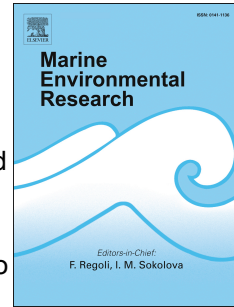# Journal Pre-proof

Role of suspension feeders in antarctic pelagic-benthic coupling: Trophic ecology and potential carbon sinks under climate change

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1 **Role of suspension feeders in Antarctic pelagic-benthic coupling: trophic ecology and**

2 **potential carbon sinks under Climate Change**

3

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18

19 ***This research is an important contribution to previously unquantified aspects***

20 ***of the effects of climate change in species-mediated energy transfer between pelagic***

21 ***and benthic Antarctic coastal areas.***

27

28

29 **HIGHLIGHTS**

30 − Food processing and energy acquisition was studied on two Antarctic filter-feeder

31 species subjected to different food sources and sediment concentrations.

32 − A general energy model was developed to assess the energy balance of an ascidian

33 and to evaluate its potential as a carbon sink in coastal Antarctic ecosystems.

34 − Food characteristics and animal densities modulate the impact of ascidians on

35 pelagic-benthic coupling and on carbon immobilisation.

36 − Increasing inputs of sediment runoff would be a major constraint in coastal areas.

37

38 **ABSTRACT**

39 Sea-ice and coastal glacier loss in the Western Antarctic Peninsula open new ice-free areas.

40 They allowing primary production and providing new seabed for colonisation, both acting as

41 a negative feedback of climate change. However, the injection of sediment-laden runoff from

42 the melting of land-terminating glaciers may reduce this feedback. Changes in particulate

43 matter will affect nutrition and excretion (faeces stoichiometry and properties) of suspension

44 feeders, reshaping coastal carbon dynamics and pelagic-benthic coupling. Absorption

45 efficiency and biodeposition of *Euphausia superba* and *Cnemidocarpa verrucosa* were

46 quantified for different food treatments and varying sediment concentrations. Both species

47 showed high overall absorption efficiency for free-sediment diets, but were negatively

48 affected by sediment addition. High sediment conditions increased krill biodeposition, while it

49 decreased in ascidians. Energy balance estimation indicated high carbon sink potential in

50 ascidians, but it is modulated by food characteristics and negatively affected by sediment

51 inputs in the water column.

52

55

56 **INTRODUCTION**

57   While the rapid temperature increase in the Antarctic Peninsula seems to be paused

58   since the late 1990s due to a short-term natural climate variability (Turner et al. 2016),

59   evident impact of climate change is observed in the West Antarctic Peninsula (WAP) over the

60   cryosphere (Rückamp et al. 2011, Cook et al. 2014, Gutt et al. 2015), the continental shelf

61   and in particular the coastal area (Meredith and King 2005, Cook et al. 2016). Furthermore,

62   climate model projections indicate that a large anthropogenic regional warming signal is likely

63   to result in substantial warming across the Peninsula over the 21st century (Bracegirdle et al.

64   2008, Etourneau et al. 2019).

65   The loss of ice shelves and the retreat of coastal glaciers in Antarctica over recent

66   decades, have created around 2.4×10^4 km^2 of new open water, enhancing planktonic

67   primary production (Peck et al. 2010, Moreau et al. 2015, Jansen et al. 2018a), but also new

68   ice-free seabed areas prone to benthic colonisation (Bowden et al. 2006, Barnes et al. 2018,

69   Jansen et al. 2018b). For instance, in Potter Cove (King George Island/Isla 25 de Mayo),

70   high macroalgae and suspension feeder abundances have been reported in new ice-free

71   areas (Quartino et al. 2013, Lagger et al. 2017, 2018). Similarly, in the Mertz Glacier Tongue

72   (East Antarctic), there has been a large increase in suspension feeder abundance after

73   massive ice loss (Jansen et al. 2018b). Such new production (planktonic and benthic)

74   represents an important food source and an increase in energy and biomass for the whole

75   ecosystem (Barnes et al. 2018, Jansen et al. 2018a). Furthermore, a high potential carbon

76   (C) sink (blue carbon storage) could act as negative feedback to climate change due to water

77   column C drawdown (Peck et al. 2010, Quartino et al. 2013, Barnes 2015, Barnes et al.

78   2018). Indeed, benthic secondary production would be an important C sink, as it involves

79   long-term carbon storage in animal biomass (Rossi et al. 2012, Barnes 2015, Barnes et al.

80   2016).

81   Some WAP coastal areas are subjected to seasonal and sporadic injections of fresh

82   water loaded with sediments due to melting of marine-terminating glaciers (Klöser et al.

83   1994, Monien et al. 2017, Meredith et al. 2018). In these areas phytoplankton and

84   macroalgae growth seem to be arrested via light-limitation (Dierssen et al. 2002, Schloss et

85 al. 2002, 2012, Quartino et al. 2013, Deregibus et al. 2016). Furthermore, low concentrations

86 of key nutrients and organic particulates occur when inorganic particle loads are high, which

87 constrains food supplies for planktonic and benthic suspension feeding species (Klöser et al.

88 1994, Pakhomov et al. 2003, Müller-Navarra 2008, Fuentes et al. 2016). A high

89 concentration of suspended sediments can also clog the filtering apparatus of these species,

90 which further constraints physiological performance (Torre et al. 2012, 2014) and can even

91 lead to massive mortality events (Pakhomov et al. 2003, Fuentes et al. 2016).

92   Suspension feeders are able to feed on a wide spectrum of food particle types and

93 sizes (Riisgård and Larsen 2010). Through their trophic activity (ingestion and faecal

94 production) these animals play a major role in pelagic-benthic coupling (PBC) and in the flow

95 of C through marine shallow ecosystems, modulating the cycling of nutrients and moving C

96 from the pelagic to the benthic realm and vice versa (Gili and Coma 1998). Sediment trap

97 studies in shallow nearshore waters (5-25 m depth) indicate that faecal pellets from krill and

98 other mesozooplanktonic consumers are important components of the organic matter (OM)

99 flux (Schloss et al. 1999, Isla et al 2001, Alurralde 2018). Antarctic krill (*Euphausia superba*)

100 is a key planktonic suspension feeder occurring in the Southern Ocean (Siegel 2016). High

101 densities are frequent in the coastal areas of the WAP (Atkinson et al. 2009, Warren and

102 Demer 2010, Steinberg et al. 2015, Belcher et al. 2016, 2017), where 66.7–96.3% of total

103 particulate organic carbon (POC) flux in shallow waters (20-180 m depth), is represented by

104 krill faeces (Isla et al. 2001, Belcher et al. 2016, 2017). In Potter Cove, krill annual

105 abundances can be as high as ~3.000 ind.100 m^{-3} (Fuentes 2006), which promote high but

106 seasonally variable inputs of faecal pellets (1.5 10^3 -7.53 10^5 mm^3.m^{-2}.d^{-1}) sinking to the

107 seafloor (Alurralde 2018). This enable benthic suspension feeders such as hydrozoans,

108 corals, glass sponges and ascidians to feed directly on them and benefit from their organic

109 contents (Orejas et al. 2000, Duineveld et al. 2004, Leys et al. 2004, Tatián et al. 2004). This

110 functional group is the dominant component of the Southern Ocean shelf benthos (Gili et al.

111 2006, Gutt et al. 2013) and in contrast to the Arctic, nearshore biomass and diversity in fjords

112 is much higher than the offshore sites (Grange and Smith 2013). Suspension feeders not

113   only enhance PBC in shallow waters (Ahn 1993, Tatián et al. 2004), but also develop

114   complex three-dimensional biogenic structures particularly on soft bottoms (Tatián et al.

115   1998, Gili et al. 2006), where epibiosis is a common phenomenon especially over solitary

116   ascidians (Rimondino et al. 2015). Solitary and compound ascidians comprise dominant

117   representatives of Antarctic epifaunal macrobenthic communities on the shelf (Gutt et al.

118   2013, Segelken-Voigt et al. 2016), fjords and coastal areas (Grange and Smith 2013, Moon

119   et al. 2015, Sahade et al. 2015, Lagger et al. 2018). In new ice-free areas of the WAP

120   ascidians reach the higher abundances (Lagger et al. 2017, 2018), which could increase

121   retention of a greater share of the productivity in their living structures for decades (Kowalke

122   et al. 2001). Nevertheless, these organisms of apparently great C sink potential in shallow

123   waters (Petersen and Riisgård 1992, Coppari et al. 2014) are generally neglected in the

124   overall equation of C circulation in our changing world (Rossi et al. 2015).

125   The abundance and distribution of benthic suspension feeders depend on the quality

126   of available food sources (Gardner 2000, Rossi et al. 2015, Jansen et al. 2018a,b). The

127   degree to which the quantity and composition of accessible food meets the consumer's

128   nutritional needs defines food quality (Müller-Navarra, 2008), while the characteristics of the

129   diet define the way in which the digestion process takes place in suspension feeders (*e.g.*

130   Jørgensen 1996, Mayer et al. 1997, Hawkins et al. 1998). Only part of the ingested food is

131   absorbed (i.e., transported across the gut wall); the rest is expelled as faeces. A fraction of

132   the absorbed food is diverted to growth and reproduction, while another fraction is used to

133   maintain resting metabolism. If the energy expended in resting metabolism is lower than the

134   energy gained through digestion, organisms are in a position of net energy gain, thus

135   enabling biomass production that immobilises C in somatic tissues. But if absorption is low, a

136   higher proportion of OM would be transferred to the seabed through faeces that will be

137   remineralised by microbial activity and hence released back into the water column later

138   (Claquin et al. 2010, Mermillod-Blondin 2014), buried in the sediments and/or consumed by

139   detritivores, a process known as biodeposition (Ahn et al. 1993, Tatián et al. 2008,

140   Mermillod-Blondin 2014). Consequently, the quantification of uptake efficiency for different

141 food sources and of biodeposition are essential to assess energy flows through benthic and

142 pelagic ecosystems.

143   Predicted changes in the properties of suspended particulate matter along the WAP

144 (Montes-Hugo et al. 2009, Schofield et al. 2010) are expected to have profound implications

145 for the trophic processes of suspension feeders, such as energy uptake (Robbins 1985,

146 Wotton and Malmqvist 2001, Atkinson et al. 2012a), which will ultimately impact their net

147 energy balance. The ecological consequences may be dramatic since the WAP supports a

148 high abundance of both planktonic (Atkinson et al. 2012b, Puigcorbé et al. 2016) and benthic

149 (Gutt et al. 2013) suspension feeders, and these species are the food supply to the

150 scavengers and carnivores that form the rest of the benthic food web. Furthermore, faecal

151 production may be affected by alterations in the rate, stoichiometry and properties of pellets

152 (Ragueneau et al. 2005, Gergs et al. 2009), with cascade effects on ecosystem functioning

153 (Claquin et al. 2010, Alcaraz et al. 2014, Coello-Camba et al. 2017). In the same way, high

154 sediment inputs in marine coastal areas could drastically impact suspension feeders

155 (Fuentes et al. 2016, Sahade et al. 2015), limiting blue carbon storage ecosystem services

156 as it occurs with ice scour disturbance (Barnes 2017, Barnes et al. 2018).

157   In the present study, we first examined the absorption efficiency (AE) and

158 biodeposition of *E. superba* and *C. verrucosa* subjected to different food conditions (diet

159 composition and sediment concentrations). These abundant and conspicuous filter feeders

160 are able to sieve particles from the water in a wide range of sizes (0.06 μm to >100 μm),

161 overlapping with other suspension feeders (Riisgård and Larsen 2010, Suh and Nemoto

162 1987) making them good representatives of the suspension feeder guild. By means of a

163 general energy budget, we assessed the energy balance of *C. verrucosa* under those food

164 conditions to evaluate its potential as a C sink and the consequences of alternative food

165 scenarios (i.e. phytoplankton- or macroalgal detritus-dominated seston, and increased

166 suspended sediment concentration). Finally krill was considered in its role of food provider

167 for benthic communities throughout biodeposition. To this end, we included krill faeces as

168 food source for ascidians.

169

170   **METHODS**

171   **Study area.** Experiments were conducted at the Argentinean-German Dallmann

172   Laboratory in the Argentinean Antarctic station Carlini (former Jubany) next to the study area

173   in Potter Cove (62º 14' S, 58º 40' W), in King George Island (25 de Mayo), South Shetland

174   Islands. The cove (Fig. 1), which is surrounded by the Fourcade Glacier on its north and east

175   sides, is 4 km long and 2.5 km wide (Al-Handal and Wulff, 2008) with a maximum depth of

176   100 m. During the summer, melt water creeks carry large amounts of sediment from the

177   land-terminating glacier (average maximum 284 mg L^{-1}), which are discharged into the cove

178   by several creeks (Monien et al. 2017). A comprehensive description of the coastal

179   ecosystem of Potter Cove can be found in Wiencke et al. (2008), and the hydrographical

180   characteristics and environmental conditions for the last two decades are reported by

181   Schloss et al. (2012) and Meredith et al. (2018).
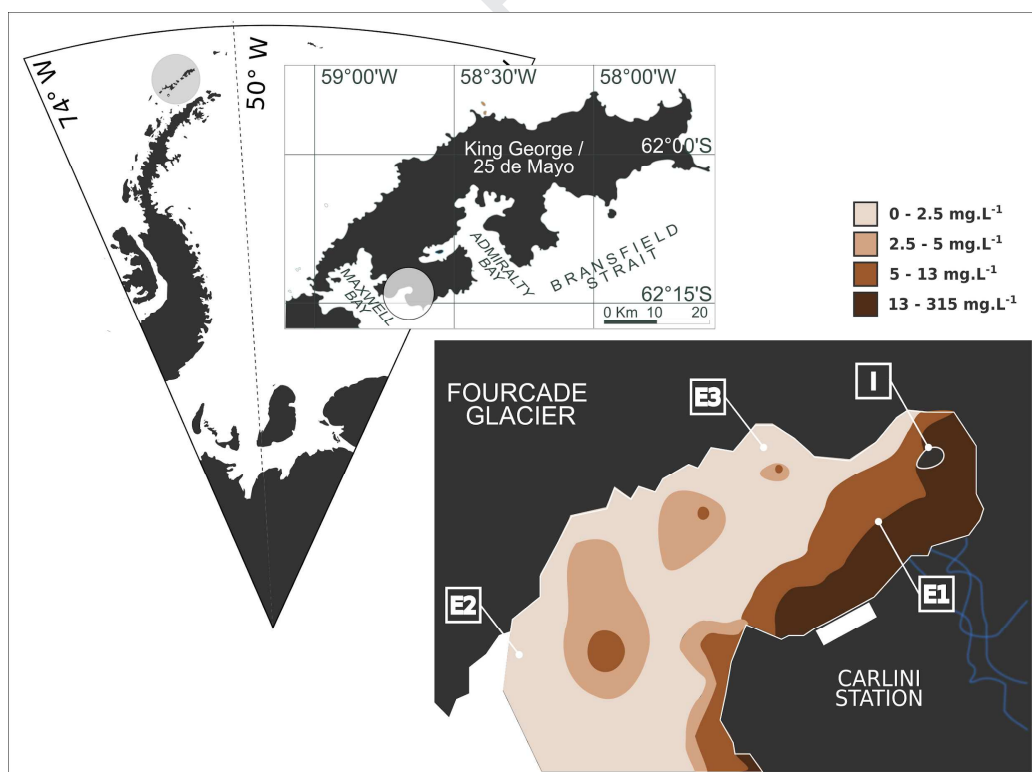
182

183

184   **Figure 1.** Location of Potter Cove, King George/25 de Mayo Island, South Shetland

185   Islands, Antarctica. Average spatial distribution of total suspended particulate matter (TSPM)

186   concentration in the surface waters of Potter Cove during summer 2010/2011 (based on

187   Figure 5a, Monien et al. 2017). E1, E2, E3, indicate the sampling stations mentioned by

188   Sahade et al. 1998 and I, the ice-free area (Island) mentioned by Lagger et al. 2018.

189

190   **Target species and collection.** During the summers of 2012/2013 and 2013/2014,

191   we collected juvenile and adult *E. superba* from the outer part of Potter Cove using a 200 μm

192   mesh Nansen net with a 2 L cod end, towed vertically and obliquely (40 m below the

193   surface). The contents of the cod end were immediately transferred to a 50 L plastic bucket

194   filled with cooled (0°C) filtered seawater and then taken directly to a cool room (0 ± 1°C),

195   where the animals were placed in a 100 L container (further details in Fuentes et al. (2016)).

196   Specimens of *C. verrucosa* were collected by SCUBA divers between 20 - 30 m depth in the

197   inner part of Potter Cove (Fig. 1). Sampled individuals were immediately transported to the

198   station aquaria in a 50 L plastic bucket filled with cooled (0 ± 1°C) seawater and

199   subsequently placed in a 100 L container after cleaning their tunics from large epibionts.

200   Both species were kept in an open flow system with natural seawater (0 ± 1°C) directly

201   pumped from the cove for at least 10 days for acclimation (Torre et al. 2012, 2014). Prior to

202   the experiments, krill specimens were starved for 48 h and ascidians for 5 days in filtered

203   seawater (0.1 μm) to allow the specimens to empty their stomachs.

204   **Experimental setup.** For both species, we used six independent cylindrical 8-L

205   aquaria with individual closed circulation systems, placed in a 90 L running seawater bath for

206   the incubation experiments at constant temperatures (0 ± 1°C). We fitted a mesh (200 μm for

207   krill and 1 mm for ascidians) 10 cm above the bottom of each cylindrical aquarium, allowing

208   water to flow and avoiding the disaggregation of the faeces in the circulating system. For

209   each treatment (see below) we used one control and five replicates. For krill incubation, we

210   placed 12 juvenile krill specimens per aquarium (range size: 35-46 mm total length). For

211   ascidian incubation, we placed 1 individual per aquarium (range size: 8-12 cm high).

212   **Test Diets.** Two types of diet were used (Table 1). Primary diets consisted of: 1)

213   natural seston (S) present in surface seawater pumped directly from the cove; 2) natural

214 phytoplankton (P); 3) macroalgal detritus (D). Natural phytoplankton was collected by towing

215 a 70 µm mesh net horizontally in the outer part of the cove to ensure the predominance of

216 phytoplankton in the sample, which was transferred to a 60 L tank of 0.1 µm filtered

217 seawater. Macroalgal detritus was collected by sieving debris directly from the water column

218 on days following storms when there were significant amounts of resuspended detrital

219 deposits. Macroalgal detritus was dried at 60⁰C, ground and sieved through a 50 µm mesh

220 before being suspended in 0.1 µm filtered seawater at a final concentration of 5 mg L^{-1}. To

221 evaluate the effect of suspended inorganic sediments, we used natural seston and natural

222 seston with the addition of two suspended sediment concentrations: 1) 20 mg L^{-1} (S and 20

223 mg of sediment per litre; S20); 2) 40 mg L^{-1} (natural seston and 40 mg of sediment per litre;

224 S40). These concentrations are within the range of the *in situ* concentrations recorded in

225 Potter Cove (Pakhomov et al. 2003, Phillipps et al. 2011, Schloss et al. 2012, Sahade et al.

226 2015). The sediment added (<50 µm) in the experiments was obtained from the surface

227 bottom sediments of the inner cove area (around 15 m depth, close to the mouth of the major

228 creek), dried at 70°C and sieved through a 50 µm mesh, following Torre et al. (2012).

229 Sediment OM content was gravimetrically estimated to correct subsequent calculations and

230 to avoid biases in the estimation of trophic parameters.

231

232 **Table 1:** Details of the diet composition (food treatments) used in the feeding experiments

233 and explanation of the abbreviations used. S, S20, S40, P were the primary diets offered to

234 *Euphausia superba* and *Cnemidocarpa verrucosa*. FS, FS20, FS40, FP and FD were the

235 secondary diets offered only to *C. verrucosa*.

236

	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
	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

237

238

239   Secondary diets (only used to feed *C. verrucosa*) consisted of krill faeces obtained

240 from krill fed on the same primary diets and sediment conditions described above. Hence, a

241 total of five secondary diets were used to feed *C. verrucosa*: 1) faeces of krill obtained after

242 animals fed on S (FS); 2) faeces of krill obtained after animals fed on S20 (FS20); 3) faeces

243 of krill obtained after animals fed on S40 (FS40); 4) faeces of krill obtained after animals fed

244 on P (FP); 5) faeces of krill obtained after animals fed on D (FD). Faeces from each condition

245 were collected, dried and suspended in 0.1 µm filtered seawater at a final concentration of 5

246 mg L^{-1}.

247   **Absorption Efficiency (AE).** We estimated the AE of the organic fraction by means

248 of the Conover ratio (Conover 1966), which assumes that only the organic component of the

249 food is significantly affected by the digestive process. We calculated the AE as the difference

250 of the ratio of mass loss after combustion of food and the corresponding percentage of mass

251 loss after combustion of faeces, as follows:

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

253 where F is the organic fraction of the food and E the organic fraction of the faeces. AE values

254 are reported as percentages.

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

256 each diet condition) we measured total suspended particulate matter (TSPM) concentration

257 gravimetrically after filtering 0.25 – 2 L of aquaria seawater through combusted (500°C, 4.5

258 h) and pre-weighed 25 mm Whatman GF/F filters. After filtration, we rinsed filters twice with

259 distilled water, dried them for 24 h at 60°C, and weighed them again to obtain the dry weight

260 (DW) of the particles in the water samples. Filters were then burned at 500°C for 4.5 h to

261 obtain ash weight of the sample, and by difference with the dry weight, the ash-free dry

262 weight (AFDW). To estimate the organic fraction in the faeces, we used the same process as

263 with the filters. In both cases, we measured the inorganic material directly as ash weight after

264 ignition at 500°C, from which ash-free dry mass was estimated by subtraction from the dry

265 weight values to determine the particulate organic matter (POM) and the particulate inorganic

266 matter (PIM).

267 **Faecal Production and Biodeposition Rates.** We calculated the Faecal Production Rate

268 (FPR) as the DW of faeces produced individual^{-1} day^{-1}, while we also presented the data as

269 the Mass-specific Faecal Production Rate (MSFPR), which was the mass of faeces produced

270 day^{-1} divided by the animal body mass (not including the tunica in the ascidians), for

271 comparison purposes with previous studies (e.g. Tatián et al. 2008, Torre et al. 2012, 2014).

272 For experiments conducted with krill, faeces were collected every 30 minutes during the first

273 6 h of incubation and hourly until 24 h incubation, following the protocol reported by Atkinson

274 et al. (2012a). For experiments conducted with ascidians, we collected faeces every 24 h

275 following the protocol of Tatián et al. (2008). After the experiments, we dried the organisms

276 at 60ºC, weighed them and then ignited them in a muffle furnace at 500ºC for, 4.5 h, when

277 they were weighed again. The organic fraction (AFDW) of each specimen was obtained from

278 the difference between the ash weight after ignition and DW. When FPR was related to

279 animal densities, we called this the Biodeposition Rate (BR).

280   **Carbon Balance.** To estimate the potential of *Cnemidocarpa verrucosa* as a C sink

281 and its role in the PBC, we followed the approach of Coppari et al. (2014). Since ammonia

282 excretion was not measured, the estimation of C balance is expected to be slightly elevated.

283 The balanced C equation (without ammonium excretion) was considered as follows:

284 $$C_i = T + R + F$$

285   where C_i is the total C ingested (as a function of the filtration rate (FR) and the C

286 content of the food: $FR*C_{food}$), T is the production of somatic and reproductive tissues, R is

287 the respiratory C loss, and F is the faeces C loss. Because the absorbed fraction (A) is the

288 product of C_i and AE, T can be expressed as the difference between C absorbed from the

289 food and C expenditure due to respiration (**T= A - R**). Hence T reflects the overall C balance

290 and the values represent estimates of C gain or loss. Positive T values reflect the C which is

291 available for biomass production (C sink potential) after meeting routine metabolic demands,

292 whereas negative T values reflect an overall deficit of C.

293   Specific daily rates of filtration were calculated for each tested diet, based on the

294 measurements of faecal pellet production by using the following relation:

295 $$FR = PR_{IF} / PIM = [FPR (1/E)] / PIM$$

296   where PR_{IF} is the inorganic fraction of Faecal Production Rate (FPR) and E is the

297 organic content of faeces, as used in the Conover equation. This calculation (Iglesias et al.

298 1998) is correct on the only assumption that inorganic matter is a conservative tracer in the

299 gut (no absorption of inorganics would occur). The oxygen consumption of *C. verrucosa*

300 wasobtained from published values for standard conditions (Kowalke et al. 2001) and after

301 sediment exposure to increased sediment loads (Torre et al. 2012). All data were

302 standardised to 1 g dry tissue weight. Oxygen consumption was converted to carbon dioxide

303 production using the respiratory quotient ($RQ = CO_2$ evolved/O_2 consumed). We assumed

304 the respiratory quotient (RQ) of 0.949 recommended for ammonotelic organisms as

305 ascidians (Lampert 1984). In 3 water sample replicates (3 x 250 ml per replicate) collected at

306 the beginning of the experiments for all treatments, we determined the C content of food

307 (after removing calcium carbonate with hydrochloric acid) using a Carlo-Erba EA1108

308 analyser.

309   Known densities of *E. superba* (Fuentes 2006) and *C. verrucosa* for Potter Cove

310 (Sahade et al. 1998, Lagger et al. 2017, 2018) and shelf areas of the WAP (Steinberg et al.

311 2015; Segelken-Voigt et al. 2016) were used to produce local scale estimates of the potential

312   biodeposition rates and C sinks.

313   **Statistical analysis.** We tested the normality of residuals using the Shapiro-Wilks

314   test (Mahibbur Rahman and Govindarajulu 1997) and confirmed homoscedasticity by

315   Levene's tests (Montgomery 1997). One-way ANOVA was employed to test the effects of the

316   independent variables (primary and secondary diets) upon each separate trophic dependent

317   variable (AE, FPR and MSFPR). The concentrations of S and P diets were uncontrolled,

318   since both reflected the natural amounts in the local seawater. Moreover, those values may

319   be related to the variables under study (especially for krill feeding). Thus, we used TSPM as

320   a covariate. In the cases where the covariate was significant, we reported ANCOVA results.

321   Finally, we performed one-way ANOVA to test differences in the carbon balance of *C.*

322   *verrucosa* related to the different treatments. In all cases, when we encountered significant

323   differences in ANOVA, we used the Tukey–Kramer method (Miller 1981) as a *post-hoc* test.

324   All statistical analyses were performed using InfoStat v. 2016 (Di Rienzo et al. 2016).

325

326   **RESULTS**

327   **Test Diets.** The composition and concentration of the different treatments tested are

328   summarized in Table 2. The initial TSPM of each treatment did not differ between

329   experiments with krill or ascidians (P > 0.05), with the exception of the P treatment, which

330   was higher in the case of ascidians (Table 2). However, the treatments showed differences

331   between experiments with krill and ascidians in terms of initial PIM, POM and the organic

332   fraction (P < 0.001). The organic component (POM) of S did not differ among krill and

333   ascidian experiments (F = 0.34; P = 0.5737). Secondary diets (krill faeces) showed no

334   difference in terms of initial TSPM nor PIM, but there was difference for the initial POM and

335   for the organic fraction, *f* (P < 0.001). Food C content varied significantly among the different

336   treatments (primary and secondary diets) for both species (P < 0.0001 in all cases, Table 2).

337   The carbon to nitrogen ratio in primary diets was significantly higher for D (P = 0.014 for krill

338   experiments, P = 0.027 for ascidian experiments), but no differences were observed for

339   secondary diets (F = 2.42; P = 0.081).

340

341 **Table 2.** Composition and concentration of diet used in the feeding experiments conducted

342 with *Euphausia superba* and *Cnemidocarpa verrucosa*. Values are given as mean ± standard

343 deviation. TSPM: Total Particulate Matter (mg L^{-1}), PIM: particulate inorganic matter (mg L^{-1}),

344 POM: particulate organic matter (mg L^{-1}), f: organic fraction (POM/TSPM), Chl a: chlorophyll

345 a (µg L^{-1}), C:N: carbon and nitrogen ratio, POC: particulate organic carbon (mg L^{-1}).

346

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

347
348

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

350 (*Euphausia superba*: 88.29% ± 0.04; *Cnemidocarpa verrucosa*: 86.05% ± 0.07), reaching

351 about 60% for the sediment-free primary diets (P and D); however, these were not

352 significantly different (P > 0.05) (Fig. 2a, b). When S was compared to S20 and S40, the

353 addition of sediment caused a 75% drop in AE in both species. Sediment concentration was

354 inversely related to krill AE and differed significantly among the three tested concentrations

355 (S, S20, S40) (F = 27.85, P < 0.0001) (Fig. 2a); the fall in AE was greater for S40 than for

356   S20 ($P < 0.05$; 15.75% ± 3.62 and 21.44% ± 15.27, respectively). The same response was

357   observed for *C. verrucosa* (F = 9.17, P = 0.0045), where its AE was reduced to 23.83% ±

358   12.44 and 15.12% ± 7.42 in the S20 and S40 treatments respectively. However, no

359   differences ($P > 0.05$) were detected between these two concentrations (Fig. 2b). For *C.*

360   *verrucosa* fed on secondary diets, the maximum mean AE (52.6% ± 5.91) was recorded in

361   the FD diet (F = 6.60; P = 0.0015), while the lowest mean AE (21.97% ± 16.19)

362   corresponded to the FS40 diet (Fig. 2c). In the remaining secondary diets (FS, FS20, FP)

363   there were no significant differences.

364   **Faecal Production Rate.** The mean FPR of *E. superba* did not differ between diets P

365   (2.9 $mg.ind^{-1}.d^{-1}$ ± 1.2) and D (3.0 $mg.ind^{-1}.d^{-1}$ ± 0.9), but it was lower for S (1.4 $mg.ind^{-1}.d^{-1}$ ±

366   0.6) (F = 12.52, $P < 0.0001$). Sediment concentration in diets S, S20 and S40 was positively

367   related (F = 82.75, $P < 0.0001$) to mean FPR, with a higher production (4.6 $mg.ind^{-1}.d^{-1}$ ± 0.3)

368   feeding on S40 (Fig. 3a). The mean MSFPR of krill exhibited a trend similar to FPR (Fig. 3a)

369   although no significant differences were detected among diets (F = 1.26, P = 0.32). Similarly

370   in krill diets S, S20 and S40 did not produce any differences in MSFPR (F = 2.45, P =

371   0.1279).

372   Faecal Production Rates (FPR and MSFPR) of *C. verrucosa* were variable for both

373   primary and secondary diets (Fig. 3b, c). For primary diets, the highest rates were recorded

374   when animals were feeding on S (FPR: F = 5.06, P = 0.0056; MSFPR: F = 4.63, P = 0.0082)

375   (Fig. 3b), while for secondary diets the highest rates were achieved under FP and FD diets

376   (FPR: F = 13.16, $P < 0.0001$; MSFPR: F = 8.73, P = 0.0003) (Fig. 3c). Sediment addition was

377   related negatively with the amount of faeces produced, and there were differences among all

378   diets (S, S20, S40) (FPR: F = 9.87, P = 0.0029; MSFPR: F = 7.22, P = 0.0088). Sediment

379   had no detectable effect among secondary diets FS, FS20 and FS40 (FPR: F = 0.91, P =

380   0.4269; MSFPR: F = 0.17, P = 0.8463).

381
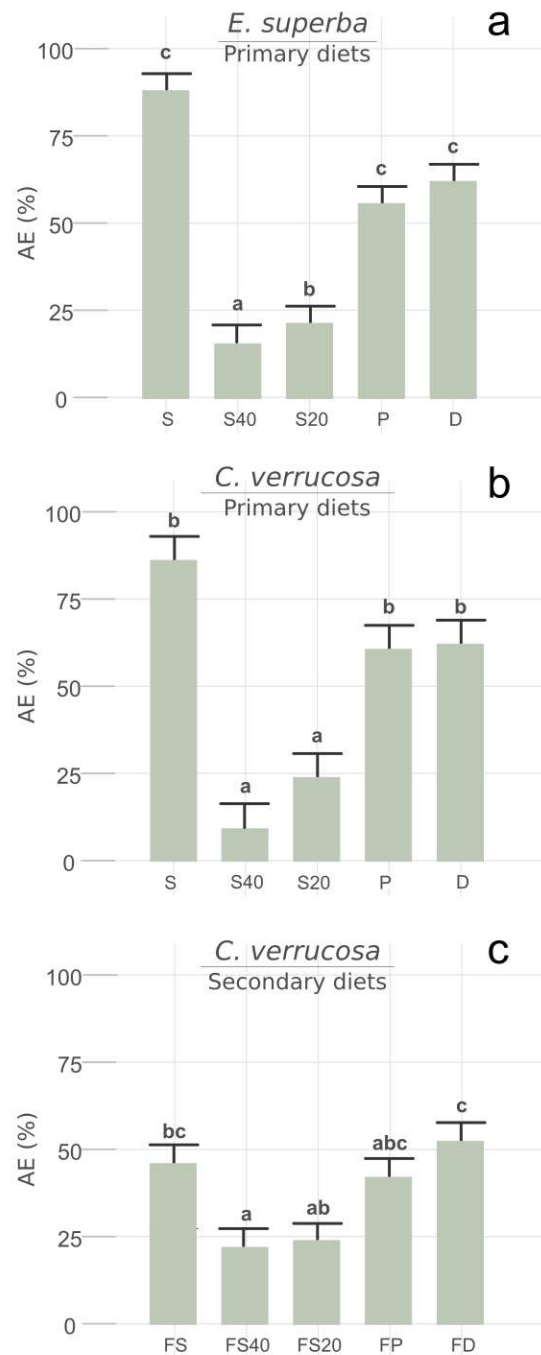
Figure 2. Absorption Efficiency (AE) (expressed in % as mean ± standard error) under the

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).
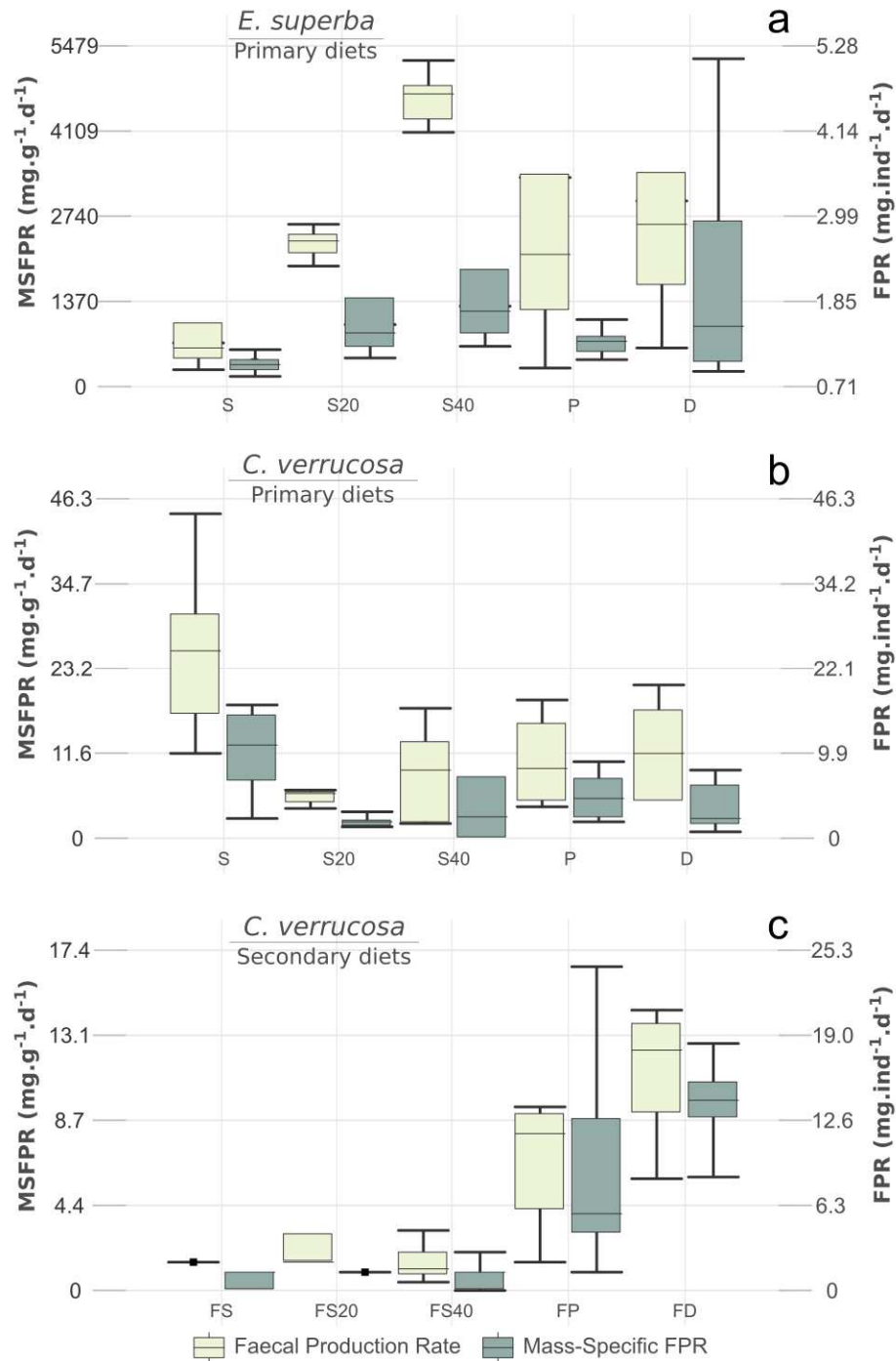
Figure 3. MassSpecific Faecal Production Rate (MSFR) expressed as mg faeces g.ind⁻¹ d⁻¹

and Faecal Production Rate (FPR) expressed as mg faeces ind⁻¹ d⁻¹. **a** *Euphausia superba*

feeding on primary diets. **b** *Cnemidocarpa verrucosa* feeding on primary diets. c *C.*

verrucosa feeding on secondary diets (krill faeces).

394   **Carbon Balance.** Based on the C content of the experimental diets and the AE

395 determined for *C. verrucosa,* maximum mean C absorption (*A*) was obtained for S (11.69±

396 8.75 mgC g^{-1} d^{-1}) followed by D (5.97±3.46 mgC g^{-1} d^{-1}), being higher than the other primary

397 diets (F = 5.50, P =0.0104; Table 3). In contrast, for secondary diets, the highest mean *A*

398 (11.38±2.82 mgC g^{-1}d^{-1}) was estimated for FD (F = 19.86, P < 0.0001; Table 3). Mean

399 respiratory C loss (*R*) differed among primary diets (F = 214.01, P < 0.0001), and there was

400 a negative effect of sediment addition. The highest sediment concentration (S40) generated

401 the highest *R* (67.68±6.76mgC g^{-1} d^{-1}), followed by the S20 diet where *R* was 55.43±8.08

402 mgC g^{-1} d^{-1}. The remaining treatments had no detectable on R (Table 3), and *R* did not differ

403 among secondary diets (P = 0.24).

404

405 **Table 3.** Estimated C ingested (C$_i$) (as a function of the filtration rate and the C content of the

406 food), C absorbed (A) (the product of C$_i$ and AE) and respiratory C loss (R) for

407 *Cnemidocarpa verrucosa* (mgC.g^{-1}d^{-1}), considering the C content of the different diets.

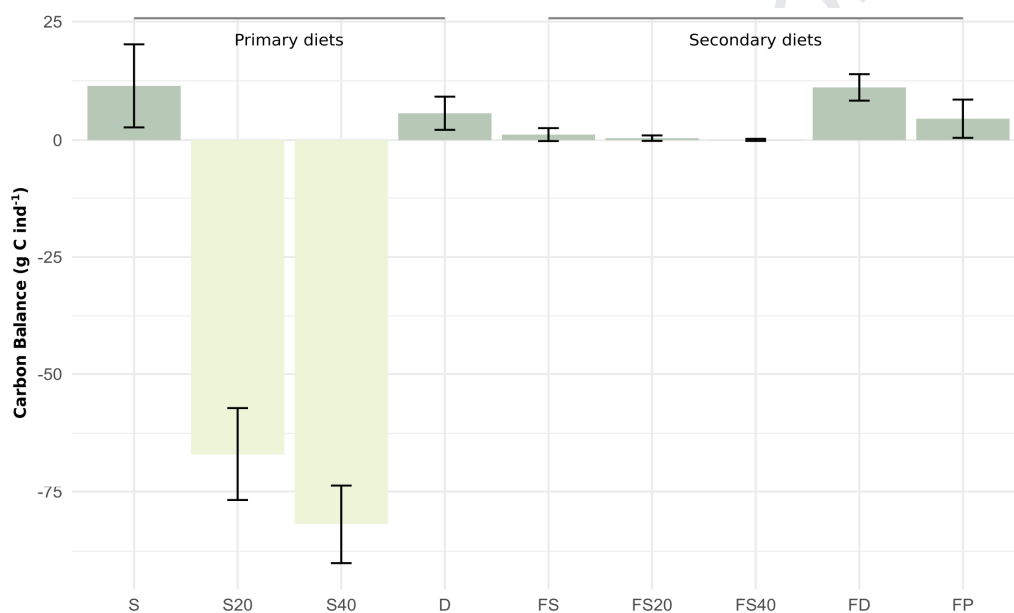408 Values are expressed as mean ± standard deviation.

409

Primary diet	C$_i$	A	R
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$_i$**	**A**	**R**
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

410

411

412   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 ±

415 8.76 mgC g^{-1} d^{-1}) was estimated for *C. verrucosa* feeding on S while the largest C deficit (-

416 81.76 ± 1.05 mgC g^{-1} 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 ± 0.39 mgC g^{-1} 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 ±

420 2.79 mgC g^{-1} d^{-1} that was significantlly higher than the remaining diets (F =20.41, P < 0.0001)

421

422 **Figure 4.** Carbon Balance of *Cnemidocarpa verrucosa* relating absorbed and respired

423   carbon from different diets. Results are expressed as mean and standard deviation.

424

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

426 (Tables 4 and 5 respectively), varied with population density at different sites and depths as

427 well as the potential of ascidians to act as C sink (Fig. 5 and 6). The highest BR for krill

428 identified here was in Potter Cove under a S40 diet (1226.4 ± 92.24 mg.m^{-3}.d^{-1}), and this

429 decreased throughout the offshore sites where lower densities of krill were reported (Table

430 4). Also for *C. verrucosa*, the highest BR (4199.47 ± 2036.26 mg.m^{-2}.d^{-1}) was calculated to

431 occur where there were high densities of ascidians, such as those reported for a new ice-free

432 area in the inner part of Potter Cove, but when feeding on the S diet (Table 5). For the same

433 diet, high BR (2755.9 mg.m^{-2}.d^{-1} ± 1136.29) was calculated for Bransfield Strait, where high

434 densities of *C. verrucosa* are also reported (Table 5). For secondary diets, the same trend

435 was observed, but for the FP (12285 mg.m^{-2}.d^{-1} ± 5365.17) and FD (18067 mg.m^{-2}.d^{-1} ±

436 5315.36) diets (Table 5). Similarly, the potential of ascidians to act as a C sink varied with

437 population density at different sites and depth in Potter Cove (Figure 5) and in Bransfield

438 Strait (Fig. 6). The highest C sink potential was calculated to be in new ice-free areas in the

439 inner part of Potter Cove (Fig. 5) followed by the Bransfield Strait (Fig. 6).

440

441 **Table 4.** Biodeposition Rate (BR, g.d^{-1}) for reported abundances of *Euphausia superba* in

442 Potter Cove and the Western Antarctic Peninsula. BR is expressed as mean ± standard

443 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±0.15	1044.17±466.06	0.03±0.01	0.01±0.01	0.003±0.00
S20	0.71±0.06	3396.40±2645.29	0.05±0.00	0.03±0.00	0.01±0.00
S40	1.23±0.09	4646.51±3639.44	0.08±0.01	0.05±0.00	0.01±0.00
P	0.77±0.31	2140.75±711.01	0.053±0.02	0.03±0.01	0.01±0.00
D	0.79±0.24	5189.28±6145.21	0.05±0.02	0.03±0.01	0.01±0.00

Table 5. Biodeposition Rate (BR, mg.m^{-2}.d^{-1}) for reported abundances of *Cnemidocarpa verrucosa* at different depths in Potter Cove and Bransfield Strait. BR is expressed as mean ± 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± 0.002	0.09± 0.04	0.20± 0.1	0.0	0.0	0.0	0.0	0.04± 0.02	0.0	0.0	0.17± 0.08	0.20± 0.10	4.20± 2.04	2.36± 1.15	3.67± 1.78	1.84± 0.89	2.76± 1.15	2.36± 0.76	1.57± 0.00
S20	0.001± 0.0002	0.01± 0.003	0.03± 0.01	0.0	0.0	0.0	0.0	0.01± 0.002	0.0	0.0	0.03± 0.01	0.03± 0.01	0.64± 0.15	0.36± 0.09	0.56± 0.13	0.28± 0.07	0.42± 0.10	0.36± 0.09	0.24± 0.06
S40	0.002± 0.001	0.04± 0.01	0.09± 0.03	0.0	0.0	0.0	0.0	0.02± 0.01	0.0	0.0	0.08± 0.03	0.09± 0.03	1.97± 0.72	1.11± 0.40	1.72± 0.63	0.86± 0.31	1.29± 0.47	1.11± 0.40	0.74± 0.27
P	0.002± 0.002	0.04± 0.03	0.10± 0.07	0.0	0.0	0.0	0.0	0.02± 0.02	0.0	0.0	0.08± 0.06	0.10± 0.07	2.02± 1.56	1.14± 0.88	1.77± 1.36	0.89± 0.68	1.33± 1.02	1.14± 0.88	0.76± 0.58
D	0.001± 0.001	0.03± 0.02	0.07± 0.05	0.0	0.0	0.0	0.0	0.02± 0.01	0.0	0.0	0.06± 0.05	0.07± 0.05	1.52± 1.14	0.86± 0.64	1.33± 1.00	0.67± 0.50	1.00± 0.75	0.86± 0.64	0.57± 0.43
Secondary Diets																			
FS	0.002± 0.01	0.04± 0.01	0.09± 0.02	0.0	0.0	0.0	0.0	0.02± 0.01	0.0	0.0	0.07± 0.02	0.09± 0.02	1.82± 0.51	1.02± 0.29	1.59± 0.45	0.80± 0.22	1.20± 0.34	1.02± 0.29	0.68± 0.19
FS20	0.004± 0.004	0.08± 0.08	0.19± 0.18	0.0	0.0	0.0	0.0	0.04± 0.04	0.0	0.0	0.15± 0.15	0.19± 0.18	3.90± 3.70	2.19± 2.08	3.41± 3.24	1.70± 1.62	2.56± 2.43	2.19± 2.08	1.46± 1.39
FS40	0.002± 0.003	0.04± 0.05	0.10± 0.12	0.0	0.0	0.0	0.0	0.02± 0.03	0.0	0.0	0.08± 0.10	0.10± 0.12	2.14± 2.55	1.20± 1.44	1.87± 2.23	0.94± 1.12	1.40± 1.68	1.20± 1.44	0.80± 0.96
FP	0.02± 0.01	0.39± 0.27	0.90± 0.63	0.0	0.0	0.0	0.0	0.20± 0.14	0.0	0.0	0.74± 0.52	0.90± 0.63	18.72± 13.16	10.53± 7.40	16.38± 11.51	8.19± 5.76	12.29± 8.64	10.53± 7.40	7.02± 4.93
FD	0.03± 0.08	0.57± 0.17	1.32± 0.39	0.0	0.0	0.0	0.0	0.29± 0.08	0.0	0.0	1.09± 0.32	1.32± 0.29	27.53± 8.10	15.49± 4.56	24.09± 7.09	12.04± 3.54	18.07± 5.32	15.49± 4.56	10.32± 3.04

448
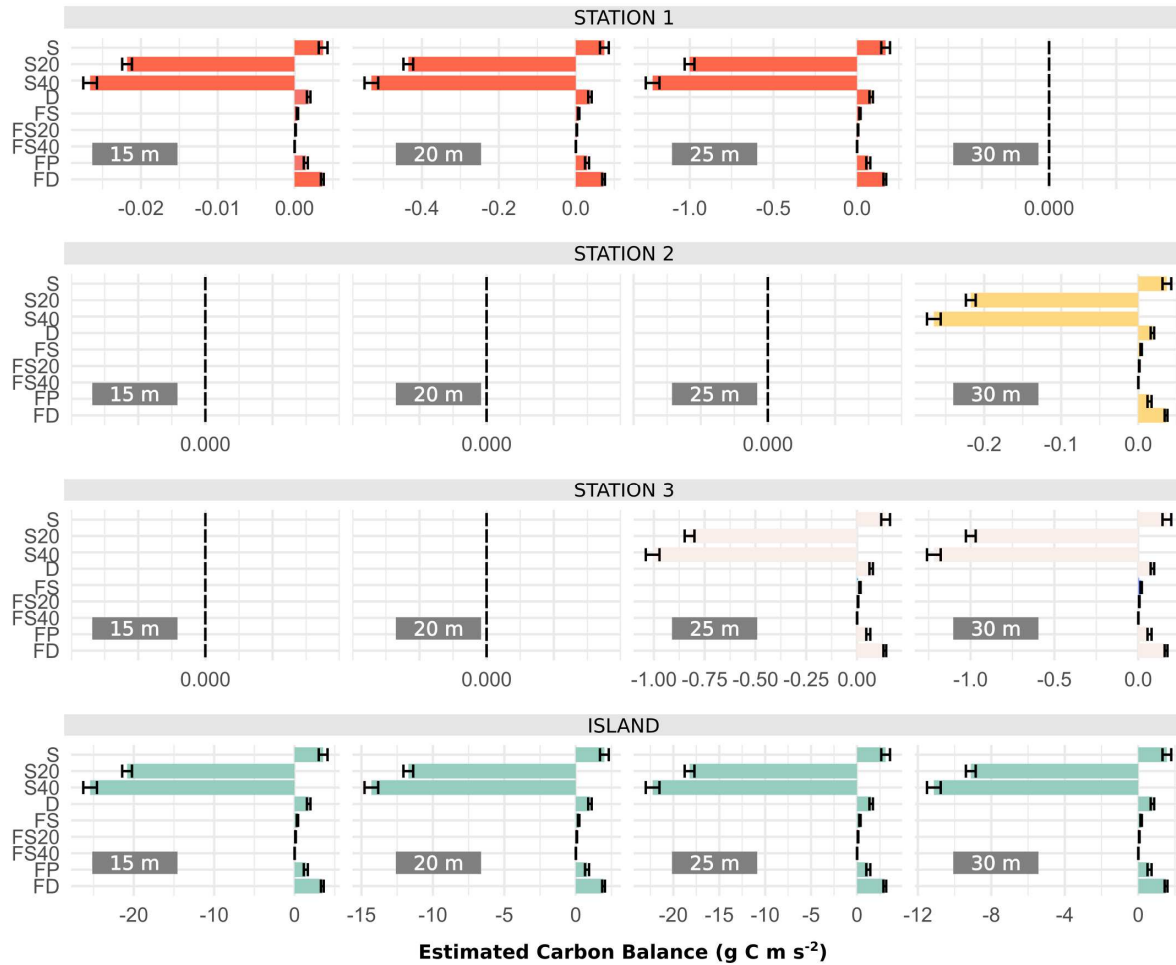
Figure 5. Estimated Carbon Balance of *Cnemidocarpa verrucosa* relating absorbed and respired carbon from different diets. Results based on abundances reported for different stations and depths in Potter Cove, are expressed as gC.m^{-2} d^{-1}. Sampling stations: E1, E2, E3, Island. 15, 20, 25, 30 indicate the depth in meters.
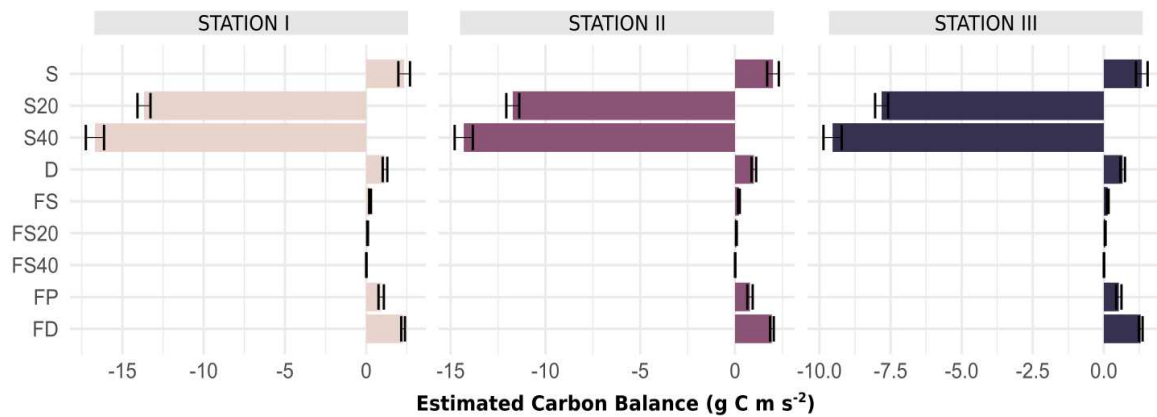
454

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).

459

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

475   krill: Schmidt et al. 2012, Fuentes et al. 2016; for ascidians: Tatián et al. 2004) and the

476   composition of particulate matter collected in sediment traps (Alurralde 2018). Furthermore,

477   we considered similar potential food sources for *E. superba* and *C. verrucosa*, since Potter

478   Cove is a shallow fjord where the water column is generally well mixed (Schloss et al. 2002).

479   Both target species displayed the expected high AE when fed primary diets free of sediment

480   (Clarke et al. 1988, Tatián et al. 2008), in accordance with their omnivore or opportunistic

481   feeding mode. Although krill AE varied among diets, this was not statistically significant,

482   which was also reported in previous studies (Atkinson et al. 2012a). The AE of *C. verrucosa*

483   did not differ among sediment free primary diets but values were higher than in previous

484   reports (Tatián et al. 2002, 2008). Several studies in filter feeding species suggest that AE is

485   strongly dependent upon food quality (Tito de Morais and Fiala-Médioni 1985, Navarro and

486   Thompson 1996, Gardner and Thompson 2001), and is particularly linked to the ratio of

487   organic to inorganic matter (Gardner 2000, Armsworthy et al. 2001). The variability observed

488   in AE estimations is therefore in line with expectations, since Potter Cove exhibits

489   considerable temporal and spatial variability in seston composition and organic to inorganic

490   ratios of particulate matter (Schloss et al. 1999, 2012, Alurralde 2018). When fed on the

491   macroalgal detritus diet, AE seems to be lower and two ascidian species, *C. verrucosa* and

492   *Pyura setosa,* are reported to be able to use up to 40% of the organic content of macroalgal

493   detritus (Tatián et al. 2008). In those experiments, Tatián et al. (2008) used a diet principally

494   based on two *Desmarestia* species that could have been unpalatable for ascidians (Amsler

495   et al. 2005). Macroalgal detritus can represent an important food source only after entry into

496   the detrital pathway (Norderhaug et al. 2003). However, recent studies show that material

497   derived from species in the order Demarestiales constitute only a minor food source,

498   because they have a high content of phlorotannins (Iken et al. 2007), which prevents

499   microbial degradation (Goecke et al. 2010, Dubois and Iken 2012, Sosik and Simenstad

500   2013). In the present study, macroalgal detritus was collected directly from the water column

501   by sieving it after resuspension events. Consequently, other macroalgae components may

502   had been present and likely had experienced a longer degradation process than in previous

503 studies, which improved AE due to an enhanced palatability (Amsler et al. 2012) after

504 mechanical breakdown and trophic upgrading by microbial activity (Quartino et al. 2015).

505 Thus different macroalgal degradation states likely affect AE in ascidians.

506   Under high suspended sediment conditions, we observed that both target species

507 reduced their AE while FPR and MSFPR responded differently in both species, probably as a

508 result of two different mechanisms for maximizing energy acquisition from low quality food.

509 Reduced AE has been previously reported for krill feeding in sediment-laden coastal waters

510 of the WAP (Clarke et al. 1988, Fuentes et al. 2016). For *C. verrucosa*, it has been

511 suggested that these ascidians could meet their energy demand (given a net year-round AE

512 of 70%) even in the presence of sediments (Tatián et al. 2002). However, our results show

513 that AE drops drastically (more than 50%) when *C. verrucosa* is subjected to high sediment

514 loads. It seems likely that the high efficiencies reported by Tatián et al. (2002) are due to

515 sediment concentrations that were up to eight times lower than those used in our

516 experiments and lower than recorded values in the area for the last decade (Schloss et al.

517 2012, Monien et al. 2017).

518   The faecal production rates (FPR and MSFPR) and OM content of krill faeces were

519 inversely related with AE as observed in wild conditions by Atkinson et al. (2012a). We

520 observed low rates of faecal production in sediment-free diets, but these increased

521 progressively with higher amounts of sediment (Fuentes et al. 2016). Probably, when the

522 amount of organic material to be digested is reduced and much diluted with sediment, krill

523 shorten their gut residence time for food which allows more space to process new food by

524 increasing faecal production (Le Vay et al. 2001), and thus favouring enzyme kinetics with

525 enough substrate to act (Jumars et al. 1989). Ingested food is macerate and crushed by the

526 gastric mill, which is located inside the stomach, and mixed with digestive enzymes (Suh and

527 Toda 1992, Suh 1996). It is then pressed through a fine filter system which allows fine food

528 particles (0.2 µm) to enter the midgut, where they are further digested and nutrients are

529 absorbed. Coarse food particles, together with small inorganic, can be transported directly to

530 the hindgut (Ullrich et al. 1991, Fuentes et al. 2016). Most probably, krill can sort and

531 accumulate inorganic material inside the stomach (Fuentes et al. 2016) exposing smaller

532 amounts of food to high enzyme activity (Mayzaud et al. 1985, Saborowski and Buchholz

533 1999, Saborowski 2012) maximizing the absorption of nutrients (Jumars 2000).

534   On the contrary, digestion in ascidians may be related inversely to the amount of

535 refractory material in the food (Karasov and Douglas 2013), as highly digestible food would

536 require less time to be hydrolysed and absorbed, with consequent higher rates of faecal

537 production (Willows 1992, Jumars 2000). Seston is easily digested by benthic filter feeders,

538 which typically consists of a mixture of phytoplankton, bacteria, protozoa, detritus and some

539 inorganic particles (Hawkins et al. 1996, Gardner 2000). Our faecal production and AE

540 results were slightly higher when *C. verrucosa* fed on natural seston than on the other

541 sediment–free diets, suggesting that a diet mainly composed of P or D may impose some

542 constraints on the digestive process, possibly due to a high content of refractory

543 components. Some benthic filter feeders have been observed to decrease their AE when fed

544 on certain species of phytoplankton (Ren et al. 2006) or when phytoplankton have a high

545 content of refractory material (Fernández-Reiriz et al. 2015). Despite tunicates possess

546 cellulase enzymes (Davison and Blaxter 2005), the refractory composition of the substrate

547 attacked by digestive enzymes may alter the efficiency of the digestive process. Hence, the

548 low faecal production rates observed for *C. verrucosa* fed on P, D or diets with high sediment

549 concentrations (S20 and S40), may be the result of keeping food longer in the digestive tract

550 to maximize AE, as has been already observed in other filtering organisms such as the

551 cockle *Cerastoderma edule* (Navarro et al. 2009, Arambalza et al. 2014).

552   Studies using isotopic tracers in shallow coastal waters like Potter Cove, indicate that

553 benthic diatoms and microphytobenthos represent important components of suspension

554 feeders diet, including *C. verrucosa* (Pasotti et al. 2015, Ha et al. 2019), since they are

555 available after detachment from benthic substrates and resuspension into the water column

556 (Ahn et al. 1997, 2016). It has been recently stated (Ha et al. 2019) that benthic diatoms are

557 the primary food sources for filter-feeders in shallow coastal Antarctic areas. However, the

558 filter-feeder fauna from Potter Cove seems to rely on a detrital-pool food supply were faecal

559   pellets are included (Pasotti et al. 2015). Krill is thought to play a major role in the

560   biodeposition process by transferring high amounts of OM to the benthos that can then feed

561   on it, because krill faeces are a dominant component of the total organic flux up to at least

562   170 m depth (Gleiber et al. 2012). In shallow coastal waters (20-180 m depth), krill would be

563   equally relevant as benthic diatoms, once high krill densities were reported for several areas

564   in the WAP (Warren and Demer 2010, Steinberg et al. 2015, Belcher et al. 2016, 2017), and

565   due to the high contribution (66.7–96.3%) of krill faecal pellets to the total particulate organic

566   carbon (POC) flux, even at very shallow depths of 20-50 m (Isla et al. 2001, Belcher et al.

567   2016, 2017). Our results indicate that krill faeces are likely to be a valuable food source for

568   the benthos, considering that *C. verrucosa* reached 25-50% AE values that varied with faecal

569   sediment content. Although this is low compared with primary diets, an AE of 25-50% is still a

570   high value compared to several ascidian species (Klumpp 1984, Tito de Morais and Fiala-

571   Medioni 1985, Armsworthy et al. 2001). Although, faecal pellets were not included so far in

572   isotopes studies, we believe that they are an important secondary food source, equally

573   available as benthic diatoms, since both have the same chance to be resuspended into the

574   water column. Moreover, depending on the considered group of benthic diatoms (epilytic,

575   epiphytic, epibionts, microphytobenthos, etc), to some extent faecal pellets would be easier

576   to resuspend than diatoms since they tend to be loosely aggregated in the seafloor, while

577   diatoms are able to attach to the surface where they grow (Al-Handal and Wulff 2008, Ahn et

578   al 2016). Faecal pellets and macroalgal detritus were the major components (mean 91%) in

579   gut contents year-round in *C. verrucosa* occurring at the inner part of Potter Cove, while

580   diatoms were a low percentage (mean 4.5%) (Tatián et al. 2004). High mean annual krill

581   abundance (from 264 to 3000 ind.100 m^{-3}) has been estimated in Potter Cove, from net-

582   towing samples (Fuentes 2006). The presence and relevance of krill in this shallow system is

583   further suggested by the high occurrence in gut contents of *Notothenia coriiceps*, a dominant

584   benthic fish in Potter Cove (Barrera-Oro and Casaux 1990) which feeds primarily on krill

585   (Fanta et al. 2003), and also by frequent massive beaching of krill on the shoreline that has

586   been observed for over a decade (Fuentes et al. 2016). Upscaling our experimental FPR to

587   the reported abundances by Fuentes (2006), we estimated a high potential input of krill

588   faeces in Potter Cove (Table 4) which matches the high proportion of these particles

589   collected in a four years (2012-2015) sediment traps study (Alurralde 2018). In that study,

590   faecal pellets inputs to the sea floor were high but seasonally variable ($1.5 \ 10^3$ - $7.53 \ 10^5$

591   $mm^3.m^{-2}.d^{-1}$). It is interesting to note that the highest biodeposition calculated in the present

592   study was for S40, and this, despite reducing krill AE, would result in a higher amount of OM

593   carried in a larger volume of faeces. Therefore, our estimated FPR and the ability of *C.*

594   *verrucosa* to feed on, highlight the role of krill in the pelagic-benthic coupling in Potter Cove.

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

596   Estimates of C held in coastal waters along the WAP suggest that, in newly opened areas

597   (ice-free), about 20 gC m^{-2} were accumulated through the development of benthic

598   communities fuelled by new primary production (Peck et al. 2010). More recently, Barnes et

599   al. (2018) argued that such estimation would be conservative and the immobilisation in

600   coastal areas would be higher when iceberg calving is considered. In addition, strong links

601   have been reported between suspended food and the abundance of sessile suspension

602   feeders (Jansen et al. 2018a), where there is a strong increase in abundance close to

603   glacier-influenced sites (Jansen et al 2018b).

604   Our estimates indicate a high C sink potential in new ice-free areas of Potter Cove

605   and also in the Bransfield Strait, in case that ascidians receive a sediment-free, or low

606   sediment content food supply. In such scenarios, our energy balance analyses indicate that

607   *C. verrucosa* ingest more than the minimum C required to cover its energy demands (0.24

608   mgC L^{-1} d^{-1}) (Kowalke et al. 2001), perhaps explaining the high abundance of ascidians in

609   Potter Cove (Sahade et al. 1998, Lagger et al. 2017, 2018) and along the WAP (Segelken-

610   Voigt et al. 2016). However, our results also indicate that this potential may be constrained

611   by the effect of suspended sediments washed from the land. It is particularly interesting that

612   high abundance of *C. verrucosa* (160 ind. m^{-2}) was observed in a new ice-free area of Potter

613   Cove (Lagger et al. 2017, 2018), close to the highest concentrations recorded of suspended

614   sediments (Schloss et al. 2012, Monien et al. 2017). Under current summer sediment loads

615 in Potter Cove, *C. verrucosa* is able to actively respond to high sediment conditions whether

616 performing squirting to expel inorganic material or closing their siphons while the exposure

617 lasts (Torre et al. 2014). If the exposure persist, the oxygen consumption is triggered (Torre

618 et al. 2012) inducing a high metabolic demand (Torre et al. 2014). This represents a high

619 energy cost for *C. verrucosa* (Torre et al. 2012) and other ascidian species, exceeding what

620 could be gained from a low-quality diet and a lower AE. According with our energy budget

621 calculations, ascidians should not be successful in Potter Cove, because high sediment

622 loads ultimately lead to a high C deficit, mediated by respiratory C loss that could scale up

623 200-fold, probably constraining animal growth (Robbins 1985, Petersen et al. 1995).

624 However, these animals would shortly go through negative energy balance, when sediment

625 loads are high in summer. The discharge and injection of sediments into the cove is strongly

626 dependent upon meteorological control of glacial meltwater discharge linked to inter-annual

627 climate variability driven by the Southern Annular Mode and the El Niño Southern Oscillation

628 (Bers et al. 2013, Meredith et al. 2018). Sedimentation in Potter Cove is estimated to last 183

629 days during which average TSPM concentration is of 15 mg.l^{-1}, but episodic maximum peaks

630 (up to 18 000 mg.l^{-1}) are observed throughout the summer (Monien et al. 2017). On the other

631 hand, the highest densities of *C. verrucosa* are reported on hard rocky substrate with steep

632 slopes, what could also reduce sedimentation effects on suspension feeders, reaching less

633 amounts of sediments per square metre compared with horizontal substrates (Lagger et al.

634 2018). This would not impairs the OM supply which is lighter than inorganic material and can

635 remain suspended for longer periods of time (Schloss et al. 1999). Hence, topographic and

636 seasonal or interannual control on sediment injection would allow this species to get positive

637 energy balances over time, and therefore be able to cope with high sediment loads.

638 However, if this is not the case, it is possibly that this ascidian population will stand until a

639 threshold limit has pushed the system to another stage where ascidians will not be dominant

640 (Sahade et al. 2015).

641   Although these calculations are approximate, the estimated C sink potential stands as

642 a first attempt at quantifying the functional role of ascidians in Antarctic waters. Peck (2018)

643   highlighted that there have been very few energy budgets constructed for Antarctic marine

644   species, and as he warns, some limitations and biases should be pointed out. In our energy

645   budget, we were unable to directly measure filtration and respiration rates, and values were

646   therefore computed from FPR and taken from the literature, respectively. Respiration were

647   constrained to rates calculated for a seston diet (Kowalke et al. 2001) or sediment

648   concentrations similar to those used in this study (Torre et al. 2012), but these rates were

649   referred to body weight excluding the tunic. The tunic organic content certainly represents a

650   significant part of the ascidian biomass (49.54±3.49 % in our study) and while our C sink

651   potential would be underestimated, growth of body parts is much faster than the tunic growth

652   (Petersen et al. 1995). Similarly, mucus production could be a relevant source of bias. It has

653   been only exceptionally considered in ascidians (Goddard and Hogget, 1982), but in some

654   species, such as gastropod molluscs, the losses to mucus can be 30% or more (Peck et al.

655   1997). Also, interannual variation in animal ecology and physiology might introduce other

656   potential biases in our carbon energy balance (Petersen et al. 1995). In addition, diet

657   (Fernández-Reiriz et al. 2015, Souster et al. 2018), temperature (Klumpp 1984, Jiang et al.

658   2008) and ascidian size (Jiang et al. 2008, Souster et al. 2018) have all been documented to

659   alter ascidian filtration and respiration rates, biasing the potential C sink (Coppari et al. 2014)

660   estimated here for *C. verrucosa*. Moreover, this potential is likely to also vary throughout the

661   year (particularly in winter), as many Antarctic marine benthic species have lower winter

662   resting metabolic requirements in response to a range of factors including temperature

663   (Brockington and Clarke 2001, Peck 2018), reduced food supplies (Fraser et al. 2002, Auer

664   et al. 2015) and reproductive investment (e.g. Grange et al. 2007). Although *C. verrucosa*

665   reproduces during winter (Sahade et al. 2004), the species seems capable of feeding

666   throughout the year even when food availability is low (Tatián et a. 2002, Lesser and Slattery

667   2015), as has also been observed in some other benthic suspension feeders, both in shallow

668   coastal areas (Barnes and Clarke 1995, Ducklow et al. 2001) and in deeper areas of the

669   Antarctic shelf (Orejas et al. 2000, Gili et al. 2001).

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

671   OM sedimentation (Buesseler et al. 2007). The variability of biological processes, however, is

672   rarely assessed, which precludes an understanding of the whole system. Several biological

673   processes are inherently species-specific and contribute to shaping ecosystem functioning

674   (Barnes and Sands 2017). There are large gaps in our understanding of the response to

675   climate-driven changes in the nearshore WAP, due to the complex interplay of negative and

676   positive feedbacks that act simultaneously. The conceptual model outlined for Potter Cove

677   (Fig. 7) illustrates the complex response of trophic processes involved in the PBC to changes

678   in suspended particle composition envisaged to be some of the major consequences of

679   climate change. Current climate conditions in the WAP are the primary cause of changes in

680   TSPM and environmental settings. Ice retreat allows for both new areas for plankton

681   production and new seabed available for benthic colonisation. Species-specific trophic

682   ecology and the characteristics of the TSPM (composition and OM proportion) will determine

683   the interplay between the intake of energy (high or low AE) and the rate of faecal production.

684   The AE will determine the OM in faeces (the higher the AE, the lower the OM), but the net

685   transfer of OM to the seabed will be modulated by the amount of faeces produced combined

686   with the AE, which in turn will be determined by food processing (FPR and MSFPR) on the

687   seabed and the density of the species involved. At the same time, food availability and the

688   AE will regulate the energy balance of the species, determining energy uptake from the

689   available food. Despite the many possible combinations of responses, when food supply has

690   low sediment loads or consists of krill faeces, the overall energy balance for ascidians is

691   positive. However, the melting of the land-terminating glacier in Potter Cove has increased

692   the amount of sediment in the water column during summer, which has lowered the AE in

693   both species studied, even if FPR and MSFPR are different. Lower AE's would result in a

694   greater transfer of OM to the seabed and to sediments. For benthic animals such as

695   ascidians, the ultimate effect would be to promote a highly negative energy balance that

696   would eventually compromise the last benthic secondary production (somatic growth) and

697   therefore C accumulation, if the exposure to suspended sediments becomes chronic.

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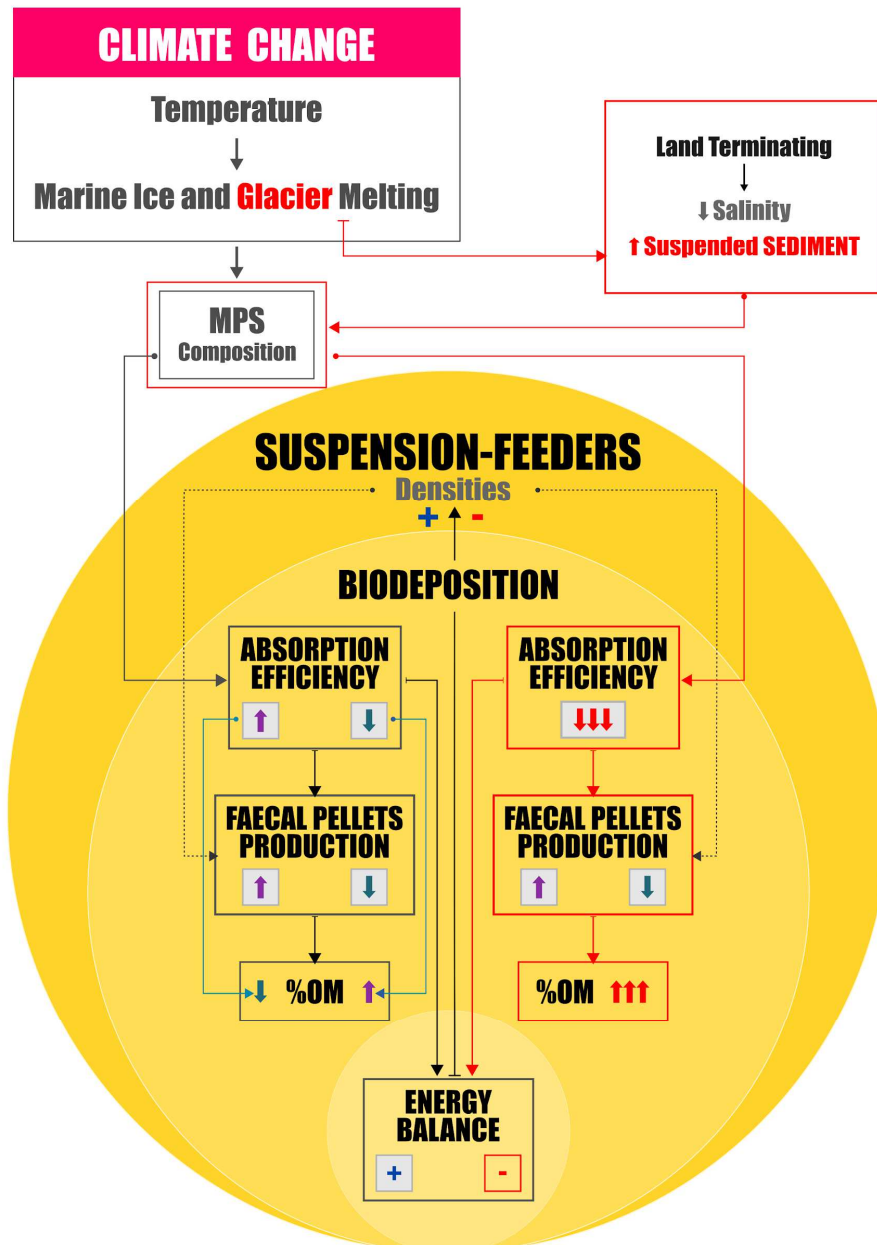
Figure 7. A conceptual model of the trophic processes involved in the PBC and their response to alternative suspended particle composition scenarios driven by climate change. PBC promoted by biodeposition mediated by suspension feeders is regulated by the characteristics of the diet, which determine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

708   vice versa (blue lines). The net transfer of OM in the faeces will therefore be regulated by the

709   species-specific production and the animal densities (dashed lines). Under high sediment

710   conditions (red boxes), AE is negatively affected in all cases (red arrows) transferring more

711   OM in the faeces, but faecal pellet production differs according to the species. Independently

712   of free-sediment diets, the energy balance would be positive (black line) assuring the survival

713   of suspension feeders and even promoting their increase (positive effect on the ecosystem).

714   Conversely, the increase of suspended sediment leads to a very negative energy balance

715   that would drastically affect the suspension feeder community (negative effect on the

716   ecosystem).

717

718   Despite a generalised marine and glacier ice loss, a high potential for benthic carbon

719   accumulation and immobilization has been estimated as a negative feedback to climate

720   change (Peck et al. 2010, Barnes 2015, Barnes and Sands 2017). The results presented

721   here generally support this view and we are confident that they are realistic and accurate for

722   the system under study in summer. They emphasise that the role of suspension feeders in

723   the flow of energy between the water column and the benthos is higher than previously

724   thought. Disentangling the effects of different pressures on the species-mediated energy

725   transfer between pelagic and benthic habitats is challenging, because our understanding of

726   how particular mechanistic processes and pressures may be modulated by environmental

727   drivers is still limited. Recent research suggests that, if warming of the WAP resume from the

728   current hiatus (Turner et al. 2016, Etourneau et al. 2019) and extensive fjordic areas follow

729   the same trend (retreating landward), it is likely that such systems will face similar conditions

730   to those reported here (Meredith et al. 2018). We highlight in this work the importance of an

731   integrated perspective for understanding how coastal ecosystems can respond to climate

732   drivers through their effects on PBC.

733

734   **Notation**

735   **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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767

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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.