Role of zooplankton in determining the efficiency of the biological carbon pump

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Abstract

The efficiency of the ocean’s biological carbon pump (BCPeff – here the product of particle export and transfer efficiencies) plays a key role in the air-sea partitioning of CO2. Despite its importance in the global carbon cycle, the biological processes that control BCPeff are poorly known. We investigate the potential role that zooplankton play in the biological carbon pump using both in situ observations and model output. Observed and modelled estimates of fast, slow and total sinking fluxes are presented from three oceanic sites: the Atlantic sector of the Southern Ocean, the temperate North Atlantic and the equatorial Pacific oxygen minimum zone (OMZ). We find that observed particle export efficiency is inversely related to primary production likely due to zooplankton grazing, in direct contrast to the model estimates. The model and observations show strongest agreement in remineralization coefficients and BCPeff at the OMZ site where zooplankton processing of particles in the mesopelagic zone is thought to be low. As the model has limited representation of zooplankton-mediated remineralization processes, we suggest that these results point to the importance of zooplankton in setting BCPeff, including particle grazing and fragmentation, and the effect of diel vertical migration. We suggest that improving parameterizations of zooplankton processes may increase the fidelity of biogeochemical model estimates of the biological carbon pump. Future changes in climate such as the expansion of OMZs may decrease the role of zooplankton in the biological carbon pump globally, hence increasing its efficiency.

Keywords

Biological carbon pump, zooplankton, remineralization
1. Introduction

The biological carbon pump plays an important role in regulating atmospheric carbon dioxide levels (Kwon et al., 2009; Parekh et al., 2006). Phytoplankton in the surface ocean convert inorganic carbon during photosynthesis to particulate organic carbon (POC), a fraction of which is then exported out of the upper ocean. As particles sink through the interior ocean they are subject to remineralization by heterotrophs, such that only a small proportion of surface produced POC reaches the deep ocean (Martin et al. 1987). The efficiency of the biological carbon pump (BCP$_{eff}$; defined as the proportion of surface primary production that is transferred to the deep ocean (Buesseler and Boyd, 2009) therefore affects the air-sea partitioning of CO$_2$ (Kwon et al., 2009). Greater understanding on the controls of this term may consequently result in more accurate assessments of the BCP’s role in the global carbon cycle.

One approach to determine BCP$_{eff}$ over long time scales (millennia) is by assessing the relative proportions of preformed and regenerated nutrients, i.e. the fraction of upwelled nutrients that is removed from surface waters by biological uptake (Hilting et al., 2008). However to assess BCP$_{eff}$ over much shorter timescales (days to weeks) we use the definition of Buesseler & Boyd (2009) where BCP$_{eff}$ is the product of particle export efficiency (PE$_{eff}$, the ratio of exported flux to mixed layer primary production) and transfer efficiency (T$_{eff}$, the ratio of deep flux to exported flux). Using these two parameters together allows a more in-depth analysis of the biological processes involved and thus the assessment of the role of zooplankton in setting BCP$_{eff}$. Additionally the attenuation coefficients Martin’s $b$ (Martin et al. 1987) and the remineralization length scale $z^*$ (Boyd and Trull,
are useful to quantify how much exported POC is remineralized in the mesopelagic zone.

PEeff varies proportionally to primary production, although uncertainty exists as to whether the relationship is inverse or positive (Aksnes and Wassmann, 1993; Cavan et al., 2015; Henson et al., 2015; Laws et al., 2000; Maiti et al., 2013; Le Moigne et al., 2016). Potential controls on PEeff include temperature (Henson et al., 2015; Laws et al., 2000), zooplankton grazing (Cavan et al., 2015), microbial cycling (Le Moigne et al., 2016), mineral ballasting (Armstrong et al., 2002; François et al., 2002; Le Moigne et al., 2012) or large export of dissolved organic carbon (Maiti et al., 2013). Teff and POC attenuation coefficients describe how much of the exported POC reaches the deep ocean and how much of it is remineralized. Essentially the attenuation of POC with depth is determined by the sinking rates of particles and how rapidly the POC is turned over (Boyd and Trull, 2007). However, these factors themselves are controlled by various other processes such as: ballasting by minerals (François et al., 2002; Le Moigne et al., 2012), epipelagic community structure (Lam et al., 2011), temperature (Marsay et al., 2015), lability of the particles (Keil et al., 2016) and zooplankton diel vertical migration (Cavan et al., 2015). Therefore it is unlikely that any single factor controls BCPeff.

The role of zooplankton in controlling the efficiency of the BCP is often overlooked, with greater focus on factors such as biominerals for ballasting (De La Rocha and Passow, 2007) or microbial respiration (Herndl and Reinthaler, 2013). Nevertheless zooplankton have the potential to significantly impact the biological carbon pump as they can consume and completely transform particles (Lampitt et al., 1990). Grazing by zooplankton results in POC either passing through the gut and being egested as a fecal pellet, being respired as CO2 or
fragmented into smaller particles through sloppy feeding (Lampitt et al., 1990). Further, zooplankton can undergo diel vertical migration, feeding on particles at night in the surface and egesting them at depth during the day (Wilson et al., 2013). Consequently a significant proportion of POC may escape remineralization in the upper mesopelagic zone (Cavan et al., 2015), where recycling of POC is most intense (Martin et al. 1987).

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

2. Methods

2.1 Site description

Three very different sites were chosen in this study: the Atlantic sector of the Southern Ocean (SO, 45 – 65 °S, 20 – 70 °W), the Porcupine Abyssal Plain (PAP) site in the temperate North Atlantic (49 °N, 17 °W) and the Equatorial Tropical North Pacific (ETNP) oxygen minimum zone (13 °N, 91 °W) (Fig. 1). The SO accounts for ~ 20 % of the global ocean CO₂ uptake (Park et al., 2010; Takahashi et al., 2002) and is a large high-nutrient-low-chlorophyll region, in part due to limited iron availability (Martin, 1990). Nevertheless, iron from oceanic
islands and melting sea ice can cause intense phytoplankton blooms, which may lead to high POC export (Pollard et al., 2009). In the temperate North Atlantic seasonality is high, with phytoplankton blooms occurring in spring and summer (Lampitt et al., 2001). The region contributes disproportionately to global export, accounting for 5 – 18 % of the annual global export (Sanders et al., 2014). In the ETNP region a strong oxygen minimum (OMZ) persists where, between 50 and 1000 m depth, dissolved oxygen concentration can fall below 2 µmol kg⁻¹ (Paulmier and Ruiz-Pino, 2009). In OMZs the low oxygen concentrations may lead to a high transfer efficiency of POC flux (Devol and Hartnett, 2001; Hartnett et al., 1998; Keil et al., 2016; Van Mooy et al., 2002).

2.2 Observations

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

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

### 2.3 Model output

The ecosystem model MEDUSA (Yool et al., 2013) was used for this study as it distinguishes detrital fluxes in two pools, fast and slow sinking. In MEDUSA, fast sinking particles are assumed to sink more rapidly than the time-step of the model and are remineralized instantaneously at all vertical levels with the flux profile determined by a ballast model (Armstrong et al., 2002). Slow sinking particles sink at 3 m d$^{-1}$ and remineralization is temperature dependent, with zooplankton grazing on slow sinking particles but not on the fast sinking particles. Zooplankton DVM is not parameterised. Primary production is modelled as non-diatom and diatom production, which is summed to give the total depth-integrated primary production. The model was run in hindcast mode at ¼ ° spatial resolution and output saved with a 5-day temporal resolution. The model output was extracted at the same locations and times as the observations were made and averaged over 12 years (1994 - 2006) to give the climatological seasonal cycle. The model outputs fluxes of particulate organic nitrogen...
(mg N m\(^{-2}\) d\(^{-1}\)) which are converted to POC (mg C m\(^{-2}\) d\(^{-1}\)) using the Redfield ratio (Redfield, 1934).

### 2.4 Data manipulation

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

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

3. Results and Discussion

3.1 Comparison of fluxes

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

3.2 Export production

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

However for the slow sinking particles the model shows an inverse relationship between PP and PEeff, similar to that seen in the observations for the fast sinking particles (power law function, $p<0.001$, $r^2=0.97$, Fig. 2 b). Potential reasons for an inverse relationship between PP and PEeff include the temporal decoupling between primary production and export (Salter et
al., 2007), seasonal dynamics of the zooplankton community (Tarling et al., 2004) or grazing by zooplankton (Cavan et al., 2015; Maiti et al., 2013; Le Moigne et al., 2016). As previously mentioned one of the differences between the fast and slow sinking detrital pools in the model is that slow sinking particles are grazed on by zooplankton and fast sinking are not. Thus when zooplankton graze on particles in the model an inverse relationship between $PE_{eff}$ and PP exists and when zooplankton grazing is not accounted for, the opposite occurs. This highlights the importance of zooplankton in determining the efficiency of the BCP.

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

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

Particles naturally sink at different rates, with one operational definition being that slow sinking particles sink at < 20 m d$^{-1}$ and fast sinking particles at > 20 m d$^{-1}$ (Riley et al., 2012). Most sediment traps cannot separately measure fluxes of fast and slow sinking particles and are unlikely to capture much of the slow sinking flux due to their deployment in the lower mesopelagic and bathypelagic zones (Buesseler et al., 2007; Lampitt et al., 2008). Slow sinking particles sink too slowly and are remineralized too quickly to reach the deep ocean unless they are formed there. Hence the MSC is a useful tool to analyse the two sinking fluxes separately.
In both the model and the observations, the slow sinking flux was consistently smaller than the fast sinking flux and generally only contributed < 40% of the total flux (Fig. S2). However in the model the proportion of slow sinking flux always decreases with depth (Figs. S2 a-c) whereas observations at the PAP site showed the proportion of slow sinking fluxes increased with depth (Figs. S2 e). Increases in slow sinking particles with depth must be from the fragmentation of larger fast sinking particles either abiotically (Alldredge et al., 1990) or from sloppy feeding by zooplankton (Lampitt et al., 1990). Sloppy feeding results in zooplankton fragmenting particles into smaller particles resulting in a larger surface area to volume ratio increasing colonization by microbes and thus remineralization (Mayor et al., 2014). Zooplankton do not graze on fast sinking particles in the model hence neither sloppy feeding nor abiotic fragmentation are represented (Yool et al., 2013). This likely explains why the contribution of slow sinking particles can only decrease with depth in the model, unlike the observations in which slow sinking particles may increase with depth.

3.4 Attenuation of POC with depth

The attenuation of POC through the water column describes how quickly POC fluxes are remineralized, with a high attenuation indicating high POC remineralization. We used the parameters b (Martin et al. 1987) and z* (Boyd and Trull, 2007) to describe the attenuation of flux with depth. A recent study suggests POC remineralization is temperature dependent (Marsay et al., 2015) hence we compared the attenuation coefficients with temperature. Calculated mean b and z* values for total (fast + slow) sinking POC from the model were similar at all sites (Figs. 3 a & b) with no correspondence with temperature, even though slow sinking particles are remineralized as a function of temperature in the model. Hence slow sinking b and z* increase and decrease respectively with temperature (Table S2). The
observations (for total sinking particles) show a non-linear relationship with temperature that
deviates away from the Marsay et al. (Marsay et al., 2015) regression, such that
remineralization increases (high attenuation) at temperatures greater than 13 °C. The
variability is much greater in the observations than the model, a feature that is consistent
across all indices (3 a & b). Apart from at the ETNP where the model and observations agree,
the observations consistently show slower POC attenuation compared to the model. The
active transfer of POC to depth via diel vertical migration (DVM) of zooplankton (Wilson et
al., 2008) may contribute to the observed slower rates of POC attenuation. Cavan et al. 2015
showed that high Southern Ocean b values were a result of DVM, a process not
parameterized in the MEDUSA model. Although active transfer via DVM is a complex
process that may be difficult to model, it is potentially important to include in
biogeochemical models, as it has been shown to account for 27 % of the total flux in the
North Atlantic (Hansen and Visser, 2016).

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

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

Even though the PAP site had the highest PP, the BCP_{eff} was lowest (< 15 %). There were also large differences (up to 15 %) in the BCP_{eff} between the model and the observations at the PAP site driven by large discrepancies in PE_{eff}. Observations of fast sinking PE_{eff} were much lower than predicted by the model (Fig. 4 a), which we suggest could result from active grazing and fragmentation of fast sinking particles by zooplankton. T_{eff} of fast sinking particles were low and consistent with model predictions, suggesting that active transfer via DVM (not parameterized in the model) plays a relatively minor role at the PAP site. Therefore mineral ballasting (Armstrong et al., 2002), which drives T_{eff} in the model, may be the main driver of T_{eff} at PAP. The modelled and observed slow sinking BCP_{eff} were similar at PAP (~ 1 %) despite a large difference in T_{eff} (Fig. 4 b). Fragmentation of fast to slow sinking particles (not included in the model) at depth could explain the difference in slow sinking T_{eff}. 


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

4. Conclusions

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

Our results highlight the crucial role that zooplankton play in regulating the efficiency of the biological carbon pump through 1) controlling particle export by grazing, 2) fragmenting large, fast sinking particles into smaller, slower sinking particles and 3) active transfer of POC to depth \textit{via} diel vertical migration. Comparisons of the model and observations in an oxygen minimum zone provide strong evidence of the importance of zooplankton in regulating the BCP. Here extremely low dissolved oxygen concentrations at depth reduce the abundance and metabolism of zooplankton in the mid-water column. Thus the ability of zooplankton to degrade or repackage particles is vastly reduced in OMZs, and as such it is here that the model, with limited zooplankton interaction with particles, shows the strongest agreement with observations.
We recommend that grazing on large, fast sinking particles and the fragmentation of fast to slow sinking particles (either via zooplankton or abiotically) is introduced into global biogeochemical models, with the aim of also incorporating active transfer. Future changes in climate such as the expansion of OMZs may decrease the role of zooplankton in the biological carbon pump globally, increasing its efficiency and hence forming a positive climate feedback.

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References


Devol, A. H. and Hartnett, H. E.: Role of the oxygen-deficient zone in transfer of organic


Fig. 1. Map showing study areas. Blue rectangle is location of sites in the Southern Ocean, red is the North Atlantic Porcupine Abyssal Plain and orange the equatorial north Pacific oxygen minimum zone.
**Fig. 2.** Primary production against particle export efficiency (PE\textsubscript{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).
Fig. 3. Total sinking POC attenuation coefficients (a) $b$ and (b) $z^*$ with temperature. Blue circles are Southern Ocean, red squares PAP and orange triangles equatorial Pacific. Filled points show model output and open points are observations. Solid line is Marsay et al. (2015) regression. Error bars are standard error of the mean and only plotted on the observations as the error is too small in the model. See Table S2 for attenuation coefficients of fast and slow sinking particles.
Fig. 4. Efficiency of the biological carbon pump for (a) fast, (b) slow and (c) total sinking particles. Particle export efficiency (PE_{eff}) is plotted against transfer efficiency (T_{eff}). Contours represent BCP_{eff} (proportion of primary production at depth). Blue circles are Southern Ocean, red squares PAP and orange triangles equatorial Pacific. Filled points show model output and open points are observations.