opportunistic feeding mode. Although krill AE varied among diets, this was not statistically significant, which was also reported in previous studies (Atkinson et al. 2012a). The AE of *C. verrucosa* did not differ among sediment free primary diets but values were higher than in previous reports (Tatián et al. 2002, 2008). Several studies in filter feeding species suggest that AE is strongly dependent upon food quality (Tito de Moraes and Fiala-Médioni 1985, Navarro and Thompson 1996, Gardner and Thompson 2001), and is particularly linked to the ratio of organic to inorganic matter (Gardner 2000, Armsworthy et al. 2001). The variability observed in AE estimations is therefore in line with expectations, since Potter Cove exhibits considerable temporal and spatial variability in seston composition and organic to inorganic ratios of particulate matter (Schloss et al. 1999, 2012, Alurralde 2018). When fed on the macroalgal detritus diet, AE seems to be lower and two ascidian species, *C. verrucosa* and *Pyura setosa*, are reported to be able to use up to 40% of the organic content of macroalgal detritus (Tatián et al. 2008). In those experiments, Tatián et al. (2008) used a diet principally based on two *Desmarestia* species that could have been unpalatable for ascidians (Amsler et al. 2005). Macroalgal detritus can represent an important food source only after entry into the detrital pathway (Norderhaug et al. 2003). However, recent studies show that material derived from species in the order Demarestiales constitute only a minor food source, because they have a high content of phlorotannins (Iken et al. 2007), which prevents microbial degradation (Goecke et al. 2010, Dubois and Iken 2012, Sosik and Simenstad 2013). In the present study, macroalgal detritus was collected directly from the water column by sieving it after resuspension events. Consequently, other macroalgae components may have been present and likely had experienced a longer degradation process than in previous

studies, which improved AE due to an enhanced palatability (Amsler et al. 2012) after mechanical breakdown and trophic upgrading by microbial activity (Quartino et al. 2015). Thus different macroalgal degradation states likely affect AE in ascidians.

Under high suspended sediment conditions, we observed that both target species reduced their AE while FPR and MSFPR responded differently in both species, probably as a result of two different mechanisms for maximizing energy acquisition from low quality food. Reduced AE has been previously reported for krill feeding in sediment-laden coastal waters of the WAP (Clarke et al. 1988, Fuentes et al. 2016). For *C. verrucosa*, it has been suggested that these ascidians could meet their energy demand (given a net year-round AE of 70%) even in the presence of sediments (Tatián et al. 2002). However, our results show that AE drops drastically (more than 50%) when *C. verrucosa* is subjected to high sediment loads. It seems likely that the high efficiencies reported by Tatián et al. (2002) are due to sediment concentrations that were up to eight times lower than those used in our experiments and lower than recorded values in the area for the last decade (Schloss et al. 2012, Monien et al. 2017).

The faecal production rates (FPR and MSFPR) and OM content of krill faeces were inversely related with AE as observed in wild conditions by Atkinson et al. (2012a). We observed low rates of faecal production in sediment-free diets, but these increased progressively with higher amounts of sediment (Fuentes et al. 2016). Probably, when the amount of organic material to be digested is reduced and much diluted with sediment, krill shorten their gut residence time for food which allows more space to process new food by increasing faecal production (Le Vay et al. 2001), and thus favouring enzyme kinetics with enough substrate to act (Jumars et al. 1989). Ingested food is macerate and crushed by the gastric mill, which is located inside the stomach, and mixed with digestive enzymes (Suh and Toda 1992, Suh 1996). It is then pressed through a fine filter system which allows fine food particles (0.2 μm) to enter the midgut, where they are further digested and nutrients are absorbed. Coarse food particles, together with small inorganic, can be transported directly to the hindgut (Ullrich et al. 1991, Fuentes et al. 2016). Most probably, krill can sort and

accumulate inorganic material inside the stomach (Fuentes et al. 2016) exposing smaller amounts of food to high enzyme activity (Mayzaud et al. 1985, Saborowski and Buchholz 1999, Saborowski 2012) maximizing the absorption of nutrients (Jumars 2000).

On the contrary, digestion in ascidians may be related inversely to the amount of refractory material in the food (Karasov and Douglas 2013), as highly digestible food would require less time to be hydrolysed and absorbed, with consequent higher rates of faecal production (Willows 1992, Jumars 2000). Seston is easily digested by benthic filter feeders, which typically consists of a mixture of phytoplankton, bacteria, protozoa, detritus and some inorganic particles (Hawkins et al. 1996, Gardner 2000). Our faecal production and AE results were slightly higher when *C. verrucosa* fed on natural seston than on the other sediment-free diets, suggesting that a diet mainly composed of P or D may impose some constraints on the digestive process, possibly due to a high content of refractory components. Some benthic filter feeders have been observed to decrease their AE when fed on certain species of phytoplankton (Ren et al. 2006) or when phytoplankton have a high content of refractory material (Fernández-Reiriz et al. 2015). Despite tunicates possess cellulase enzymes (Davison and Blaxter 2005), the refractory composition of the substrate attacked by digestive enzymes may alter the efficiency of the digestive process. Hence, the low faecal production rates observed for *C. verrucosa* fed on P, D or diets with high sediment concentrations (S20 and S40), may be the result of keeping food longer in the digestive tract to maximize AE, as has been already observed in other filtering organisms such as the cockle *Cerastoderma edule* (Navarro et al. 2009, Arambalza et al. 2014).

Studies using isotopic tracers in shallow coastal waters like Potter Cove, indicate that benthic diatoms and microphytobenthos represent important components of suspension feeders diet, including *C. verrucosa* (Pasotti et al. 2015, Ha et al. 2019), since they are available after detachment from benthic substrates and resuspension into the water column (Ahn et al. 1997, 2016). It has been recently stated (Ha et al. 2019) that benthic diatoms are the primary food sources for filter-feeders in shallow coastal Antarctic areas. However, the filter-feeder fauna from Potter Cove seems to rely on a detrital-pool food supply were faecal

pellets are included (Pasotti et al. 2015). Krill is thought to play a major role in the biodeposition process by transferring high amounts of OM to the benthos that can then feed on it, because krill faeces are a dominant component of the total organic flux up to at least 170 m depth (Gleiber et al. 2012). In shallow coastal waters (20-180 m depth), krill would be equally relevant as benthic diatoms, once high krill densities were reported for several areas in the WAP (Warren and Demer 2010, Steinberg et al. 2015, Belcher et al. 2016, 2017), and due to the high contribution (66.7–96.3%) of krill faecal pellets to the total particulate organic carbon (POC) flux, even at very shallow depths of 20-50 m (Isla et al. 2001, Belcher et al. 2016, 2017). Our results indicate that krill faeces are likely to be a valuable food source for the benthos, considering that *C. verrucosa* reached 25-50% AE values that varied with faecal sediment content. Although this is low compared with primary diets, an AE of 25-50% is still a high value compared to several ascidian species (Klumpp 1984, Tito de Moraes and Fiala-Medioni 1985, Armsworthy et al. 2001). Although, faecal pellets were not included so far in isotopes studies, we believe that they are an important secondary food source, equally available as benthic diatoms, since both have the same chance to be resuspended into the water column. Moreover, depending on the considered group of benthic diatoms (epilytic, epiphytic, epibionts, microphytobenthos, etc), to some extent faecal pellets would be easier to resuspend than diatoms since they tend to be loosely aggregated in the seafloor, while diatoms are able to attach to the surface where they grow (Al-Handal and Wulff 2008, Ahn et al 2016). Faecal pellets and macroalgal detritus were the major components (mean 91%) in gut contents year-round in *C. verrucosa* occurring at the inner part of Potter Cove, while diatoms were a low percentage (mean 4.5%) (Tatián et al. 2004). High mean annual krill abundance (from 264 to 3000 ind.100 m⁻³) has been estimated in Potter Cove, from net-towing samples (Fuentes 2006). The presence and relevance of krill in this shallow system is further suggested by the high occurrence in gut contents of *Notothenia coriiceps*, a dominant benthic fish in Potter Cove (Barrera-Oro and Casaux 1990) which feeds primarily on krill (Fanta et al. 2003), and also by frequent massive beaching of krill on the shoreline that has been observed for over a decade (Fuentes et al. 2016). Upscaling our experimental FPR to

the reported abundances by Fuentes (2006), we estimated a high potential input of krill faeces in Potter Cove (Table 4) which matches the high proportion of these particles collected in a four years (2012-2015) sediment traps study (Alurralde 2018). In that study, faecal pellets inputs to the sea floor were high but seasonally variable ($1.5 \cdot 10^3 - 7.53 \cdot 10^5 \text{ mm}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). It is interesting to note that the highest biodeposition calculated in the present study was for S40, and this, despite reducing krill AE, would result in a higher amount of OM carried in a larger volume of faeces. Therefore, our estimated FPR and the ability of *C. verrucosa* to feed on, highlight the role of krill in the pelagic-benthic coupling in Potter Cove.

The role of *Cnemidocarpa verrucosa* in the PBC and its potential as a C sink.

Estimates of C held in coastal waters along the WAP suggest that, in newly opened areas (ice-free), about 20 gC m^{-2} were accumulated through the development of benthic communities fuelled by new primary production (Peck et al. 2010). More recently, Barnes et al. (2018) argued that such estimation would be conservative and the immobilisation in coastal areas would be higher when iceberg calving is considered. In addition, strong links have been reported between suspended food and the abundance of sessile suspension feeders (Jansen et al. 2018a), where there is a strong increase in abundance close to glacier-influenced sites (Jansen et al 2018b).

Our estimates indicate a high C sink potential in new ice-free areas of Potter Cove and also in the Bransfield Strait, in case that ascidians receive a sediment-free, or low sediment content food supply. In such scenarios, our energy balance analyses indicate that *C. verrucosa* ingest more than the minimum C required to cover its energy demands ($0.24 \text{ mgC L}^{-1} \text{ d}^{-1}$) (Kowalke et al. 2001), perhaps explaining the high abundance of ascidians in Potter Cove (Sahade et al. 1998, Lager et al. 2017, 2018) and along the WAP (Segelken-Voigt et al. 2016). However, our results also indicate that this potential may be constrained by the effect of suspended sediments washed from the land. It is particularly interesting that high abundance of *C. verrucosa* (160 ind. m^{-2}) was observed in a new ice-free area of Potter Cove (Lager et al. 2017, 2018), close to the highest concentrations recorded of suspended sediments (Schloss et al. 2012, Monien et al. 2017). Under current summer sediment loads

in Potter Cove, *C. verrucosa* is able to actively respond to high sediment conditions whether performing squirting to expel inorganic material or closing their siphons while the exposure lasts (Torre et al. 2014). If the exposure persists, the oxygen consumption is triggered (Torre et al. 2012) inducing a high metabolic demand (Torre et al. 2014). This represents a high energy cost for *C. verrucosa* (Torre et al. 2012) and other ascidian species, exceeding what could be gained from a low-quality diet and a lower AE. According with our energy budget calculations, ascidians should not be successful in Potter Cove, because high sediment loads ultimately lead to a high C deficit, mediated by respiratory C loss that could scale up 200-fold, probably constraining animal growth (Robbins 1985, Petersen et al. 1995). However, these animals would shortly go through negative energy balance, when sediment loads are high in summer. The discharge and injection of sediments into the cove is strongly dependent upon meteorological control of glacial meltwater discharge linked to inter-annual climate variability driven by the Southern Annular Mode and the El Niño Southern Oscillation (Bers et al. 2013, Meredith et al. 2018). Sedimentation in Potter Cove is estimated to last 183 days during which average TSPM concentration is of 15 mg.l^{-1} , but episodic maximum peaks (up to $18\,000 \text{ mg.l}^{-1}$) are observed throughout the summer (Monien et al. 2017). On the other hand, the highest densities of *C. verrucosa* are reported on hard rocky substrate with steep slopes, what could also reduce sedimentation effects on suspension feeders, reaching less amounts of sediments per square metre compared with horizontal substrates (Lagger et al. 2018). This would not impair the OM supply which is lighter than inorganic material and can remain suspended for longer periods of time (Schloss et al. 1999). Hence, topographic and seasonal or interannual control on sediment injection would allow this species to get positive energy balances over time, and therefore be able to cope with high sediment loads. However, if this is not the case, it is possibly that this ascidian population will stand until a threshold limit has pushed the system to another stage where ascidians will not be dominant (Sahade et al. 2015).

Although these calculations are approximate, the estimated C sink potential stands as a first attempt at quantifying the functional role of ascidians in Antarctic waters. Peck (2018)

highlighted that there have been very few energy budgets constructed for Antarctic marine species, and as he warns, some limitations and biases should be pointed out. In our energy budget, we were unable to directly measure filtration and respiration rates, and values were therefore computed from FPR and taken from the literature, respectively. Respiration were constrained to rates calculated for a seston diet (Kowalke et al. 2001) or sediment concentrations similar to those used in this study (Torre et al. 2012), but these rates were referred to body weight excluding the tunic. The tunic organic content certainly represents a significant part of the ascidian biomass (49.54 ± 3.49 % in our study) and while our C sink potential would be underestimated, growth of body parts is much faster than the tunic growth (Petersen et al. 1995). Similarly, mucus production could be a relevant source of bias. It has been only exceptionally considered in ascidians (Goddard and Hogget, 1982), but in some species, such as gastropod molluscs, the losses to mucus can be 30% or more (Peck et al. 1997). Also, interannual variation in animal ecology and physiology might introduce other potential biases in our carbon energy balance (Petersen et al. 1995). In addition, diet (Fernández-Reiriz et al. 2015, Souster et al. 2018), temperature (Klumpp 1984, Jiang et al. 2008) and ascidian size (Jiang et al. 2008, Souster et al. 2018) have all been documented to alter ascidian filtration and respiration rates, biasing the potential C sink (Coppari et al. 2014) estimated here for *C. verrucosa*. Moreover, this potential is likely to also vary throughout the year (particularly in winter), as many Antarctic marine benthic species have lower winter resting metabolic requirements in response to a range of factors including temperature (Brockington and Clarke 2001, Peck 2018), reduced food supplies (Fraser et al. 2002, Auer et al. 2015) and reproductive investment (e.g. Grange et al. 2007). Although *C. verrucosa* reproduces during winter (Sahade et al. 2004), the species seems capable of feeding throughout the year even when food availability is low (Tatián et al. 2002, Lesser and Slattery 2015), as has also been observed in some other benthic suspension feeders, both in shallow coastal areas (Barnes and Clarke 1995, Ducklow et al. 2001) and in deeper areas of the Antarctic shelf (Orejas et al. 2000, Gili et al. 2001).

Future perspectives. PBC is usually examined in terms of nutrient exchange and

OM sedimentation (Buesseler et al. 2007). The variability of biological processes, however, is rarely assessed, which precludes an understanding of the whole system. Several biological processes are inherently species-specific and contribute to shaping ecosystem functioning (Barnes and Sands 2017). There are large gaps in our understanding of the response to climate-driven changes in the nearshore WAP, due to the complex interplay of negative and positive feedbacks that act simultaneously. The conceptual model outlined for Potter Cove (Fig. 7) illustrates the complex response of trophic processes involved in the PBC to changes in suspended particle composition envisaged to be some of the major consequences of climate change. Current climate conditions in the WAP are the primary cause of changes in TSPM and environmental settings. Ice retreat allows for both new areas for plankton production and new seabed available for benthic colonisation. Species-specific trophic ecology and the characteristics of the TSPM (composition and OM proportion) will determine the interplay between the intake of energy (high or low AE) and the rate of faecal production. The AE will determine the OM in faeces (the higher the AE, the lower the OM), but the net transfer of OM to the seabed will be modulated by the amount of faeces produced combined with the AE, which in turn will be determined by food processing (FPR and MSFPR) on the seabed and the density of the species involved. At the same time, food availability and the AE will regulate the energy balance of the species, determining energy uptake from the available food. Despite the many possible combinations of responses, when food supply has low sediment loads or consists of krill faeces, the overall energy balance for ascidians is positive. However, the melting of the land-terminating glacier in Potter Cove has increased the amount of sediment in the water column during summer, which has lowered the AE in both species studied, even if FPR and MSFPR are different. Lower AE's would result in a greater transfer of OM to the seabed and to sediments. For benthic animals such as ascidians, the ultimate effect would be to promote a highly negative energy balance that would eventually compromise the last benthic secondary production (somatic growth) and therefore C accumulation, if the exposure to suspended sediments becomes chronic.

699

700 **Figure 7.** A conceptual model of the trophic processes involved in the PBC and their
 701 response to alternative suspended particle composition scenarios driven by climate change.
 702 PBC promoted by biodeposition mediated by suspension feeders is regulated by the
 703 characteristics of the diet, which determine different digestive processing (absorption
 704 efficiency and faeces production) in different species, which will regulate the amount of OM
 705 transferred, and finally by the densities of the species considered. A free-sediment food
 706 provision (black boxes) can increase (violet arrow) or reduce (green arrow) the AE and the
 707 faeces production. A high AE will determine a low content of OM in the faeces (%OM) and

vice versa (blue lines). The net transfer of OM in the faeces will therefore be regulated by the species-specific production and the animal densities (dashed lines). Under high sediment conditions (red boxes), AE is negatively affected in all cases (red arrows) transferring more OM in the faeces, but faecal pellet production differs according to the species. Independently of free-sediment diets, the energy balance would be positive (black line) assuring the survival of suspension feeders and even promoting their increase (positive effect on the ecosystem). Conversely, the increase of suspended sediment leads to a very negative energy balance that would drastically affect the suspension feeder community (negative effect on the ecosystem).

Despite a generalised marine and glacier ice loss, a high potential for benthic carbon accumulation and immobilization has been estimated as a negative feedback to climate change (Peck et al. 2010, Barnes 2015, Barnes and Sands 2017). The results presented here generally support this view and we are confident that they are realistic and accurate for the system under study in summer. They emphasise that the role of suspension feeders in the flow of energy between the water column and the benthos is higher than previously thought. Disentangling the effects of different pressures on the species-mediated energy transfer between pelagic and benthic habitats is challenging, because our understanding of how particular mechanistic processes and pressures may be modulated by environmental drivers is still limited. Recent research suggests that, if warming of the WAP resume from the current hiatus (Turner et al. 2016, Etourneau et al. 2019) and extensive fjordic areas follow the same trend (retreating landward), it is likely that such systems will face similar conditions to those reported here (Meredith et al. 2018). We highlight in this work the importance of an integrated perspective for understanding how coastal ecosystems can respond to climate drivers through their effects on PBC.

Notation

A Absorbed fraction: the product of C_i and AE

736 **AE** Absorption Efficiency
 737 **BR** Biodeposition Rate
 738 **C** carbon
 739 **C_i** total C ingested
 740 **E** Organic fraction of the faeces
 741 **F** Organic fraction of the food
 742 **FPR** Faecal Production Rate
 743 **MSFPR** Mass-specific Faecal Production Rate
 744 **OM** Organic Matter
 745 **PBC** Pelagic-benthic coupling
 746 **PIM** Particulate Inorganic Matter
 747 **POM** Particulate Organic Matter
 748 **R** Respiratory C loss
 749 **T** Overall C balance
 750 **TSPM** Total Suspended Particulate Matter

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HIGHLIGHTS

Journal Pre-proof

- Food processing and energy acquisition was studied on two Antarctic filter-feeder species subjected to different food sources and sediment concentrations.
- A general energy model was developed to assess the energy balance of an ascidian and to evaluate its potential as a carbon sink in coastal Antarctic ecosystems.
- Food characteristics and animal densities modulate the impact of ascidians on pelagic-benthic coupling and on carbon immobilisation.
- Increasing inputs of sediment runoff would be a major constraint in coastal areas.

Journal Pre-proof