



1 **Role of zooplankton in determining the efficiency of the biological**  
2 **carbon pump**

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23 **Abstract**

24 The efficiency of the ocean's biological carbon pump ( $BCP_{eff}$  – here the product of particle  
25 export and transfer efficiencies) plays a key role in the air-sea partitioning of  $CO_2$ . Despite  
26 its importance in the global carbon cycle, the biological processes that control  $BCP_{eff}$  are  
27 poorly known. We investigate the potential role that zooplankton play in the biological  
28 carbon pump using both *in situ* observations and model output. Observed and modelled  
29 estimates of fast, slow and total sinking fluxes are presented from three oceanic sites: the  
30 Atlantic sector of the Southern Ocean, the temperate North Atlantic and the equatorial Pacific  
31 oxygen minimum zone (OMZ). We find that observed particle export efficiency is inversely  
32 related to primary production likely due to zooplankton grazing, in direct contrast to the  
33 model estimates. The model and observations show strongest agreement in remineralization  
34 coefficients and  $BCP_{eff}$  at the OMZ site where zooplankton processing of particles in the  
35 mesopelagic zone is thought to be low. As the model has limited representation of  
36 zooplankton-mediated remineralization processes, we suggest that these results point to the  
37 importance of zooplankton in setting  $BCP_{eff}$ , including particle grazing and fragmentation,  
38 and the effect of diel vertical migration. We suggest that improving parameterizations of  
39 zooplankton processes may increase the fidelity of biogeochemical model estimates of the  
40 biological carbon pump. Future changes in climate such as the expansion of OMZs may  
41 decrease the role of zooplankton in the biological carbon pump globally, hence increasing its  
42 efficiency.

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44 **Keywords**

45 Biological carbon pump, zooplankton, remineralization

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## 48 1. Introduction

49

50 The biological carbon pump plays an important role in regulating atmospheric carbon dioxide  
51 levels (Kwon et al., 2009; Parekh et al., 2006). Phytoplankton in the surface ocean convert  
52 inorganic carbon during photosynthesis to particulate organic carbon (POC), a fraction of  
53 which is then exported out of the upper ocean. As particles sink through the interior ocean  
54 they are subject to remineralization by heterotrophs, such that only a small proportion of  
55 surface produced POC reaches the deep ocean (Martin et al. 1987). The efficiency of the  
56 biological carbon pump ( $BCP_{eff}$ ; defined as the proportion of surface primary production that  
57 is transferred to the deep ocean (Buesseler and Boyd, 2009) therefore affects the air-sea  
58 partitioning of  $CO_2$  (Kwon et al., 2009). Greater understanding on the controls of this term  
59 may consequently result in more accurate assessments of the BCP's role in the global carbon  
60 cycle.

61

62 One approach to determine  $BCP_{eff}$  over long time scales (millennia) is by assessing the  
63 relative proportions of preformed and regenerated nutrients, i.e. the fraction of upwelled  
64 nutrients that is removed from surface waters by biological uptake (Hilting et al., 2008).  
65 However to assess  $BCP_{eff}$  over much shorter timescales (days to weeks) we use the  
66 definition of Buesseler & Boyd (2009) where  $BCP_{eff}$  is the product of particle export  
67 efficiency ( $PE_{eff}$ , the ratio of exported flux to mixed layer primary production) and transfer  
68 efficiency ( $TE_{eff}$ , the ratio of deep flux to exported flux). Using these two parameters together  
69 allows a more in-depth analysis of the biological processes involved and thus the assessment  
70 of the role of zooplankton in setting  $BCP_{eff}$ . Additionally the attenuation coefficients  
71 Martin's  $b$  (Martin et al. 1987) and the remineralization length scale  $z^*$  (Boyd and Trull,



72 2007) are useful to quantify how much exported POC is remineralized in the mesopelagic  
73 zone.  
74  
75  $PE_{eff}$  varies proportionally to primary production, although uncertainty exists as to whether  
76 the relationship is inverse or positive (Aksnes and Wassmann, 1993; Cavan et al., 2015;  
77 Henson et al., 2015; Laws et al., 2000; Maiti et al., 2013; Le Moigne et al., 2016). Potential  
78 controls on  $PE_{eff}$  include temperature (Henson et al., 2015; Laws et al., 2000), zooplankton  
79 grazing (Cavan et al., 2015), microbial cycling (Le Moigne et al., 2016), mineral ballasting  
80 (Armstrong et al., 2002; François et al., 2002; Le Moigne et al., 2012) or large export of  
81 dissolved organic carbon (Maiti et al., 2013).  $Te_{eff}$  and POC attenuation coefficients describe  
82 how much of the exported POC reaches the deep ocean and how much of it is remineralized.  
83 Essentially the attenuation of POC with depth is determined by the sinking rates of particles  
84 and how rapidly the POC is turned over (Boyd and Trull, 2007). However, these factors  
85 themselves are controlled by various other processes such as: ballasting by minerals  
86 (François et al., 2002; Le Moigne et al., 2012), epipelagic community structure (Lam et al.,  
87 2011), temperature (Marsay et al., 2015), lability of the particles (Keil et al., 2016) and  
88 zooplankton diel vertical migration (Cavan et al., 2015). Therefore it is unlikely that any  
89 single factor controls  $BCP_{eff}$ .  
90  
91 The role of zooplankton in controlling the efficiency of the BCP is often overlooked, with  
92 greater focus on factors such as biominerals for ballasting (De La Rocha and Passow, 2007)  
93 or microbial respiration (Herndl and Reinthaler, 2013). Nevertheless zooplankton have the  
94 potential to significantly impact the biological carbon pump as they can consume and  
95 completely transform particles (Lampitt et al., 1990). Grazing by zooplankton results in POC  
96 either passing through the gut and being egested as a fecal pellet, being respired as  $CO_2$  or



97 fragmented into smaller particles through sloppy feeding (Lampitt et al., 1990). Further,  
98 zooplankton can undergo diel vertical migration, feeding on particles at night in the surface  
99 and egesting them at depth during the day (Wilson et al., 2013). Consequently a significant  
100 proportion of POC may escape remineralization in the upper mesopelagic zone (Cavan et al.,  
101 2015), where recycling of POC is most intense (Martin et al. 1987).

102

103 In this study we combine observations (made using Marine Snow Catchers, MSCs) and  
104 model output to investigate the role of zooplankton in setting the efficiency of the biological  
105 carbon pump in three different oceanic regions: the Atlantic sector of the Southern Ocean  
106 (SO), the Porcupine Abyssal Plain (PAP) site in the temperate North Atlantic and the  
107 Equatorial Tropical North Pacific (ETNP) oxygen minimum zone. The ecosystem model  
108 used here, MEDUSA (Yool et al., 2013), was chosen as it separates particle fluxes into slow  
109 and fast sinking groups. Additionally the only interactions of zooplankton with particles in  
110 MEDUSA are through the production of particles (fecal pellets) and by grazing on slow  
111 sinking particles only. Here we compare various indices of  $BCP_{eff}$  between the observations  
112 and model to infer the role of zooplankton in controlling  $BCP_{eff}$ .

113

## 114 2. Methods

### 115 2.1 Site description

116 Three very different sites were chosen in this study: the Atlantic sector of the Southern Ocean  
117 Ocean (SO, 45 – 65 °S, 20 – 70 °W), the Porcupine Abyssal Plain (PAP) site in the temperate  
118 North Atlantic (49 °N, 17 °W) and the Equatorial Tropical North Pacific (ETNP) oxygen  
119 minimum zone (13 °N, 91 °W) (Fig. 1). The SO accounts for ~ 20 % of the global ocean CO<sub>2</sub>  
120 uptake (Park et al., 2010; Takahashi et al., 2002) and is a large high-nutrient-low-chlorophyll  
121 region, in part due to limited iron availability (Martin, 1990). Nevertheless, iron from oceanic



122 islands and melting sea ice can cause intense phytoplankton blooms, which may lead to high  
123 POC export (Pollard et al., 2009). In the temperate North Atlantic seasonality is high, with  
124 phytoplankton blooms occurring in spring and summer (Lampitt et al., 2001). The region  
125 contributes disproportionately to global export, accounting for 5 – 18 % of the annual global  
126 export (Sanders et al., 2014). In the ETNP region a strong oxygen minimum (OMZ) persists  
127 where, between 50 and 1000 m depth, dissolved oxygen concentration can fall below 2  $\mu\text{mol}$   
128  $\text{kg}^{-1}$  (Paulmier and Ruiz-Pino, 2009). In OMZs the low oxygen concentrations may lead to a  
129 high transfer efficiency of POC flux (Devol and Hartnett, 2001; Hartnett et al., 1998; Keil et  
130 al., 2016; Van Mooy et al., 2002).

131

## 132 2.2 Observations

133 Particles were collected using Marine Snow Catchers (MSCs) (Riley et al., 2012) from the  
134 three oceanic sites as shown in Fig. 1. In total 27 stations were sampled, 18 in the SO, 5 at  
135 PAP and 4 in the ETNP (Table S1). MSCs have the advantage of being able to separate  
136 particles intact into two groups dependent on their sinking rate, fast ( $> 20 \text{ m d}^{-1}$ ) or slow ( $<$   
137  $20 \text{ m d}^{-1}$ ). MSCs were deployed below the mixed layer depth (MLD), which was determined  
138 as the depth with the steepest gradient of salinity and temperature, and usually occurred  
139 between 20 and 70 m (Table S1). The shallowest MSC was deployed 10 m below the MLD  
140 and another 100 m deeper than this for the Southern Ocean (Cavan et al., 2015) and the PAP  
141 site. In the ETNP MSCs were also deployed deeper into the water column to a maximum  
142 depth of 220 m.

143

144 Fast and slow sinking particles were collected from the MSC following the protocol by Riley  
145 et al. (Riley et al., 2012). Images of fast sinking particles were taken to estimate the  
146 equivalent spherical diameter (ESD) of the particles and ESD converted to POC mass *via*



147 conversion factors (Alldredge, 1998; Cavan et al., 2015). Slow sinking and suspended  
148 particles were filtered onto ashed (400 °C, overnight) GF/F filters and run in a HNC  
149 elemental analyser to determine POC mass. Sinking rates were estimated for fast sinking  
150 particles in the SO and at PAP by placing particles into a measuring cylinder filled with *in*  
151 *situ* sea water and timing how long it took each particle to pass a discrete point (Cavan et al.,  
152 2015). At the ETNP a FlowCAM was used to measure fast particle sinking rates (Bach et al.,  
153 2012). All slow sinking particle rates were calculated using the SETCOL method (Bienfang,  
154 1981). Fluxes ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) were calculated by dividing the mass of POC (mg) by the area  
155 of the MSCs ( $\text{m}^2$ ) and the sinking time of the particles (d) (Cavan et al., 2015). Primary  
156 production (PP) was estimated from 8-day satellite-derived data using the Vertically  
157 Generalised Productivity Model (Behrenfeld and Falkowski, 1997) applied to MODIS data.

158

### 159 **2.3 Model output**

160 The ecosystem model MEDUSA (Yool et al., 2013) was used for this study as it distinguishes  
161 detrital fluxes in two pools, fast and slow sinking. In MEDUSA, fast sinking particles are  
162 assumed to sink more rapidly than the time-step of the model and are remineralized  
163 instantaneously at all vertical levels with the flux profile determined by a ballast model  
164 (Armstrong et al., 2002). Slow sinking particles sink at  $3 \text{ m d}^{-1}$  and remineralization is  
165 temperature dependent, with zooplankton grazing on slow sinking particles but not on the fast  
166 sinking particles. Zooplankton DVM is not parameterised. Primary production is modelled as  
167 non-diatom and diatom production, which is summed to give the total depth-integrated  
168 primary production. The model was run in hindcast mode at  $\frac{1}{4}^\circ$  spatial resolution and output  
169 saved with a 5-day temporal resolution. The model output was extracted at the same locations  
170 and times as the observations were made and averaged over 12 years (1994 - 2006) to give  
171 the climatological seasonal cycle. The model outputs fluxes of particulate organic nitrogen



172 (mg N m<sup>-2</sup> d<sup>-1</sup>) which are converted to POC (mg C m<sup>-2</sup> d<sup>-1</sup>) using the Redfield ratio (Redfield,  
173 1934).

174

#### 175 **2.4 Data manipulation**

176 For both the observations and the model output the fast and slow sinking fluxes were  
177 summed to calculate the total sinking POC flux. Model output was available at fixed depths  
178 of 100 and 200 m, which introduces an offset with our at-sea observations (Table S1). This  
179 study is therefore assessing  $BCP_{eff}$  in the upper ocean only. Parameters calculated to test the  
180 efficiency of the biological carbon pump were the percentage contribution of fast and slow  
181 sinking particles to the total sinking flux, particle export efficiency ( $PE_{eff}$ ), the attenuation of  
182 flux with depth expressed as  $b$  and  $z^*$  and transfer efficiency ( $Te_{eff}$ ).

183

184  $PE_{eff}$  is the proportion of surface produced primary production (PP) that is exported out of  
185 the mixed layer (observations) or at 100 m (model) and is calculated by dividing the exported  
186 flux by PP. To estimate the attenuation of flux over the upper mesopelagic zone the  
187 exponents  $b$  (Martin et al. 1987) and  $z^*$  (Buesseler and Boyd, 2009) were calculated, where  
188 fluxes at the export depth and 100 m below were used for observations and fluxes at 100 and  
189 200 m from the model. The  $b$  exponent is dimensionless and generally ranges from 0 to 1.5  
190 with low values indicating low attenuation, thus low remineralization, and higher values  
191 representing high attenuation and remineralization. The  $z^*$  (m) exponent is the  
192 remineralization length scale, or the depth by which only 37 % of the reference flux (here at  
193 the export depth) remains. Thus a large  $z^*$  suggests low attenuation and low remineralization  
194 of the particle flux. The  $Te_{eff}$  is another parameter that represents how much flux reaches the  
195 deeper ocean and hence is not remineralized. This is simply calculated by dividing the deep  
196 flux (125 – 220 m in observations and 200 m in model) by the export flux. All indices are



197 dimensionless apart from the proportion of slow and fast sinking flux which is expressed as a  
198 percentage and  $z^*$  which is in metres.

199

### 200 **3. Results and Discussion**

#### 201 **3.1 Comparison of fluxes**

202 We compare model output with satellite-derived estimates of primary production (PP) POC  
203 export and deep (150 - 300 m) fluxes in the upper ocean (Fig. S1). Overall, modelled PP  
204 compares well compared to satellite-derived estimates with a strong positive correlation  
205 between the two ( $p < 0.001$ ,  $r^2 = 0.84$ , Fig. S1 a), although the model slightly overestimates  
206 PP. When comparing the total sinking export fluxes and total deep fluxes, most points lie  
207 below the 1:1 line, suggesting that the model is overestimating POC flux (Figs. S1 b & c).

208

#### 209 **3.2 Export production**

210 The traditional view of export production is that as PP increases, so does POC export out of  
211 the mixed layer (Laws et al., 2000). However recent analyses from the Southern Ocean (SO)  
212 observe the opposite relationship, that an inverse relationship between  $PE_{eff}$  and PP exists  
213 (Cavan et al., 2015; Maiti et al., 2013; Le Moigne et al., 2016). We find that for fast sinking  
214 particles the model shows  $PE_{eff}$  increases with PP (Fig. 2 a) according to a power law  
215 function ( $p < 0.001$ ,  $r^2 = 0.6$ ) while the observations show an inverse relationship (logarithmic  
216 function,  $p < 0.001$ ,  $r^2 = 0.4$ ), even when including sites outside of the SO.

217

218 However for the slow sinking particles the model shows an inverse relationship between PP  
219 and  $PE_{eff}$ , similar to that seen in the observations for the fast sinking particles (power law  
220 function,  $p < 0.001$ ,  $r^2 = 0.97$ , Fig. 2 b). Potential reasons for an inverse relationship between PP  
221 and  $PE_{eff}$  include the temporal decoupling between primary production and export (Salter et



222 al., 2007), seasonal dynamics of the zooplankton community (Tarling et al., 2004) or grazing  
223 by zooplankton (Cavan et al., 2015; Maiti et al., 2013; Le Moigne et al., 2016). As previously  
224 mentioned one of the differences between the fast and slow sinking detrital pools in the  
225 model is that slow sinking particles are grazed on by zooplankton and fast sinking are not.  
226 Thus when zooplankton graze on particles in the model an inverse relationship between  $PE_{eff}$   
227 and PP exists and when zooplankton grazing is not accounted for, the opposite occurs. This  
228 highlights the importance of zooplankton in determining the efficiency of the BCP.

229

230 The observed slow sinking  $PE_{eff}$  were generally very low ( $< 0.05$ ) and thus had little  
231 influence on the  $PE_{eff}$  for total sinking POC flux, which also had a non-linear inverse  
232 relationship with PP ( $p < 0.001$ ,  $r^2 = 0.4$ , Fig. 2 c). It is important to note that high values of  
233 PP ( $> 1000 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) were only present at PAP, and that the SO had the greatest range of  
234 PP, so drives a large part of the inverse relationship. Therefore measuring  $PE_{eff}$  in other  
235 regions with large PP ranges is fundamental to see if this relationship holds outside the sites  
236 from this study.

237

### 238 3.3 Contribution of fast and slow sinking POC fluxes

239 Particles naturally sink at different rates, with one operational definition being that slow  
240 sinking particles sink at  $< 20 \text{ m d}^{-1}$  and fast sinking particles at  $> 20 \text{ m d}^{-1}$  (Riley et al., 2012).  
241 Most sediment traps cannot separately measure fluxes of fast and slow sinking particles and  
242 are unlikely to capture much of the slow sinking flux due to their deployment in the lower  
243 mesopelagic and bathypelagic zones (Buesseler et al., 2007; Lampitt et al., 2008). Slow  
244 sinking particles sink too slowly and are remineralized too quickly to reach the deep ocean  
245 unless they are formed there. Hence the MSC is a useful tool to analyse the two sinking  
246 fluxes separately.



247

248 In both the model and the observations, the slow sinking flux was consistently smaller than  
249 the fast sinking flux and generally only contributed < 40 % of the total flux (Fig. S2).  
250 However in the model the proportion of slow sinking flux always decreases with depth (Figs.  
251 S2 a-c) whereas observations at the PAP site showed the proportion of slow sinking fluxes  
252 increased with depth (Figs. S2 e). Increases in slow sinking particles with depth must be from  
253 the fragmentation of larger fast sinking particles either abiotically (Alldredge et al., 1990) or  
254 from sloppy feeding by zooplankton (Lampitt et al., 1990). Sloppy feeding results in  
255 zooplankton fragmenting particles into smaller particles resulting in a larger surface area to  
256 volume ratio increasing colonization by microbes and thus remineralization (Mayor et al.,  
257 2014). Zooplankton do not graze on fast sinking particles in the model hence neither sloppy  
258 feeding nor abiotic fragmentation are represented (Yool et al., 2013). This likely explains  
259 why the contribution of slow sinking particles can only decrease with depth in the model,  
260 unlike the observations in which slow sinking particles may increase with depth.

261

### 262 **3.4 Attenuation of POC with depth**

263 The attenuation of POC through the water column describes how quickly POC fluxes are  
264 remineralized, with a high attenuation indicating high POC remineralization. We used the  
265 parameters  $b$  (Martin et al. 1987) and  $z^*$  (Boyd and Trull, 2007) to describe the attenuation of  
266 flux with depth. A recent study suggests POC remineralization is temperature dependent  
267 (Marsay et al., 2015) hence we compared the attenuation coefficients with temperature.  
268 Calculated mean  $b$  and  $z^*$  values for total (fast + slow) sinking POC from the model were  
269 similar at all sites (Figs. 3 a & b) with no correspondence with temperature, even though slow  
270 sinking particles are remineralized as a function of temperature in the model. Hence slow  
271 sinking  $b$  and  $z^*$  increase and decrease respectively with temperature (Table S2). The



272 observations (for total sinking particles) show a non-linear relationship with temperature that  
273 deviates away from the Marsay et al. (Marsay et al., 2015) regression, such that  
274 remineralization increases (high attenuation) at temperatures greater than 13 °C. The  
275 variability is much greater in the observations than the model, a feature that is consistent  
276 across all indices (3 a & b). Apart from at the ETNP where the model and observations agree,  
277 the observations consistently show slower POC attenuation compared to the model. The  
278 active transfer of POC to depth *via* diel vertical migration (DVM) of zooplankton (Wilson et  
279 al., 2008) may contribute to the observed slower rates of POC attenuation. Cavan et al. 2015  
280 showed that high Southern Ocean *b* values were a result of DVM, a process not  
281 parameterized in the MEDUSA model. Although active transfer *via* DVM is a complex  
282 process that may be difficult to model, it is potentially important to include in  
283 biogeochemical models, as it has been shown to account for 27 % of the total flux in the  
284 North Atlantic (Hansen and Visser, 2016).

285

286 The strong alignment of the modelled and observed attenuation at the ETNP is likely because  
287 of the lack of particle processing by zooplankton, by design in the model and naturally in  
288 oxygen minimum zones (OMZs). The daytime depth of vertically migrating zooplankton is  
289 reduced in OMZs due to low dissolved oxygen concentrations (Bianchi et al., 2013), which at  
290 the ETNP reach  $< 2 \mu\text{mol kg}^{-1}$  by 120 m. Further the population of zooplankton below this  
291 depth is almost non-existent in OMZs (Wishner et al., 2013) and those that are there feed on  
292 particles at the surface, not in the OMZ core (Williams et al., 2014). Thus zooplankton  
293 consumption and manipulation of particles is greatly reduced in OMZs and is non-existent in  
294 the MEDUSA model.

295

296 **3.5 Efficiency of the biological carbon pump**



297 To calculate  $BCP_{eff}$  (proportion of mixed layer primary production found at depth, here 150 -  
298 300 m) we replicated the  $BCP_{eff}$  plots of Buesseler & Boyd (2009) by plotting  $PE_{eff}$  against  
299 transfer efficiency ( $T_{eff}$ ) for fast, slow and total sinking particles (Fig. 4). According to the  
300 observations, the SO had the highest total sinking  $BCP_{eff}$  at 40 %, similar to the maximum  
301 observed by Buesseler & Boyd (2009) in the North Atlantic. The SO observations showed a  
302 higher  $BCP_{eff}$  than the model by about 10 % across all sinking fluxes (Fig. 4). This  
303 difference was largely due to a very high  $T_{eff}$  ( $> 1$ ) estimated from observations, which  
304 implies fluxes increased at depth. This could be due to active fluxes by vertically migrating  
305 zooplankton, possibly krill (Cavan et al., 2015). Active fluxes could account for high  
306 observed  $T_{eff}$  in the slow sinking particles, as well as fragmentation of larger particles at  
307 depth (Mayor et al., 2014).

308

309 Even though the PAP site had the highest PP, the  $BCP_{eff}$  was lowest ( $< 15$  %). There were  
310 also large differences (up to 15 %) in the  $BCP_{eff}$  between the model and the observations at  
311 the PAP site driven by large discrepancies in  $PE_{eff}$ . Observations of fast sinking  $PE_{eff}$  were  
312 much lower than predicted by the model (Fig. 4 a), which we suggest could result from active  
313 grazing and fragmentation of fast sinking particles by zooplankton.  $T_{eff}$  of fast sinking  
314 particles were low and consistent with model predictions, suggesting that active transfer via  
315 DVM (not parameterized in the model) plays a relatively minor role at the PAP site.

316 Therefore mineral ballasting (Armstrong et al., 2002), which drives  $T_{eff}$  in the model, may be  
317 the main driver of  $T_{eff}$  at PAP. The modelled and observed slow sinking  $BCP_{eff}$  were similar  
318 at PAP ( $\sim 1$  %) despite a large difference in  $T_{eff}$  (Fig. 4 b). Fragmentation of fast to slow  
319 sinking particles (not included in the model) at depth could explain the difference in slow  
320 sinking  $T_{eff}$ .

321



322 Finally the  $BCPe_{eff}$  for the ETNP is very similar between the model and observations for all  
323 sinking fluxes (Fig. 4). The similarity in the  $BCPe_{eff}$  here echoes the similarity shown for  
324 POC attenuation with depth. This reiterates our hypothesis that the model and observations  
325 agree on  $BCPe_{eff}$  only in areas of the global ocean where processing of particles by  
326 zooplankton is reduced due to very low dissolved oxygen concentrations.

327

#### 328 4. Conclusions

329 We have used observations and model output from the upper mesopelagic zone in 3  
330 contrasting oceanic regions to assess the influence of zooplankton on the efficiency of the  
331 biological carbon pump. We separately collected *in situ* fast and slow sinking particles, which  
332 are also separated into discrete classes in the MEDUSA model. The model has limited  
333 processing of particles by zooplankton with only slow sinking detrital POC being grazed  
334 upon.

335

336 Our results highlight the crucial role that zooplankton play in regulating the efficiency of the  
337 biological carbon pump through 1) controlling particle export by grazing, 2) fragmenting  
338 large, fast sinking particles into smaller, slower sinking particles and 3) active transfer of  
339 POC to depth *via* diel vertical migration. Comparisons of the model and observations in an  
340 oxygen minimum zone provide strong evidence of the importance of zooplankton in  
341 regulating the BCP. Here extremely low dissolved oxygen concentrations at depth reduce the  
342 abundance and metabolism of zooplankton in the mid-water column. Thus the ability of  
343 zooplankton to degrade or repackage particles is vastly reduced in OMZs, and as such it is  
344 here that the model, with limited zooplankton interaction with particles, shows the strongest  
345 agreement with observations.

346



347 We recommend that grazing on large, fast sinking particles and the fragmentation of fast to  
348 slow sinking particles (either *via* zooplankton or abiotically) is introduced into global  
349 biogeochemical models, with the aim of also incorporating active transfer. Future changes in  
350 climate such as the expansion of OMZs may decrease the role of zooplankton in the  
351 biological carbon pump globally, increasing its efficiency and hence forming a positive  
352 climate feedback.

353

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358

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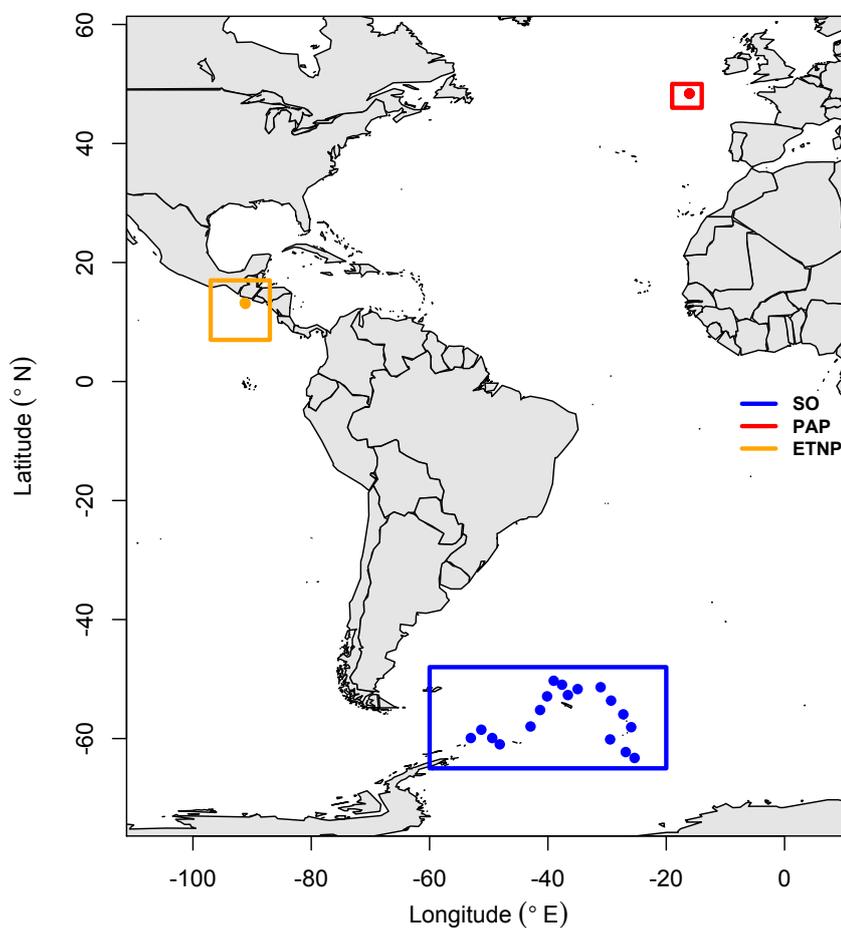
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519 **Fig. 1.** Map showing study areas. Blue rectangle is location of sites in the Southern Ocean,

520 red is the North Atlantic Porcupine Abyssal Plain and orange the equatorial north Pacific

521 oxygen minimum zone.

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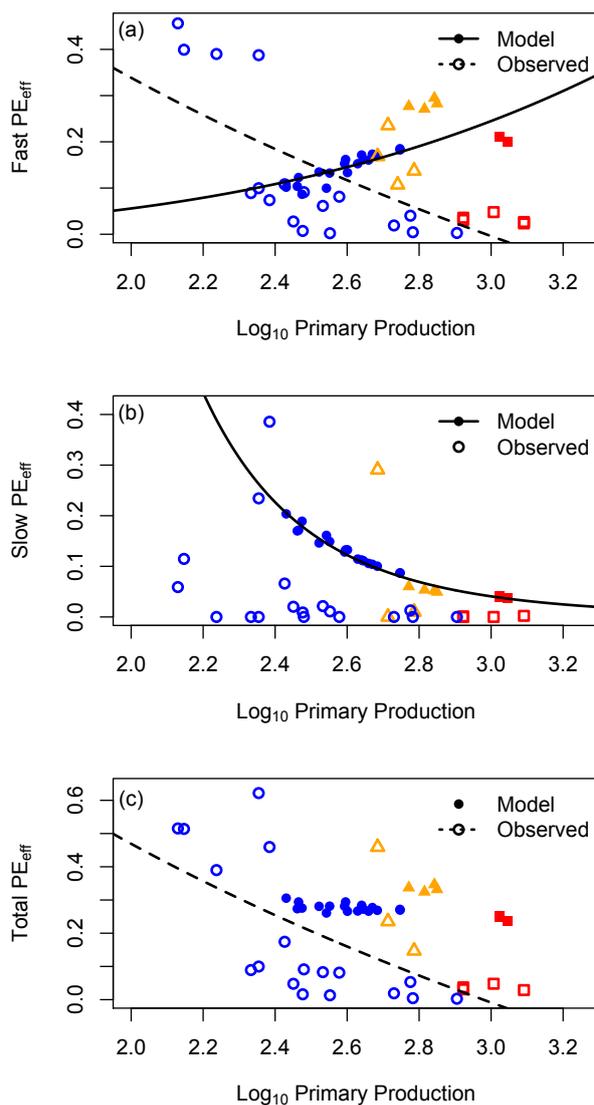
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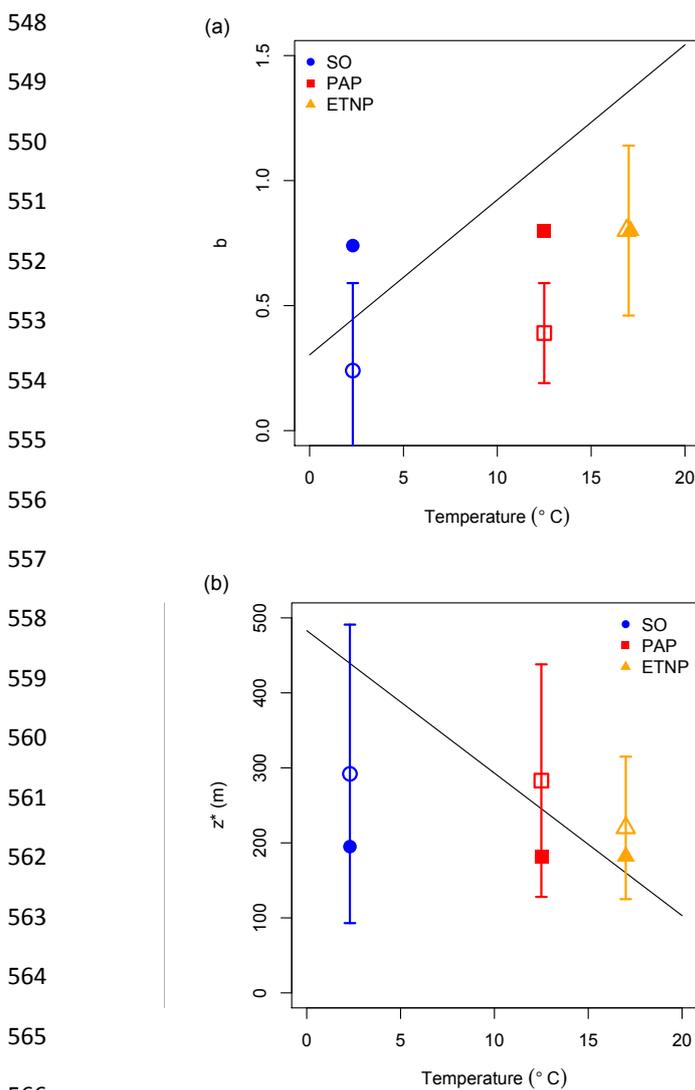
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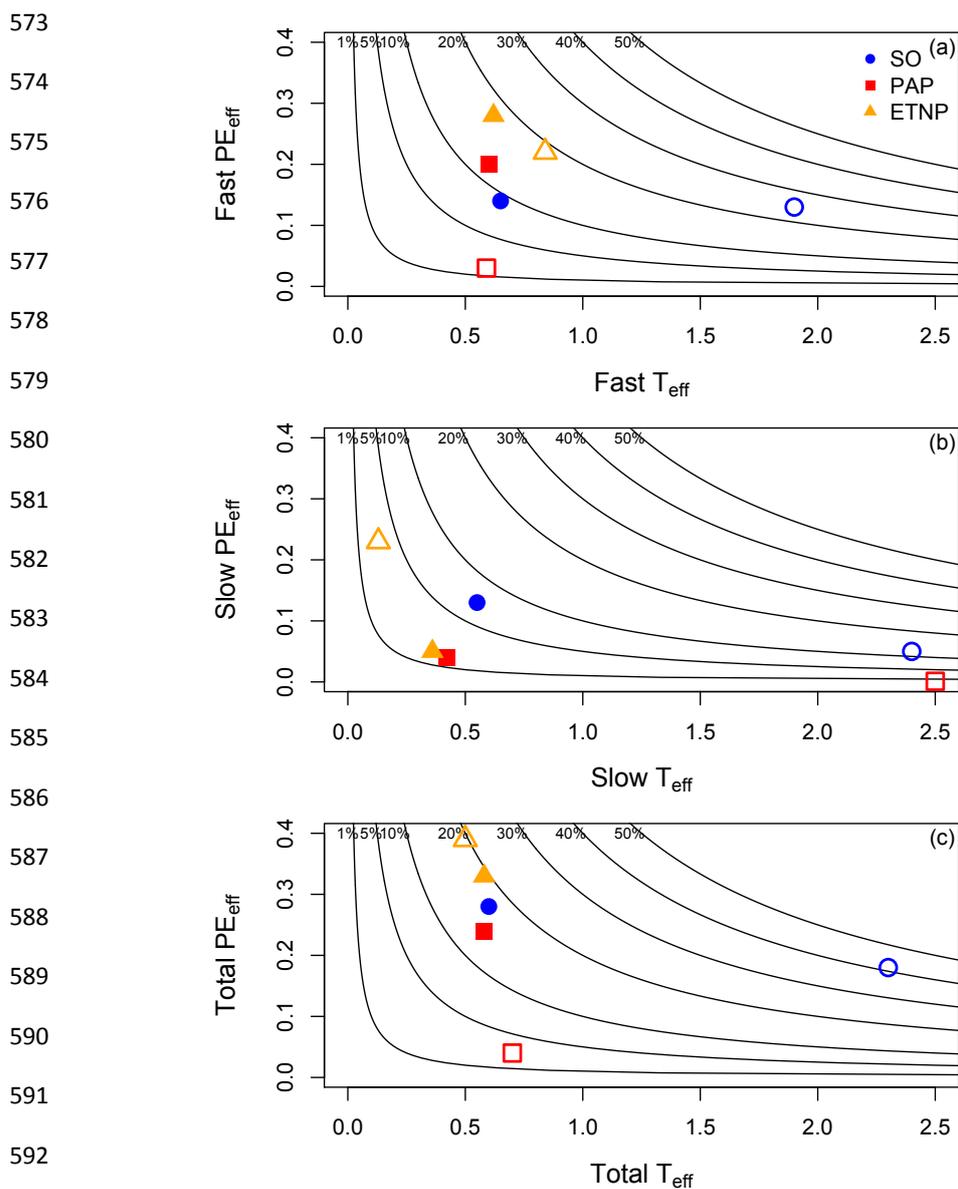
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**Fig. 2.** Primary production against particle export efficiency ( $PE_{eff}$ ) for (a) fast sinking, (b) slow sinking and (c) total sinking particles. Blue circles are Southern Ocean, red squares PAP and orange triangles equatorial Pacific. Filled circles and solid black lines show model output and open circles and dashed lines are observations. All fitted lines are statistically significant to at least the 95 % level (see text for details).



567 **Fig. 3.** Total sinking POC attenuation coefficients (a)  $b$  and (b)  $z^*$  with temperature. Blue  
 568 circles are Southern Ocean, red squares PAP and orange triangles equatorial Pacific. Filled  
 569 points show model output and open points are observations. Solid line is Marsay et al. (2015)  
 570 regression. Error bars are standard error of the mean and only plotted on the observations as  
 571 the error is too small in the model. See Table S2 for attenuation coefficients of fast and slow  
 572 sinking particles.



593 **Fig. 4.** Efficiency of the biological carbon pump for (a) fast, (b) slow and (c) total sinking  
 594 particles. Particle export efficiency (PE<sub>eff</sub>) is plotted against transfer efficiency (T<sub>eff</sub>).  
 595 Contours represent BCPE<sub>eff</sub> (proportion of primary production at depth). Blue circles are  
 596 Southern Ocean, red squares PAP and orange triangles equatorial Pacific. Filled points show  
 597 model output and open points are observations.