



Fear and loathing in the pelagic: How the seascape of fear impacts the biological carbon pump

Pinti, Jérôme; Visser, André W.; Serra-Pompei, Camila; Andersen, Ken H.; Ohman, Mark D.; Kiørboe, Thomas

Published in:
Limnology and Oceanography

Link to article, DOI:
[10.1002/lno.12073](https://doi.org/10.1002/lno.12073)

Publication date:
2022

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Pinti, J., Visser, A. W., Serra-Pompei, C., Andersen, K. H., Ohman, M. D., & Kiørboe, T. (2022). Fear and loathing in the pelagic: How the seascape of fear impacts the biological carbon pump. *Limnology and Oceanography*, 67(6), 1238-1256. <https://doi.org/10.1002/lno.12073>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Fear and loathing in the pelagic: How the seascape of fear impacts the biological carbon pump

Jérôme Pinti ^{1*}, André W. Visser,¹ Camila Serra-Pompei,^{1,2} Ken H. Andersen ¹, Mark D. Ohman ³,
Thomas Kiørboe ¹

¹VKR Centre for Ocean Life, Technical University of Denmark, Kongens Lyngby, Denmark

²Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts

³Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California

Abstract

The biological carbon pump transports photosynthetically fixed carbon from surface waters to depths. It removes carbon from the atmosphere and sequesters it in the deep ocean, playing an important role in global climate regulation. As the biological carbon pump is directly related to biological processes, it is heavily influenced by the biomass and trophic interactions between populations in the ecosystem. However, behavioral responses and adaptations to predation risk change trophic interactions, potentially having larger impacts than direct effects on trophic interactions and population abundances. Thus, predation risk may play an important role in shaping the biological carbon pump's strength (how much carbon leaves the euphotic zone) and efficiency (what fraction of detritus reaches a certain depth without being degraded). Except in the case of active carbon transport by vertically migrating organisms, this role of risk is not generally recognized. Here, we synthesize the existing knowledge on the consequences of anti-predation responses on the biological carbon pump. First, we consider a generic anti-predation response and investigate the different direct, indirect, and cascading effects that the response can induce. Then, we focus on pelagic anti-predation responses and detail how they can specifically alter the different components of the pump. Finally, we discuss points to consider in biological carbon pump studies and highlight directions for future research. In particular, there is a need for more quantitative research to evaluate the importance of anti-predation responses in shaping the biological carbon pump.

The ocean exerts a strong control on global climate because of its ability to sequester carbon away from the atmosphere (Boyd et al. 2019). Biological processes play an important role in carbon sequestration through the export of photosynthetically fixed carbon from surface waters to depths—a mechanism known as the biological carbon pump (Volk and Hoffert 1985; Falkowski et al. 1998; Boyd et al. 2019). It is estimated that atmospheric pCO₂ would be approximately 200 ppm higher than the current

400 ppm without the biological carbon pump (Maier-Reimer et al. 1996). The biological carbon pump is composed of several pathways (Boyd et al. 2019), chief of which are (i) the biological gravitational pump, that is, the passive sinking of particulate organic matter (POM; Boyd et al. 2019), and (ii) the migrant pump, that is, the active transport of carbon by daily or seasonally vertically migrating organisms (Bianchi et al. 2013; Jónasdóttir et al. 2015). It is becoming increasingly clear that passive sinking of detrital particles is not the only component of the biological pump, and that metazoans play a major role in setting both its strength (how much carbon leaves the euphotic zone) and efficiency (what depths carbon leaving the euphotic zone reaches) (Davison et al. 2013; Henson et al. 2019; Cavan and Hill 2022; Pinti et al. 2021b; Saba et al. 2021; Serra-Pompei et al. 2021).

Population dynamics and trophic interactions among primary producers, predators, and bacteria are the main determinants of how much carbon is exported or transferred to higher trophic levels. However, trophic interactions and population dynamics may be modified by anti-predation responses (Schmitz et al. 2004, 2008; Wirsing et al. 2021; Pinti et al. 2021a), sometimes more than by direct predation (Peacor and Werner 2001; Schmitz et al. 2004). Anti-predation responses refer here to

*Correspondence: jpinti@udel.edu

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Additional Supporting Information may be found in the online version of this article.

[†]Present address: College of Earth, Ocean, and Environment, University of Delaware, Lewes, Delaware

Author Contribution Statement: JP and CSP designed the study. JP conducted the study under the supervision of AWW, KHA and TK. JP wrote the manuscript with contributions from all authors.

behavioral responses adopted to deal with predation pressure—for example, chain formation and toxin production in phytoplankton, or schooling and diel vertical migration (DVM) in fish (see Fig. 1 for illustrations of anti-predation responses).

Behavioral responses to risk disrupt trophic interactions and thereby alter the routes by which carbon is channeled into the biological pump (Pinti et al. 2021a). Predation risk is inhomogeneous in the environment, shaping a seascape of fear (analogous to the terrestrial landscape of fear; Laundré et al. 2010) in which organisms adjust to varying levels of risk with different defense mechanisms (also called anti-predation responses). For example, DVM of marine organisms, where organisms hide from visual predation at depth during daytime while foraging at the surface during nighttime, varies depending on the predator and prey in the water column (Ohman 1990; Pinti et al. 2019), thus impacting trophic transfer efficiency and carbon export (Pinti et al. 2021a). Understanding and quantifying the ways in which anti-predation behavior shapes the biological carbon pump under different circumstances will support a more accurate mechanistic description of carbon export and sequestration.

Here, we use simple trait-based mechanistic models to illustrate how anti-predation behaviors affect the biological carbon pump. We review the possible consequences of defense mechanisms for the biological pump by highlighting how they can impact both carbon export and sequestration in the pelagic. Even though they are important components of the biological carbon pump, marine snow and phytoplankton aggregates are excluded from this review, as they are not directly related to defense behaviors. We first consider the different mechanisms through which anti-predation responses can alter carbon export without focusing on any specific behavior. We illustrate this with a series of trait-based toy models (i.e., simple conceptual models) of increasing complexity considering successively individuals, populations, and ecosystems. Second, we review different properties of the biological carbon pump (production of organic matter, efficiency of the biological carbon pump, active transport, and spatiotemporal aspects) and examine how they may be impacted by different anti-predation responses. Third, we discuss various important effects of anti-predation processes to consider in relation to the biological carbon pump in the pelagic. Finally, we highlight directions and perspectives for further research.

The biological carbon pump from individual to ecosystem

Predation risk has not only direct effects on prey, but also indirect effects that cascade through food-webs. A conceptual framework to approach the effect of predation risk on food webs is illustrated in Fig. 2 (Peacor et al. 2020). Direct consumptive effects decrease prey abundances, but prey trait responses (i.e., anti-predation behavior) can also lead to changes in abundances via nonconsumptive effects. For example, zooplankton taking refuge at depths during the day will eat less phytoplankton, thus lowering their growth rate and population size

compared to a zooplankton population not subject to predation. The intensity of an anti-predation response is adjusted to the local seascape of fear to balance the level of risk an individual is facing (Fig. 2). Different levels of predation risk elicit different prey trait responses through anti-predation mechanisms. The abundance of prey varies because of both consumptive and non-consumptive effects. Prey have, in turn, an influence on other species (resources, competitors, and sometimes also predators) via density-mediated indirect effects, if the effect is driven by a change in prey abundance, or via trait-mediated indirect effects, if the effect is driven by a change in prey behavior or life-history trait. For example, a response to both trait- and density-mediated indirect effect is when a prey performs reverse DVM in response to a large zooplankton that performs DVM, therefore staying close to the surface during daytime where it is too dangerous for their zooplankton predators (Ohman 1990). These third species can also have further consequences on the food web through cascading indirect effects (Fig. 2). As all trophic levels contribute in their own way to carbon export, any change in anti-predation response can modify carbon export.

Here, we demonstrate how anti-predation responses and their cascading consequences for food web dynamics impact both the strength and the efficiency of the biological carbon pump (see Box 1 for a definition of both terms). We start with a very simple toy model considering only prey abundance, and then successively add a number of effects due to predation risk to highlight the consequences that they can have on food-webs and carbon export. For simplicity, we focus on the gravitational pump, but similar illustrations can be developed for the migrant pump.

Direct consumptive effects

In a hypothetical world where primary producers were perfectly defended (no grazing, Fig. 2 dashed box a) the vertical flux of carbon would peak at the bottom of the euphotic zone and then attenuate with depth as sinking material is degraded by microbes (Fig. 3, blue line; see Supporting Information Appendix S1 for equations and parameters for this and the following toy models). However, phytoplankton defense is not perfect and zooplankton consume phytoplankton. Zooplankton grazing reduces the flux from phytoplankton but at the same time redirects a fraction of it into fast sinking fecal pellet (Fig. 2 dashed box b, Eppley and Peterson 1979; Turner 2002; Stamieszkin et al. 2015). Large zooplankton and fish can create fecal pellets that sink at speeds of several hundred m day^{-1} , reaching bathyal depths in 2–5 d (Robison and Bailey 1981; Saba and Steinberg 2012; Saba et al. 2021). Including zooplankton grazing, because fecal pellets sink fast (see Supporting Information Table S1), the attenuation of the flux with depth is much slower in the presence than in the absence of zooplankton. That is, the efficiency of the biological carbon pump increases. These differences in strength and efficiency of the biological carbon pump can be observed in the field, where zooplankton fecal pellets usually account for less than 25% of the flux at depths less than 200 m (Turner 2002) but can account for up

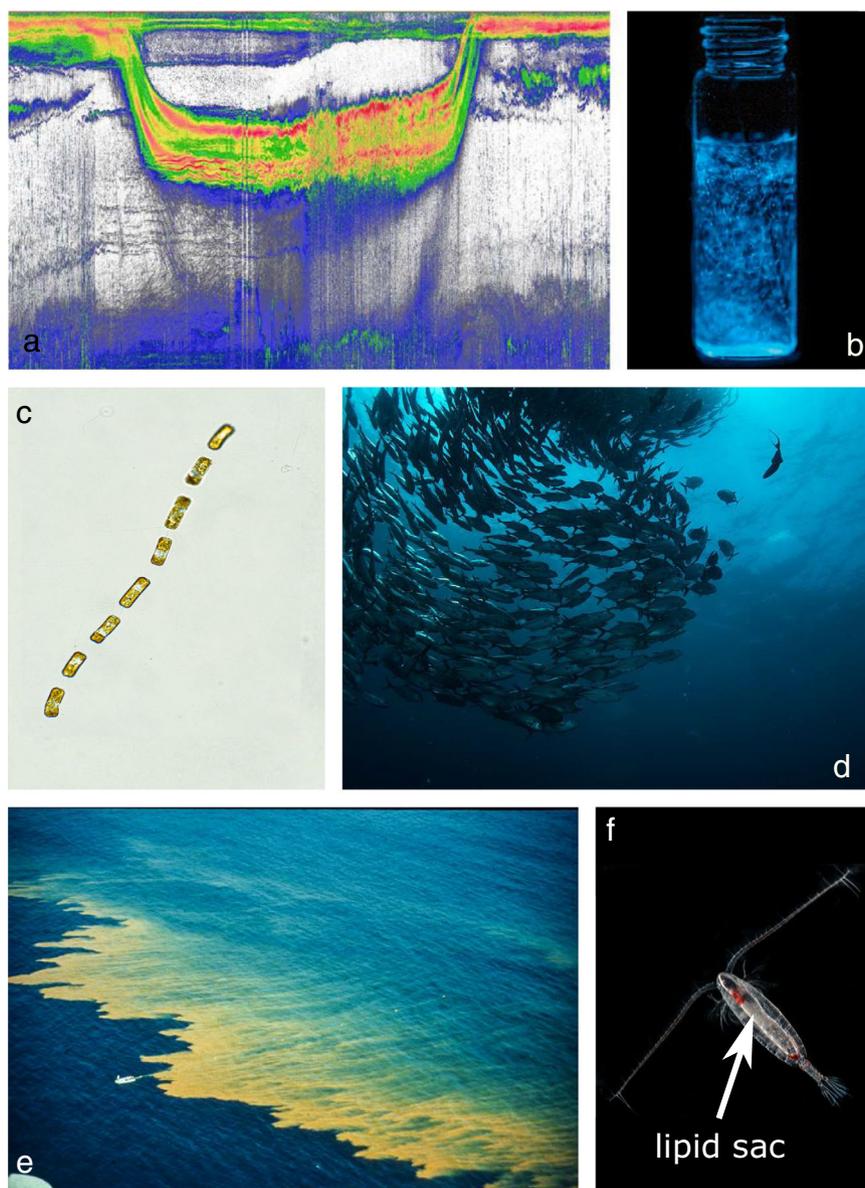


Fig. 1. Anti-predation responses in the pelagic, observed at the individual, population, or ecosystem level. **(a)** Echogram in the East Pacific realized over a daily cycle. Organisms remain close to the surface at night, migrate down at dawn, remain at depths during daytime (thus escaping visual predation) before migrating up again at dusk. **(b)** A vial of bioluminescent algae *Lingulodinium polyedra*. Bioluminescence can deter predators. **(c)** A chain of diatoms *Thalassiosira nordenskiöldii*. Diatom chains offer protection against small grazers that can handle single cells but not larger chains. **(d)** A school of black jack *Caranx lugubris* in the water column. Schooling decreases per capita predation pressure. **(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. Toxic compounds released in the water column protect against grazers. **(f)** A copepod *Calanus glacialis* with a visible lipid sac—a necessary energy reserve to undergo diapause. Diapause offers a defense against visual surface predators when food resources are low. 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.

to 99% of the flux below 400 m (Bishop et al. 1977). Note that phytodetritus also increase the efficiency of the biological pump (Laurenceau-Cornec et al. 2015). However, since marine snow is not a result of behavioral effects we do not include it in this review (Laurenceau-Cornec et al. 2015).

Indirect effects on prey and predators

It appears that defense has a potential impact on the counter-balanced metrics of export and sequestration. However, there is an additional dimension, namely that defense comes at a cost (Litchman and Klausmeier 2008; Grønning

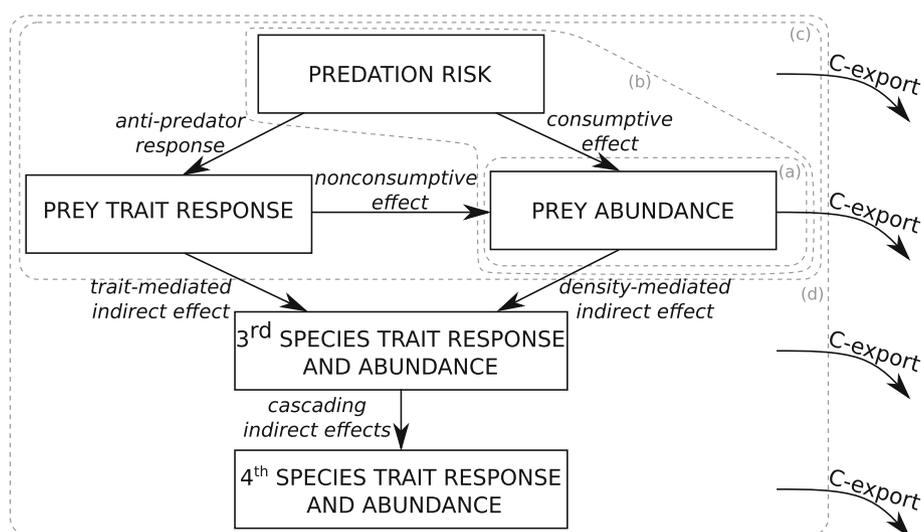


Fig. 2. Conceptual framework of the consequences of predation risk on the food web. Dashed boxes (a–d) refer to the different toy models presented here. Predation pressure decreases prey abundance, through either direct consumptive effects or through indirect nonconsumptive effects. The consequences in terms of both trait response and prey abundance can cascade through the entire food web. Each trophic level then contributes to carbon export, and predation pressure can alter (positively or negatively) the strength of the carbon flux produced by all populations of the food web. See the text for more details. Modified from Peacor et al. (2020).

and Kiørboe 2020), and the trade-offs along the defense benefit–cost axis have consequences for population dynamics (Pinti et al. 2021a).

We illustrate the importance of variable levels of defense with a simple example where two populations interact with different levels of prey defense and associated trade-offs (Fig. 2 dashed box c, equations are detailed in Supporting Information Section A.3). For example, the system can consist of populations of colony-forming diatoms and copepods, or of toxic dinoflagellates and copepods. The prey defense level is set by S , which can vary between 0 (prey not defended at all) and 1 (prey perfectly defended). The trade-off is that with increasing defense levels (and thus reducing predation) comes a reduction in growth rate. Detritus (sinking organic material) originate from prey and predators. Detritus refers to both fecal pellets and deadfalls, that is, dead cells for phytoplankton and carcasses for metazoans. Deadfall production rate is assumed to be equal to natural nonpredation mortality rates. In the particular case where phytoplankton are the prey, fecal pellet production is replaced by leakage of surplus dissolved organic material (DOM) that does not sink. A more complete model would have to consider that leaked DOM can be taken up again by primary producers, thus stimulating production. Various levels of defense for the prey lead to different equilibrium population sizes (Fig. 4). In our example, the optimal defense level for prey is around $S = 0.6$ —this corresponds to the level where the predator goes extinct and any further investment in defense will not decrease predation risk further, but will still diminish growth. Natural mortality losses are directly proportional to population sizes, but fecal pellet production depends on ingestion rate. Consequently, the maximum detritus

production rate does not necessarily correspond to the maximum population size. Furthermore, predators create bigger and faster-sinking detritus than their prey, 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 (Fig. 5). Interestingly, the optimal defense level for prey does not correspond to the defense level with the highest carbon flux. This toy model shows that, except at highest defense levels, detritus created by predators tend to dominate the carbon flux. Thus, this model again suggests that high levels of defense reduce the efficiency of the biological carbon pump.

At high defense levels, detritus originating from prey dominate the carbon flux (Fig. 5). An example of highly defended prey that leads to high—not lower—carbon export is toxin production, prevalent in many bloom-forming phytoplankton. Ungrazed cells may sink and toxic material has been found in sediment traps up to 800 m below the surface (Schnetzer et al. 2007). Toxins may further affect the bacterial community, decrease remineralization rate, and hence increase export efficiency (Bach et al. 2019). Toxin production in phytoplankton may also have cascading effects as toxins may accumulate in the food web (Petitpas et al. 2014), all the way to marine mammals (Schnetzer et al. 2007). Deadfalls of large animals may lead to very high local fluxes (Smith et al. 2015). This suggests that cascading effects in the food web can be important in determining carbon flux and carbon export efficiency.

Cascading ecosystem effects

Defense behaviors that affect the trophic interactions between a predator and its prey, as described above, may have

Box 1. Strength and efficiency of the biological carbon pump.

The importance of the biological carbon pump can be assessed with two factors: its strength (how much carbon sinks out of the euphotic zone) and its efficiency (what fraction of detritus reaches a certain depth without being degraded). A common way to assess the strength of the biological carbon pump in a given ecosystem is through the EZ-ratio, defined as the fraction of net primary production (NPP) that sinks below the euphotic zone (Buesseler and Boyd 2009):

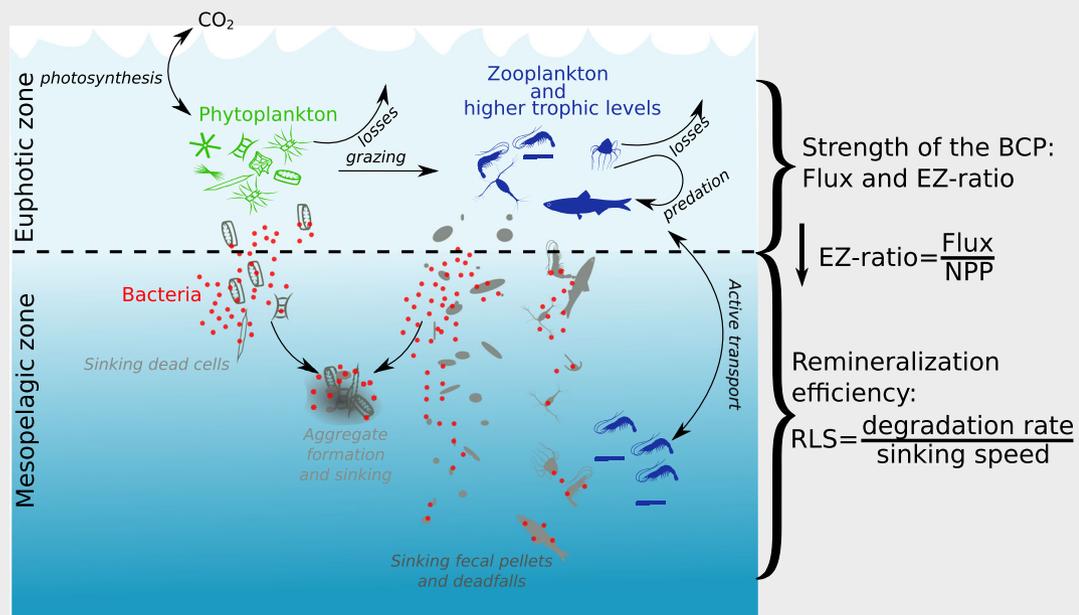
$$\text{EZ-ratio} = \frac{\text{Export below euphotic zone}}{\text{NPP}} \quad (1)$$

The efficiency of the carbon pump is linked to the remineralization length scale (RLS):

$$\text{RLS} = \frac{\text{Degradation rate}}{\text{Sinking speed}}, \quad (2)$$

sometimes also called the L-ratio (Feinberg and Dam 1998). The RLS (in m^{-1}) is the fraction of detritus that is remineralized per meter sinking. The lower the RLS, the higher the fraction of carbon export that reaches a specific depth—and thus the more efficient the biological carbon pump is. Both the strength and the efficiency of the biological carbon pump determine how much carbon is exported at a certain depth, and ultimately how much carbon sequestration a system can mediate—even though most studies tend to focus on the EZ-ratio or on the flux at a certain depth, typically 100 m (Henson et al. 2015, 2019; Archibald et al. 2019).

A common misunderstanding of biological carbon pump studies is the difference between carbon export and sequestration. “Carbon export” typically refers to the sinking flux (in, e.g., PgC yr^{-1}) of carbon below a specific depth (e.g., the limit of the euphotic zone), while “carbon sequestration” refers to the amount of carbon (in PgC) that is sequestered in the ocean’s interior (DeVries and Holzer 2019; Holzer et al. 2021; Pinti et al. 2021b). The latter gives a different, albeit more complete, description of the biological carbon pump, as it combines both the export flux and the remineralization efficiency. Organic carbon settling out of the euphotic zone can remain stored in the ocean’s interior for periods ranging from months to millenia before returning to the surface. This sequestration time scale (that can be assessed by dividing carbon sequestration by export) depends on the remineralization length scale of particles, but also on where the export occurs—for example, export in deep-water formation zones will tend to sequester carbon on a much longer time scale than export in upwelling areas.



Sketch of the biological pump: Phytoplankton fix CO_2 through photosynthesis, before being grazed upon by consumers that can be, in turn, preyed upon by higher trophic levels. As detritus sinks, bacteria degrade it into dissolved inorganic carbon (DIC),

Continued

Box 1 Strength and efficiency of the biological carbon pump.—cont'd

but also dissolved organic carbon (DOC), nutrients, and other dissolved material. The strength of the biological carbon pump is set in the euphotic zone, while its efficiency depends on processes mainly taking place below the euphotic zone (Buesseler and Boyd 2009). For a representation of the biological carbon pump that includes the microbial loop, see Steinberg and Landry (2017).

cascading effects that impact the structure of the entire food web (Fig. 2 dashed box d, Peacor and Werner 2001; Schmitz et al. 2004). Food web structure is now recognized as important for carbon export efficiency (Guidi et al. 2009; Henson et al. 2019; Stukel et al. 2019), and anti-predation responses consequently have the potential to control the biological carbon pump through indirect effects. How such indirect effects translate precisely in terms of carbon flux is hard to estimate due to the difficulty of separating the different effects from each other. Theoretical models based on Lotka-Volterra equations of predator-prey interactions are appropriate tools to explore such effects as they allow tracking carbon ingestion and egestion by each population, and thus can help disentangling the relative contributions of different populations to carbon export.

We use a simple model to illustrate and explore these cascading effects (Fig. 6). We consider a food web with an intra-guild predation motif (i.e., a predator that can prey on another predator with which it shares a resource; Polis et al. 1989), casting a diatom as prey R , a ciliate C as consumer that can

change its defense level, and a copepod as the intra-guild predator (Fig. 6a). Depending on the intensity of the defense of the consumer and the shape of the competition-defense trade-off, this system has different potential outcomes: (i) only diatoms are present, (ii) only diatoms and ciliates are present, (iii) only diatoms and copepods are present, or (iv) all three species coexist (Holt and Polis 1997). Examples are provided for different trade-off parameters in Fig. 6b. In particular, well-defended ciliates go extinct (Fig. 6b, purple lines) because of the competition-defense trade-off: investing in defense means that resource acquisition decreases—up to a point where the population can no longer be sustained.

Although the three different simulations have comparable total equilibrium biomasses, the biomasses of each group and the resulting biological carbon pump differs significantly (Fig. 6c), 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 community composition due to behavioral adaptations even without changes in total biomass can have major consequences for carbon export.

A real-world example that describes food web effects qualitatively is offered by the large-scale trait effects of copepod predation pressure on planktonic food webs (Selander et al. 2019). Many colony-forming phytoplankton modify colony size in response to copepod chemical cues, and plasticity of colony size helps adapt to the size of grazers (Long et al. 2007; Bjærke et al. 2015). Likewise, many phytoplankton increase their toxicity in the presence of their predators (Selander et al. 2006). Selander et al. (2019) showed that the release of copepod cues in the natural environment was sufficient to decrease chain formation in diatoms and to double the production of domoic acid by toxic diatoms during ca. 90% of the year. The decrease in colony size pushes carbon flow toward small microzooplankton, ciliates and heterotrophic dinoflagellates rather than mesozooplankton. Without quantifying carbon flux, Selander et al. (2019) argue that this leads to an overall decreased carbon flux and carbon pump strength compared to an idealized system without behavioral responses to predation risk.

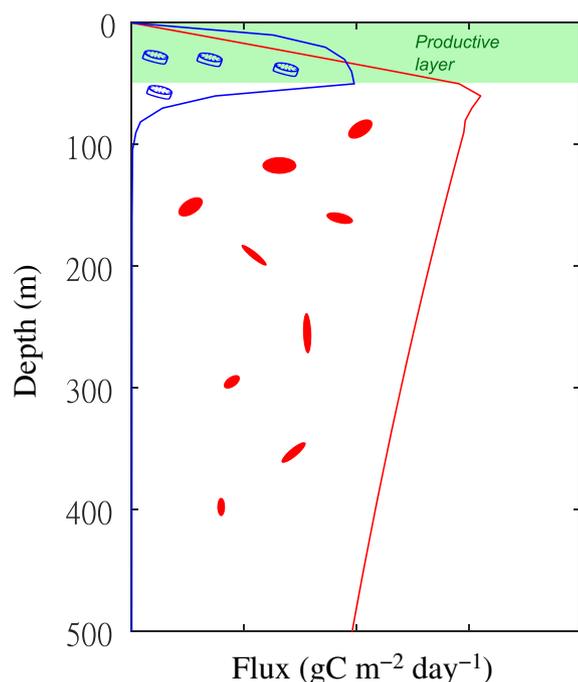


Fig. 3. POC flux as a function of depth if the flux originates entirely from dead phytoplankton cells (blue) or entirely from zooplankton fecal pellets (red).

Modeling the effects of risk mitigation behaviors

These three models indicate how anti-predator responses may significantly impact both the strength and the efficiency

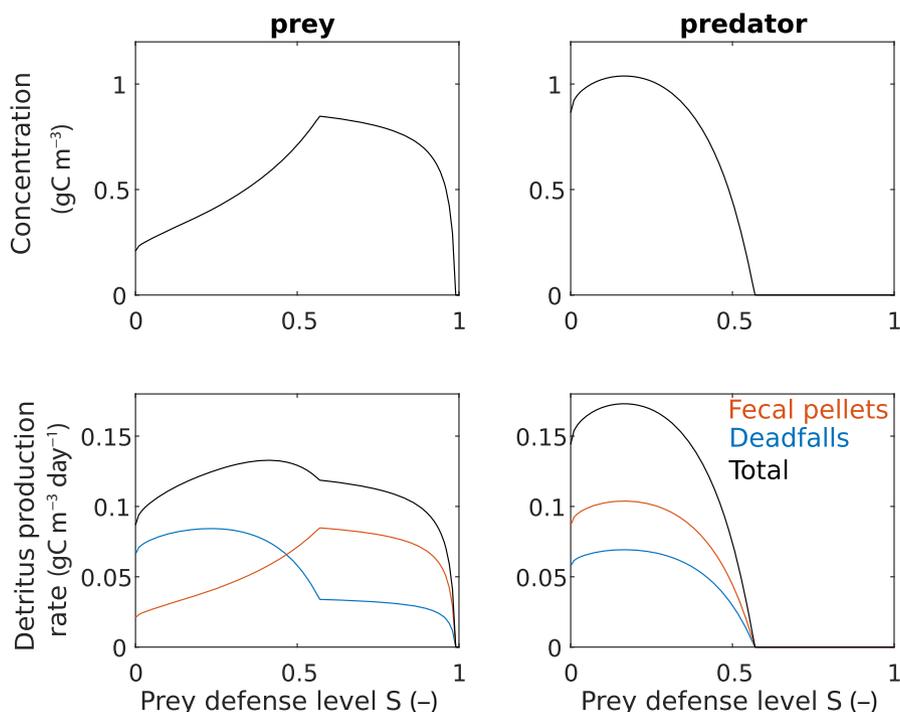


Fig. 4. Example of a predator–prey system for different levels of prey defense. Top: Equilibrium biomasses of prey (left) and predator (right). Bottom: Ensuing detritus production rates as fecal pellets (orange) or deadfalls (blue) for prey (left) and predator (right).

of the biological carbon pump. Generally, defense responses that change the plankton size spectrum toward smaller sizes will reduce the efficiency of the pump, because smaller particles sink more slowly. Assessing the effect of any particular system requires a more specific model, which may involve a number of complications. First, for simplicity, our toy models only considered the gravitational pump and ignored the migration pump that may be quantitatively very significant, as it directly transports carbon to depths, bypassing remineralization during descent (Davison et al. 2013). Second, we only considered steady state, whereas environmental forcing lead to highly dynamic systems and temporal mismatch between predators and prey. Furthermore, seasonal pulses in

surface productivity lead to time-delayed pulses in carbon flux at depth (Henson et al. 2015, 2019; Laws and Maiti 2019). Third, as is typically the case for NPZ-type models of pelagic ecosystems, our models ignore life histories. However, multicellular organisms—which have a dominant role on the biological carbon pump—have ontogenetic development that can have a major impact on the strength of the pump (Serra-Pompei et al. 2021). Finally, we have considered only one-way defensive responses of prey to the presence of predators, while in reality, the predators may counter-respond. This may elicit behavioral trait cascades, both up and down the food web (Schmitz et al. 2004; Van Someren Gréve et al. 2019). That is, organisms from multiple populations and trophic levels co-

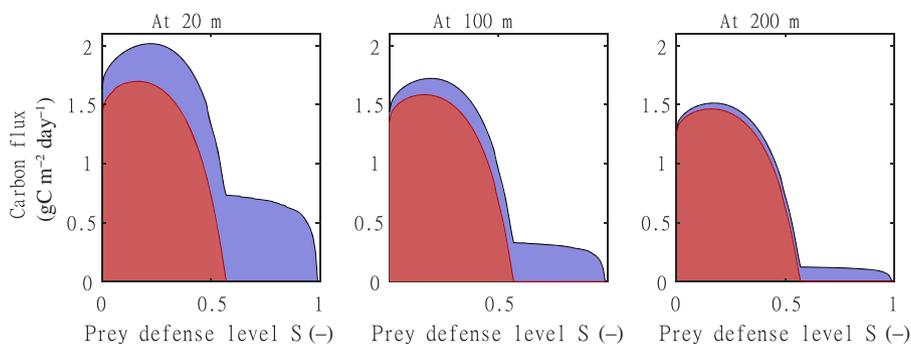


Fig. 5. Carbon fluxes originating from detritus (both fecal pellets and deadfalls) for prey (blue) and predators (red) at 20, 100, and 200 m assuming a productive layer of 20 m.

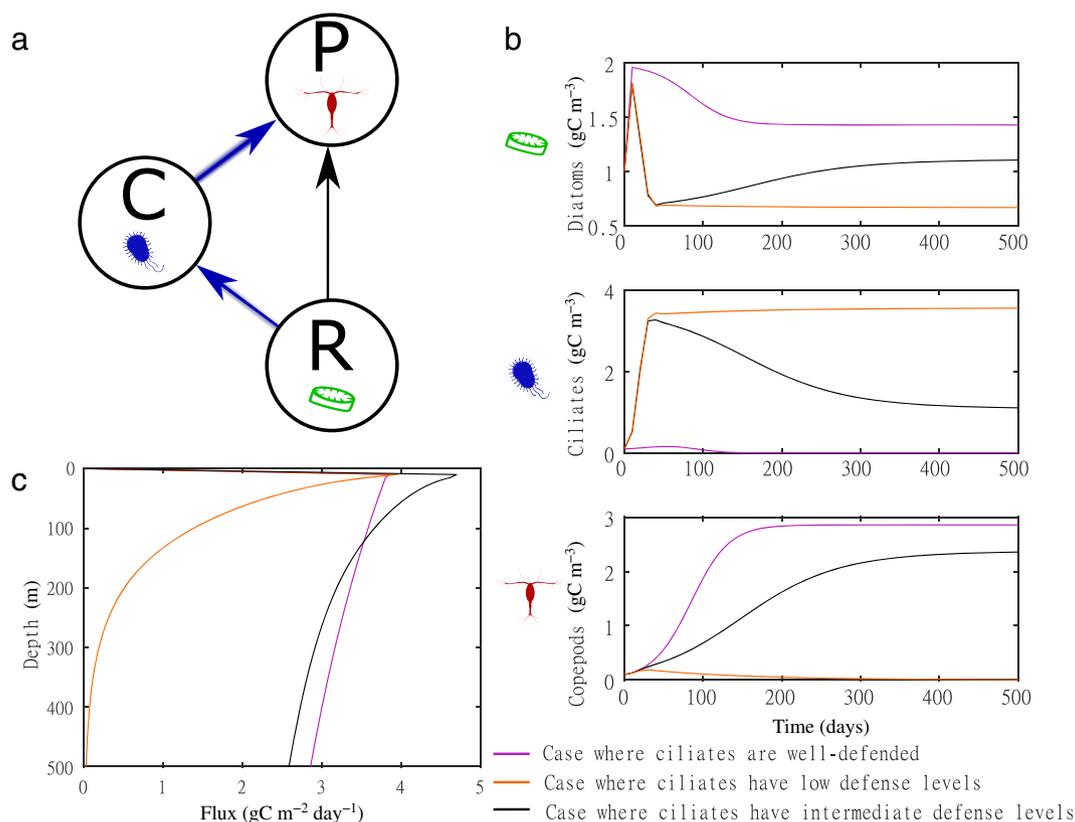


Fig. 6. (a) Intraguild predation motif. Diatoms (*R*) are prey for both ciliates (*C*) and copepods (*P*). Copepods can prey on both diatoms and ciliates, and in this way reduce competition with ciliates for the resource. However, ciliates can modulate their defense, for example, through changing foraging activity, with consequences for the ability of the copepod to act as an intraguild predator (blue arrows illustrate changing interaction strengths). (b) Population dynamics under three levels of ciliate defense. Well-defended ciliates go extinct, because even if they do not suffer from predation their resource acquisition ability is too low for their own survival (there is a trade-off between defense and competition abilities). (c) Carbon flux at equilibrium as a function of depth. For (b) and (c), purple lines are for simulations with well-defended ciliates $(\tau, S) = (0.8, 0.8)$, orange lines with poorly-defended ciliates $(\tau, S) = (0.4, 0.6)$, and black lines with intermediate defense $(\tau, S) = (0.5, 0.5)$. S and τ are parameters related to the competition-defense trade-off (level of defense and shape of the defense-competition trade-off, respectively), detailed in Supporting Information.

adapt, all trying to simultaneously optimize their fitness. Resolving such co-adaptation requires game theory. Game theory has been applied to examine DVM involving several trophic levels, where all players optimize their vertical behavior relative to what their predators, competitors, and prey do (Iwasa 1982; Hugie and Dill 1994; Pinti and Visser 2019). Because game theoretical approaches have had success in predicting the diverse vertical migration behaviors observed in nature (Pinti et al. 2019, 2021b), they have the potential to also predict the effects of risk on different behaviors.

Anti-predation responses in the pelagic

Until now, our discussion has focused on defense in a generic and abstract sense. In nature, a considerable array of defense mechanisms have evolved among pelagic organisms (Fig. 1), and these may have different impacts on the biological carbon pump. In this section, we review the ways in which the different components of the biological pump are impacted by specific anti-predation responses. Table 1 lists the anti-predation responses among pelagic organisms that we find particularly important

and summarizes their potential consequences for the biological carbon pump, while Table 2 breaks down the components of the pump and how they are affected directly, or indirectly, by various anti-predation behaviors. In the following, we discuss how anti-predation responses may affect four components of the biological carbon pump: the production of organic matter, the efficiency of the carbon pump (that depends on the detritus sinking speed and the degradation rate in the water column), the active transport of carbon (the migrant pump), and the spatiotemporal aspect of the pump.

Production of POM

The amount of detritus that sinks out of the euphotic zone (the strength of the pump) depends directly on the quantity and the type of organic matter produced as deadfalls, fecal pellets, or other kind of detritus. Anti-predation responses can modify the production of particulate matter by releasing organic material directly in the water column, or by inducing population size variations resulting in changes in detritus production. The direct release of material is likely of limited

Table 1. Summary of pelagic anti-predation responses. We list possible direct effects on carbon flux, trait-mediated indirect interactions and their cascading effects on carbon flux. We do not list biomass changes and density-dependent indirect effects, as they are mostly similar for all behaviors: Better protected organisms will have higher population sizes, sustaining higher flux, but the decrease in predation success will decrease predator sizes and hence carbon flux originating from higher trophic levels. References relate to the trait-mediated indirect effect, or, when we could not find previous study investigating it directly, to the description of the response itself.

Anti-predation response	Trophic level	Direct effect for carbon flux	Trait-mediated indirect effect	Indirect effect for carbon flux	Reference
Chain formation or dislocation	Phytoplankton, diatoms	Formation: ↑ sinking speed Dislocation: ↓ sinking speed	Breaking diatom chains favors microzooplankton predator and disfavors large predators	↓ Sinking speed from predator fecal pellets	Selander et al. (2019)
Frustule thickening	Phytoplankton (diatoms)	↑ Flux locally	Reduces predation	↓ Flux from predators ↑ Sinking speed of predator fecal pellets through ballasting (↑ efficiency)	Gronning and Kjørboe (2020)
Swarming	Zooplankton, krill	↑ Flux locally	Attracts piscivorous predators Overwhelms bacterial community locally	↑ Flux from fast-sinking fish fecal pellets ↓ Local bacterial degradation rate	Kaartvedt et al. (2005), Atkinson et al. (2012), Belcher et al. (2019), Cavan et al. (2019)
Schooling	Fish	↑ Increases flux locally	Overwhelms bacterial community locally	↓ Local bacterial degradation rate	Pavlov and Kasumyan (2000)
Toxin production	Phytoplankton and mixotrophs	↑ Flux during toxic blooms ↑ Sinking speed in case of released organic material and mucus in the water column	Toxins affect bacterial community Toxins increase background mortality of higher trophic levels	↓ Bacterial degradation rate ↑ Flux of carcasses	Bach et al. (2019), Schnetzer et al. (2007)
Bioluminescence	All	↑ Flux with the release of bioluminescent material and sacrificial tag	Attracts higher order predators with the “burglar alarm mechanism” Bioluminescent shunt: bioluminescent detritus is more consumed	↑ Detritus production at depth ↑ Flux in case of repackaging, ↓ flux in case of sloppy feeding/coprohexy	Childress (1995), Tanet et al. (2020)
Molting	Zooplankton, krill	↑ Flux of fast-sinking molts			Cavan et al. (2019)
Daily horizontal migrations	Nekton	Redistributes flux locally	Fertilizes places that would have slower growth rates otherwise	↑ Flux	Robinson et al. (1995)
Seasonal horizontal migrations	Nekton	↑↓ Redistributes flux seasonally	Some prey and predator may migrate in response to variable predation pressure	↑↓ Redistributes the flux even more	

(Continues)

Table 1. Continued

Anti-predation response	Trophic level	Direct effect for carbon flux	Trait-mediated indirect effect	Indirect effect for carbon flux	Reference
Diel vertical migrations	Plankton and nekton	↑ Increases active transport to depths	Triggers DVM in other organisms, prey and predators, maybe to even deeper depths (Vinogradov's ladder)	↑ Increases active transport and depths of the active transport	Vinogradov (1962)
Seasonal vertical migrations and diapause	Zooplankton	↑ Increases active transport			Jónasdóttir et al. (2015)

Table 2. Summary of behaviors that can impact the different parts of the biological carbon pump, through direct or indirect effects.

	<i>Quantity of organic matter produced</i>
Direct	<ul style="list-style-type: none"> • Krill and zooplankton molts • Extra cellular toxins released in the environment • TEP release
Indirect	<ul style="list-style-type: none"> • Release of bioluminescent material and sacrificial tags • All behaviors as they modify trophic interactions and ingestion rates • Toxins kill more higher trophic level organisms • Bioluminescent burglar alarms increase predation by higher order predators
	<i>Detritus sinking speed</i>
Direct	<ul style="list-style-type: none"> • Thickness of frustules and calcium carbonate shells • Chain and aggregate formation • TEP release
Indirect	<ul style="list-style-type: none"> • Faster sinking of ballasted fecal pellets (by frustules and shells) • Behavioral cascades, as changing the size of the community changes • The size spectrum of detritus produced and hence its sinking rate
	<i>Detritus degradation rate</i>
Direct	<ul style="list-style-type: none"> • Toxic compounds can affect bacteria • Bioluminescent shunt
	<i>Active transport</i>
Direct	<ul style="list-style-type: none"> • Diel vertical migrations • Seasonal vertical migrations
Indirect	<ul style="list-style-type: none"> • DVM induced by other organisms (reverse DVM, fish following their prey, or also Vinogradov's ladder)
	<i>Spatio-temporal changes</i>
Direct	<ul style="list-style-type: none"> • School and swarms • Horizontal daily and seasonal migrations
Indirect	<ul style="list-style-type: none"> • Trophic-mediated changes in spatial distributions

quantitative importance. It includes, for example, discarded exoskeletons from molting krill (Buchholz 1991; Cavan et al. 2019) suggested to function as decoys to visual predators

(Hamner et al. 1983), or bioluminescent material released by crustaceans and squids to distract predators (Herring 1988; Robison et al. 2003)—even in the form of glowing body parts (sacrificial tags, Robison et al. 2003). If ingested by predators, such sacrificial tags may continue to glow and attract predators and thus function as a “burglar alarm” attracting the predators of the predator (Childress 1995).

Sinking speed of POM

The efficiency of the biological carbon pump is in large part determined by the sinking speed and remineralization rate of detrital material. Thus, defense behaviors that affect these attributes of detritus can significantly impact the pump efficiency.

Sinking speeds, for instance, can be enhanced or reduced by defense mechanisms. For example, mineralized defensive exoskeletons of phytoplankton such as the calcium carbonate plates of coccolithophores or silica frustules of diatoms are well known to act as ballast, enhancing the sinking speeds of their consumers' fecal pellets (Francois et al. 2002; Martin et al. 2011). Furthermore, diatom frustules thickness can be increased under the presence of grazers (Grønning and Kjørboe 2020), increasing their contribution to mineral ballasting. Although live diatoms regulate their buoyancy and avoid sinking (Gemmell et al. 2016), the elevated density of their predators' fecal pellets (Feinberg and Dam 1998) or particle loaded discarded mucus feeding webs result in faster sinking detritus. Similarly, the ballasting effects of diatom frustules and coccoliths when incorporated into marine snow may increase the sinking speed of the latter (Francois et al. 2002; Engel et al. 2009; Bach et al. 2019).

The role of the silica frustule in carbon sequestration may be more complex in some instances. Highly defended diatoms with thick frustules, such as *Fragilariopsis kerguelensis* that dominate in the Antarctic Circumpolar Current, efficiently resist grazing, but sink mainly as empty-shelled frustules to the seafloor with most of their organic carbon lost in the surface ocean (Assmy et al. 2013). In contrast, other less defended thinner-shelled diatoms are either grazed and sink in the form of fecal pellets, or

form rapidly sinking aggregates that transport organic carbon to the ocean interior. In fact, there is evidence that aggregation can be induced by grazers (Toullec et al. 2019) and thus be a means by which diatoms may escape predation and survive in the sediments until growth conditions again become favorable. For these diatom species, sinking is an integral part of their life history and they thus play a major quantitative role in the biological carbon pump (Smetacek 1999).

The breakup of colonies in response to grazers also affects sinking speed. It is well documented that diatoms and dinoflagellates may reduce colony size (chain length) in response to grazer cues (Selander et al. 2011; Bjærke et al. 2015). Other species, such as colonial *Phaeocystis* sp. may increase or decrease colony size in response to microzooplankton and mesozooplankton grazers, respectively (Jakobsen and Tang 2002; Long et al. 2007; Lundgren and Granéli 2011). To a first order, sinking speed scales with the square of the linear dimension of the particle (i.e., a long chain will always sink faster than any of its sections in isolation, although shape and buoyancy regulation may modify this). Therefore, defensive colony-size regulation may impact sinking speed and, thus, carbon sequestration.

The case with colonial dinoflagellates is different from that of other colonial phytoplankton since dinoflagellates are motile and, hence, do not sink. However, a reduced colony size reduces swimming speed and the ability of dinoflagellates to perform DVM (Selander et al. 2011). The diurnal migration of dinoflagellates allows the flagellates to collect nutrients below the pycnocline at night and photosynthesize in the euphotic zone during day (MacIntyre et al. 1997; Fauchot et al. 2005). Although it leads to a net downward flux of carbon due to night respiration, dinoflagellates rarely migrate below the euphotic zone, so the total effect may be limited. However, their migration leads to a net upward transport of nutrients, thus increasing the production in the surface layer and the amount of detritus that enters the gravitational pump (cf. Discussion).

An increase in toxin production or shell thickness of a prey can lead to prey-switching by a predator, hence modifying the density and sinking rate of its fecal pellets. These behaviorally mediated trophic cascades can be observed in the field under particular conditions only (Ohman 1990; Romare and Hansson 2003; Selander et al. 2019) as they are often embedded within complex food webs and depend on highly dynamic variables. They can also be exhibited in lab experiments (Peacor and Werner 1997; Van Someren Gréve et al. 2019; Kville et al. 2021) or numerical models (Křivan and Schmitz 2004). Coupling or revisiting these models to include fecal pellet density, when relevant, would help shed light on the consequences of these highly nonlinear effects (Křivan and Schmitz 2004) on carbon export.

Detritus degradation rate

The efficiency of the biological carbon pump is also determined by the rate at which detrital aggregates are remineralized by bacteria (Grossart et al. 2003), together with

the rate at which they are consumed by zooplankton and fish (Miller et al. 2011; Möller et al. 2012). Microorganisms, both bacteria and their protozoan predators, rapidly colonize sinking detrital particles (Kjørboe et al. 2003), and attached bacteria defend themselves against grazing by forming microcolonies and producing toxins (Matz and Kjelleberg 2005), allowing high bacterial densities and rapid remineralization. Net remineralization rates also vary with temperature and oxygen, which together with other temperature-dependent processes results in temperature-dependence of the biological carbon pump (Guidi et al. 2015; Marsay et al. 2015).

Bacteria may also be affected by toxic compounds (Bach et al. 2019). Defensive phytoplankton toxins can be found in detritus (Lehtiniemi et al. 2002; Petitpas et al. 2014) persisting to depths down to 800 m below the surface (Sekula-Wood et al. 2009). These toxins may slow bacterial degradation rate and increase carbon export efficiency, but may on the other hand also reduce grazing, thus reducing the biological carbon pump efficiency.

Finally, bioluminescence presents an anti-predation mechanism that can modify detritus degradation rates. Deep-sea organisms such as fish and squids emit light via intrinsic or symbiotic bioluminescence (Haddock et al. 2010). Bioluminescence can be used to hide via counter-illumination, to distract predators with “smoke screens” and sacrificial body tags, or to startle predators with light flashes. These can result in bioluminescent particulate organic carbon release, and luminous bacteria growing on particulate matter may produce enough light to be visible by other organisms, resulting in a higher consumption of luminous particles. This process, termed the “bioluminescent shunt” was recently reviewed by Tanet et al. (2020). Whether the extra consumption would come from lower trophic levels degrading the matter through sloppy feeding and coprophagy (fragmentation of pellets) or higher trophic levels repackaging detritus, thus increasing their sinking speed and the pump efficiency, is unknown. Describing mechanistically the processes involved will help understanding the importance of bioluminescence for deep-sea remineralization (how does it impact bacterial degradation rate? how does it vary with depth?), as well as implications for the carbon pump. We can posit that larger organisms will consume relatively more glowing particles than small organisms, as the latter do not use vision to find food—resulting in an increased sinking speed for glowing material at depth. Nevertheless, the mechanistic description of bioluminescent interactions is an exciting avenue for future deep-sea research. Given the slow metabolic rates typical at mesopelagic and bathypelagic depths (Drazen and Seibel 2007), even a minimal effect on bacterial degradation rate is likely to contribute significantly to carbon sequestration at a global scale.

Active transport: The migrant pump

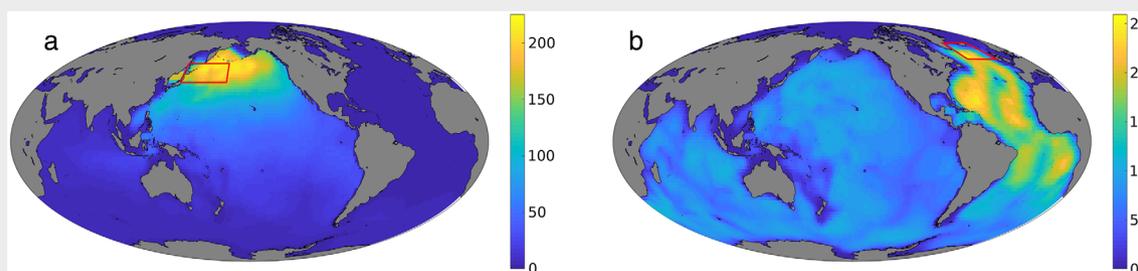
Active transport refers to the downward transport of organic material by vertically migrating organisms. DVM can

Box 2. Seasonal vertical migration and carbon sequestration.

Every year, copepods from polar and subpolar latitudes fill up with lipid reserves before migrating to great depths to spend winter. They can remain at depths of up to 1000–3000 m (Visser et al. 2017) for more than 60–80% of the year. While at depth, they respire their lipid reserves, thus directly exporting carbon from the surface to great depths. Export flux is estimated to vary between 0.6 and 6.0 gC m⁻² yr⁻¹ (Kobari et al. 2003; Jónasdóttir et al. 2015; Visser et al. 2017). By coupling this respiration term to a global ocean circulation model (DeVries and Holzer 2019; Holzer et al. 2021), we can compute the equilibrium concentration of DIC in the oceans due to diapausing copepod respiration. Dividing the total sequestration (in, e.g., PgC) by the respiration rate (in, e.g., PgC yr⁻¹) yields a sequestration time scale, an estimation of the efficiency of the process.

We compute these estimates for two population of copepods: *C. finmarchicus* in the North Atlantic, and *Neocalanus* spp. in the Western North Pacific. We assume respiration rates of 2.3 gC m⁻² yr⁻¹ (North Atlantic; Jónasdóttir et al. 2015) and 4.3 gC m⁻² yr⁻¹ (North Pacific; Kobari et al. 2003), and a residency depth of 1000 m. Total sequestration (in PgC) is not very informative because of the incomplete spatial and species coverage of our simulations, but sequestration time scales indicate the efficiency of the process. Sequestration time scale is around 530 years in the North Pacific and 560 years in the North Atlantic, suggesting that this process is extremely efficient at sequestering carbon away from the atmosphere (for comparison, sinking fecal pellets of mesozooplankton are assumed to be sequestered for ~140 years on average; Pinti et al. 2021b).

Because of the structure of ocean currents, carbon respired in the North Atlantic is eventually advected all around the oceans, while carbon respired in the North Pacific largely remains local (see figure below)—but the efficiency of the lipid pump in the two areas is nevertheless similar.



Equilibrium DIC concentrations in gC m⁻² due to copepod respiration during diapause in the North Pacific (**a**) and North Atlantic (**b**). Red squares indicate where diapausing copepods are located in these illustrative illustrations, but their distribution is much wider in nature. We assume that copepods are normally distributed around 1000 m depth (with standard deviation of 50 m) during their diapause. The resulting residence time of DIC produced by diapausing copepods is 560 and 528 years for the North Atlantic and North Pacific, respectively.

often be considered an anti-predation response, as conventionally it allows phytoplankton grazers to forage in the surface layer at night while seeking refuge from visual predators at depth during day (Zaret and Suffern 1976). DVM may elicit a trait-cascade of DVM behaviors because the predators of the grazers, and their predators in turn, may follow their respective prey while at the same time minimizing their own predation risk (Ohman 1990; Pinti et al. 2019; Bandara et al. 2021; Pinti et al. 2021b). Vertical migration also occurs on a seasonal scale due to organisms diapausing at depth during wintertime in a low-predation environment (Jónasdóttir et al. 2015). Active transport by the migrant pump is very efficient as it bypasses the degradation during descent that affects sinking detritus.

The active transport on a seasonal time scale is linked to the need for zooplankton, and especially copepods, to undergo diapause during wintertime when there is not enough food at the surface (Visser and Jónasdóttir 1999). At

higher latitudes in both hemispheres, overwintering copepods migrate from the surface to depths of 1000–3000 m to enter diapause (Visser et al. 2017). These copepods are filled with carbon-rich lipids that constitute their energy reserve for their diapause (Fig. 1f). Throughout the winter, they slowly respire this carbon at depth. This process is called the “lipid pump” (Jónasdóttir et al. 2015) and releases between 0.6 and 6 gC m⁻² yr⁻¹ at depth, depending on the species and location considered (Jónasdóttir et al. 2015; Visser et al. 2017). Because this dissolved inorganic carbon is produced at depths and in down-welling areas (Schmitz 1996), it will likely be stored on very long time scales. Box 2 details the calculation of the carbon sequestration mediated by the seasonal vertical migrations of two groups of copepods in the North Atlantic and North Pacific.

DVM is one of the most conspicuous behaviors in the oceans, as it is present in all ocean basins (Bianchi et al. 2013; Klevjer et al. 2016) and involves many different taxa such as

copepods, krill, mesopelagic fish, squids, and jellyfish. There can be huge variations in realized DVM patterns, both spatially (Klevjer et al. 2016) and temporally (Prihartato et al. 2015), and are likely due to the different trade-offs faced by migrants (Ohman 1990; Ohman and Romagnan 2016; Pinti et al. 2019). The carbon draw-down mediated by actively migrating organisms has been widely explored, especially for zooplankton (Longhurst et al. 1990; Archibald et al. 2019; Kelly et al. 2019), and more recently also for fish (Davison et al. 2013; Pinti et al. 2021b) and jellyfish (Luo et al. 2020; Pinti et al. 2021b). Climate-driven changes in the distribution of copepods also impact the spatial patterns of copepod-mediated carbon fluxes, but it remains unclear whether the magnitudes have also changed (Brun et al. 2019). Some studies suggest an active transport of carbon equivalent to 14–18% of the passive sinking flux at the base of the euphotic zone for zooplankton (Archibald et al. 2019) and 14–16% for fish (Davison et al. 2013; Saba et al. 2021; Pinti et al. 2021b), although these values are known to vary spatially with the structure of the food web (Kelly et al. 2019). Global carbon sequestration mediated by metazoan DVM was recently estimated to be between 400 and 1200 PgC (Pinti et al. 2021b).

Spatiotemporal considerations

Horizontal spatial movements can play a role similar to DVM, to allow nighttime foraging in productive areas and daytime residency in low productive but safe locations. With large gradients in food availability perpendicular to the coast, forage fish can exhibit large inshore-offshore movements, migrating up and inshore during night time in rich but risky places, and down and offshore at dawn (Robinson et al. 1995). Similar to DVM, this may increase carbon sequestration as residency offshore leads to the release of fecal pellets in deeper areas than closer to shore. The global significance of daily horizontal migrations is, to our knowledge, currently unknown.

The formation of dense swarms and schools of organisms such as krill and fish are behaviors that decrease per capita predation pressure (Pitcher and Parrish 1993). These formations can locally reach very high concentrations of organisms—up to 660 ind m⁻³ for krill (Cresswell et al. 2009) and several tens of individuals per m³ for fish schools (Pavlov and Kasumyan 2000). Some krill swarms can be very large, extending over 100 km² and containing 2 million tonnes of krill (Tarling and Fielding 2016). Such high concentrations of organisms produce large amounts of detritus that may overwhelm consumers and decrease the net degradation of sinking material, and increase the export efficiency (Atkinson et al. 2012; Belcher et al. 2019; Cavan et al. 2019). Specifically, it has been estimated that flux attenuation rates are dependent on the krill density in overlying waters (Belcher et al. 2017). This spatiotemporal discrepancy may be important at global scales as seasonal krill-related export has been found to account for ~35% (range 17–61%) of the total

carbon export below 100 m in the Southern Ocean marginal ice zone (Belcher et al. 2019). A failure to consider the patchiness of organisms' distributions can severely underestimate export, impairing our ability to predict future changes in the biological carbon pump (Belcher et al. 2019).

Discussion

The biological pump is of paramount importance to climate regulation, as models predict that its absence would result in atmospheric CO₂ concentrations being 200 ppm 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). As such, understanding the consequences of anti-predation behavior on the biological carbon pump is an important question not only for the ecology of the organisms involved, but also for Earth system science.

We highlight here the different ways in which anti-predation mechanisms can affect the biological carbon pump in the pelagic. We stress that detritus production is not the only way in which behavior and food web dynamics can modify the biological carbon pump. Export flux (strength of the biological pump) depends very much on the quantity of detritus produced, but a complete description of the biological carbon pump must also consider its efficiency. This is necessary to assess how much carbon is ultimately stored in the oceans via different mechanisms. For example, mechanisms leading to few fast sinking particles may yield a higher sequestration than many slowly sinking particles (Buesseler et al. 2020; Pinti et al. 2021b). For an exhaustive description, biological carbon pump research must then strive to assess the efficiency of the pump, and not just the export at the base of the euphotic zone or at an artificially set depth.

One aspect not covered by our toy models is mass balance and the stoichiometry of sinking detritus. The downward flux of any limiting element cannot, in the long run, exceed the input of this element to the euphotic zone, independently of the composition of the pelagic community (i.e., export production equals new production, Eppley and Peterson (1979)). In addition, organisms that migrate vertically on a daily or a seasonal basis and respire at depth typically preferentially metabolize carbon-rich substances, for example, fat, rather than nitrogen-rich substances, such as proteins, and therefore enhance carbon sequestration (Jónasdóttir et al. 2015).

Despite the diversity of anti-predation responses that can arise and the multitude of effects they can trigger, it appears that non-consumptive and indirect effects can have important consequences on food web dynamics (Peacor and Werner 2001; Schmitz et al. 2004), and thus on carbon export. Traditionally, effects of predation risk are seen as top-down effects, but they can also spiral toward higher trophic levels. For example, DVM of small organisms can force DVM in larger organisms who need to follow their prey (Pinti and Visser 2019). Krill swarms are

patrolled by piscivorous fish that prey on planktivorous fish attracted to the krill (Kaartvedt et al. 2005). Bioluminescent fish or squid releasing a sacrificial tag that is ingested by a predator may attract their own predators' predators through the burglar alarm mechanism (Childress 1995). This vast array of indirect effects can be cast in terms of game theory. Game theory considers that all organisms in a food web behave optimally and adjust their behaviors simultaneously and not iteratively. The optimal distribution in the strategy space (i.e., the set of behaviors that organisms can adopt) is attained when a Nash equilibrium is reached (Nash 1951)—that is, when no organism can increase its fitness by unilaterally changing its behavior. This method has now been widely applied to DVMs (Iwasa 1982; Hugie and Dill 1994; Pinti et al. 2019; Pinti and Visser 2019), but to our knowledge, not to other anti-predation responses in aquatic environments. Indeed, game theoretic approaches provide a framework to predict behaviors that propagate through food webs as organisms trade off feeding opportunity with predation risk. Given proper mechanistic descriptions of the processes involved, adjusting mathematical models developed for DVM to other behaviors in the pelagic should be relatively straightforward.

Anti-predation behavior and defense mechanisms rest on the existence of trade-offs with competitive abilities (Våge et al. 2014; Cadier et al. 2019). But there can also be a trade-off within the defense mechanism itself: a defense cannot be efficient against all types of predators, and organisms need to choose what defense to adopt in response to the local risk seascape. For example, nocturnal descent is a very efficient response against visual predation, but it is virtually useless in response to tactile predation. On the contrary, it can be beneficial to remain at the surface in broad daylight and perform reverse vertical migration in the presence of tactile predators that perform DVM because of their own predators (Ohman 1990). Diatom chains may offer an efficient defense strategy against micro zooplankton grazers, but are useless against copepods that can “eat them like spaghetti.” Consequently, there may not be such a thing as a maximum defense level, and the level to adopt may depend on the trophic assemblage in the water column, creating not only a unique seascape of fear but a combination of different seascapes that prey need to deal with. One-sided optimization methods (considering predators' behaviors fixed) and game theoretic approaches (where both prey and predators adapt their response) are particularly well-suited tools for answering these questions related to the optimal behavior of marine organisms.

Although different species impose different types of risks, organisms can respond to risk by varying not just a defense level, but the kind (or number) of defense mechanism(s) that they adopt. Anti-predation responses are (often) not mutually exclusive, and can be coupled for increased efficiency. For example, fish can couple diel vertical and horizontal migrations (Robinson et al. 1995), fish and krill can perform DVM and school during part of the day (Nilsson et al. 2003; Cavan et al. 2019), and high-latitude copepods can couple diel and

seasonal vertical migrations over a yearly cycle (Bandara et al. 2018). Most studies to date focus on one behavior, but do not consider the consequences that interacting behaviors can have on the carbon cycle. In particular, fish often couple schooling and DVM, and these behaviors may work in synergy—by actively transporting carbon to depth and by generating strong localized pulses of detritus that may overwhelm the local bacterial community—thus multiplying carbon sequestration at depth.

In most population-based studies, all organisms of a population are assumed to adopt uniformly the same anti-predator behavior. This disregards the fact that within populations, organisms can elicit different responses to the same stimulus. For example, in a population of Baltic Sea copepods predominantly performing DVM, some individuals exhibit the opposite behavior and perform reverse vertical migration (Möller et al. 2020). The diversity of behavioral responses can be due to individual personalities (Carter et al. 2013), such as different boldness traits (Christiansen et al. 2021), and to the plasticity in their response to environmental variations (Dingemanse et al. 2010). Behavioral states (e.g., energy and fat reserves, gut fullness) can also alter anti-predator responses (Beltran et al. 2021). In a DVM context, this is what is called the hunger-satiation hypothesis (Pearre 2003), in which organisms would migrate to the surface to eat when they are hungry and migrate down at depths once satiated. A recent study of vertical migration of mesopelagic fish and crustaceans highlighted the role of behavioral states (in that case, gut fullness) in the vertical migrations of the mesopelagic layer. By investigating the gut fullness level of both the migrating and the resident mesopelagic community, they showed that gut fullness could partially explain the decision of individual organisms from different mesopelagic species to migrate (Bos et al. 2021). Finally, without considering individual variations in populations, game theory approaches also predict mixed strategies to arise (Pinti and Visser 2019). Considering individual variation in anti-predator response is important, as a few organisms with responses different from the majority of the community could contribute disproportionately to the biological carbon pump. We acknowledge that it is currently a challenge to address this issue for biological pump studies, as we are just beginning to recognize and consider these individual effects in studies of food web dynamics.

Finally, as anthropogenic impacts on marine ecosystems become stronger, organisms need to adapt to the new conditions that they are facing. At the ecosystem level, this means that organisms may migrate to new areas, biomasses of different species may increase or decrease, and trophic interactions in general will likely be modified (Kwiatkowski et al. 2019; Lotze et al. 2019). Individual organisms can try to cope with these changes by adjusting their behavior, but only within the bounds of their innate plasticity. The emerging picture of pelagic food webs is that their function is controlled not only by the abundance of its various players, but also by the complex web of ever-changing behavioral strategies that they

adopt (Pinti et al. 2021a). As is the nature of all complex systems, abrupt transitions and tipping points may occur. We have here reviewed a wide variety of behaviors and explored their impact on the biological carbon pump, and all behaviors may react differently to global change. Consequently, assessing the future of the behavioral impacts to the biological pump depends on many different factors, and is also behavior specific. How the biological carbon pump will respond to future changes in organisms' behavior, abundance, and distribution is an important question for future Earth system research.

Future directions

- Make direct, quantitative estimates of the importance of different anti-predator behaviors for the biological carbon pump—both in terms of carbon export and carbon sequestration. To date, most discussions are qualitative. Except for active transport (both diel and seasonal vertical migrations; Jónasdóttir et al. 2015; Visser et al. 2017; Aumont et al. 2018; Archibald et al. 2019), the importance of behavior to the biological pump is not quantified. Quantifying these potential effects would help redirect efforts toward the most important contributors, both for carbon export and sequestration.
- Increase research effort on deep-sea processes. So far, most biological pump studies focused on carbon export at the base of the euphotic zone, but deep-sea processes are of paramount importance when it comes to carbon sequestration. Midwater and deep-sea processes can dramatically affect the relative importance of metazoan and bacterial oxidation rates. Considering the time scale on which carbon is sequestered when it reaches depths deeper than ~1000 m, a precise mechanistic description of deep-water processes rather than a constant (or, in best cases, temperature dependent) bacterial degradation rate would increase the confidence in estimations of carbon sequestration in the ocean's interior. For example, including bioluminescence and its trade-offs in mechanistic models may be of importance for the biological pump (Tanet et al. 2020).
- Is there a simple way to account for a behavioral response? Nowadays, most models considering behavior rely on heuristic principles (Aumont et al. 2018; Archibald et al. 2019) or on optimization procedures that can be computationally intensive (Pinti et al. 2021a). Incorporating behavior more consistently in global biogeochemical models would be feasible only if it does not substantially increase computing costs. Developing a framework to model it accurately, perhaps similar to the formalization of ingestion rates as Holling's functional responses (Holling 1959) with appropriate prey refuges (Chenillat et al. 2021), would certainly be a big step forward.
- How will anti-predator behavior and the biological carbon pump evolve in the future? Anti-predator behavior is an adaptation to other organisms of the ecosystem, but is also modulated by local environmental conditions. As local

conditions and trophic assemblages change because of global change, will organisms be able to adjust their behavior in response? To what degree are individual anti-predation responses plastic, to both predation levels but also to environmental changes? What will be the cascading consequences for the biological pump? For example, increased temperature and deoxygenation in the California Current System will likely shallow the daytime residency depth of the mesopelagic layer, decreasing the efficiency of active transport (Netburn and Koslow 2015).

Data availability statement

The MATLAB codes necessary to run the models presented in this article are deposited in the following repository: https://gitlab.gbar.dtu.dk/jppi/Fear-loathing_BCP

References

- Archibald, K. M., D. A. Siegel, and S. C. Doney. 2019. Modeling the impact of zooplankton diel vertical migration on the carbon export flux of the biological pump. *Global Biogeochem. Cycl.* **33**: 181–199.
- Assmy, P., and others. 2013. Thick-shelled, grazer-protected diatoms decouple ocean carbon and silicon cycles in the iron-limited Antarctic Circumpolar Current. *Proc. Natl. Acad. Sci. USA* **110**: 20633–20638.
- Atkinson, A., K. Schmidt, S. Fielding, S. Kawaguchi, and P. A. Geissler. 2012. Variable food absorption by Antarctic krill: Relationships between diet, egestion rate and the composition and sinking rates of their fecal pellets. *Deep-Sea Res. Part II Topical Stud. Oceanogr.* **59–60**: 147–158.
- Aumont, O., O. Maury, S. Lefort, and L. Bopp. 2018. Evaluating the potential impacts of the diurnal vertical migration by marine organisms on marine biogeochemistry. *Global Biogeochem. Cycl.* **32**: 1–22.
- Bach, L. T., P. Stange, J. Taucher, E. P. Achterberg, M. Algueró-Muñoz, H. Horn, M. Esposito, and U. Riebesell. 2019. The influence of plankton community structure on sinking velocity and remineralization rate of marine aggregates. *Global Biogeochem. Cycl.* **33**: 971–994.
- Bandara, K., Ø. Varpe, R. Ji, and K. Eiane. 2018. A high-resolution modeling study on diel and seasonal vertical migrations of high-latitude copepods. *Ecol. Model.* **368**: 357–376.
- Bandara, K., Ø. Varpe, L. Wijewardene, V. Tverberg, and K. Eiane. 2021. Two hundred years of zooplankton vertical migration research. *Biol. Rev.* **96**: 1547–1589.
- Belcher, A., and others. 2017. The potential role of Antarctic krill faecal pellets in efficient carbon export at the marginal ice zone of the South Orkney Islands in spring. *Polar Biol.* **40**: 2001–2013.
- Belcher, A., and others. 2019. Krill faecal pellets drive hidden pulses of particulate organic carbon in the marginal ice zone. *Nat. Commun.* **10**: 1–8.

- Beltran, R. S., and others. 2021. Lightscares of fear: How mesopredators balance starvation and predation in the open ocean. *Sci. Adv.* **7**: 1–8.
- Bianchi, D., C. Stock, E. D. Galbraith, and J. L. Sarmiento. 2013. Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochem. Cycles* **27**: 478–491.
- Bishop, J. K., J. M. Edmond, D. R. Ketten, M. P. Bacon, and W. B. Silker. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. *Deep-Sea Res.* **24**: 511–548.
- Bjærke, O., P. R. Jonsson, A. Alam, and E. Selander. 2015. Is chain length in phytoplankton regulated to evade predation? *J. Plankton Res.* **37**: 1110–1119.
- Bos, R. P., T. T. Sutton, and T. M. Frank. 2021. State of satiation partially regulates the dynamics of vertical migration. *Front. Mar. Sci.* **8**: 607228.
- Boyd, P. W., H. Claustre, M. Levy, D. A. Siegel, and T. Weber. 2019. Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* **568**: 327–335.
- Brun, P., K. Stamieszkin, A. W. Visser, P. Licandro, M. R. Payne, and T. Kiørboe. 2019. Climate change has altered zooplankton-fuelled carbon export in the North Atlantic. *Nat. Ecol. Evol.* **3**: 416–423.
- Buchholz, F. 1991. Moults cycle and growth of Antarctic krill *Euphausia superba* in the laboratory. *Mar. Ecol. Prog. Ser.* **69**: 217–229.
- Buesseler, K. O., and P. W. Boyd. 2009. Shedding light on processes that control particle export and flux attenuation in the twilight zone of the open ocean. *Limnol. Oceanogr.* **54**: 1210–1232.
- Buesseler, K. O., P. W. Boyd, E. E. Black, and D. A. Siegel. 2020. Metrics that matter for assessing the ocean biological carbon pump. *Proc. Natl. Acad. Sci.* **117**: 201918114.
- Cadier, M., K. H. Andersen, A. W. Visser, and T. Kiørboe. 2019. Competition–defense tradeoff increases the diversity of microbial plankton communities and dampens trophic cascades. *Oikos* **128**: 1027–1040.
- Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlshaw, and R. Heinsohn. 2013. Animal personality: What are behavioural ecologists measuring? *Biol. Rev.* **88**: 465–475.
- Cavan, E. L., and others. 2019. The importance of Antarctic krill in biogeochemical cycles. *Nat. Commun.* **10**: 1–13.
- Cavan, E. L., and S. L. Hill. 2022. Commercial fishery disturbance of the global ocean biological carbon sink. *Glob. Chang. Biol.* **28**: 1212–1221.
- Chenillat, F., P. Rivière, and M. D. Ohman. 2021. On the sensitivity of plankton ecosystem models to the formulation of zooplankton grazing. *PLoS One* **16**: 1–27.
- Childress, J. J. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends Ecol. Evol.* **10**: 30–36.
- Christiansen, S., T. A. Klevjer, A. Røstad, D. L. Aksnes, and S. Kaartvedt. 2021. Flexible behaviour in a mesopelagic fish (*Maurollicus muelleri*). *ICES J MarSci.* **78**: 1623–1635.
- Cresswell, K. A., G. A. Tarling, S. E. Thorpe, M. T. Burrows, J. Wiedenmann, and M. Mangel. 2009. Diel vertical migration of Antarctic krill (*Euphausia superba*) is flexible during advection across the Scotia Sea. *J. Plankton Res.* **31**: 1265–1281.
- Davison, P. C., D. M. Checkley, J. A. Koslow, and J. Barlow. 2013. Carbon export mediated by mesopelagic fishes in the Northeast Pacific Ocean. *Prog. Oceanogr.* **116**: 14–30.
- DeVries, T., and M. Holzer. 2019. Radiocarbon and helium isotope constraints on deep ocean ventilation and mantle-3He sources. *J. Geophys. Res. Oceans* **124**: 3036–3057.
- Dingemanse, N. J., A. J. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: Animal personality meets individual plasticity. *Trends Ecol Evol* **25**: 81–89.
- Drazen, J. C., and B. A. Seibel. 2007. Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. *Limnol. Oceanogr.* **52**: 2306–2316.
- Engel, A., J. Szlosek, L. Abramson, Z. Liu, and C. Lee. 2009. Investigating the effect of ballasting by CaCO₃ in *Emiliania huxleyi*: I. formation, settling velocities and physical properties of aggregates. *Deep-Sea Res Part II Topic. Stud. Oceanogr.* **56**: 1396–1407.
- Eppley, R. W., and B. J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**: 677–680.
- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* **281**: 200–206.
- Fauchot, J., M. Levasseur, and S. Roy. 2005. Daytime and nighttime vertical migrations of *Alexandrium tamarens* in the St. Lawrence estuary (Canada). *Mar. Ecol. Prog. Ser.* **296**: 241–250.
- Feinberg, L. R., and H. G. Dam. 1998. Effects of diet on dimensions, density and sinking rates of fecal pellets of the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* **175**: 87–96.
- Francois, R., S. Honjo, R. Krishfield, and S. Manganini. 2002. Factors controlling the flux of organic carbon to the bathypelagic zone of the ocean. *Global Biogeochem. Cycl.* **16**: 34-1–34-20.
- Gemmell, B. J., G. Oh, E. J. Buskey, and T. A. Villareal. 2016. Dynamic sinking behaviour in marine phytoplankton: Rapid changes in buoyancy may aid in nutrient uptake. *Proc. Roy. Soc. B Biol. Sci.* **283**: 20161126.
- Grønning, J., and T. Kiørboe. 2020. Diatom defence: Grazer induction and cost of shell-thickening. *Funct. Ecol.* **34**: 1790–1801.
- Grossart, H. P., T. Kiørboe, K. Tang, and H. Ploug. 2003. Bacterial colonization of particles: Growth and interactions. *Appl. Environ. Microbiol.* **69**: 3500–3509.
- Gruber, N., and others. 2019. The oceanic sink for anthropogenic CO₂ from 1994 to 2007. *Science* **363**: 1193–1199.

- Guidi, L., L. Legendre, G. Reygondeau, J. Uitz, L. Stemmann, and S. A. Henson. 2015. A new look at ocean carbon remineralization for estimating deepwater sequestration. *Global Biogeochem. Cycl.* **29**: 1044–1059.
- Guidi, L., L. Stemmann, G. A. Jackson, F. Ibanez, H. Claustre, L. Legendre, M. Picheral, and G. Gorsky. 2009. Effects of phytoplankton community on production, size and export of large aggregates: A world-ocean analysis. *Limnol. Oceanogr.* **54**: 1951–1963.
- Haddock, S. H., M. A. Moline, and J. F. Case. 2010. Bioluminescence in the sea. *Ann. Rev. Mar. Sci.* **2**: 443–493.
- Hamner, W. M., P. P. Hamner, S. W. Strand, and R. W. Gilmer. 1983. Behavior of Antarctic Krill, *Euphausia superba*: Chemoreception, feeding, schooling, and molting. *Science* **220**: 433–435.
- Henson, S., F. Le Moigne, and S. Giering. 2019. Drivers of carbon export efficiency in the global ocean. *Global Biogeochem. Cycl.* **33**: 891–903.
- Henson, S. A., A. Yool, and R. Sanders. 2015. Global biogeochemical cycles carbon export: A model study. *Global Biogeochem. Cycl.* **29**: 33–45.
- Herring, P. J. 1988. Copepod luminescence. *Hydrobiologia* **167-168**: 183–195.
- Holling, C. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**: 385–398.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *Am. Nat.* **149**: 745–764.
- Holzer, M., T. DeVries, and C. de Lavergne. 2021. Diffusion controls the ventilation of a Pacific Shadow Zone above abyssal overturning. *Nat. Commun.* **12**: 1–13.
- Hugie, D. M., and L. M. Dill. 1994. Fish and game: A game theoretic approach to habitat selection by predators and prey. *J. Fish Biol.* **45**: 151–169.
- Iwasa, Y. 1982. Vertical migration of zooplankton: A game between predator and prey. *Am. Nat.* **120**: 171–180.
- Jakobsen, H. H., and K. W. Tang. 2002. Effects of protozoan grazing on colony formation in *Phaeocystis globosa* (Prymnesiophyceae) and the potential costs and benefits. *Aquat. Microb. Ecol.* **27**: 261–273.
- Jónasdóttir, S. H., A. W. Visser, K. Richardson, and M. R. Heath. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proc. Natl. Acad. Sci.* **112**: 12122–12126.
- Kaartvedt, S., A. Røstad, Ø. Fiksen, W. Melle, T. Torgersen, M. T. Breien, and T. A. Klevjer. 2005. Piscivorous fish patrol krill swarms. *Mar. Ecol. Prog. Ser.* **299**: 1–5.
- Kelly, T. B., P. C. Davison, R. Goericke, M. R. Landry, M. D. Ohman, and M. R. Stukel. 2019. The importance of mesozooplankton diel vertical migration for sustaining a mesopelagic food web. *Front. Mar. Sci.* **6**: 1–18.
- Kjørboe, T., K. Tang, H. P. Grossart, and H. Ploug. 2003. Dynamics of microbial communities on marine snow aggregates: Colonization, growth, detachment, and grazing mortality of attached bacteria. *Appl. Environ. Microbiol.* **69**: 3036–3047.
- Klevjer, T. A., X. Irigoien, A. Røstad, E. Fraile-Nuez, V. M. Benítez-Barrios, and S. Kaartvedt. 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci. Rep.* **6**: 19873.
- Kobari, T., A. Shinada, and A. Tsuda. 2003. Functional roles of interzonal migrating mesozooplankton in the western subarctic Pacific. *Prog. Oceanogr.* **57**: 279–298.
- Křivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. *Oikos* **107**: 239–250.
- Kvile, K. Ø., D. Altin, L. Thommesen, and J. Titelman. 2021. Predation risk alters life history strategies in an oceanic copepod. *Ecology* **102**: 1–11.
- Kwiatkowski, L., O. Aumont, and L. Bopp. 2019. Consistent trophic amplification of marine biomass declines under climate change. *Glob. Chang. Biol.* **25**: 218–229.
- Laundré, J. W., L. Hernandez, and W. J. Ripple. 2010. The landscape of fear: Ecological implications of being afraid. *Open Ecol. J.* **3**: 1–7.
- Laurenceau-Cornec, E. C., and others. 2015. The relative importance of phytoplankton aggregates and zooplankton fecal pellets to carbon export: Insights from free-drifting sediment trap deployments in naturally iron-fertilised waters near the Kerguelen Plateau. *Biogeosciences* **12**: 1007–1027.
- Laws, E. A., and K. Maiti. 2019. The relationship between primary production and export production in the ocean: Effects of time lags and temporal variability. *Deep Sea Res. Part 1 Oceanogr. Res. Pap.* **148**: 100–107.
- Lehtiniemi, M., J. Engström-Öst, M. Karjalainen, B. Kozłowski-Suzuki, and M. Viitasalo. 2002. Fate of cyanobacterial toxins in the pelagic food web: Transfer to copepods or to faecal pellets? *Mar. Ecol. Prog. Ser.* **241**: 13–21.
- Litchman, E., and C. A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.* **39**: 615–639.
- Long, J. D., G. W. Smalley, T. Barsby, J. T. Anderson, and M. E. Hay. 2007. Chemical cues induce consumer-specific defenses in a bloom-forming marine phytoplankton. *Proc. Natl. Acad. Sci. USA* **104**: 10512–10517.
- Longhurst, A., A. Bedo, W. Harrison, E. Head, and D. Sameoto. 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. *Deep Sea Res. Part A Oceanogr. Res. Pap.* **37**: 685–694.
- Lotze, H. K., and others. 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. USA* **116**: 12907–12912.
- Lundgren, V., and E. Granéli. 2011. Influence of altered light conditions and grazers on *Scrippsiella trochoidea* (Dinophyceae) cyst formation. *Aquat. Microb. Ecol.* **63**: 231–243.
- Luo, J. Y., R. H. Condon, C. A. Stock, C. M. Duarte, C. H. Lucas, K. A. Pitt, and R. Cowen. 2020. Gelatinous zooplankton-mediated carbon flows in the global oceans: A

- data-driven modeling study. *Global Biogeochem. Cycl.* **34**: e2020GB006704.
- MacIntyre, J. G., J. J. Cullen, and A. D. Cembella. 1997. Vertical migration, nutrition and toxicity in the dinoflagellate *Alexandrium tamarense*. *Mar. Ecol. Prog. Ser.* **148**: 201–216.
- Maier-Reimer, E., U. Mikolajewicz, and A. Winguth. 1996. Future ocean uptake of CO₂: Interaction between ocean circulation and biology. *Climate Dynam.* **12**: 711–722.
- Marsay, C. M., R. J. Sanders, S. A. Henson, K. Pabortsava, E. P. Achterberg, and R. S. Lampitt. 2015. Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci. USA* **112**: 1089–1094.
- Martin, P., R. S. Lampitt, M. Jane Perry, R. Sanders, C. Lee, and E. D'Asaro. 2011. Export and mesopelagic particle flux during a North Atlantic spring diatom bloom. *Deep Sea Res. Part 1 Oceanogr. Res. Pap.* **58**: 338–349.
- Matz, C., and S. Kjelleberg. 2005. Off the hook—How bacteria survive protozoan grazing. *Trends Microbiol.* **13**: 302–307.
- Miller, M., T. Otake, J. Aoyama, S. Wouthuyzen, S. Suharti, H. Sugeha, and K. Tsukamoto. 2011. Observations of gut contents of leptocephali in the North Equatorial Current and Tomini Bay, Indonesia. *Coast. Mar. Sci.* **35**: 277–288.
- Möller, K. O., M. S. John, A. Temming, J. Floeter, A. F. Sell, J. P. Herrmann, and C. Möllmann. 2012. Marine snow, zooplankton and thin layers: Indications of a trophic link from small-scale sampling with the Video Plankton Recorder. *Mar. Ecol. Prog. Ser.* **468**: 57–69.
- Möller, K. O., and others. 2020. Predation risk triggers copepod small-scale behavior in the Baltic Sea. *J. Plankton Res.* **044**: 1–12.
- Montenegro, A., V. Brovkin, M. Eby, D. Archer, and A. J. Weaver. 2007. Long term fate of anthropogenic carbon. *Geophys. Res. Lett.* **34**: 1–5.
- Nash, J. 1951. Non-cooperative games. *Ann. Math.* **54**: 286.
- Netburn, A. N., and J. A. Koslow. 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. *Deep Sea Res. Part I* **104**: 149–158.
- Nilsson, L. A., U. H. Thygesen, B. Lundgren, B. F. Nielsen, J. R. Nielsen, and J. E. Beyer. 2003. Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. *Aquat. Liv. Res.* **16**: 317–324.
- Ohman, M. D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* **60**: 257–281.
- Ohman, M. D., and J.-B. Romagnan. 2016. Nonlinear effects of body size and optical attenuation on diel vertical migration by zooplankton. *Limnol. Oceanogr.* **61**: 765–770.
- Pavlov, D., and A. Kasumyan. 2000. Patterns and mechanisms of schooling behaviour in fish: A review. *J. Ichthyol.* **40**: 163–231.
- Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology* **78**: 1146–1156.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA* **98**: 3904–3908.
- Peacor, S. D., B. T. Barton, D. L. Kimbro, A. Sih, and M. J. Sheriff. 2020. A framework and standardized terminology to facilitate the study of predation-risk effects. *Ecology* **101**: 1–10.
- Pearre, S. 2003. Eat and run? The hunger satiation hypothesis in vertical migration: History, evidence and consequences. *Biol. Rev.* **78**: 1–79.
- Petitpas, C. M., and others. 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 Res. Part II Topic. Stud. Oceanogr.* **103**: 350–367.
- Pinti, J., and A. W. Visser. 2019. Predator-prey games in multiple habitats reveal mixed strategies in diel vertical migration. *Am. Nat.* **193**: E65–E77.
- Pinti, J., T. Kjørboe, U. H. Thygesen, and A. W. Visser. 2019. Trophic interactions drive the emergence of diel vertical migration patterns: A game-theoretic model of copepod communities. *Proc. Roy. Soc. B Biol. Sci.* **286**: 20191645.
- Pinti, J., K. H. Andersen, and A. W. Visser. 2021a. Co-adaptive behavior of interacting populations in a habitat selection game significantly impacts ecosystem functions. *J. Theor. Biol.* **523**: 110663.
- Pinti, J., and others. 2021b. Metazoans, migrations, and the ocean's biological carbon pump. *BioRxiv* 1–12.
- Pitcher, T. and Parrish, J. (1993). Functions of shoaling behaviour in teleosts. In Pitcher, T., editor, *The behaviour of teleost fishes* (2nd ed.), pages 363–439. Chapman and Hall.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**: 297–330.
- Prihartato, P. K., D. L. Aksnes, and S. Kaartvedt. 2015. Seasonal patterns in the nocturnal distribution and behavior of the mesopelagic fish *Maurollicus muelleri* at high latitudes. *Mar. Ecol. Prog. Ser.* **521**: 189–200.
- Robinson, C. J., F. V. Arenas, and G. J. Gomez. 1995. Diel vertical and offshore-inshore movements of anchovies off the central Baja California coast. *J. Fish Biol.* **47**: 877–892.
- Robison, B. H., and T. G. Bailey. 1981. Sinking rates and dissolution of midwater fish fecal matter. *Mar. Biol.* **65**: 135–142.
- Robison, B. H., K. R. Reisenbichler, J. C. Hunt, and S. H. Haddock. 2003. Light production by the arm tips of the deep-sea cephalopod *Vampyroteuthis infernalis*. *Biol. Bull.* **205**: 102–109.
- Romare, P., and L. A. Hansson. 2003. A behavioral cascade: Top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnol. Oceanogr.* **48**: 1956–1964.
- Saba, G. K., and D. K. Steinberg. 2012. Abundance, composition, and sinking rates of fish fecal pellets in the Santa Barbara channel. *Sci. Rep.* **2**: 1–6.

- Saba, G. K., and others. 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* **66**: 1–26.
- Schmitz, W. J., Jr. 1996. On the World Ocean circulation: Volume I—Some global features/North Atlantic circulation. Technical report. Woods Hole Oceanographic Institution.
- Schmitz, O. J., V. Křivan, and O. Ovadia. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecol. Lett.* **7**: 153–163.
- Schmitz, O. J., J. H. Grabowski, B. L. Peckarsky, E. L. Preisser, G. C. Trussell, and J. R. Vonesh. 2008. From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. *Ecology* **89**: 2436–2445.
- Schnetzer, A., and others. 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**: 372–387.
- Sekula-Wood, E., and others. 2009. Rapid downward transport of the neurotoxin domoic acid in coastal waters. *Nat. Geosci.* **2**: 272–275.
- Selander, E., P. Thor, G. Toth, and H. Pavia. 2006. Copepods induce paralytic shellfish toxin production in marine dinoflagellates. *Proc. Roy. Soc. B Biol. Sci.* **273**: 1673–1680.
- Selander, E., H. H. Jakobsen, F. Lombard, and T. Kiørboe. 2011. Grazer cues induce stealth behavior in marine dinoflagellates. *Proc. Natl. Acad. Sci. USA* **108**: 4030–4034.
- Selander, E., and others. 2019. Copepods drive large-scale trait-mediated effects in marine plankton. *Sci. Adv.* **5**: 3–9.
- Serra-Pompei, C., B. A. Ward, J. Pinti, A. W. Visser, T. Kiørboe, and K. H. Andersen. 2021. Zooplankton trophic dynamics drive carbon export efficiency. *BioRxiv* 1–23.
- Smetacek, V. 1999. Diatoms and the ocean carbon cycle. *Protoplast* **150**: 25–32.
- Smith, C. R., A. G. Glover, T. Treude, N. D. Higgs, and D. J. Amon. 2015. Whale-fall ecosystems: Recent insights into ecology, paleoecology, and evolution. *Ann. Rev. Mar. Sci.* **7**: 571–596.
- Stamieszkin, K., A. J. Pershing, N. R. Record, C. H. Pilskaln, H. G. Dam, and L. R. Feinberg. 2015. Size as the master trait in modeled copepod fecal pellet carbon flux. *Limnol. Oceanogr.* **60**: 2090–2107.
- Steinberg, D. K., and M. R. Landry. 2017. Zooplankton and the ocean carbon cycle. *Ann. Rev. Mar. Sci.* **9**: 413–444.
- Stukel, M. R., M. D. Ohman, T. B. Kelly, and T. Biard. 2019. The roles of suspension-feeding and flux-feeding zooplankton as gatekeepers of particle flux into the mesopelagic ocean in the Northeast Pacific. *Frontiers in marine science* **6**: 1–16.
- Tanet, L., S. Martini, L. Casalot, and C. Tamburini. 2020. Reviews and syntheses: Bacterial bioluminescence—Ecology and impact in the biological carbon pump. *Biogeosci. Discuss.* **17**: 3757–3778.
- Tarling, G. A., and S. Fielding. 2016. Swarming and behaviour in Antarctic krill, p. 279–319. *In* V. Siegel [ed.], *Biology and ecology of Antarctic krill*. Springer. Cham
- Toullec, J., D. Vincent, L. Frohn, P. Miner, M. Le Goff, J. Devesa, and B. Moriceau. 2019. Copepod grazing influences diatom aggregation and particle dynamics. *Front. Mar. Sci.* **6**: 751.
- Turner, J. T. 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat. Microb. Ecol.* **27**: 57–102.
- Våge, S., J. E. Storesund, J. Giske, and T. F. Thingstad. 2014. Optimal defense strategies in an idealized microbial food web under trade-off between competition and defense. *PLoS One* **9**: e101415.
- Van Someren Gréve, H., T. Kiørboe, and R. Almeda. 2019. Bottom-up behaviourally mediated trophic cascades in plankton food webs. *Proc. Roy. Soc. B Biol. Sci.* **286**: 20181664.
- Vinogradov, M. 1962. Feeding of the deep-sea zooplankton. *ICES Rep.* **18**: 114–120.
- Visser, A. W., and S. H. Jónasdóttir. 1999. Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. *Fish. Oceanogr.* **8**: 100–106.
- Visser, A. W., J. Grønning, and S. H. Jónasdóttir. 2017. *Calanus hyperboreus* and the lipid pump. *Limnol. Oceanogr.* **62**: 1155–1165.
- Volk, T., and M. I. Hoffert. 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO₂ changes, p. 99–110. *In* *The carbon cycle and atmospheric CO₂: Natural variations Archean to present*, v. **32**. Wiley.
- Wirsing, A. J., M. R. Heithaus, J. S. Brown, B. P. Kotler, and O. J. Schmitz. 2021. The context dependence of non-consumptive predator effects. *Ecol. Lett.* **24**: 113–129.
- Zaret, T. M., and S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**: 804–813.

Acknowledgments

We thank Fredrik Ryderheim, Peter Franks and Erik Selander for providing pictures for Fig. 1, and Tim DeVries for providing us with the transport matrix that was used for the simulations in Box 2. This work was supported by the Gordon and Betty Moore Foundation (Grant #5479), by the Centre for Ocean Life, a VKR Centre of excellence funded by the Villum Foundation, and by the U.S. National Science Foundation through support to MDO for the California Current Ecosystem LTER site. We thank Emma Cavan and an anonymous reviewer for their contributions that helped us improve this manuscript.

Conflict of Interest

We declare we have no conflict of interest.

Submitted 21 October 2021

Revised 02 February 2022

Accepted 14 March 2022

Associate editor: Anja Engel