

# Fear and loathing in the pelagic: how behaviour impacts the biological carbon pump

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## Abstract

## 1 Introduction

The ocean exerts a strong control on global climate because of its ability to sequester carbon away from the atmosphere (Boyd et al., 2019). This sequestration is due to a persisting gradient of dissolved inorganic carbon (DIC) between the oceans' surface and depth (Sarmiento and Gruber, 2006). DIC surface concentrations are approx. 2000  $\mu\text{mol /kg}$ , but DIC concentrations are around 2300  $\mu\text{mol /kg}$  at depth (Sarmiento and Gruber, 2006). This difference means that around 4000 PgC are sequestered in the oceans' interior (figure 1). The biological carbon pump is responsible for around 90 % of this sequestration, while oceanic pumps (mainly the solubility pump – colder waters lead to a higher CO<sub>2</sub> solubility) are responsible for the remainder (Sarmiento and Gruber, 2006; Boyd et al., 2019). The biological pump is paramount to climate regulation, as model predicts that its absence would result in atmospheric CO<sub>2</sub> concentrations around two-fold higher (Maier-Reimer et al., 1996). It is estimated that the ocean presently contains roughly 31% of anthropogenic carbon released during the Anthropocene (Gruber et al., 2019), and it will eventually sequester most of the released anthropogenic carbon (Montenegro et al., 2007).

The biological carbon pump (BCP) is the transport of photosynthetically-fixed carbon from the surface of the oceans to the depths (Volk and Hoffert, 1985; Falkowski et al., 1998; Le Moigne, 2019). It consists mostly of the biological gravitational pump (Boyd et al., 2019), that is the passive sinking of organic matter (the so-called marine snow that consists of fecal pellets, shells, exoskeletons, carcasses, and aggregates of organic matter from different sources). But the downward flux can also occur through the active transport of carbon by marine organisms via diel or seasonal vertical migrations (Bianchi et al.,

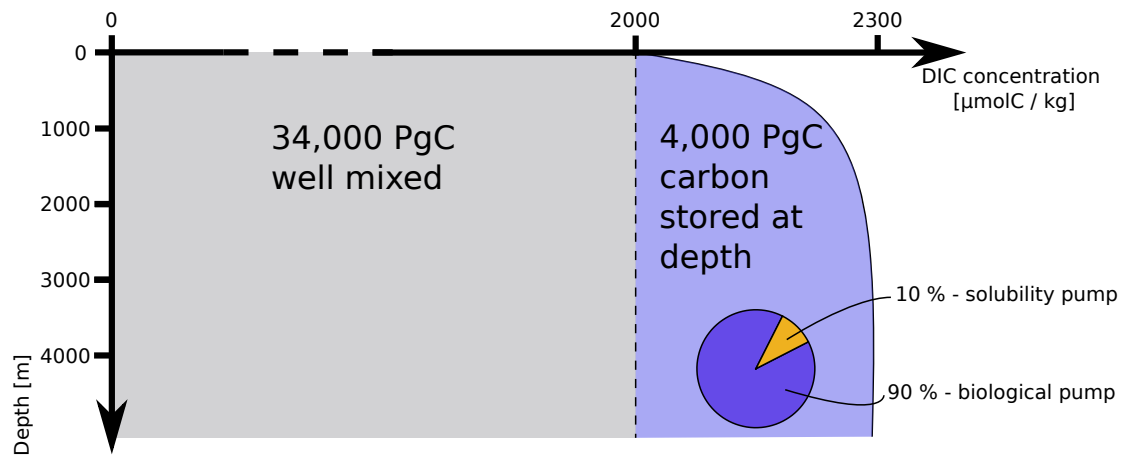


Figure 1: DIC concentration in the oceans as a function of depth and corresponding DIC sequestered.

2013; Jónasdóttir et al., 2015), or through the advection of neutrally buoyant organic matter entrained by downwellings and/or mixing. The BGP is responsible for the export of more than 6 PgC / yr below the euphotic zone, the migrant pump for more than 3 PgC / yr, and flux due to mixing and advection accounts for around 1 PgC / yr (Boyd et al., 2019). In the following of this work, because of its limited importance and because it is mostly driven by physico-chemical (as opposed to biological) processes, we will not consider flux due to mixing and consider the BCP as the sum of the gravitational and the migrant pump – an assertion in agreement with most recent studies of the BCP (Aumont et al., 2018; Archibald et al., 2019).

Because of its very nature, the BCP is very sensitive to biological processes and the functioning of marine ecosystems. In particular, marine organisms have the ability to modify and influence trophic interactions and population dynamics through their behaviour (Schmitz et al., 2004, 2008; Wirsing et al., 2021). As the funding element of the migrant pump, the migration behaviour of marine organisms is already recognized as an important parameter driving carbon export (Aumont et al., 2018; Archibald et al., 2019; Jónasdóttir et al., 2015; Visser et al., 2017), but other behaviours may also be important in shaping carbon flux intensity. For example, colony-forming phytoplankton cells (colonies that can be induced by the presence of predators (Lürling and Van Donk, 1996; Van Donk et al., 1999)) are better protected against predation (Lürling and Van Donk, 1996; Pančić and Kiørboe, 2018). As such, they benefit from a higher growth rate, and increasing population sizes will ultimately increase carbon flux through the sinking of more dead phytoplankton cells (and they will sink faster as cells will aggregate). But conversely, better protected cells decreases predation risk, thus decreasing food intake from predators – and consequently fecal pellet excretion, reducing carbon export mediated by higher trophic levels.

Here, we review the possible consequences of anti-predatory behaviour for the biological pump. We will adopt a mechanistic trait-based approach, where organisms are defined by a few key traits interrelated through trade-offs rather than by their taxonomic affiliation, as this approach has proven to be more

efficient at describing complex ecosystems in simple ways (Kjørboe et al., 2018). We define behaviour as a set of traits that can be altered more or less rapidly, and potentially only temporarily. As such, the chain-forming ability of phytoplankton, the toxin production capacity of dinoflagellates, or the diel vertical migrations of fish are all examples of behaviour. In contrast, the size of an organism is a well-defined trait, but it is not a behaviour as it cannot be modified rapidly nor only temporally (with a few notable exceptions – such as puffer fish and gulper eels, and in this case, the trait is size at rest and the behaviour is the ability to increase its size).

A notable group of behaviour is anti-predatory behaviours, i.e. behaviours aimed at decreasing predation risk. Specifically, anti-predatory behaviours serve one (or more) of the following goals: detect predators, evade predators, or resist their attacks (Ohman, 1988; Wirsing et al., 2021). For example, fish schooling helps to resist predators as predators are less able to catch prey within schools (Brock and Riffenburgh, 1960; Fréon and Misund, 1999), but it also increases detection as information travels faster within fish schools than with dispersed individuals (Gerlotto et al., 2006; Handegard et al., 2012). Diel vertical migration helps evading predators, as its motive is to reduce detectability by hiding in darker waters during daytime (Zaret and Suffern, 1976).

Notwithstanding the ultimate goal of the anti-predatory behaviour, there is always a trade-off and a cost has to be paid for any benefit, e.g. in terms of reduced growth, missed feeding or mating opportunity (Litchman and Klausmeier, 2008). For instance, being in a school reduces feeding opportunities because of competition with conspecifics, and performing diel vertical migration decreases feeding rates because the migrant has access to food-rich surface waters only during part of the day. As a consequence, anti-predatory behaviours can also have indirect effects on other levels of the food-web, through direct or indirect effects (trait-mediated indirect interactions, TMII or density-mediated indirect interactions, DMII). These indirect effects can be as important as or more important than direct effects (Kotler and Holt, 1989; Peacor and Werner, 2001; Schmitz et al., 2004), and can therefore have important cascading consequences when it comes to carbon export.

The aim of this article is to highlight how anti-predatory behaviour of marine organisms can impact carbon export in the pelagic. First, we consider the different mechanisms through which anti-predatory behaviour can alter carbon export, with the help of three mechanistic models of increasing complexity considering successively individuals, populations, and ecosystems. Second, we review the different aspects of the biological carbon pump (production of organic matter, efficiency of the biological carbon pump, active transport, and spatio-temporal aspects) and relate how the different behaviours observed in the pelagic can impact them. Third, we discuss various important effects to consider with behaviour in relation to the biological carbon pump in the pelagic. Finally, we highlight directions and perspectives for further research.

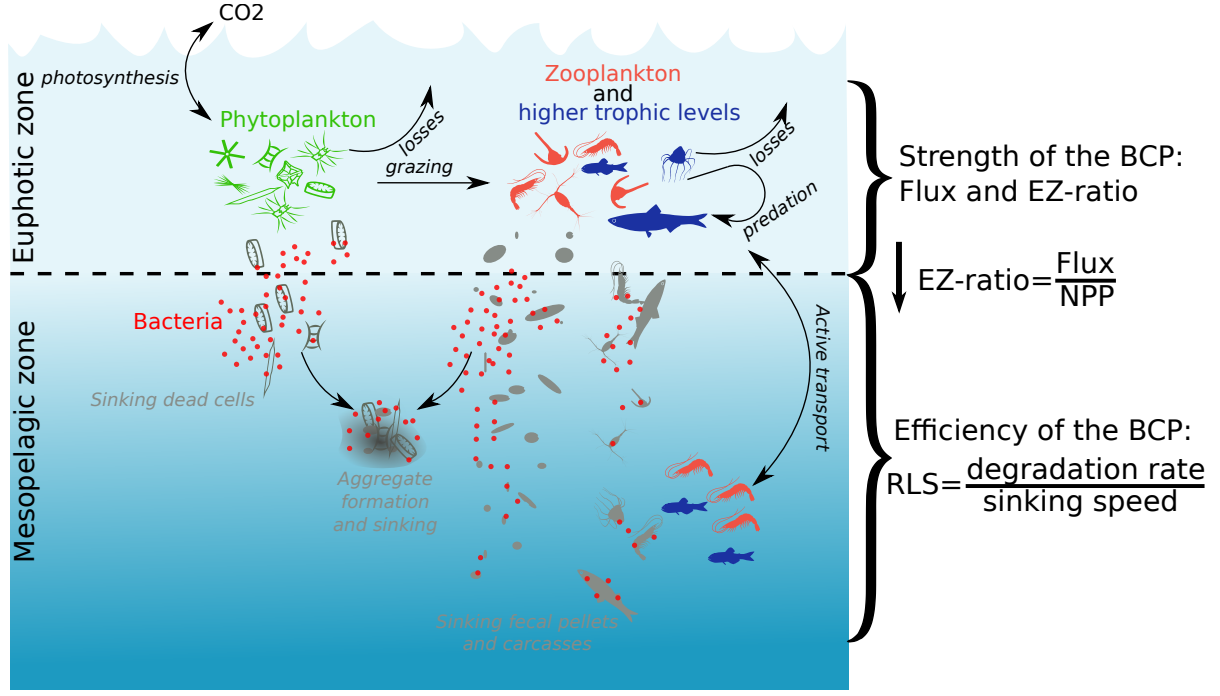


Figure 2: Sketch of the biological pump. Phytoplankton fix  $\text{CO}_2$  through photosynthesis, before being grazed upon by consumers that can be, in turn, preyed upon by higher trophic levels. The fraction of NPP that sinks (as dead cells, fecal pellets, carcasses or aggregates of all these) or is transported (by actively migrating organisms) below the euphotic zone is the EZ-ratio (Buesseler and Boyd, 2009). As detritus sink, bacteria degrade them into DIC. The ratio between detritus degradation rate (in  $\text{day}^{-1}$ ) and sinking rate (in  $\text{m day}^{-1}$ ) is the remineralization length scale (RLS, in  $\text{m}^{-1}$ ), a measure of the efficiency of the BCP (Bach et al., 2019). As such, the strength of the BCP is set in the euphotic zone, while its efficiency depends on processes mainly taking place below the euphotic zone Buesseler and Boyd (2009).

## 2 The biological carbon pump, from individuals to ecosystems

A common way to assess mechanistically the strength of the BCP in a given ecosystem is through the EZ-ratio, defined as (Buesseler and Boyd, 2009):

$$EZ - ratio = \frac{\text{export below euphotic zone}}{NPP}, \quad (1)$$

while the efficiency of the carbon pump is defined by the remineralization length scale (Bach et al., 2019):

$$RLS = \frac{\text{degradation rate}}{\text{sinking speed}}. \quad (2)$$

Knowledge of both the strength and the efficiency of the BCP is necessary to assess how much carbon is exported below a given depth (figure 2).

The definition of the EZ-ratio emphasizes the importance of new primary production (NPP) for the export flux. However, the EZ-ratio can be modified by several other factors. Thus far, efforts have focused on the importance of bacterial remineralization (Belcher et al., 2016; Buchan et al., 2014; Buesseler et al., 2007; Le Moigne et al., 2016), phytoplankton community structure (Buesseler, 1998; Boyd and Newton,

1999; Francois et al., 2002), and zooplankton (Hansen and Visser, 2016; Steinberg et al., 2002; Archibald et al., 2019; Cavan et al., 2019) for the export flux, demonstrating observationally (Buesseler, 1998) and with modelling (Wassmann, 1998; Henson et al., 2015) that the export flux is unlikely to be constant spatially or temporally.

The efficiency of the biological pump depends on detritus sinking speed that is directly related to the trophic assemblage in the water column, and on the degradation rate of bacteria, usually assumed to be food-web-independent (even though it can be modified, during e.g. bloom events or with the sinking of toxic material (Bach et al., 2019)).

Here, we demonstrate how considering marine organisms behaviour and its cascading consequences for food-web dynamics increases our mechanistic understanding of carbon fluxes, by affecting both the strength and the efficiency of the BCP, and in particular of the gravitational pump. Active transport of carbon by migrating organisms is a particular behaviour that constitutes a different pump (the migrant pump), and to remain general we will not include this behaviour in this section.

The lowest level of complexity when considering the biological carbon pump is to interpret the *EZ* – *ratio* literally, and to consider only primary production in relation to the carbon flux. In a system at equilibrium, the export flux would be equal to NPP (Eppley and Peterson, 1979), for a total carbon export of 2.0 – 4.5 GtC / yr, at around 10 % of the total primary production.

We illustrate this with a simple example. Disregarding zooplankton (i.e. assuming that phytoplankton cells are perfectly defended), detritus in the water column originates only from dead phytoplankton cells. The concentration of detritus  $D_\varphi$  in the water column is then governed by:

$$\frac{\partial D_\varphi}{\partial z} = \frac{S(z) - \alpha D_\varphi}{\omega_\varphi}, \quad (3)$$

with  $S$  the source term of detritus (i.e. the natural mortality rate of phytoplankton),  $\alpha$  the degradation rate of detritus in the water column due to bacterial respiration and  $\omega_\varphi$  the sinking speed of dead phytoplankton cells. The carbon flux  $F_\varphi$  at any depth is

$$F_\varphi = \omega_\varphi D_\varphi. \quad (4)$$

However, zooplankton play an important role in carbon flux by repackaging phytoplankton cells in fast-sinking fecal pellets (Eppley and Peterson, 1979; Stamieszkin et al., 2015; McDonnell and Buesseler, 2010; Turner, 2002, 2015). With a set-up similar to eq. 3, we consider that zooplankton consume all phytoplankton (so cells end up being ingested rather than sinking). The concentration of detritus in the water column  $D_P$  is then:

$$\frac{\partial D_P}{\partial z} = \frac{\tilde{S}(z) - \alpha D_P}{\omega_P}, \quad (5)$$

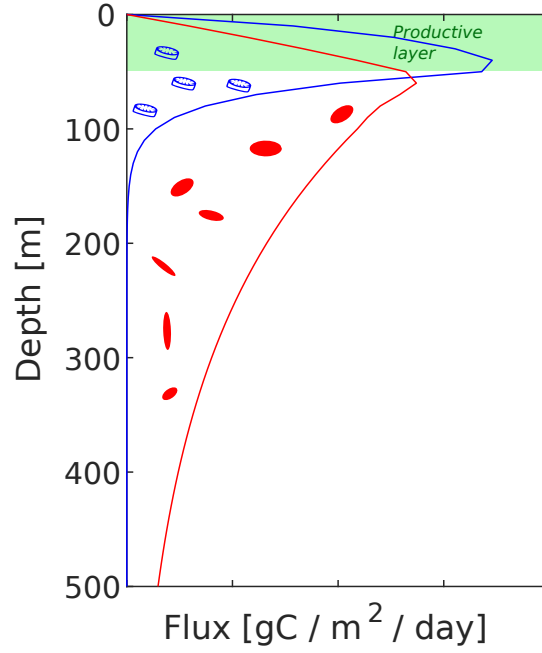


Figure 3: POC flux as a function of depth if all flux originates from dead phytoplankton cells (blue) or from zooplankton fecal pellets (red).

with  $\omega_P$  the sinking rate of zooplankton fecal pellets and  $\tilde{S}$  the detritus source term, equal to  $\tilde{S} = (1 - \varepsilon_P)S$ ,  $\varepsilon_P$  being the assimilation efficiency of zooplankton. The carbon flux is defined by

$$F_P = \omega_P D_P. \quad (6)$$

Both fluxes  $F_\varphi$  and  $F_P$  are pictured in figure 3. Assuming a constant production term in the euphotic zone (assumed here to be in the first 50 m of the water column), the flux directly below the euphotic zone is more important in the absence of zooplankton predation. This is because only a little fraction of what is ingested gets excreted as fecal pellets, as an important fraction of carbon ingested by zooplankton is assimilated by the organisms. However, as zooplankton fecal pellets sink faster, the RLS is higher for phytoplankton than zooplankton detritus. Therefore,  $F_P$  attenuates much less than  $F_\varphi$ , and is already 8 times larger than  $F_\varphi$  at 100 m depth. This difference in carbon export efficiency at depth is visible in the field, as zooplankton fecal pellets usually account for less than 25 % of the flux below 200 m (Turner, 2002) but can account up to more than 99 % of the flux below 400 m in some cases (Bishop et al., 1977) – even though the relative proportion of fecal zooplankton fecal pellets in carbon flux can vary tremendously both spatially and temporally, from less than 2 to more than 90 % (Lalande et al., 2011; Stukel et al., 2013; Turner, 2015).

These discrepancies in flux variation originating from zooplankton fecal pellets highlight the need to consider predator-prey interactions and trophic levels higher than phototrophs to assess the strength

of the carbon flux. An important factor that modifies trophic couplings is the level to which prey are defended. The previous cases mimic two idealized situations where (i) phytoplankton are not defended and subject to predation vs. (ii) where phytoplankton are perfectly defended and thus where zooplankton are unable to survive. But while defense mechanisms offer protection, they come at a cost which can have consequences for population dynamics. It is therefore important to consider the consequences that defense levels can have on population dynamics, and consequently on carbon flux.

Again, we illustrate this by a simple example, where two populations interact in a productive layers following Lotka-Volterra equations:

$$\begin{cases} \frac{\partial N}{\partial t} &= rN(1 - \frac{N}{K})f_{compet}(S, \tau) - \beta f_{gain}(S, \tau)N \frac{P}{w_P} - \mu_N N, \\ \frac{\partial P}{\partial t} &= \varepsilon_P \beta f_{gain}(S, \tau)N \frac{P}{w_P} - \mu_P P, \end{cases} \quad (7)$$

with  $N$  and  $P$  the prey and predator concentration respectively,  $r$  the maximum prey growth rate,  $K$  the prey carrying capacity,  $\beta$  the predator clearance rate,  $w_P$  the predator carbon mass, and  $\mu_N$  and  $\mu_P$  the prey and predator background mortality, respectively. We consider that prey can change its defense level (e.g. toxicity, shell thickness). This provides them with a decrease in predation risk  $f_{gain}$ , but also a decrease in net growth rate  $f_{compet}$ . The shape of the trade-off, i.e. the relationship between  $f_{gain}$  and  $f_{compet}$  is modulated by  $\tau$  (Våge et al., 2014; Cadier et al., 2019).  $S$  is the level of defense of individuals:  $S = 0$  is for populations not defended while  $S = 1$  is for populations completely defended. The cost to pay for any defense can either occur as an extra metabolic cost, or as a decrease in foraging or nutrient acquisition capacity (Cadier et al., 2019; Chakraborty et al., 2019). Here, we assumed that the cost only occurred as a decrease in resource acquisition capacity, and we have (Cadier et al., 2019):

$$\begin{cases} f_{gain}(S, \tau) &= 1 - S^\tau, \\ f_{compet}(S, \tau) &= (1 - S)^\tau. \end{cases} \quad (8)$$

The relation between  $f_{gain}$  and  $f_{compet}$  is shown in figure 4.

Based on eq. 7, the creation rate of detritus, originating from carcasses and fecal pellets of prey and predators are:

$$\begin{cases} S_{FP,N} &= \frac{1-\varepsilon_N}{\varepsilon_N} r(1 - \frac{N}{K})N f_{compet}(S, \tau), \\ S_{C,N} &= \mu_N N, \\ S_{FP,P} &= (1 - \varepsilon_P) \beta f_{gain}(S, \tau)N \frac{P}{w_P}, \\ S_{C,P} &= \mu_P P, \end{cases} \quad (9)$$

with  $S_{FP,N}$  and  $S_{C,N}$  the creation term originating from prey fecal pellets and carcasses (respectively), and similarly for predators and  $S_{FP,P}$  and  $S_{C,P}$ .

The defense-competition trade-off leads to different equilibrium population sizes depending on the

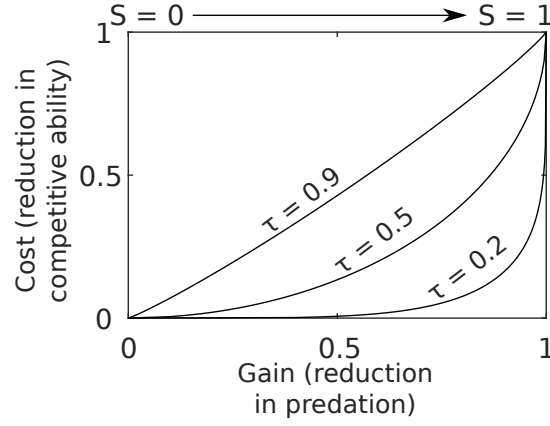


Figure 4: Shape of the defense-competition trade-off for different values of  $\tau$ .  $S = 0$  means that the organism is not defended, whereas  $S = 1$  means that the organism is perfectly defended. Adapted from Cadier et al. (2019).

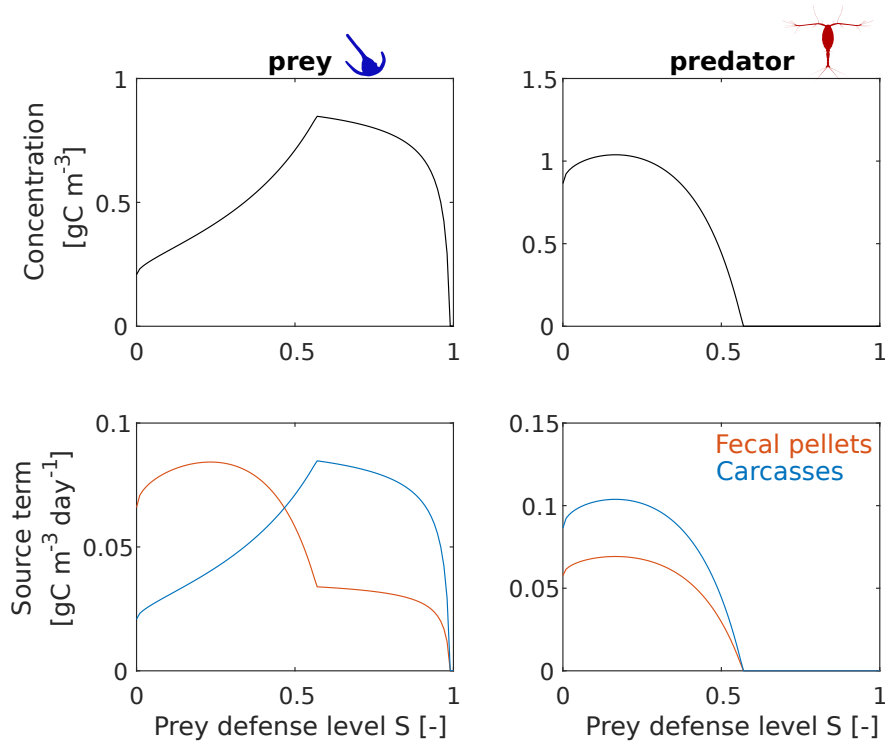


Figure 5: Top: Equilibrium biomasses of prey (left) and predator (right). Bottom: Ensuing production rates of detritus as fecal pellets (orange) or carcasses (blue) for prey (left) and predator (right).



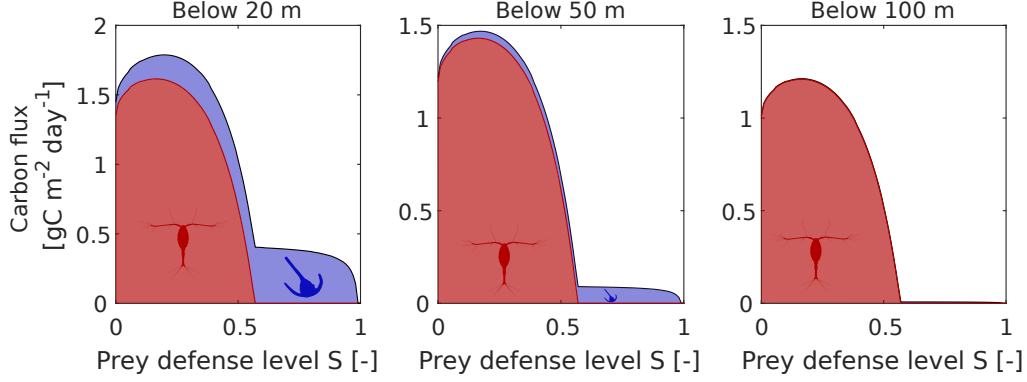


Figure 6: Carbon fluxes originating from both fecal pellets and carcasses for prey (blue) and predators (red) at 20, 50, and 100 m assuming a productive layer of 20 m.

level of defense of the prey (figure 5). In our example, the optimal defense level for prey is around  $S = 0.6$  – this corresponds to the level where predator go extinct. Indeed, after this point, any further investment in defense is a waste as it will not decrease predation risk further while still diminishing food intake. Natural mortality losses are directly proportional to population sizes, but fecal pellets production depends on ingestion rate. Consequently, the maximum detritus production rate does not necessarily correspond with the maximum population size. Further, copepods create bigger and faster-sinking detritus, so as long as they are present in the system they are responsible for the majority of the flux below the euphotic zone – and this share increases with depth (figure 6). Interestingly, the optimal defense level for prey does not correspond to the defense level that would optimize carbon flux.

In nature, an increase in defense level can also incur an increase in sinking speed for both prey carcasses and predator fecal pellets, for example because of heavier prey shells (Besiktepe and Dam, 2002) or increased coagulation due to the presence of transparent exopolymer particles (TEP, Engel et al., 2004). Without modifying the production rate of detritus (strength of the BCP), this directly impacts the RLS and thus the efficiency of the pump. This increase can be modelled as:

$$\begin{cases} \tilde{\omega}_{C,N}(S) &= (S + 1)\omega_{C,N} \\ \tilde{\omega}_{FP,P}(S) &= (S + 1)\omega_{FP,P}, \end{cases} \quad (10)$$

with  $\omega_{C,N}$  and  $\omega_{FP,P}$  the reference sinking speeds of prey carcasses and predator fecal pellets, respectively.

Considering this relation between defense level and sinking speed does not fundamentally change carbon export (figure 7), except at depth ( $> 50$  m) at high defense levels, where the increased sinking speed of phytoplankton carcasses means that a larger fraction of them reaches the depths. Even if this simple exercise disregards temporal dynamics that can be important to consider, it still highlights the importance of well-defended phytoplankton blooms (diatoms, toxic algae) for carbon export. For instance, during blooms, diatoms can account for the bulk of carbon export. In Disko Bay (Greenland), diatoms were found to account for most of the strength of the BCP, representing 60 % of the carbon flux below 50

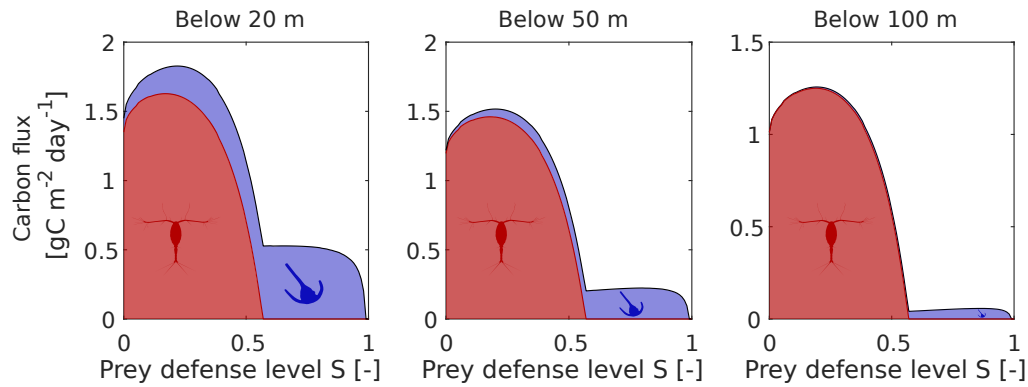


Figure 7: Carbon fluxes originating from both fecal pellets and carcasses for prey (blue) and predators (red) at 20, 50, and 100 m as prey carcasses and predator fecal pellet sinking speeds are proportional to the prey defense level, assuming a productive layer of 20 m.

m (Dünweber et al., 2010). In the North Atlantic, during a spring diatom bloom, 25 to 43 % of the export that reached 100 m reached 750 m, highlighting the high efficiency of this carbon export pathway (Martin et al., 2011). This flux consisted almost entirely of ungrazed diatoms and TEP. In the Southern Ocean, similar results were found when an iron fertilization experiment led to a diatom bloom, of which more than 50 % sank below 1000 m (Smetacek et al., 2012), and phytoplankton blooms can sink well below that as deep sea sedimentation of phytoplankton blooms has been recorded across the globe (Smetacek, 1985; Beaulieu, 2002). Toxic blooms also lead to high export efficiency, and toxic material has been found in sediment traps 800 m below the surface (Schnetzler et al., 2007). Toxic material can also affect the bacterial community, decreasing remineralization rate and hence increasing export efficiency (Bach et al., 2019). Toxicity as a defense mechanism can also incur carbon export thanks to other mechanisms. First, through the release of toxins directly in the water column, as toxins can sink and agglomerate with other organisms (Schnetzler et al., 2007). Fecal pellets are thus not the only kind of organic detritus that can be released by organisms. Second, through cascading effects in the food-web. Indeed, toxins can directly affect other marine organisms. Toxins can accumulate in zooplankton and up the food-web (Petitpas et al., 2014), all the way to marine mammals that can then die of poisoning (Schnetzler et al., 2007). An increased mortality then leads to an increased sinking of carcasses in the water column, and thus potentially to a very high local flux as large fish and marine mammals sink all the way to the seafloor.

Further, cascading effects appear to be important in determining carbon flux and carbon export efficiency. Lack of significant statistical relationships between biomass and DIC production in mesocosm experiments highlights the importance of the microbial food-web in determining dissolved inorganic carbon (DIC) production (Engel et al., 2004). Food-web structure is now recognized as an important proxy for computing carbon export efficiency (Guidi et al., 2009, 2015; Henson et al., 2019; Bach et al., 2019), something logical considering the impact that different food-web structures can have in terms of biomass production and trophic transfer efficiency.

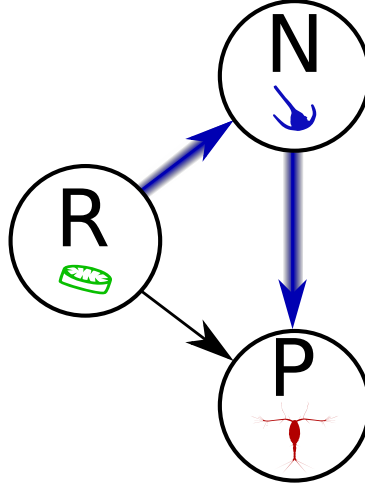


Figure 8: Intraguild predation. Diatoms ( $R$ ) are prey for both ciliates ( $N$ ) and copepods ( $P$ ). Copepods can prey on both diatoms and ciliates, and ciliates are the intraguild predator. Further, ciliates can modulate their defense investment, with consequences for their ingestion rate.

Behavioural activities can have far-reaching consequences on food-webs, as it is recognized that they can have indirect effects as important as, or even more important than direct predation effects (Kotler and Holt, 1989; Peacor and Werner, 2001; Schmitz et al., 2004). It is hard to measure in the field how these translate in terms of carbon flux, due to the difficulty to separate the different effects arising. However, numerical studies offer the adequate tools to understand the mechanistic effects that can arise.

As an illustrative example, we consider a food-web with intra-guild predation, for example casting a diatom prey  $R$ , a copepod predator  $P$  and a ciliate as the intra-guild consumer  $N$  (figure 8). If we allow ciliates to change their defense strategies in a similar fashion as in the previous example, the system can be represented by the following differential equations:

$$\begin{cases} \frac{\partial R}{\partial t} = rN(1 - \frac{R}{K})R - f_{compet}(S, \tau)\beta_N R \frac{N}{w_N} - \beta_{PR} R \frac{P}{w_P} - \mu_R R, \\ \frac{\partial N}{\partial t} = \varepsilon_N f_{compet}(S, \tau)\beta_N R \frac{N}{w_N} - f_{gain}(S, \tau)\beta_{PN} N \frac{P}{w_P} - \mu_N N, \\ \frac{\partial P}{\partial t} = \varepsilon_P (\beta_{PR} R + f_{gain}(S, \tau)\beta_{PN} N) \frac{P}{w_P} - \mu_P P, \end{cases} \quad (11)$$

with  $\beta_N$  the clearance rate of ciliates,  $\beta_{PR}$  and  $\beta_{PN}$  the clearance rates of copepod foraging diatoms and ciliates respectively,  $w_N$  and  $w_P$  the carbon mass of ciliates and copepods respectively, and  $\mu_R$ ,  $\mu_N$ ,  $\mu_P$  the background mortality rates of diatoms, ciliates and copepods respectively.

Depending on the shape of the competition-defense trade-off, this system has different outcomes: only diatoms are present, only diatoms and ciliates or diatoms and copepods, or all three species (Visser et al., 2012; Holt and Polis, 1997). Examples are provided for different values of  $(\tau, S)$  in figure 9.

While the three different runs had comparable equilibrium biomasses, resulting BCP differ largely (figure 10), both in terms of strength (export below the euphotic zone) and efficiency (attenuation as a function of depth). Simulations with surviving copepods yield much higher export flux at depth, because of the fast sinking speed of both their fecal pellets and carcasses. This highlights that changes in

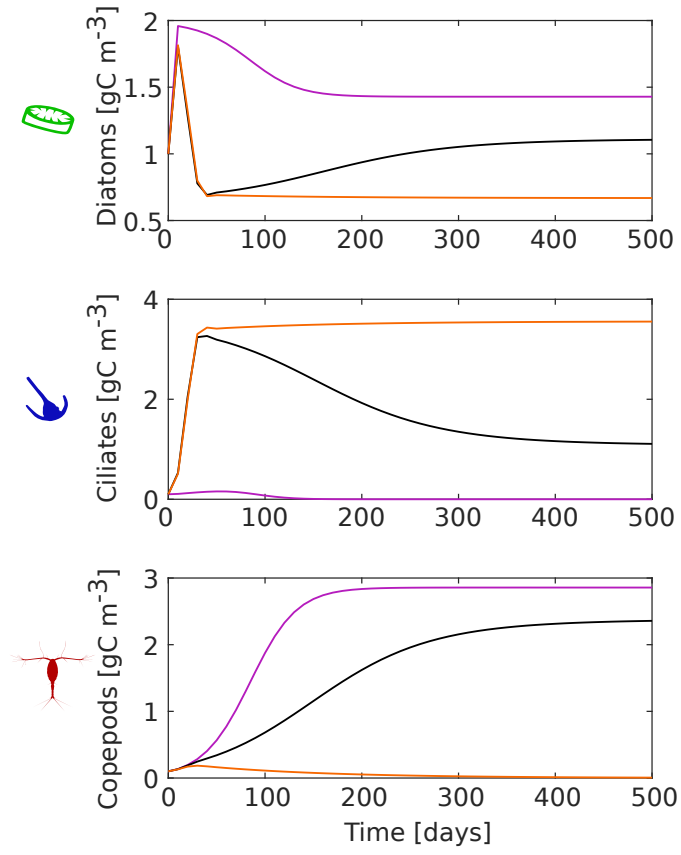


Figure 9: Population dynamics in a trophic food-web with intraguild predation. Purple lines are for  $(\tau, S) = (0.8, 0.8)$ , orange lines for  $(\tau, S) = (0.4, 0.6)$  and black lines for  $(\tau, S) = (0.5, 0.5)$ .

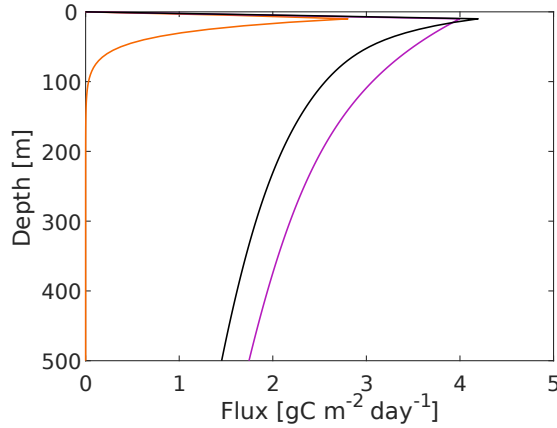


Figure 10: Carbon flux. Purple lines are for  $(\tau, S) = (0.8, 0.8)$ , orange lines for  $(\tau, S) = (0.4, 0.6)$  and black lines for  $(\tau, S) = (0.5, 0.5)$ .

community composition due to behavioural adaptations even without changes in total biomass can have drastic consequences for carbon export.

This three illustrating models are fairly simple, and should be interpreted as such. Accurate mechanistic models of the biological carbon pump ought to consider more complex dynamics and interactions that arise in nature.

First, our mechanistic description of behaviour is intently unspecified as to not lose in generality. However, many behaviour have different more ways of impacting the flux than modifying the production rate of detritus. For example, the production of TEP greatly increases the formation rate of aggregates (Engel, 2000) and has thus an impact in the deep carbon export of phytoplankton blooms (Kjørboe et al., 1994) – even though the positive buoyancy of TEP can also have the opposite effect (Mari et al., 2017). The production of toxins can also decrease bacterial activity, hence increasing directly the efficiency of the BCP (Bach et al., 2019). Another example is diel vertical migrations (Brierley, 2014), a behaviour that directly transports carbon to depths (Ducklow et al., 2001; Davison et al., 2013), consequently bypassing remineralization in the upper levels of the water column. Considering the effects of such behaviours on the biological pump requires to consider their specificity directly at the risk of overlooking important details.

Second, we consider here only the equilibrium biomasses of organisms, whereas environmental forcing lead to highly dynamic systems. In particular, analysing the onset and termination of blooms requires considering transient states of mechanistic systems. Because of the time that detritus takes to reach certain depths, field studies also need to take into account time dynamics when comparing surface productivity and carbon export at depth (Henson et al., 2019).

Third, we assume here that populations are homogeneous, which is far from being the case. Organisms grow and reproduce, sometimes even going through different ontogenetic changes and molting several times throughout their life cycle (Melle et al., 2004; Cavan et al., 2019). Modelling these ontogenetic

changes is crucial to understand the discrepancies that can be observed in the EZ-ratio at a global scale (?).

Finally, unlike what is assumed here, organisms do not have a fixed behaviour. They adapt their behaviour to the prevailing conditions to behave in the best way possible. Models can consider this behaviour changes thanks to optimization procedures (Fiksen and Giske, 1995; Varpe et al., 2007; Hansen and Visser, 2016). But it is important to keep in mind that organisms adjust to prevailing conditions simultaneously in what is in fact a survival game. As such, it might be necessary to consider the co-adaptations of organisms from multiple populations and multiple trophic levels. A method to do so is game theory (Maynard Smith, 1976). This technique has been applied to multiple habitat selection games, and in particular to diel vertical migrations involving several trophic levels (Iwasa, 1982; Gabriel and Thomas, 1988; Hugie and Dill, 1994; Sainmont et al., 2013; Thygesen and Patterson, 2018; Pinti and Visser, 2019; Pinti et al., 2019) - but hasn't, to our knowledge, been applied to other kind of behaviour in the pelagic, such as bioluminescently-mediated interactions at depths or toxin production and trophic interactions close to the surface.

### 3 Anti-predatory behaviours in the pelagic

We review here the different ways in which pelagic behaviours (figure 11 displays observations of different behaviour at the individual, population or ecosystem level) can impact carbon flux. We divided this section in four sub-sections: the production of organic matter, the efficiency of the carbon pump (that depends on the characteristic of the particulate matter produced and the flux attenuation in the water column), the active transport of detritus, and the spatio-temporal aspect of the BCP.

#### 3.1 Production of particulate matter

#### 3.2 Efficiency of the BCP

##### 3.2.1 Characteristics of the particulate matter

##### 3.2.2 Flux attenuation in the water column

#### 3.3 Active transport

#### 3.4 Spatio-temporal considerations

### Acknowledgements

We thank Fredrik Ryderheim, Peter Franks and Erik Selander for providing pictures for figure XXXX. This work was supported by the Centre for Ocean Life, a VKR Centre of excellence funded by the Villum

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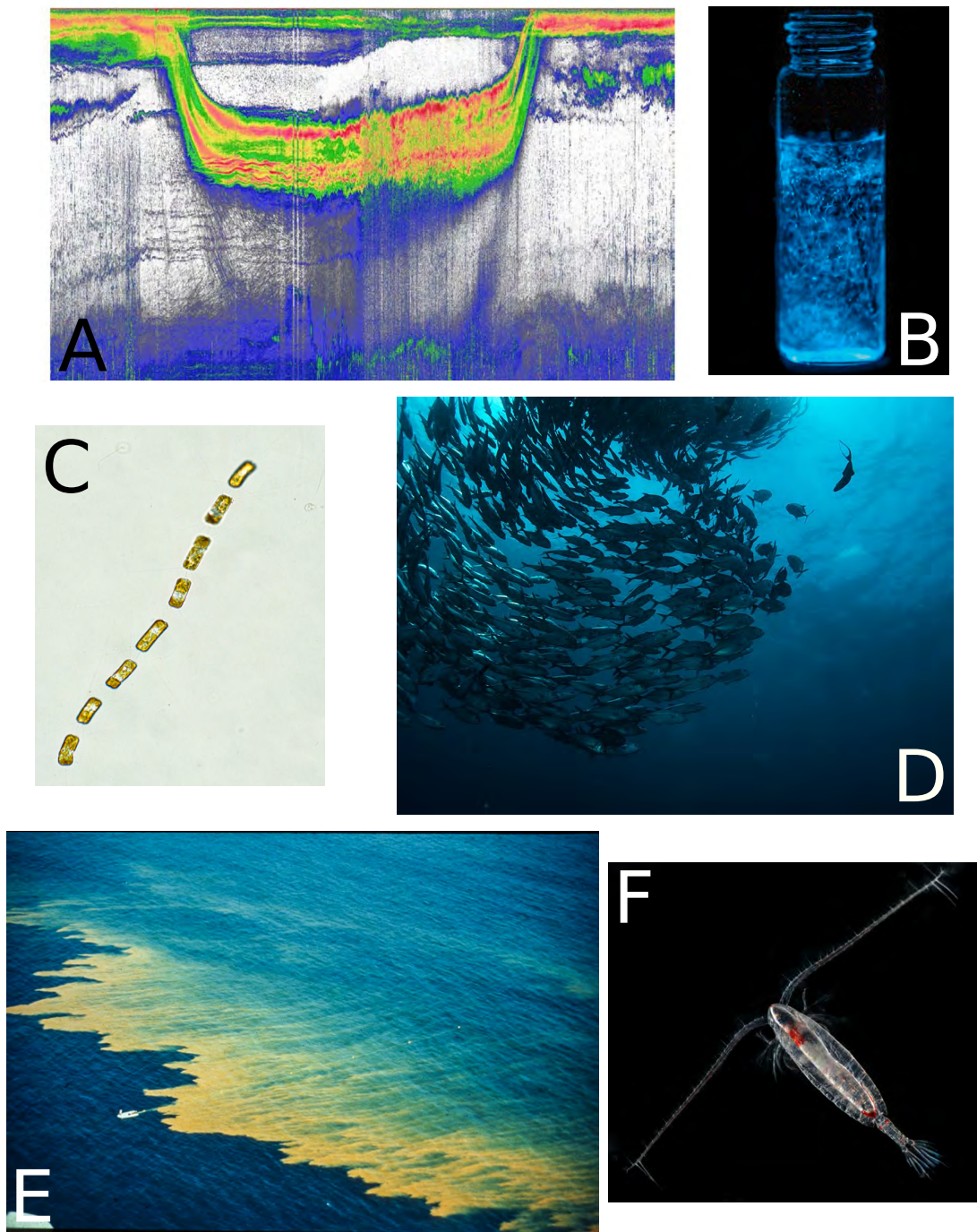


Figure 11: Different behaviours in the pelagic, observed at the individual, population or ecosystem level. (A) Echogram in the East Pacific realized over a daily cycle. Organisms remain close to the surface at night, migrate down at dawn, remain at depths during daytime before migrating up again at dusk. (B) A fiol of bioluminescent algae *Lingulodinium polyedra*. (C) A chain of diatoms *Thalassiosira nordenskiöldii*. (D) A school of black jack *Caranx lugubris* in the water column. (E) A red tide, a bloom of *Noctiluca scintillans* in 1995 off San Diego, California (USA). The floats on the line behind the boat are spaced 20 m apart. (F) A copepod *Calanus glacialis* with a visible lipid sac. These are necessary energy reserves to go under diapause. Figure credits: A, Thor Klevjer CC BY 4.0, reproduced from Klevjer et al. (2016), B,F Erik Selander, University of Gothenburg, Sweden, C, Fredrik Ryderheim, Technical University of Denmark, Denmark, D, Anna Varona, CC BY 4.0, E, Peter Franks, Scripps Institution of Oceanography, University of California San Diego, California, USA.

Foundation, and by the Gordon and Betty Moore Foundation (grant #5479).

## References

- Archibald, K. M., Siegel, D. A., and Doney, S. C. (2019). Modeling the impact of zooplankton diel vertical migration on the carbon export flux of the biological pump. *Global Biogeochemical Cycles*, 33:181–199.
- Aumont, O., Maury, O., Lefort, S., and Bopp, L. (2018). Evaluating the Potential Impacts of the Diurnal Vertical Migration by Marine Organisms on Marine Biogeochemistry. *Global Biogeochemical Cycles*, 32(11):1–22.
- Bach, L. T., Stange, P., Taucher, J., Achterberg, E. P., Algueró-Muñiz, M., Horn, H., Esposito, M., and Riebesell, U. (2019). The Influence of Plankton Community Structure on Sinking Velocity and Remineralization Rate of Marine Aggregates. *Global Biogeochemical Cycles*, 33(8):971–994.
- Beaulieu, S. (2002). Accumulation and fate of phytodetritus on the sea floor. *Oceanography and Marine Biology: an annual review*, 40:171–232.
- Belcher, A., Iversen, M., Giering, S., Riou, V., Henson, S. A., Berline, L., Guilloux, L., and Sanders, R. (2016). Depth-resolved particle-associated microbial respiration in the northeast Atlantic. *Biogeo-sciences*, 13(17):4927–4943.
- Besiktepe, S. and Dam, H. G. (2002). Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. *Marine Ecology Progress Series*, 229:151–164.
- Bianchi, D., Stock, C., Galbraith, E. D., and Sarmiento, J. L. (2013). Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochemical Cycles*, 27(2):478–491.
- Bishop, J. K., Edmond, J. M., Ketten, D. R., Bacon, M. P., and Silker, W. B. (1977). The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. *Deep-Sea Research*, 24(6).
- Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T. (2019). Multi-faceted particle pumps drive carbon sequestration in the ocean.
- Boyd, P. W. and Newton, P. P. (1999). Does planktonic community structure determine downward particulate organic carbon flux in different oceanic provinces? *Deep-Sea Research Part I: Oceanographic Research Papers*, 46(1):63–91.
- Brierley, A. S. (2014). Diel vertical migration. *Current Biology*, 24(22):R1074–R1076.



309 Brock, V. E. and Riffenburgh, R. H. (1960). Fish schooling: a possible factor in reducing predation.  
310 *ICES Journal of Marine Science*, 25(3):307–317.

311 Buchan, A., LeClerc, G. R., Gulvik, C. A., and González, J. M. (2014). Master recyclers: features and  
312 functions of bacteria associated with phytoplankton blooms. *Nature reviews. Microbiology*, 12(10):686–  
313 698.

314 Buesseler, K. O. (1998). The decoupling of production and particulate export in the surface ocean. *Global*  
315 *Biogeochemical Cycles*, 12(2):297–310.

316 Buesseler, K. O. and Boyd, P. W. (2009). Shedding light on processes that control particle export and  
317 flux attenuation in the twilight zone of the open ocean. *Limnology and Oceanography*, 54(4):1210–1232.

318 Buesseler, K. O., Lamborg, C. H., Boyd, P. W., Lam, P. J., Trull, T. W., Bidigare, R. R., Bishop, J.  
319 K. B., Casciotti, K. L., Dehairs, F., Elskens, M., Honda, M., Karl, D. M., Siegel, D. a., Silver, M. W.,  
320 Steinberg, D. K., Valdes, J., Mooy, B. V., and Wilson, S. (2007). Revisiting carbon flux through the  
321 ocean’s twilight zone. *Science*, 316(April):567–570.

322 Cadier, M., Andersen, K. H., Visser, A. W., and Kiørboe, T. (2019). Competition–defense tradeoff  
323 increases the diversity of microbial plankton communities and dampens trophic cascades. *Oikos*,  
324 128(7):1027–1040.

325 Cavan, E. L., Belcher, A., Atkinson, A., Hill, S. L., Kawaguchi, S., McCormack, S., Meyer, B., Nicol, S.,  
326 Ratnarajah, L., Schmidt, K., Steinberg, D. K., Tarling, G. A., and Boyd, P. W. (2019). The importance  
327 of Antarctic krill in biogeochemical cycles. *Nature Communications*, 10(1):1–13.

328 Chakraborty, S., Pančić, M., Andersen, K. H., and Kiørboe, T. (2019). The cost of toxin production in  
329 phytoplankton: the case of PST producing dinoflagellates. *ISME Journal*, 13(1):64–75.

330 Davison, P. C., Checkley, D. M., Koslow, J. A., and Barlow, J. (2013). Carbon export mediated by  
331 mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography*, 116:14–30.

332 Ducklow, H. W., Steinberg, D. K., and Buesseler, K. O. (2001). Upper Ocean Carbon Export and the  
333 Biological Pump. *Oceanography*, 14(4):50–58.

334 Dünweber, M., Swalethorp, R., Kjellerup, S., Nielsen, T. G., Arendt, K. E., Hjorth, M., Tønnesson,  
335 K., and Møller, E. F. (2010). Succession and fate of the spring diatom bloom in Disko Bay, western  
336 Greenland. *Marine Ecology Progress Series*, 419:11–29.

337 Engel, A. (2000). The role of transparent exopolymer particles (TEP) in the increase in apparent particle  
338 stickiness ( $\alpha$ ) during the decline of a diatom bloom. *Journal of Plankton Research*, 22(3):485–497.

- Engel, A., Delille, B., Jacquet, S., Riebesell, U., Rochelle-Newall, E., Terbrüggen, A., and Zondervan, I. (2004). Transparent exopolymer particles and dissolved organic carbon production by *Emiliania huxleyi* exposed to different CO<sub>2</sub> concentrations: A mesocosm experiment. *Aquatic Microbial Ecology*, 34(1):93–104.
- Eppley, R. W. and Peterson, B. J. (1979). Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, 282(5740):677–680.
- Falkowski, P. G., Barber, R. T., and Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science*, 281(5374):200–206.
- Fiksen, Ø. and Giske, J. (1995). Vertical distribution and population dynamics of copepods by dynamic optimization. *ICES Journal of Marine Science*, 52(3-4):483–503.
- Francois, R., Honjo, S., Krishfield, R., and Manganini, S. (2002). Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. *Global Biogeochemical Cycles*, 16(4):34–1–34–20.
- Fréon, P. and Misund, O. (1999). *Dynamics of Pelagic Fish Distribution and Behaviour: Effects on fisheries and stock assessment*. Blackwell Science, Oxford.
- Gabriel, W. and Thomas, B. (1988). Vertical Migration of Zooplankton as an Evolutionarily Stable Strategy. *The American Naturalist*, 132(2):199–216.
- Gerlotto, F., Bertrand, S., Bez, N., and Gutierrez, M. (2006). Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. *ICES Journal of Marine Science*, 63(8):1405–1417.
- Gruber, N., Clement, D., Carter, B. R., Feely, R. A., van Heuven, S., Hoppema, M., Ishii, M., Key, R. M., Kozyr, A., Lauvset, S. K., Monaco, C. L., Mathis, J. T., Murata, A., Olsen, A., Perez, F. F., Sabine, C. L., Tanhua, T., and Wanninkhof, R. (2019). The oceanic sink for anthropogenic CO<sub>2</sub> from 1994 to 2007. *Science*, 363(6432):1193–1199.
- Guidi, L., Legendre, L., Reygondeau, G., Uitz, J., Stemmann, L., and Henson, S. A. (2015). A new look at ocean carbon remineralization for estimating deepwater sequestration. *Global Biogeochemical Cycles*, 29:1044–1059.
- Guidi, L., Stemmann, L., Jackson, G. A., Ibanez, F., Claustre, H., Legendre, L., Picheral, M., and Gorsky, G. (2009). Effects of phytoplankton community on production, size and export of large aggregates: A world-ocean analysis. *Limnology and Oceanography*, 54(6):1951–1963.
- Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjøstheim, D. B., and Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology*, 22(13):1213–1217.

- Hansen, A. N. and Visser, A. W. (2016). Carbon export by vertically migrating zooplankton: An optimal behavior model. *Limnology and Oceanography*, 61(2):701–710.
- Henson, S., Le Moigne, F., and Giering, S. (2019). Drivers of Carbon Export Efficiency in the Global Ocean. *Global Biogeochemical Cycles*, pages 891–903.
- Henson, S. A., Yool, A., and Sanders, R. (2015). Global Biogeochemical Cycles carbon export : A model study. *Global Biogeochemical Cycles*, 29:33–45.
- Holt, R. D. and Polis, G. A. (1997). A theoretical framework for intraguild predation. *American Naturalist*, 149(4):745–764.
- Hugie, D. M. and Dill, L. M. (1994). Fish and Game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology*, 45(Supplement A):151–169.
- Iwasa, Y. (1982). Vertical migration of zooplankton: a game between predator and prey. *The American naturalist*, 120(2):171–180.
- Jónasdóttir, S. H., Visser, A. W., Richardson, K., and Heath, M. R. (2015). Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proceedings of the National Academy of Sciences*, 112(39):12122–12126.
- Kjørboe, T., Lundsgaard, C., Olesen, M., and Hansen, J. L. (1994). Aggregation and sedimentation processes during a spring phytoplankton bloom: A field experiment to test coagulation theory. *Journal of Marine Research*, 52:297–323.
- Kjørboe, T., Visser, A., and Andersen, K. H. (2018). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, 75(6):1859–1863.
- Klevjer, T. A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V. M., and Kaartvedt, S. (2016). Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Scientific Reports*, 6(1):19873.
- Kotler, B. P. and Holt, R. D. (1989). Predation and Competition: The Interaction of Two Types of Species Interactions. *Oikos*, 54(2):256.
- Lalande, C., Bauerfeind, E., and Nöthig, E. M. (2011). Downward particulate organic carbon export at high temporal resolution in the eastern Fram Strait: Influence of Atlantic Water on flux composition. *Marine Ecology Progress Series*, 440:127–136.
- Le Moigne, F. A. (2019). Pathways of Organic Carbon Downward Transport by the Oceanic Biological Carbon Pump. *Frontiers in Marine Science*, 6(October):1–8.

- Le Moigne, F. A., Henson, S. A., Cavan, E., Georges, C., Pabortsava, K., Achterberg, E. P., Ceballos-Romero, E., Zubkov, M., and Sanders, R. J. (2016). What causes the inverse relationship between primary production and export efficiency in the Southern Ocean? *Geophysical Research Letters*, 43(9):4457–4466.
- Litchman, E. and Klausmeier, C. A. (2008). Trait-Based Community Ecology of Phytoplankton. *Annual Review of Ecology, Evolution, and Systematics*, 39(1):615–639.
- Lürling, M. and Van Donk, E. (1996). Zooplankton-induced unicell-colony transformation in *Scenedesmus acutus* and its effect on growth of herbivore *Daphnia*. *Oecologia*, 108(3):432–437.
- Maier-Reimer, E., Mikolajewicz, U., and Winguth, A. (1996). Future ocean uptake of CO<sub>2</sub>: Interaction between ocean circulation and biology. *Climate Dynamics*, 12(10):711–722.
- Mari, X., Passow, U., Migon, C., Burd, A. B., and Legendre, L. (2017). Transparent exopolymer particles: Effects on carbon cycling in the ocean. *Progress in Oceanography*, 151:13–37.
- Martin, P., Lampitt, R. S., Jane Perry, M., Sanders, R., Lee, C., and D’Asaro, E. (2011). Export and mesopelagic particle flux during a North Atlantic spring diatom bloom. *Deep-Sea Research Part I: Oceanographic Research Papers*, 58(4):338–349.
- Maynard Smith, J. (1976). Evolution and the Theory of Games. *American Scientist*, 64(1):41–45.
- McDonnell, A. M. and Buesseler, K. O. (2010). Variability in the average sinking velocity of marine particles. *Limnology and Oceanography*, 55(5):2085–2096.
- Melle, W., Ellertsen, B., and Skjoldal, H. R. (2004). Zooplankton: the link to higher trophic levels. In *The Norwegian Sea Ecosystem*, pages 137–202.
- Montenegro, A., Brovkin, V., Eby, M., Archer, D., and Weaver, A. J. (2007). Long term fate of anthropogenic carbon. *Geophysical Research Letters*, 34(19):1–5.
- Ohman, M. D. (1988). Behavioral responses of zooplankton to predation. *Bulletin of Marine Science*, 43(3):530–550.
- Pančić, M. and Kiørboe, T. (2018). Phytoplankton defence mechanisms: traits and trade-offs. *Biological Reviews*, 93(2):1269–1303.
- Peacor, S. D. and Werner, E. E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences of the United States of America*, 98(7):3904–3908.

- Petitpas, C. M., Turner, J. T., Deeds, J. R., Keafer, B. A., McGillicuddy, D. J., Milligan, P. J., Shue, V., White, K. D., and Anderson, D. M. (2014). PSP toxin levels and plankton community composition and abundance in size-fractionated vertical profiles during spring/summer blooms of the toxic dinoflagellate *Alexandrium fundyense* in the Gulf of Maine and on Georges Bank, 2007, 2008, and 2010: 2. Plank. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 103:350–367.
- Pinti, J., Kiørboe, T., Thygesen, U. H., and Visser, A. W. (2019). Trophic interactions drive the emergence of diel vertical migration patterns: a game-theoretic model of copepod communities. *Proceedings of the Royal Society B: Biological Sciences*, 286(1911):20191645.
- Pinti, J. and Visser, A. W. (2019). Predator-Prey Games in Multiple Habitats Reveal Mixed Strategies in Diel Vertical Migration. *The American Naturalist*, 193(3):E000–E000.
- Sainmont, J., Thygesen, U. H., and Visser, A. W. (2013). Diel vertical migration arising in a habitat selection game. *Theoretical Ecology*, 6(2):241–251.
- Sarmiento, J. L. and Gruber, N. (2006). Chapter 8 - Carbon Cycle. In *Ocean Biogeochemical Dynamics*, pages 318–358.
- Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., and Vonesh, J. R. (2008). From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology*, 89(9):2436–2445.
- Schmitz, O. J., Křivan, V., and Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2):153–163.
- Schnetzer, A., Miller, P. E., Schaffner, R. A., Stauffer, B. A., Jones, B. H., Weisberg, S. B., DiGiacomo, P. M., Berelson, W. M., and Caron, D. A. (2007). Blooms of *Pseudo-nitzschia* and domoic acid in the San Pedro Channel and Los Angeles harbor areas of the Southern California Bight, 2003-2004. *Harmful Algae*, 6(3):372–387.
- Smetacek, V., Klaas, C., Strass, V. H., Assmy, P., Montresor, M., Cisewski, B., Savoye, N., Webb, A., D’Ovidio, F., Arrieta, J. M., Bathmann, U., Bellerby, R., Berg, G. M., Croot, P., Gonzalez, S., Henjes, J., Herndl, G. J., Hoffmann, L. J., Leach, H., Losch, M., Mills, M. M., Neill, C., Peeken, I., Röttgers, R., Sachs, O., Sauter, E., Schmidt, M. M., Schwarz, J., Terbrüggen, A., and Wolf-Gladrow, D. (2012). Deep carbon export from a Southern Ocean iron-fertilized diatom bloom. *Nature*, 487(7407):313–319.
- Smetacek, V. S. (1985). Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology*, 84(3):239–251.

- Stamieszkin, K., Pershing, A. J., Record, N. R., Pilskaln, C. H., Dam, H. G., and Feinberg, L. R. (2015). Size as the master trait in modeled copepod fecal pellet carbon flux. *Limnology and Oceanography*, 60(6):2090–2107.
- Steinberg, D. K., Goldthwait, S. A., and Hansell, D. A. (2002). Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep Sea Research Part I*, 49:1445–1461.
- Stukel, M. R., Ohman, M. D., Benitez-Nelson, C. R., and Landry, M. R. (2013). Contributions of mesozooplankton to vertical carbon export in a coastal upwelling system. *Marine Ecology Progress Series*, 491:47–65.
- Thygesen, U. H. and Patterson, T. A. (2018). Oceanic diel vertical migrations arising from a predator-prey game. *Theoretical Ecology*.
- Turner, J. T. (2002). Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquatic Microbial Ecology*, 27:57–102.
- Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean’s biological pump. *Progress in Oceanography*, 130:205–248.
- Våge, S., Storesund, J. E., Giske, J., and Thingstad, T. F. (2014). Optimal defense strategies in an idealized microbial food web under trade-off between competition and defense. *PLoS ONE*, 9(7).
- Van Donk, E., Lüring, M., and Lampert, W. (1999). Consumer-induced changes in phytoplankton: inducibility, costs, benefits, and the impact on grazers. In Tollrian, R. and Harvell, C., editors, *The Ecology and Evolution of Inducible Defenses*, pages 89–103. Princeton University Press, New Jersey.
- Varpe, Ø., Jørgensen, C., Tarling, G. A., and Fiksen, Ø. (2007). Early is better: Seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos*, 116(8):1331–1342.
- Visser, A. W., Grønning, J., and Jónasdóttir, S. H. (2017). Calanus hyperboreus and the lipid pump. *Limnology and Oceanography*, 62(3):1155–1165.
- Visser, A. W., Mariani, P., and Pigolotti, S. (2012). Adaptive behaviour, tri-trophic food-web stability and damping of chaos. *Journal of The Royal Society Interface*, 9(71):1373–1380.
- Volk, T. and Hoffert, M. I. (1985). Ocean Carbon Pumps: Analysis of Relative Strengths and Efficiencies in Ocean-Driven Atmospheric CO<sub>2</sub> Changes. In *The Carbon Cycle and Atmospheric CO<sub>2</sub>: Natural Variations Archean to Present*, volume 32, pages 99–110.
- Wassmann, P. (1998). Retention versus export food chains: Processes controlling sinking loss from marine pelagic systems. *Hydrobiologia*, 363:29–57.

491 Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., and Schmitz, O. J. (2021). The context  
492 dependence of non-consumptive predator effects. *Ecology Letters*, 24:113–129.

493 Zaret, T. M. and Suffern, S. (1976). Vertical migration in zooplankton as a predator avoidance mechanism.  
494 *Limnology and Oceanography*, 21(6):804–813.