The effect of plankton vertical migration on primary productivity in a warmer more stratified ocean

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Abstract

Marine primary production sustains ocean ecosystems and plays a central role in regulating the global carbon cycle. Current projections suggest that ocean warming will enhance water stratification, limiting the resupply of inorganic nutrients to surface waters, and consequently reduce primary production. This view neglects possible biological feedback mechanisms such as vertical migration by plankton communities. Through active vertical movements, both photosynthetic organisms and their grazers transport nutrients from depth to the surface, effectively functioning as a biological nutrient pump. While the existence of these processes is well established, translating vertical migration into quantitative nutrient fluxes at ecosystem or regional scales remains a major challenge. Here, we synthesize the current understanding of vertical migration in both primary producers and grazers and assess its potential to shape nutrient transport in the ocean. We argue that vertical migration will have implications for nutrient cycling in a warmer, more stratified ocean. Specifically, any climate-driven shifts in plankton community composition towards taxa better capable of vertical migrating may diminish the projected decrease in primary production. Finally, we discuss how recent technological advances provide new opportunities to quantify this biological nutrient pump and improve predictions of its role in future ocean scenarios.

Key words: biogeochemical cycles, inorganic nutrients, mixoplankton, phytoplankton, zooplankton

1. Introduction

Approximately half the global primary production takes place in the ocean, mainly by photosynthetic plankton (Falkowski & Raven, 2013; Field et al., 1998). Ocean productivity is central to global biogeochemical cycles, and in the context of increasing atmospheric CO_2, considerable attention has focused on the biological carbon pump, whereby organic matter produced in the sunlit surface sinks into the deep ocean where it is sequestered for the foreseeable future (Volk & Hoffert, 1985). Yet, alongside this well-studied downward flux, there exists another process, a biological nutrient pump, mediated by the active transport of nutrients from depth to the surface through migration of plankton. Vertical migration can be achieved through active motility and swimming behavior (Durham and Stocker 2012) or by biochemically modulating cell density (Miettinen et al., 2024). Although vertical migration of plankton has been studied for a long time, its contribution to nutrient budgets and primary production remains poorly quantified and is rarely represented in predictive models, resulting in uncertainty about how this biological nutrient pump will operate in a warmer ocean and how strongly it is linked to the biological carbon pump.

Some attempts to quantify nutrient transport rates in the oligotrophic ocean have suggested that vertical migration can constitute a substantial part of the total nutrient input to the upper mixed layer (Villareal et al., 1999; Villareal et al., 2014), reinforced by more recent modelling studies (Wirtz & Smith, 2020; Wirtz et al., 2022). This constitutes ‘new’ production by the migrating species, and if these nutrients are subsequently remineralized in the upper mixed layer, this activity supports ‘regenerated’ production, benefitting the broader planktonic community. This transport mechanism is not limited to primary producers as there are also examples of grazers bringing up nutrients from the deep to fertilize primary production at the surface (Schmidt et al., 2011).

Climate change projections have largely framed ocean primary production through the lens of physical processes. Although regional differences exist, warming is expected to intensify stratification, suppress vertical mixing, and reduce the upward supply of inorganic nutrients, leading to declines in net primary production (NPP) across most of the global ocean (Krumhardt et al., 2017; Moore et al., 2018; Ryan-Keogh et al., 2025; Silsbe et al., 2025). This paradigm underpins the expectation that marine ecosystems will become progressively more nutrient-limited in the coming century, reducing NPP and shifting communities towards smaller phytoplankton due to their higher surface to volume ratio, which leads to higher nutrient uptake efficiency (Moore et al., 2018; Steinacher et al., 2010). However, decreasing concentrations of inorganic nutrients in the upper part of the water column would make vertical migration an advantageous trait, a strategy which has not received much attention to date in this context. A possible analog is mixotrophy (Wilken et al., 2013, Gonzalez et al., 2022, Moeller et al., 2024), which is prevalent in stratified oligotrophic ecosystems (Hartmann et al., 2012) and has been shown, using theoretical approaches, to increase cell size, trophic transfer, and export (Ward and Follows 2016). Like mixotrophy, vertical migration may facilitate the survival of large cells, particularly in ecosystems where diurnal migration to the nutricline is feasible (e.g., temperate, polar). A shift towards more abundant vertically migrating taxa, increasing the biological nutrient pump, has the potential to counteract the projected reduction in the physical supply (i.e. mixing) of inorganic nutrients, but to what extent remains an open question.

Here, we highlight the role of vertical migration as a biological nutrient pump, by synthesizing the current understanding of vertical migration in both primary producers (i.e., phytoplankton and mixoplankton), highly motile mixoplanktonic ciliates (a special case), and grazers (i.e., zooplankton and mixoplankton) and its potential to shape inorganic nutrient transport in the oceans. By contrasting this process against the prevailing paradigm of declining primary production under warming, we emphasize the need for better understanding biological feedback mechanisms that

may offset projected declines in NPP. Finally, we discuss recent technological advances that open new research avenues for quantifying how this biological nutrient pump might operate in a warmer, more stratified ocean.

2. Projected reduction in net primary production

Earth system models and coupled biogeochemical models routinely project that anthropogenic warming will enhance upper-ocean stratification, reduce vertical mixing, and thereby suppress the upward supply of inorganic nutrients (e.g. nitrate and trace metals like iron) into the euphotic zone (e.g., Kwiatkowski et al., 2020; Li et al., 2020; Cheng et al., 2025). In many model ensembles, these effects translate to ~ 2-20 % declines in global marine NPP by 2100, depending on emission scenario, regional dynamics, and nutrient limitation regimes (e.g. Steinacher et al. 2010; Moore et al. 2018). These model frameworks typically treat nutrient supply as a multi-scale physical process, driven through a combination of vertical mixing, diffusion, upwelling, mesoscale and sub-mesoscale eddy processes, and lateral advection, and do not explicitly represent active biological transport across density gradients. High-resolution regional models, improving the representation of physical processes, have in some cases projected weaker declines in marine NPP (e.g. Couespel et al. 2021). In contrast, there are also studies that point to the reductions in NPP being underestimated (Ryan-Keogh et al., 2025). In addition, projected changes in NPP are expected to vary substantially among regions. For example, NPP will likely increase at high latitudes as sea-ice cover retreats and the growing season lengthens (Arrigo et al., 2008), partly offsetting declines projected at low and mid latitude regions. There is still an unaddressed gap in not including biological processes in these models that could potentially offset any constraints to the physical nutrient resupply. Thus, present model projections may understate the resilience of marine productivity.

3. Vertical migration by primary producers

3.1. Benefits and mechanisms

Vertical migration has long been established in most photosynthetic plankton groups such as diatoms and green algae (Round & Palmer, 1966), dinoflagellates (Eppley et al., 1968) and cyanobacteria (Van Rijn & Shilo, 1985). Most studies on this topic have focused on physiological or ecological aspects of vertical migration for individual species, demonstrating benefits in combining photosynthesis in the sunlit layer with inorganic nutrient uptake at greater depths where inorganic nutrients are more abundant. In addition, motility reduces the thickness of the diffusive boundary layer, with both geometry and swimming speed enhancing mass transfer across the cell-fluid interface (Jiang and Johnson 2017, Wheeler et al., 2019). Although there are clear benefits with motility, there are some tradeoffs as well, e.g., increased risks associated with vertical migration due to higher predator/grazer encounter rates (Titelman & Kiørboe, 2003) and reduced time for photosynthesis (Wirtz & Smith, 2020). Motility also comes with a metabolic cost, although these costs are theoretically low relative to total cellular metabolism (Lavoie et al., 2016; Raven & Richardson, 1984, Wan 2024).

There are several mechanisms used by photosynthetic plankton species to migrate vertically that can broadly be divided into: (a) motility using appendages such as flagella or cilia in motile groups (e.g., dinoflagellates, ciliates); or (b) buoyancy regulation by species that are otherwise classified as non-motile (e.g., diatoms, cyanobacteria). Flagellates propel themselves forward using the flagellar apparatus that may consist of one, two or four flagella that come in various configurations (van den Hoek et al., 1995), while ciliated organisms typically utilize the hundreds of cilia present on their body for coordinated motion. Buoyancy regulation can be achieved using a combination of ballasting to sink and positive buoyancy to ascend. There are several intracellular processes that can regulate ballasting and buoyancy such as shifts in polysaccharide storage, lipid storage, formation of gas vesicles, and addition or release of ‘heavy’ inorganic ions, either intracellularly or as part of the cell wall (Boyd & Gradmann, 2002; Moore & Villareal, 1996; Pfeifer, 2012). The mechanisms

144 behind downward or upward migration are also diverse, but likely related to chemotaxis, phototaxis,
145 geotaxis and/or a circadian clock (Byrne et al., 1992; Kamykowski et al., 1998).
146
147 3.2. Phytoplankton
148 Photosynthetic dinoflagellates are perhaps the longest and best studied organisms when it comes to
149 vertical migration and positioning in phytoplankton (Gran, 1915; Hasle, 1950). They contain two
150 flagella, typically one anterior and one transverse flagellum that propels the cell forward while
151 turning around its own axis (Fenchel, 2001). Many species exhibit pronounced diel vertical
152 migration, including *Tripos* spp. (syn. *Ceratium*), *Lingulodinium polyedra*, *Akashiwo sanguinea*,
153 and *Karenia brevis*, typically ascending during daytime for photosynthesis and descending at night
154 to access deeper nutrient pools (Eppley et al., 1968; Kamykowski et al., 1998). This can in some
155 cases fuel harmful algal blooms, e.g. for *L. polyedra* (Zheng et al 2023). Some species, such as
156 *Cochlodinium polykrikoides* and *Peridiniella catenata*, form long, multicell chains with the benefit
157 of reducing drag and increasing swimming speeds (Sohn et al., 2011), potentially enhancing vertical
158 migration capacity under turbulent conditions (Lovecchio et al., 2019).
159
160 Diatoms have a siliceous cell wall, termed a frustule, whose production has a relatively low
161 metabolic cost compared with other structural cell materials. This may contribute to the typical
162 rapid growth rates and opportunistic ecological strategies of many diatom species (Inomura et al.,
163 2023). The silicate also adds ballast, and most diatoms sink quickly out of the euphotic zone
164 without turbulence. However, there are also diatoms with a slower growing strategy that can
165 migrate vertically by buoyancy regulation in the oligotrophic gyres of the ocean (Villareal et al.,
166 1999; Villareal et al., 2014). In the central north Pacific, *Rhizosolenia* mats, clusters of large
167 *Rhizosolenia* spp., tend to be negatively buoyant when nitrogen starved, and by sinking they are
168 effectively able to “mine” deep nitrate pools and return to the surface at >6m h^{-1}, completing the
169 cycle over ~3-5 days (Villareal et al., 1996). Buoyancy regulation in diatoms has been linked to

changes in carbohydrate (Richardson and Cullen 1995) and lipid quantity and type (Zhang et al., 2023), however the biochemical pathways regulating this phenomenon remain poorly understood.

Several cyanobacteria are known to regulate their buoyancy by creating gas vesicles. These are formed by adding hollow intracellular spaces that are gradually filled with gasses dissolved in the surrounding water that can be regulated by light (Kinsman et al 1991; Pfeifer, 2012). Some taxa additionally regulate buoyancy through diel changes in cellular carbohydrate ballast, accumulating dense photosynthetic products during periods of high irradiance and metabolizing them under low-light or dark conditions, thereby altering cell density and vertical position in the water column (Kromkamp and Mur 1984). Large filaments of cyanobacteria can effectively regulate vertical positioning when turbulence is low, and different depth optima can create niche differentiation between co-occurring species (Hajdu et al., 2007; Moore et al., 2019). Pico-sized cyanobacteria are an important component of marine phytoplankton; however, the large migrating cyanobacterial colonies such as *Aphamizomenon* sp are mostly absent in open ocean ecosystems but can be regionally important in some coastal seas such as in the Baltic Sea. Cyanobacteria are also a dominant taxa in many freshwater systems. Similarly, some species of green algae are well known to migrate, but they are predominantly in the freshwater realm.

Coccolithophores are a major bloom forming photosynthetic protist group whose distribution is primarily controlled by turbulence. Their cells are characterized by their calcium carbonate shells (coccoliths) that serve as a protective outer shield. The coccoliths fulfil a ballasting function, increasing the sinking speed of the cells at least when they are nutrient starved (Lecourt et al., 1996). Coccolithophores are also known to form internal lipid storages, which can serve as a buoyancy-regulating mechanism, and they do have flagella enabling motility during some life stages (Paasche, 2001). However, the extent to which coccolithophores can vertically position

themselves is likely limited, but the groups can have significant implications to future NPP due to their high abundance and biomass distributions globally (O'Brien et al., 2013).

3.3. Kleptoplastidic ciliates

Ciliates are key members of plankton communities, and many of the more prominent species are both highly motile and capable of contributing to primary production by stealing plastids (i.e., kleptoplastids) (Stoecker et al., 2009). Ciliates within the *Mesodinium rubrum* / *major* species complex are among the fastest moving of all protists (Fenchel and Hansen 2006, Jiang and Johnson 2017), have a global distribution in marine and brackish water, and can form 'red tides' (discoloration of the water due to high abundance) in many parts of the world (e.g., Herfort et al., 2011). *Mesodinium* spp ciliates are well documented to form thin layers (Owen et al., 1992, Sjöqvist and Lindholm 2011) and have been shown to vertically migrate in stratified water columns in various neritic ecosystems (Crawford and Purdie 1991, Villarino et al., 1995, Crawford and Lindholm 1997). *M. rubrum*-like ciliates host cryptophyte kleptoplasts that they can also divide, a remarkable phenomenon made possible by also retaining a transcriptionally active prey nucleus (e.g. Johnson et al., 2007, Hansen et al., 2013; Drumm et al., 2021). Ciliates from the *M. rubrum* complex take up inorganic nutrients in the form of nitrate and phosphate (Tong et al., 2015) and are obligate phototrophs that function as phytoplankton (Crawford 1989). With maximum swimming speeds approaching 1 cm s^{-1} (>30 m h^{-1}), and reports of migration down to 20 m depth and back in 24 h (Lips & Lips, 2017), they clearly have potential to overcome mixing velocity. Lips and Lips (2017) suggested that upward transport of nutrients by *M. rubrum* is important for nutrient cycles and summer communities of phytoplankton in the Baltic Sea, but with limited data also highlighted the need for further studies of its vertical migration.

Vertical migration has also been documented in kleptoplastidic oligotrich ciliates, which are functionally distinct from *Mesodinium* ciliates in that their retention of kleptoplastids is highly

transient and their metabolism is more mixotrophic (McManus et al., 2012). Indeed, a mixotrophic oligotrich ciliate, *Laboea strobila,* is known to acquire vertical migration speeds of up to ~ 8 times their body length per second (Buskey et al., 1993). Photosynthesis in mixotrophic oligotrich ciliates is also obligate, requiring near-constant replacement of kleptoplastids by foraging on pico- and nano-flagellates (e.g., Stoecker et al., 1988, 1990). Vertical movement of mixotrophic oligotrichs has been proposed to be related to finding optimal light levels (Stoecker et al. 1988). Using an in situ holographic imaging approach that facilitated high resolution vertical profiles of plankton community within the water column, a dynamic thin layer of *L. strobila* was recently documented in the Mid-Atlantic Bight (Fig 1). The layer moved deeper in the water column for several hours after noon, and that appeared to be driven by a combination of behavior and physical forcing (Barua et al. 2024). This was the clearest demonstration of a thin layer by an oligotrich ciliate, with cell densities 1-2 orders of magnitude higher (~60 cells ml^{-1}; ~93 mg C L^{-1}) than typically reported in situ concentrations for this species, and > 6 times higher than the highest previous record. In contrast to *Mesodinium* spp ciliates, oligotrichs do not take up enough nitrate to support their growth, but rather, rely more on recycled nitrogen acquired by digesting prey (Schoener and McManus 2017). This factor, combined with their mixotrophic metabolism sustained largely by phagotrophy, suggest that mixotrophic oligotrichs are not important vectors of new nitrogen like *Mesodinium* spp., but rather stimulate nutrient recycling, likely while tracking vertical movements of prey. By efficiently repackaging small photosynthetic plankton biomass into a larger size class, they also provide important links to higher trophic levels.

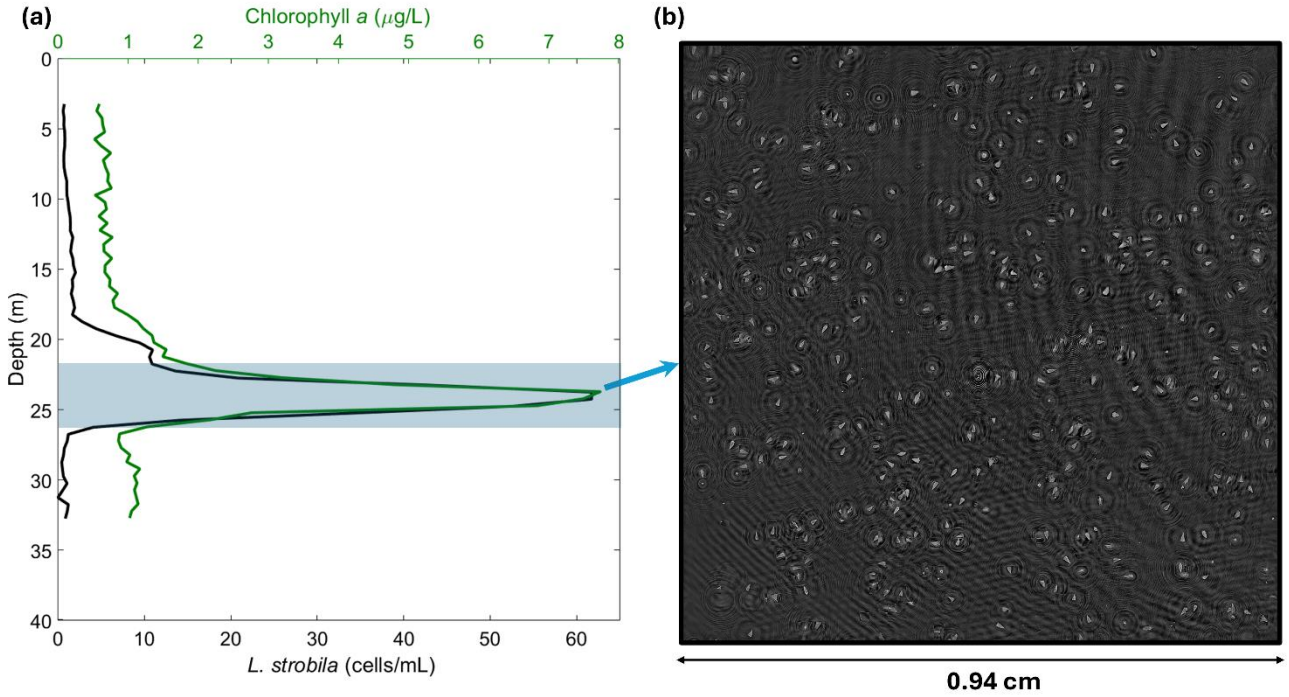

Figure 1: A high resolution vertical profile of a thin layer of the oligotrich ciliate, *Laboea strobila*, recorded in the Delaware shelf of the Atlantic Ocean on May 1, 2018. (a) Vertical abundance of *L. strobila* is strongly correlated with simultaneously recorded chlorophyll-a, with dramatic increase in concentration within the thin layer, indicated by the shaded region; (b) A sample processed hologram qualitatively showing the high abundance of *L. strobila* within the layer at 24 m depth. Figure generated from data published in Barua et al. (2024).

4. Vertical migration of heterotrophic grazers

Vertical migration of mesozooplankton has been more extensively studied than in phytoplankton and is typically inverse to phytoplankton migration, involving nocturnal grazing / feeding near the surface and seeking refuge from visual predation at depth during daytime. This diel vertical migration (DVM) is among the largest synchronized animal movements on Earth and occurs across a wide range of taxa including copepods, euphausiids, amphipods, salps and larval fish (Bandara et al., 2021). Although the migration of mesozooplankton takes place for other reasons than to combine nutrient uptake at depth with acquiring light at the surface, it might have implications for nutrient cycling and primary production (Bandara et al., 2021).

One of the best-known examples of nutrient input from mesozooplankton vertical migration is from the Southern Ocean where krill fertilizes primary production by excreting iron in the upper mixed zone (Cavan et al., 2019; Schmidt et al., 2011). Because iron strongly limits primary production across large regions of the Southern Ocean, iron fertilization by krill may have ecosystem-scale consequences for primary production. Many fish and marine mammals also migrate vertically in search of food and to some extent the vertical migration at different trophic levels can be coupled in 'cascading migrations' to either find prey or avoid predators (Bollens et al., 2011). Any excretion of waste products at the surface by the heterotrophic community would fertilize primary producers. In a scenario with reduced top-down control, any fertilization stimulating primary production could facilitate a form of phytoplankton gardening analogous to the microbial gardening hypothesis (Mayor et al 2014).

5. Future scenarios and possible effect on biogeochemical cycles

In their modelling study, Wirtz et al. (2022) surprisingly found that primary production increases in a future ocean due to vertical migration. However, as pointed out by Dunne (2022), there are some uncertainties in this approach: 1) nutrient uptake by vertical migration might diminish physical mixing of nutrients to the surface; 2) the model ignores self-shading by vertical migration; and 3) there are other physical and biological processes that could affect vertical migration which are yet to be resolved. Any climate-driven increase in stratification could select for plankton communities in which vertically migrating species play an increasingly dominant role. Under this scenario, we would hypothesize a shift towards higher abundance of mixotrophic ciliates or long-chained dinoflagellates in ecosystems where diel migration is feasible, together with greater importance of mat-forming diatoms in oligotrophic gyres, where longer but slower vertical migrations may provide access to deep nutrient pools (Fig 2). There are some shifts known regionally that could

affect overall vertical migration, for example the mixotrophic ciliate *M. rubrum* becoming more dominant in parts of the Baltic Sea (Kuosa et al., 2017), and chain forming photosynthetic dinoflagellate *Margalefidinium polykrikoides* in Korean waters (Lee et al., 2013). However, there are also other environmental drivers besides stratification affecting community shifts (e.g., eutrophication), and understanding the complex interactions between different drivers is a challenge going forward.

There are several key questions that have yet to be addressed when it comes to the biological nutrient pump. First and foremost, a combination of observation and modelling will need to resolve whether vertical migratory taxa increase in abundance, causing a shift in the community composition with increased intensity and duration of stratification. If so, the effects on the rest of the community, i.e. the extent of regeneration and secondary production, will require answers through experimentation and modelling. Follow on questions for laboratory and field studies should address whether increasing stratification becomes an increasingly difficult barrier to cross for vertical migration, creating a threshold where vertical migration loses its effect. Another open question is if nutrient uptake at (or right below) the nutricline would reduce the diffusive nutrient pump. Interaction effects between vertical migration and physical, chemical and biological changes in the marine environment should be addressed through experimentation, observation and modelling.

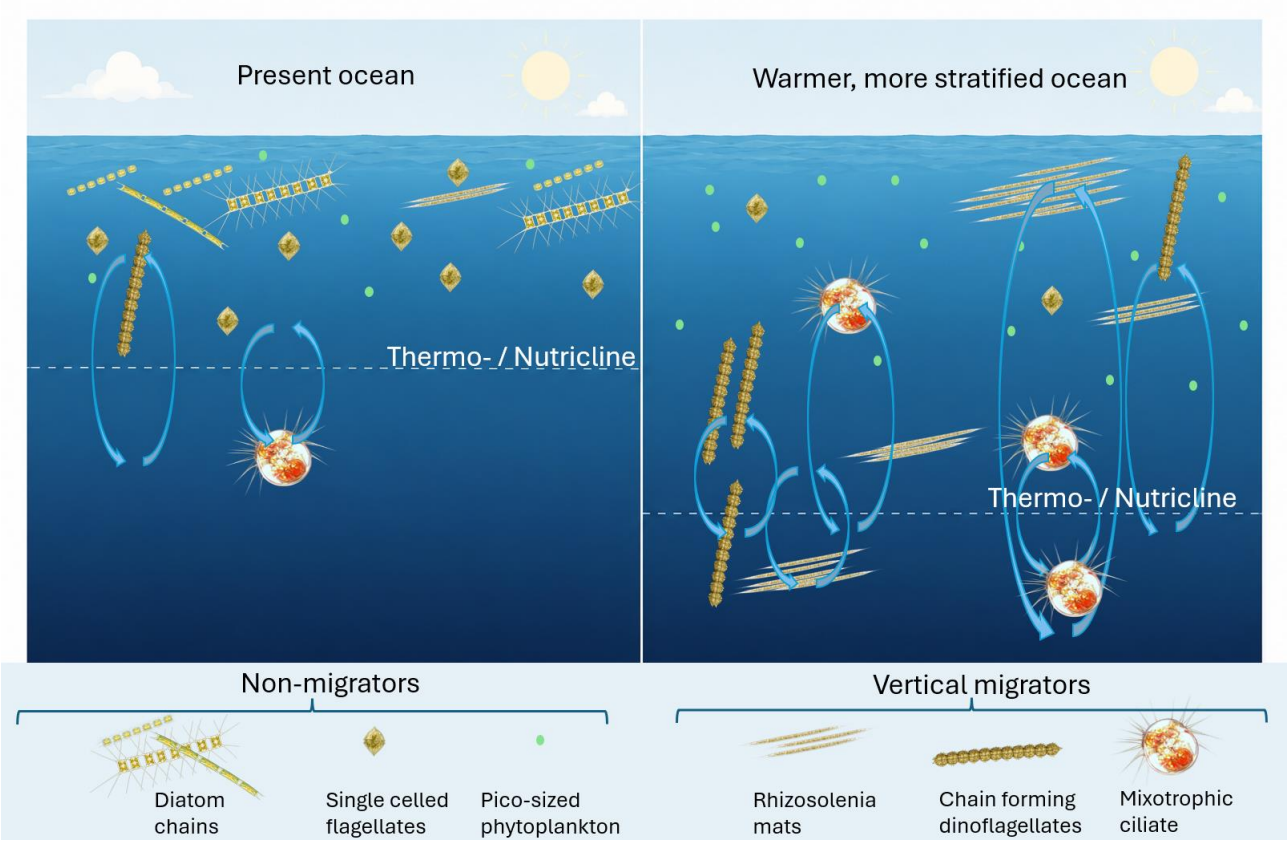

Fig 2. Conceptual model illustrating how vertically migrating phytoplankton/mixoplankton may become relatively more dominant in a warmer, more stratified ocean, where access to deep nutrients gives them a stronger competitive advantage. This mechanism could partially offset the reduced nutrient supply from physical mixing and increase the ecological importance of vertical migration as a biological nutrient pump. Picophytoplankton has also been projected to become more important as their higher surface to volume ration is beneficial at low nutrient concentration.

6. New research opportunities for studying vertical migration

Determining vertical migration in phytoplankton is challenging, as it is virtually impossible to follow individual cells over time in their natural environment. Traditionally, vertical migration in phytoplankton has been studied by sampling discrete depths frequently over time (e.g. over 24 h) to follow the population distribution, or alternatively, to follow a population in an experimental setting. However, the latter tends to come with much shorter migrating distances so that it is hard to

quantify any nutrient fluxes by vertical migration in a natural environment. Acoustic technologies are well-established methods to track DVM in zooplankton (e.g., Brierley, 2014; Bianchi and Mislan, 2016; Parra et al., 2019), however, they cannot typically resolve the smaller scales associated with phytoplankton. In situ imaging approaches facilitate high-resolution observations of both particles and organisms in the µm – cm size range (based on the instrument in question), offering a compelling means to study fluxes and species-specific abundances in the water column (Barth and Stone, 2024; Nayak and Twardowski, 2020). Additionally, emerging approaches such as digital holographic imaging and particle tracking (e.g., Nayak et al., 2021), may enable direct in situ quantification of plankton swimming behavior. Other options include simpler camera systems that can be set up to measure in situ particle movement (Simoncelli et al 2019). These techniques can resolve three-dimensional movement trajectories of individual cells and colonies under natural conditions, providing estimates of swimming speed, orientation, and migration behavior that could improve representation of active transport processes in ecosystem and biogeochemical models. These instruments also advance the collection of non-intrusive, vertical profiles of plankton composition, and can be repeated from profiling stations. Whilst these methods do not measure individual migration directly, repeated observations of swimming speed and direction of individuals provide bulk statistics on the overall direction and speed of the population allowing quantification of mass transport on a population level, as evidenced by recent studies (Garefelt et al., 2026). The recent advances in machine learning based approaches for automated classification across different imaging platforms (e.g., Irisson et al., 2022) have paved the path for the oceanographic community to increasingly embrace these instruments in research studies; however, the development of low-cost sensors is imperative to further scale these observations, including in geographical regions where data is currently limited (Nayak et al., 2025).

Ocean color satellite sensors provide ocean climate records through measurements of optical properties such as reflectance, absorption, scattering and transparency, together with derived

346 estimates of the biogeochemical state of the global ocean. Multi-decadal observations of the surface
347 ocean can already be realized; with up-to-daily global coverage at 300m resolution for most of the
348 past decade. A key observable biogeochemical product from remote sensing is chlorophyll a (Chl-a)
349 as a proxy of phytoplankton biomass. Using Chl-a to interpret green biomass has its limitations, as
350 both physiological and taxonomical differences modulate the Chl-a to C relationship. The recent
351 operationalization of hyperspectral satellites (PRISMA, EnMAP, PACE) may be used to explore
352 and quantify Chl-a derived biomass alongside taxonomic group presence based on diagnostic
353 secondary pigmentation, size classes, and carbon content. This could open avenues to observe
354 vertically migrating groups that have distinct pigmentation, while they are in the sunlit layer. For
355 example, *M. rubrum* has a distinct coloration and fluorescence profile due to the presence of
356 phycoerythrin that is uncoupled from photosynthetic antennae resulting in a high fluorescent yield,
357 resulting in light scattering properties that are distinct from the cryptophyte from where it derives its
358 chloroplasts. These features are not readily observed through the multispectral configurations of
359 conventional ocean color sensors, but visible from hyperspectral observations (Dierssen et al 2015).
360 Another option could be to couple Chl-a concentration with secondary indicators of particle size
361 (derived from the intensity and slope of backscattering), giving a good indication of Chl-a per size
362 class. Observing region to basin-scale population distributions in combination with vertical
363 profiling of diagnostic fluorescence using e.g. Argo floats, gliders, or stationary profiling buoys,
364 could be used to quantify vertical migration and upward flux of inorganic nutrients at
365 unprecedented scales.
366

367 7. Conclusion

368 Anthropogenic combustion of fossil fuels has profoundly altered the global carbon balance,
369 increasing atmospheric CO_2 concentrations and accelerating ocean warming. A dominant paradigm
370 emerging from earth system models is that enhanced upper-ocean stratification will suppress
371 nutrient resupply to the euphotic zone, leading to widespread declines in marine primary

production. While this framework has proven powerful for identifying first-order climate impacts, it does not consider possible biological feedback mechanisms. One such potential feedback mechanism is the capacity of plankton communities to actively redistribute nutrients across density gradients through vertical migration.

Here, we have reviewed both primary producers' and grazers' ability to engage in vertical movements that can modify nutrient fluxes in stratified waters. From buoyancy-regulated migrations by diatoms that access deep nutrient pools to diel migrations of zooplankton that may transport nutrients from depth to the surface, these processes collectively constitute a biological nutrient pump that operates alongside physical mixing. Importantly, these mechanisms are not rare or exceptional but are widespread across taxa, geographical regions, and trophic levels, and have likely contributed to sustaining productivity in oligotrophic and seasonally stratified systems throughout Earth's history.

Recognizing vertical migration as an integral component of marine biogeochemical cycling has important implications for projections of future ocean productivity. Rather than responding passively to increased stratification, plankton communities may partially buffer nutrient limitation through biologically mediated transport, with consequences for primary production, food-web structure, biodiversity, and carbon export efficiency. The strength, spatial extent, and net climatic feedback of this biological nutrient pump are likely to vary across ecosystems and environmental regimes, underscoring the need for ecosystem dependent assessments rather than globally uniform assumptions.

Recent technological advances including autonomous platforms, bio-optical and acoustic sensors, molecular tools, and trait-based and individual-based models provide new opportunities to quantify vertical migration and its biogeochemical consequences at relevant spatial and temporal scales.

Integrating these observations into next-generation biogeochemical and Earth system models represents biological feedback to ocean change, which could have implications for primary production in the future ocean.

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