# Main title: Carbon export by vertically migrating zooplankton: an optimal behaviour model

## Short title: Optimal vertical migration and carbon export

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## Abstract

## Through diel vertical migration (DVM), zooplankton add an active transport to the otherwise passive sinking of detrital material that constitutes the biologic pump. This active transport has proven difficult to quantify. We present a model that estimates both the temporal and depth characteristic of optimal DVM behaviour based on a trade-off between feeding opportunity and predation risk; factors that vary with latitude, time of year and the size of the migrating animal. This behavioural component, coupled to a nutrient-phytoplankton-zooplankton (NPZ) productivity model provides estimates of the active export flux of carbon by different size fractions of the migrating zooplankton population as functions of time and space. The approach is motivated by the difficulty in incorporating behavioural aspects of carbon transport into large scale carbon budgets of the world’s oceans. The results show that despite their lower abundance, large zooplankton (length circa 1 - 2 mm) migrate deeper and transport approximately twice as much carbon as do small zooplankton (length circa 0.2 - 0.3 mm). In mid- latitudes (30° to 50° N) where pronounced spring blooms are observed, about 20% more carbon is transported than at either equatorial or boreal latitudes. We estimate that the amount of carbon transported below the mixed layer by migrating zooplankton in the North Atlantic Ocean constitutes 27% (16% -30%) of the total export flux associated with the biological pump in that region.

## Introduction

The oceans play a major role in regulating global climate, one aspect of which is their potential to remove anthropogenic CO2 from the atmosphere. Primary producers assimilate CO2 in the euphotic layer to produce organic matter, a fraction of which is exported to the deep ocean as detrital material (e.g. sinking as aggregates, marine snow and faecal pellets). On its way from the surface mixed layer through the meso-pelagic ocean 80% to 90% of this detrital material is remineralized (Martin et al. 1987, Burd et al. 2010, Giering et al. 2014). The remaining fraction reaches the depths where it is sequestered in the ocean bottom or in deep circulation currents. This mechanism is part of the biologic pump which together with the solubility pump are the main sequesters of carbon from the atmosphere into the deep ocean (Volk and Hoffert 1985; Longhurst and Harrison 1989; Ducklow et al. 2001; Boyd and Trull 2007).

The biological pump is strongly regulated by the resident zooplankton community (Steinberg et al 2000). Meso-zooplankton in particular process a up to 40 % of the primary production, either in direct grazing on phytoplankton or feeding on micro-zooplankton consumers (Frangoulis et al. 2005), producing fast sinking faecal pellets that contribute significantly to export flux (Bishop et al. 1978; Honjo and Roman 1978; Smith et al. 2009). Other processes mediated by zooplankton include feeding and disruption of particle fluxes (Alldredge and Silver 1988; Steinberg et al. 2008b), and active carbon transport by vertical migrators (Dam et al. 1995; Steinberg et al. 2002; Jonasdottir et al. 2015). With regards to the latter, many meso-zooplankton grazers perform diel vertical migration (DVM), feeding in the surface at night and finding refuge at depth during sunlight hours (Longhurst 1976). This behaviour can bring them below the euphotic zone where they leave behind excreted organic matter and respired CO2 (Longhurst et al. 1990; Steinberg et al. 2000), thus contributing to the export flux. Despite its importance for the biological pump and the export of CO2 from the surface ocean, this active component remains poorly quantified (Steinberg et al. 2000, 2001), particularly in terms of the global carbon budget. There is a need to investigate the role of zooplankton DVM in the sequestering of carbon from the atmosphere, especially as the biologic pump is predicted to weaken in response to climate change (Buesseler and Boyd 2009, Steinacher et al. 2010). Changes in the ocean productivity and zooplankton community might have large implications for the sequestration of CO2 from the atmosphere and hence the global climate (Sarmiento et al. 1998; Smith et al. 2009,).

Several studies have observed the active flux of organic and respiratory carbon from migrating zooplankton (Longhurst et al. 1990; Morales 1999; Steinberg et al. 2000; Stukel et al. 2013). However, all of these are based on limited spatial and temporal information which is susceptible to seasonal and latitudinal variations in both primary and secondary productivity (Burd et al. 2010). Therefore extrapolation of the findings into global oceanic carbon budget remains a challenge. This study uses a dynamic approach to predict the optimal DVM behaviour under given physical and biotic conditions and estimates how this impacts the active carbon by migrating animals. It is applied to North Atlantic Ocean as an example, but is otherwise general. The model is simple enough to be implemented in ocean general circulation models (OGCMs), providing regional and seasonal estimates of the active carbon flux by migrating zooplankton in the global assessments of CO2 dynamics.

## Method

### An optimal behaviour model of diel vertical migration

The model presented here considers the trade-off between gaining energy for growth and reproduction and avoiding predation. This trade-off has been modelled several times before (Gilliam and Fraser 1987; Houston et al. 1993; De Robertis 2002; Visser 2007) and concerns the classic dilemma that a high energy gain nearly always comes at a cost of a high predation risk (Lima and Dill 1990; Houston et al. 1993). Many zooplankton graze in the surface layers at night, but migrate vertically into darkness during the day where their vulnerability to visual predators is reduced (Fig. 1). A simple heuristic that reflects this trade-off is Gilliam’s rule (Gilliam and Fraser 1987; Kristiansen et al. 2009; Sainmont et al. 2015) where optimal behaviour can be estimated as that which maximizes net energy gain over mortality rate. Applying Gilliam’s rule to migrating zooplankton, the functional form of fitness depends on the depth of migration ($z\_{max}$) and the fraction of the day spent migrating ($τ$) (Eq. 1):

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|  | $$f\left(z\_{max},τ\right)= \frac{g\left(1-τ\right)-c(z\_{max},τ)}{μ(z\_{max},τ)}$$ | (1) |

where $g$ is the energy gain (J day-1), $c$ is the energetic cost (J day-1) and $μ$ is the mortality rate (day-1). Hence, $f$ is an estimate of the zooplankton fitness in terms of its net energy gain (J) during its expected lifetime assuming an unchanging environment (i.e. the animal has no knowledge of future change) (Gilliam and Fraser 1987, De Robertis 2002, Sainmont et al 2015). The energetic gain from feeding can be written as

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|  | $$g\left(1-τ\right)= e\_{p}βc\_{surf}ε\_{assim}(1-τ)$$ | (2) |

depending on the fraction of a day zooplankton spend grazing,$ 1-τ$. The fraction of day the zooplankton spend migrating (down from the surface, resting at depth and returning to surface) will be referred to as "migration time" (Fig. 1). $e\_{p}$ is the energy content of the prey (J gC-1), $β$ is the maximum clearance rate ($β=ar^{3}$ (m3 day-1), where $r$ is the radius of the zooplankton (m) and $a$ $≈$ 4 × 106 day-1, which is an empirical scaling that states the clearance rate is proportional to the volume of the organism (Kiørboe 2013).). $c\_{surf}$ is the phytoplankton abundance (gC m-3) and $ε\_{assim}$ is the assimilation efficiency. We use a Hollings type I functional response with a maximum ingestion rate set to 200 % of body carbon per day if the zooplankton is feeding full time. This parameter will typically depend on the diet of the zooplankton; Besiktepe and Dam (2002) found variations between 92 % - 610 % of body carbon consumed per day in *Acartia tonsa* fed on different species of phytoplankton. As neither zooplankton nor phytoplankton species are modelled explicitly, 200 % per day seems a reasonable estimate.

The mortality $μ$ is proportional to the mean daily light exposure (Eq. 3). Zooplankton are observed to attempt to follow isolumes in their migration to depth (Heywood 1996; Sainmont et al. 2014), which makes the proportionality to light exposure a realistic assumption regarding mortality. Specifically

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|  | $$μ\left(z\_{max}τ\right)= μ\_{0}(1+m\_{fac}\hat{L}(z\_{max},τ))$$ | (3) |

where µ0 is the background mortality (day-1) , which is the mortality experienced in total darkness (i.e. mortality not by visual predators, starvation or disease, but just the inverse of the expected lifetime of a zooplankter). $\hat{L}(z\_{max},τ)$ is the daily mean light exposure of zooplankton on its path of migration (see supplementary material for details on calculation). It is assumed that the risk of mortality is 20 times higher in maximum daylight than in darkness, and hence the light risk factor$ m\_{fac}=20$. De Robertis (2002) has used a similar argument for the timing of DVM, setting the risk of mortality from visual predators 10 times higher than from all non-visual sources combined. In this model, we assume visual predation risk to be size independent. There are processes that place an allometric scaling on mortality. On the one hand, while larger prey are visually more conspicuous (Aksnes and Giske 1993), they also have greater escape ability as well as fewer predators (Hirst and Kiørboe 2002). Rather than make this an ambiguous model effect, we choose to use a size neutral mortality risk depending solely on light level.

As the zooplankton migrate vertically there is an associated energetic cost $c$ (J day-1) depending on the maximum depth of migration $z\_{max}$ and $τ$:

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|  | $$c\left(z\_{max}τ\right)= q\frac{1}{τ}k(\left|z\_{max}-z\_{0}\right|)^{2}$$ | (4) |

where $q$ is the cost of swimming ($q\left(r\right)={6πrν\_{kin}}/{ε\_{swim}}$, W m2 s-2) and $z\_{0}$ is the grazing depth (m). $k$ is a constant arising from integrating along the migration path ($ζ$, Eq. 6d), which relates the cost to the swimming so that higher speed comes at a higher energy cost (Visser 2007).

Table 1 provides values and descriptions of all model parameters.

### Application of the model

To provide the DVM model with estimates of phytoplankton abundance, we use a simple nutrient-phytoplankton-zooplankton (NPZ) model. The set-up is identical to the one made by Evans and Parslow (1985), with a the deep ocean nutrient concentration tuned (from 10 to 4 mM N m-3) to keep the resulting plankton abundance realistic (peak values of the order 100 mgC m-3) The NPZ model is forced with a growth rate based on an annual light cycle (as a function of latitude) and a time-series of mixed layer depth (see supplementary material for further explanation and visualization of the NPZ model results). The model is adjusted to simulate the North Atlantic conditions and reproduces the magnitude and timing of the spring blooms observed in northern latitudes (Colebrook 1979, Townsend et al. 1994). In keeping with the NPZ model construction, the simulated zooplankton population is assumed to be herbivorous with their growth fuelled only from grazing on phytoplankton. While not explicitly considered in this simple model, part of the zooplankton diet also consists of mirco-zooplankton consumers, a process that is to some extent modelled in the zooplankton net grazing rate. It is assumed that the zooplankton population consist of copepods, such as e.g. *Calanus spp.*, which are often dominating the zooplankton community and typically exhibit a strong DVM behaviour (Hays 1996; Dale and Kaartvedt 2000; Irigorien et al. 2004).

The optimal migration strategy is found by maximizing relative fitness, $f$ (Eq. 1) with regards migration depth $z\_{max}$ and migration time $τ$ for given environmental conditions, both physical and biotic. Different optimal strategies will emerge for different environmental conditions. The optimal $z\_{max}$ and $τ$ are used to estimate how much carbon is consumed in the surface and subsequently excreted and respired below the mixed layer ($F\_{ML}$) by migrating zooplankton. That is

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|  | $$Flux\_{ML}=g(z\_{opt},τ\_{opt})\frac{1}{e\_{p}}Zε\_{c}τ\_{ML}$$ | (5) |

where $g\left(z\_{opt},τ\_{opt}\right) $is the gain (J day-1 ind-1) achieved when choosing the optimal migration strategy, $e\_{p}$ (J gC-1) is the energy content of the phytoplankton and $Z$ (ind m-2) is the number of migrating zooplankton in the water column (estimated using carbon contents (mg C ind-1) derived from regressions of zooplankton length to carbon content from Mauchline (1998)). It is assumed that all zooplankton perform optimal DVM. $ε\_{c}$ is the fraction of the ingested carbon excreted as faecal pellets or respired as CO2, and $τ\_{ML} $is the fraction of a day spend below the mixed layer (mixed layer as used in the NPZ model (Fig. S1)). This method of estimating carbon export is similar to the approach applied by Dam et al. (1995) and Steinberg et al. (2000) who estimated zooplankton respiratory carbon flux across the mixed layer from observations on migrant biomass and respiration rates assuming equal time spent above and below the mixed layer (i.e. $τ\_{ML}$ = 0.5). In contrast, in our model $τ\_{ML}$ is an emergent property of optimal DVM behaviour, and can vary substantially as a function of latitude, time of year, zooplankter size, and phytoplankton biomass.

To predict the amount of carbon transported vertically, the migration distance is separated into 20 meter intervals (referred to as depth “bins”). By applying Eq. 5 it is assumed that excretion is continuous throughout the day with no temperature or pressure dependence. The optimal gain and the cost depend on the size of the organism. For simplicity, we assume the zooplankton biomass is distributed according to a logarithmic size spectrum ranging 200-2000 µm (Sheldon and Parsons 1967) which is split into five different size-classes. In reality, zooplankton size compositions will vary both over season and latitude, but this assumption provides some estimate of zooplankton size distribution in natural populations. During the rest of the study organisms in the high end of this size spectrum (1 – 2 mm) are referred to as large zooplankton and those towards the low end (200 – 300 µm) as small zooplankton.

To illustrate the predictions of the model in detail, two latitudes in the North Atlantic are selected; 31°N (Bermuda) and 60°N (Iceland). These sites are chosen to represent two different annual cycles; Iceland has a phytoplankton bloom in spring, followed by a zooplankton (Colebrook 1979), while the phytoplankton abundance at Bermuda is more constant throughout the year (less than an order of magnitude changes in abundance (Steinberg et al. 2001)).

## Results

### Optimal migration patterns

Due to the low phytoplankton abundance off Iceland from October to April, the model predicts no migration in this period, and zooplankton first begin migrating as the bloom is initiated (Fig. 2). At Bermuda, zooplankton perform DVM during most of the year, except for the winter months from November to January (Fig. 2). During the winter, phytoplankton abundance is so low that it is not energetically feasible for zooplankton to migrate. In addition, in the Iceland Basin light levels are low during winter which diminishes visual predation risk and reduces the need to migrate.

During the spring bloom, zooplankton migrate deeper than during the rest of the year (Fig. 2A, solid lines) as their food resources becomes more abundant and they can afford to spend energy on migrating deeper. The contour lines in Fig 3 provide an estimate of the sensitivity of fitness to actual migration strategy. The stretching of fitness contours with depth (Fig 3) is a consequence of the exponential attenuation of light in the water column. This means that the relative increase in fitness for a migration depth interval is much greater in the surface than at depth.

Large zooplankton are consistently predicted to migrate deeper than smaller zooplankton, as they are capable of acquiring more energy to spend on migration (Fig. 2). Specifically, energy gained from feeding has a cubic relation with zooplankton size (Eq. 2), while cost is has a linear dependence (Eq. 4), so that energetic gain from feeding can offset the cost of migration more readily for larger zooplankton. Consequently large zooplankton can migrate deeper. The model predicts that large zooplankton migrate down to a maximum depth of about 100 m, giving them a net migration amplitude of up to 90 m (from $z\_{0}$ to $z\_{max}$) (Table 2).

### Carbon transport by migrating zooplankton

As DVM occurs during most of the year at Bermuda, a larger amount of organic carbon is transported there compared to Iceland (Fig. 4). At Iceland, spring blooms are essential for the active transport, as almost all active flux occurs in the short period during the bloom where both phytoplankton and zooplankton abundances are high (Fig. 4A).

Large zooplankton have higher ingestion rates and they are responsible for a large fraction of the active transport (Fig. 4 right panels and Fig. 5). This means that although there are considerably fewer individuals compared to smaller size classes, large zooplankton are more important on a larger scale: they migrate deeper and thus can transport carbon further away from the surface mixed layer. This is in line with observations that find large zooplankton migrating deeper and showing significantly stronger DVM (Wiebe et al. 1992; Hays et al. 1994). In this model, all size classes contribute to the active export flux, but the large zooplankton (length 1 – 2 mm) are responsible for almost 50% as they ingest more carbon and are capable of migrating deeper (Fig. 5).

Intermediate latitudes (~30°N-~45°N) have the highest active carbon transport (Fig. 5). This is a result of the relatively high annual productivity at these latitudes predicted by the NPZ model, exhibiting a significant spring bloom on top of phytoplankton concentrations above 10-20 mg C m-2 the rest of the year (Fig. S1). This combination results in approximately 20 % higher active carbon export in latitudes ~30°N-~45°N compared to the either boreal or equatorial latitudes (Fig. 5). Integrating this over the whole North Atlantic (0oN – 66oN) suggests a total active transport contribution to the export flux of 0.34 (0.2-0.37) Gt carbon per year, an estimate that is in the same range as observations (Table 1). Alternatively, in terms of the mean POC export flux of 1.27 Gt C yr-1 in the North Atlantic (Sanders et al. 2014), 27% (16 - 29) % is mediated through the transport by zooplankton DVM.

## Discussion

### Optimal DVM

The predicted migration depths of the large zooplankton are comparable to observations made on meso-zooplankton in the high end of the size spectrum (Longhurst and Harrison 1990; Heywood 1996; Irigorien 2004; Steinberg et al. 2008; Sainmont et al 2014). Irigorien et al (2004) studied migration amplitudes of several different species and stages of species in the central Irish Sea; here he found that large copepods of the *Calanus spp.* have migration amplitudes of 50-70 m and smaller species and stages have migration amplitudes up to 40 m, both in line with the model predictions. Wiebe et al. (1992) found that large copepods migrate deeper than small ones, which is also consistent with one of the key patterns produced by the model.

The model predicts very little size dependence on $τ$ the time spent migrating per day, though it seems that large zooplankton spend a slightly higher fraction of the day on migration than the small ones (Fig. 2B). In contrast, De Robertis (2002) finds that large zooplankton descent earlier and ascent later than small ones, making them spend a larger fraction of the day on migration, a result quantitatively supported by observations (Wiebe et al. 1992). This short fall in our model may be due to the scaling of mortality risk to size, where large zooplankton are visually more conspicuous (Aknses & Giske, De Robertis).

According to the model, large zooplankton migrate at an average speed of 20-23 mm s-1 1 (from $z\_{0}$ to $z\_{max}$) (Table 2), which is high compared to observed swimming speeds from Mauchline (1998) that range from 4.2 mm s-1 for upward migration to 13 mm s-1 for downward migration for adult *Calanus finmarchicus*. However, Wiebe et al. (1992) found high migration speeds of above 20 mm s-1, which is in line with the model predictions. For large zooplankton, time spent migrating from the surface to the maximum depth is within the time interval for typical gut clearance rate of copepods (Table 2). Wiebe et al. 1992 finds that it takes about 30-60 minutes for a copepod to migrate back towards the surface from its day refuge. Gut clearance over this time interval means that the zooplanktons’ gut is cleared as it reaches maximum depth, and therefore the excretion only occurs on half of the migration path and not continuously as assumed in this study. This might lead to an overestimation of the active flux, but due to the large variation in the gut clearance rate for different species, sizes and life stages, it is unclear whether inclusion of the aspect would considerably improve the active flux estimates.

### Export Flux

Generally, the estimated ingestion and respiration and excretion rates are in the high end compared to observations (Table 2). These rates are related to the assumed constant efficiency $ε\_{c}$ that is set to 1/3. The fact that ingestion rates and consequently the excretion and respiration rates are in the high end results in the model overestimating the active flux.

Several estimates of the active flux in comparison to the total export flux have been made mostly based on observation from shorter periods (Longhurst et al 1990; Dam et al. 1995; Steinberg et al. 2000; Stukel et al. 2013). Compared to these, the model estimate is clearly at the high end of the observed range (Table 2). Especially, the active flux during spring bloom at Iceland is very high, but compared to spring bloom POC flux observations by Caron et al. (2004) and Buesseler et al (1992) the model estimate constitute 51 % (Table 2). The models percent wise comparison of the active flux to mean POC flux performs generally better. For instance, Dam et al. (1995) found at Bermuda that the respiratory carbon flux from migrating zooplankton across 150 meters during spring constituted on average 34 (±16) % of the gravitational particulate organic carbon (POC) flux. At same location Steinberg et al. (2000) finds the migratory carbon flux ranging 0 – 39 % of the mean POC. This indicates that while the model seems to overestimate some aspects, it performs well when estimating the proportional importance of the active flux.

### Impacts of model dynamics and assumptions

The motivation for this study has been in part to demonstrate the proof-of-concept for the introduction of active carbon transport by migrating zooplankton into GOCM’s as a dynamic element, an issue that is seen as a limiting factor in accurate representations of the biological pump (Steinberg et al. 2000). In this, we have demonstrated the feasibility of the approach and have verified the model results in terms of broad spatial and temporal patterns. There are however several points where the model can be improved. For instance, while allowing for a dynamic migration behaviour in response to changes in the light and food availability, our model is not fully dynamic. The DVM model has no coupling back to the NPZ model. For instance, DVM will modulate the effective grazing pressure on phytoplankton,. In addition, active transport by DVM removes nitrogen from the mixed layer along with carbon, which in a fully dynamic model also would impact the phytoplankton growth. Likewise, there are game theoretic aspects to consider, where optimal behaviour also depends on the emergent behaviour of predators, prey and competitors (Sainmont et al. 2013). The DVM model also assumes no future change in conditions, either in the environment or the organism, which is the so-called myopic assumption (Sainmont 2015). In reality, the choices made by a zooplankton will affect its lifetime fitness (Mangel and Clark 1988, Houston and McNamarra 1999) as the organism grows and contends with seasonal variations. In this, both the state and the stage of the organism are important; is it hungry or full, is it trying to find a mate, is winter coming? Such aspects can influence the outcome of choices in ways not predicted by myopic optimal behaviour based on Gilliam’s rule.

The model incorporates a simple representation of zooplankton size that assumes a uniform distribution of biomass within logarithmic length classes. As well as latitudinal variations (San Martin et al. 2006), zooplankton size will reflect species succession and ontogeny through a seasonal cycle with small zooplankton in dominating in early spring and fall and larger individuals dominating during the summer. Subsequently, variations in size distribution within the zooplankton community will introduce variations in the active carbon export, and would require a size structured zooplankton model (e.g. Ward et al. 2012) to be resolved.

We admit that several parameters in the model are not very well constrained. These are parameters that in nature are very variable in time and space like the background mortality $μ\_{0}$, and the mortality factor $m\_{fac}$ . While this might add uncertainty to the model results, we stress that the aim of study is as much about producing general spatial and seasonal patterns of DVM and active carbon transport by zooplankton as it is about exact predictions in given locations.

## Conclusion

We have demonstrated a general method by which the effects of DVM can be incorporated into models of carbon export. The method is dynamic in nature, being driven by the optimization of feeding opportunity against the risk of predation. The general patterns, both spatially and temporally, are in broad agreement with observations. The size of the zooplankton is resolved, and it appears that the greatest flux is driven by a small number of large animals.

The findings of this model study support earlier studies and suggest, that the active transport of carbon by diel vertically migrating zooplankton is substantial and should be considered when making estimates of the oceans atmospheric carbon sequestration. Even more importantly, the model proposes a simple way to include the dynamics of the active transport into global scale carbon budgets.

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Fig. 1. A conceptual overview of the diel vertical migration (DVM) model. During hours of darkness, zooplankton graze in the surface, but retreat to depth during day light hours as they become more vulnerable to visual predators. The zooplankton can vary the time they spend on migration ($τ$) and their maximum migration depth ($z\_{max}$) to optimize their fitness as a trade-off between feeding, cost of migration and mortality risk; factors that can be expected to vary with latitude, time of year, and zooplankton size. During DVM the zooplankton excrete and respire carbon, which in this model is assumed to occur continuously on the migration path.

Fig. 2. (A) The optimal migration depth ($z\_{max}$) and (B) the optimal migration time ($τ$) as a fraction of the day. The shading of the black indicates decreasing zooplankton size (what are the sizes??). Iceland is in solid lines and Bermuda is in dashed lines.

Fig. 3. Contours of the fitness surface indicating 99%, 95% and 90% of optimal fitness for a day during the spring bloom (black contours) and a day during fall (grey contours) for the Iceland site (size ??).

Fig. 4. Estimates of carbon respiration and defecation with depth; daily estimates left and yearly estimates right from A) Iceland and B) Bermuda. The different shades in the right panels show the contribution of zooplankton of decreasing sizes (the largest size class in black).

Fig. 5. Estimate of the total active transport of excreted and respired carbon integrated across all size classes (200 – 2000 m) to below the mixed layer at all latitudes ranging 0° N - 66° N (solid line). The grey shading indicates the variance in transport associated with a 95% spread in relative fitness with regards optimal migration depth, and the dashed line indicates the contribution of only the largest zooplankton size class (length 1 – 2 mm).