Impact of finescale currents on biogeochemical cycles in a changing ocean

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Abstract

Fine-scale currents, O(1-100 km, days-months), are actively involved in the transport and transformation of biogeochemical tracers in the ocean. However, their overall impact on large-scale biogeochemical cycling on the time scale of years remains poorly understood due to the multi-scale nature of the problem. Here we summarize these impacts and critically review current estimates. We examine how eddy-fluxes and upscale connections enter into the large-scale balance of biogeochemical tracers. We show that the overall contribution of eddy-fluxes to primary production and carbon export may not be as large as for oxygen ventilation. We highlight the importance of finescales to low-frequency natural variability through upscale connections, and show that they may also buffer the negative effects of climate change on the functioning of biogeochemical cycles. Significant interdisciplinary efforts are needed to properly account for the cross-scale effects of finescales on biogeochemical cycles in climate projections.

Contents

Photosynthesis: Conversion of CO_2 and other inorganic nutrients (nitrate, iron, ..) into organic molecules using light energy

Remineralization: Breakdown of organic matter into inorganic forms using an oxydant (such as oxygen, when available)

Euphotic zone: Well-lit upper layer of the ocean ($\sim 0 - 150m$) where photosynthesis occurs

Twilight zone: Below the euphotic zone ($\sim 150 - 1000m$) where remineralization prevails

1. INTRODUCTION

Marine biogeochemical cycles refer to the transport and transformation of key chemical elements, such as carbon, nitrogen, phosphorus and oxygen, between different reservoirs within the ocean. These cycles are critical to the regulation of the Earth's climate, and they are being disrupted by climate change at an unprecedented rate. Understanding biogeochemical cycles mechanistically and predicting their evolution in a changing climate is a formidable scientific challenge. Phytoplankton are at the heart of these cycles, transforming carbon and limiting nutrients through **photosynthesis** between inorganic and living pools, and producing oxygen. Oxygen is then used to **remineralize** the dead organic material back into inorganic form (see textbook by Sarmiento & Gruber 2006).

A crucial difference between marine and terrestrial biogeochemical cycles is that the net production of the living organic pool and the remineralization of the detritic organic material are highly spatially decoupled in the ocean. Vertical decoupling results from the absorption of light in the upper water column combined with gravitation; in the euphotic zone, available inorganic nutrients are rapidly assimilated, and the organic material that is produced is exported to the twilight zone, mainly by gravitational settling, causing a biological pump of carbon. In the twilight zone, the organic material is then slowly remineralized, replenishing the nutrient reservoir and also driving oxygen depletion (Figure 1). Horizontal decoupling further results from the transport of organic and inorganic pools by ocean currents. Finally, temporal decoupling, from months to years, occurs between photosynthesis and remineralization.

Importantly, vertical exchanges are required to balance the biological pump and resupply the euphotic layer with remineralized carbon and nutrients, and to deliver oxygen to the twilight zone. The strength of these vertical exchanges are primarily shaped by the ocean general circulation and are particularly powerful in regions of convection, subduction and

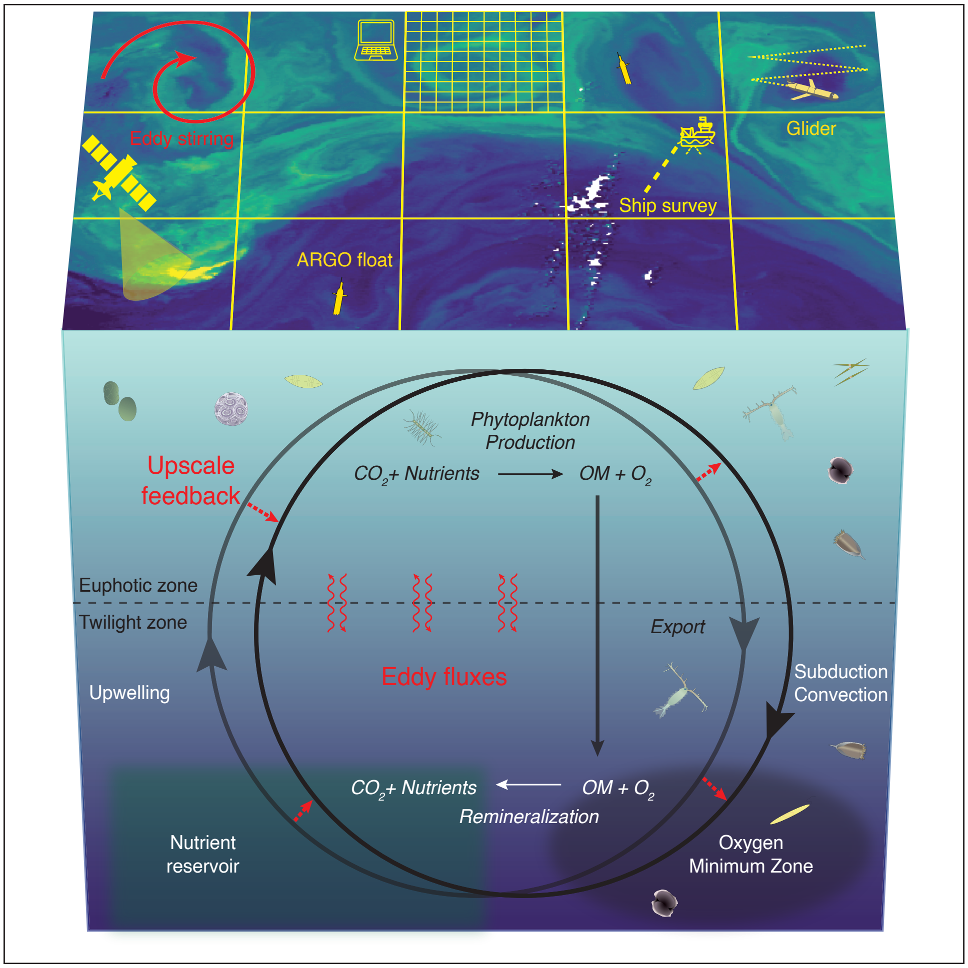

Figure 1

Illustration of the influence of finescales on marine biogeochemical cycles (red colors). (Top, surface view) Sea surface chlorophyll on 22/04/2007 from MODIS-aqua ocean color satellite L2 data binned on 1km grid. Stirring by mesoscale eddies and submesoscale fronts creates finescale patterns in the phytoplankton distribution. Overlaid are the model grids used in high-resolution Ocean General Circulation Models (OGCMs), and in coarse resolution Earth System Models (ESMs). The scales resolved by monitoring plateforms (in yellow) is also shown. (Bottom, cutaway view) Schematic representation of ocean biogeochemical cycles driven by the large scale circulation (large grey loop). Finescales impact these cycles through local eddy-fluxes and through upcale feedback which modifies the large-scale transport.

upwelling (Figure 1). Moreover, these contrasts in supply drive distinct large-scale **biogeochemical provinces**. Thus, marine biogeochemical cycles operate at the spatial scale of these provinces and over temporal scales of years (see textbook by Williams & Follows 2011). This is a critical element in the context of this review which focuses on processes occurring on much smaller and faster scales with a particular focus on their influence on the larger-scales.

Biogeochemical provinces: Large-scale ecosystems under coherent physical forcing and environmental conditions

In the late 1990s, the idea arose that large-scale exchanges could not fully explain the cycling of elements. This stemmed from apparent observational discrepancies between nutrient supply and export production in the North Atlantic oligotrophic subtropical gyre, which suggested that sporadic nutrient injections at unresolved scales were necessary to close the budget (McGillicuddy et al. 1998, Oschlies 2002). It was initially assumed that these small-scale nutrient transports were driven by **mesoscale eddies** (see review by McGillicuddy 2016), which are ubiquitous in the global ocean, particularly close to western boundary currents, such as the Gulf Stream, where they are generated.

It then became clear that vertical velocities occurring at the **submesoscale** also played a role since they are even more intense than at the mesoscale (see review by Klein & Lapeyre 2009). Submesoscale currents are flow structures in the form of sharp density fronts and filaments, or coherent vortices, created from mesoscale eddies and strong currents, whose dynamical characteristics have been the topic of several inspiring reviews (McWilliams 2016, 2019, Gula et al. 2022, Taylor & Thompson 2022).

Submesoscale and mesoscale circulations are strongly intertwined, one feeding the other and vise-versa (Sasaki et al. 2020, Balwada et al. 2022, Naveira Garabato et al. 2022, Taylor & Thompson 2022), and often act in conjunction (Uchida et al. 2019, Freilich & Mahadevan 2019, Balwada et al. 2021). Biogeochemical studies based on high-resolution models or high-resolution satellite or in-situ observations do not always isolate their respective roles, and we will use the generic term of finescales to describe them.

Mesoscale and submesoscale dynamics can be modeled accurately with the hydrostatic, Boussinesq equations that form the core of Ocean General Circulation Models (OGCMs) (Mahadevan & Tandon 2006). They emerge when the horizontal grid spacing used to solve the model equations has kilometer-scale (Capet et al. 2008, Lévy et al. 2012b, Pietri et al. 2021). But finescales are not explicitly resolved when OGCMs are embedded within Earth System Models (ESMs) used for biogeochemical climate projections (Bopp et al. 2013), which involve long and global simulations, because computational capabilities limit grid spacing. In ESMs, the effects of finescales must be included through sub-grid parameterizations, whose development is an area of active research (Mak et al. 2018, Bolton & Zanna 2019, Frezat et al. 2022) and one of the great challenges in ocean modeling (Fox-Kemper et al. 2019).

Much progress has been made recently in the understanding, observation and modeling of the vertical circulation in the mesoscale to submesoscale range (Mahadevan et al. 2020). An important aspect is that the surface intensified submesoscale density fronts are associated with three-dimensional cross-frontal circulation. Provided that they reach deep enough into the nutricline, there is now a plethora of evidence that intense upwelling on the warm side of submesoscale fronts locally fertilizes the euphotic layer and increases **primary production** (see previous reviews by Mahadevan 2016, Levy et al. 2012, 2018). The downwelling on the cold side of submesoscale fronts is equally important for biogeochemical cycles, directing fluid and tracers from the euphotic zone to the twilight zone; submesoscale downwelling velocities contribute to the biological export of organic carbon via the **eddy pump** (Boyd et al. 2019), to the sequestration of anthropogenic CO2 (Balwada et al. 2018), and act as the primary mechanism supplying subsurface oxygen to **Oxygen Minimum Zones** (Lévy et al. 2022). Thus submesoscale cross-frontal circulations act as miniature motors of marine biogeochemical cycles, refueling the surface layer with limiting nutrients, participating in the export of organic carbon, and ventilating the ocean interior (Figure 1).

Mesoscale eddies: Coherent rotating vortices with horizontal and time scales O(10-100 km, months)

Submesoscales: Dynamical features with horizontal and time scales just below the mesoscale O(1-10km, days)

Finescales: Dynamical features in the submesoscale to mesoscale range O(1-100 km, days-months)

Ocean General Circulation Models (OGCMs): Computer code that estimates the solution of fluid motions in the ocean on a three-dimensional grid under prescribed atmospheric forcing

Earth System Models (ESMs): Computer code that simulates climate relevant aspects of the Earth System coupled to one another

Primary production: Amount of phytoplankton production by unit time

Eddy pump: Organic carbon export by finescale transport that complements the gravitational pump

Oxygen Minimum Zones (OMZs): Poorly ventilated hypoxic waters located in the twilight zone crucially important for climate and resources

The previous reviews on bio-physical couplings at finescales (McGillicuddy 2016, Mahadevan 2016, Levy et al. 2012, 2018) have focused on quantifying and understanding the local processes involved. Now that we have ample evidence and a much better understanding of how these processes act at the local scale of fronts and eddies, what remains more uncertain, and will be the focus of this review, is the extent to which these finescale flows participate in the global cycling of elements in the ocean on the timescale of years, their natural variability on the timescale of decades and their response to climate change on the timescale of centuries.

In addition to their local impact, submesoscale and mesoscale flows transfer energy to larger scales, and thus contribute to the large-scale balance of ocean circulation (Taylor & Thompson 2022), its natural variability (Penduff et al. 2011) and its evolution under climate change (Hewitt et al. 2022). Thus finescales may impact biogeochemical cycles both through **eddy fluxes** at their own scale, and through **upscale connections** (Figure 1). These two aspects will be discussed with regard to the mean state, natural variability and response to climate change of biogeochemical cycles.

Eddy fluxes: Advective transport of elements by finescale currents

Upscale connections: Modifications of the ocean circulation through energy transfer from finescales to large-scales

In section 2, we introduce how finescales may impact marine biogeochemical cycles and how this impact may be quantified. Then we present a review of current estimates of the impact of finescales on the mean state of biogeochemical cycles (section 3), their natural variability (section 4) and their response to climate change (section 5). This review focuses on the rapidly expanding body of knowledge in the literature since a previous review article on the topic (Levy et al. 2018).

2. EVALUATING THE IMPACTS OF FINESCALES ON BIOGEOCHEMICAL CYCLES

Evaluating the impacts of finescale processes implies measuring how they contribute to the large-scale biogeochemical balance. This poses challenges because finescales are difficult to observe and model, and because the spatio-temporal averaging at which this quantification is meaningful (biogeochemical provinces, > 1 year) is much larger than the scales at which submesoscale fluxes can be observed (targeted fronts, <1-2 months) or modeled. It is all the more challenging that their contribution takes multiple forms. Here we introduce the biogeochemical balance, we present the different finescale impacts conceptually, and the limitations of the current methods that are used to evaluate them.

2.1. Biogeochemical balance

The balance equation for biogeochemical tracers can be summarized as follows:

$$\partial_t C = -\nabla \cdot (Cv) + \partial_z(k_z \partial_z C) + B(C) \qquad 1.$$

C is the biogeochemical tracer (such as dissolved inorganic carbon, phytoplankton, nitrate or oxygen), v is the three-dimensional velocity, k_z is the vertical mixing coefficient, and $B(C)$ includes the biogeochemical reactions of C; for instance in the case of oxygen, $B(C)$ will include oxygen production by photosynthesis minus oxygen removal by remineralization; for phytoplankton, $B(C)$ will include phytoplankton production by primary production minus phytoplankton losses through mortality and predation.

Due to the spatio-temporal decoupling between the different terms in this equation, which is particularly pronounced at finescales (Estapa et al. 2015, McGillicuddy et al. 2019),

Large-scale biogeochemical balance: Balance between upward fluxes of elements, downward fluxes and transformations in the euphotic zones and twilight zones, after integration over the scale of biogeochemical provinces and over the year

this balance is not at equilibrium locally (i.e. $\partial_t C \neq 0$), but may emerge after integrating equation 1 over sufficiently large spatio-temporal scales, i.e. typically the year and over biogeochemical provinces, and over the euphotic (resp. twilight) layer (i.e. $\langle \partial_t C \rangle = 0$). The braquets $\langle . \rangle$ represent this **large-scale** integration. At equilibrium over the euphotic (resp. twilight) layer, the amplitude of the biogeochemical reactions $\langle B(C) \rangle$ is set by the magnitude of the transport terms, advection and vertical diffusion. The natural low-frequency variability of these cycles, and response to anthropogenic disturbances, are manifested as positive or negative trends in $\langle \partial_t C \rangle$. Hence marine biogeochemical cycles can be pictured as a balance between the upward and downward fluxes of elements across the separation between the euphotic zone and twilight zone, and the transformation of these elements between organic and inorganic forms in the euphotic zone and twilight zone, respectively (Figure 1).

To highlight the importance of finescale dynamics on the advective transport of biogeochemical material, we can further separate the advective term of Equation 1 into mean and eddy components, following a classical Reynolds decomposition:

$$\overline{Cv} = \overline{C}\,\overline{v} + \overline{C'v'} \qquad 2.$$

The over-barre represents a monthly mean operator and/or a spatial mean operator over boxes larger than the mesoscale (typically 1° to 2° wide, which is the size of coarse-resolution ocean models grid), and the prime is the deviation from this mean. Due to their non-linear nature, biogeochemical reactions can also be decomposed in a similar manner into eddy ($\overline{B'(C')}$) and mean ($\overline{B}(\overline{C})$) components.

With this decomposition, the large-scale biogeochemical balance becomes:

$$\langle \overline{\partial_t C} \rangle = -\langle \nabla \cdot (\overline{C}\,\overline{v}) \rangle - \langle \nabla \cdot (\overline{C'v'}) \rangle + \langle \partial_z \overline{(k_z \partial_z C)} \rangle + \langle \overline{B}(\overline{C}) \rangle + \langle \overline{B'(C')} \rangle \qquad 3.$$

Finescales naturally enter this balance through the eddy advection term $\langle \nabla \cdot (\overline{C'v'}) \rangle$ and through the biogeochemical eddy term $\langle \overline{B'(C')} \rangle$. In addition, submesoscale dynamics affects both the large-scale circulation ($\overline{v}$) and small-scale turbulence ($\overline{k_z}$) by redistributing energy upscale and downscale (Taylor & Thompson 2022); thus through these scale connections, finescales enter the balance through the mean advection $\langle \nabla \cdot (\overline{C}\,\overline{v}) \rangle$, and mean vertical diffusion $\langle \partial_z \overline{(k_z \partial_z C)} \rangle$. This review focuses on the impact of eddy advective fluxes and upscale connections, nevertheless for completeness in the next section we also discuss the other possible pathways, i.e. biogeochemical eddy terms and downscale connections.

2.2. The different impacts of finescales

2.2.1. Impact of finescales through local eddy fluxes.

2.2.1.1. Vertical eddy advective fluxes. Finescale vertical advection associated with mesoscale eddies and submesoscale fronts (Mahadevan 2016, Levy et al. 2012, 2018) supplies the euphotic layer with nutrients (Lévy et al. 2001), exports organic carbon (Lévy et al. 2001, Omand et al. 2015) or excess nutrients (Gruber et al. 2011), and ventilates the ocean interior with oxygen (Resplandy et al. 2012). Indeed submesoscale ($w' \sim 10 - 100 mday^{-1}$, Pietri et al. 2021) and mesoscale ($w' \sim 0.1 - 10 mday^{-1}$, Pietri et al. 2021) vertical velocities are much larger than the strongest mean large-scale vertical velocities ($\overline{w} \sim 0.1 - 0.5 mday^{-1}$ Liao et al. 2022), leading to eddy vertical advection fluxes $\overline{C'w'}$ that may largely exceed the mean vertical advection flux $\overline{C}\overline{w}$. However, it has also been argued that the shallow penetration of w' at some submesoscale fronts (Ramachandran et al. 2014), as well as their strong seasonality (Callies et al. 2015), may limit the strength of vertical eddy fluxes in some cases (Levy et al. 2018). Moreover, because vertical eddy fluxes operate at the local scale of eddies and fronts and over relatively short period of time, while mean vertical transport - either advective or diffusive - operates at much larger spatio-temporal scales, it is not guaranteed that the large-scale contribution of vertical eddy fluxes $\langle\overline{C'w'}\rangle$ dominates over the other transport fluxes $\langle\overline{C}\overline{w}\rangle$ and $\langle\overline{k_z\partial_z C}\rangle$.

2.2.1.2. Stirring. Horizontal eddy advection is often called stirring because mesoscale eddies and submesoscale flows are responsible for the stirring of biogeochemical tracers (Lehahn et al. 2007, d'Ovidio et al. 2010). Patterns in sea-surface phytoplankton clearly reflect the influence of stirring (Figure 1), and constitute what have been termed drifting forests (Lehahn et al. 2017a), which can spread over thousands of kilometers (Sergi et al. 2020). In opposition to vertical eddy advection, stirring at the sea-surface mostly reorganizes the tracers without significantly affecting their quantity. To reflect that, vertical eddy advection was referred to as active in a previous review, in opposition to passive horizontal stirring at the ocean surface (Levy et al. 2018). But away from the sea surface, the preferential direction for stirring motions are the inclined **isopycnal surfaces**, leading to an eddy transport along these isopycnals which is often described as isopycnal diffusion (Abernathey et al. 2022). Isopycnal diffusion is important for replenishing nutrients at sub-surface (Spingys et al. 2021), and for oxygen ventilation(Lachkar et al. 2016).

Isopycnal surfaces: Surfaces of constant density along which water parcels can move freely

2.2.2. Impact of finescales through scale connections.

2.2.2.1. Upscale connection. The energy transfer from finescales to the large-scale contributes to the dynamical and thermodynamical adjustment of the ocean, and thus in setting $\overline{v}$. Quantification of this upscale feedback is emerging in recent literature, as the resolution of OGCMs increases. Let us compare two simulations of the same model configuration, one explicitly resolving finescales (HR), the other including finescales through parameterizations (CR). Due to scale connections, the mean advection will not be the same in the two simulations; the upscale feedback can be estimated as $\langle\nabla\cdot(\overline{C}\overline{v})\rangle_{HR} - \langle\nabla\cdot(\overline{C}\overline{v})\rangle_{CR}$. $\overline{v}_{HR}$ is often closer to observations than $\overline{v}_{CR}$ (Chassignet et al. 2020). Observational evidence of this energy transfer has recently been shown in the Gulf of Mexico (Balwada et al. 2022).

2.2.2.2. Downscale connection. There are complex interactions between submesoscale vertical transport and vertical mixing. Indeed, as they develop, many submesoscale processes increase the vertical density stratification in, or restratify, the upper ocean (Taylor & Thompson 2022). The seasonal restratification of the **mixing-layer** following the development of submesoscales has been shown to advance seasonal phytoplankton blooms (Karleskind et al. 2011, Mahadevan et al. 2012). This effect is not associated with changes in the annual fluxes of elements, but rather when a time shift of a couple weeks (Haeck et al. 2023). The finescale heterogeneity of vertical mixing also affects the annual export of carbon, by enhancing the export rate associated with gravitational settling (Taylor et al. 2020) and by creating hot spots of export through entrainment (Resplandy et al. 2019). OGCMs are not able to capture the full complexity of the interactions between submesoscales and vertical turbulence in the mixing-layer, but these can be examined with more

Mixing-layer: Upper layer of up to 1000m depth characterized by strong vertical mixing.

complex models such as Large Eddy Simulations (LES, Whitt & Taylor 2017). LES models can only be used in very small domains and do not yet allow meaningful quantification, nevertheless, with a biogeochemical LES model, (Whitt et al. 2019) have been able to show that submesoscales could enhance storm-driven vertical mixing of nutrients. The effects discussed in this paragraph need to be further quantified and are not considered thereafter.

2.2.3. Impact of fine scales on biogeochemical reactions. There have been only few attempts to quantify $\langle\overline{B'(C')}\rangle$, which makes it difficult at this stage to discuss further their global relevance. The first evaluations (Lévy & Martin 2013, Martin et al. 2015) concluded on a negligible contribution in the case of primary production. We should also mention here that transport and reactive processes are linked. For instance, the strength of the eddy nutrient supply affects the structuring of the planktonic ecosystem, with certain plankton species favored and others not (Mangolte et al. 2022, Guo et al. 2022); the modified structuring may affect, in turn, affect the export efficiency (Treguer et al. 2018, Serra-Pompei et al. 2022). Another example is the feedback between the phytoplankton growth rate and the eddy vertical nutrient flux (Freilich et al. 2022), as the former sets the vertical gradient on which the latter acts. We can also mention the link between horizontal stirring and phytoplankton biomass accumulation through adjustment of ecosystem (Lehahn et al. 2017b). These aspects call for future studies before they can be quantified at large-scale, and are not considered thereafter.

2.3. Methodological challenges

2.3.1. Local field studies. Much of the recent work on the biogeochemical impacts of submesoscales has relied on local field surveys (Marrec et al. 2018, Little et al. 2018, de Verneil et al. 2019, Ruiz et al. 2019, Tzortzis et al. 2021). Such field campaigns are extremely difficult to implement due to the inherent difficulty of sampling submesoscales, which are constantly and rapidly changing. Today, there are no direct observations of finescale currents from space, as the currents derived from satellite altimetry maps only represent scales larger than 100 km (Chelton et al. 2011), although this might change in the near future thanks to the new Surface Water and Ocean Topography satellite mission (d'Ovidio 2019). But field surveys have been extremely useful to reconstruct the cross-frontal submesoscale circulation (D'Asaro et al. 2018, Buongiorno Nardelli et al. 2018, Siegelman et al. 2020, Tarry et al. 2021, 2022, Garcia-Jove et al. 2022, Cutolo et al. 2022, Comby et al. 2022). These local field studies have been useful in providing estimates of $\overline{T'v'}$, but are difficult to extrapolate to $\langle\overline{T'v'}\rangle$. Another caveat of these local field studies is that they tend to target strong cases, which may not be always representative of the mean ocean.

2.3.2. Biogeochemical argo floats. Biogeochemical argo floats have also been used to detect anomalies in the vertical distribution of tracers, that can be related with past submesoscale events but the link to eddy fluxes in not straightforward (Llort et al. 2018, Wilson 2021). Moreover, although more and more floats are progressively being deployed, the number of events that they can capture is still very limited. For instance Wilson (2021) identified a dozen of nitrate injection events in the North Pacific subtropical gyre representing less than 1% of the total number of profiles recorded.

2.3.3. High resolution models. Modeling studies are also pushed to their limits due to the current computational power, which remains insufficient for the use of high-resolution models over large domains and/or long periods of time (Hewitt et al. 2022). When the grid resolution is increased in OGCMs, the finescales that emerge at higher resolution feed more eddy fluxes and also feedback onto the large-scale circulation. But models need to be integrated over sufficiently long periods for the time-mean circulation to equilibrate, and the required spin-up gets more challenging as the grid is refined. Thus the upscale feedback is often not present in short short integrations of high resolution regional models (Rosso et al. 2014, Kessouri et al. 2020).

2.3.4. Ocean color data. The only biogeochemical dataset with sufficient spatial and temporal resolution to estimate the global impact of finescales is the satellite ocean color record, which has been continuously increasing in length since 1998 and provides daily estimates of surface chlorophyll at a resolution now approaching 1 km. The information contained in this database is imperfect in many respects, notably because the data relate to chlorophyll (a proxy for phytoplankton biomass) and not fluxes, are restricted to the surface, and limited by clouds. Nevertheless, they are valuable in that they can be used to examine variability in surface phytoplankton across a range of scales. Finescale chlorophyll patterns reflect the influence of stirring, of vertical nutrient eddy fluxes, but also of other factors such as wind bursts (Nicholson et al. 2021) or intrinsic ecological interactions, such as predator-prey interactions or competition for resources (Mayersohn et al. 2022). The analysis of these highly dynamic ocean color patches has involved a variety of methodologies, from the Eulerian analysis of their shape, possibly in relation to pre-identified physical features, to the Lagrangian perspective of tracking their formation, where ocean color data has been used alone, or in conjunction with other datasets such as satellite sea surface height or temperature to relate phytoplankton patchiness to specific physical finescale features. We present in the next section how the methods have evolved to allow the extraction of the impact of vertical transport from surface observations.

3. IMPACT OF FINESCALES ON THE MEAN STATE OF BIOGEOCHEMICAL CYCLES

Below we present recent attempts to estimate the impact of finescales on primary production, carbon export and oxygen ventilation, which illustrate the high degree of uncertainty in our current knowledge. We first present estimates from ocean color data, then move to estimates of carbon, nitrogen and oxygen eddy fluxes derived from in-situ data, argo floats and regional model studies, and we end with estimates of the upscale feedback of finescales from longer model integrations.

3.1. Impact of finescales on surface phytoplankton

3.1.1. Stirring. Spatial geostatistical analysis provides statistical confirmation that phytoplankton spatial variability at the global scale is dominated by horizontal stirring (Glover et al. 2018). Keerthi et al. (2022) quantified this role by considering finescales through their temporal, rather than spatial, footprint; at each location in the global ocean, the sub-seasonal component (defined as associated with timescales <3 months) of phytoplankton was extracted, and shown to be largely associated with fine spatial scales (<100 km) and to contribute roughly 30% of the total variance at the global scale. There were strong regional disparities in this contribution, for it varied between 30 and 55% instance in the Gulf stream region (yellow bars in Figure 2). These results were confirmed by an independent study which used a different approach based on the analysis of the dominant timescale of variability (Jönsson et al. 2023).

3.1.2. Highlighting vertical inputs. In order to isolate the influence of vertical inputs of nutrients driving net growth, Jönsson et al. (2011) proposed a Lagrangian framework in which satellite ocean color data are projected onto surface trajectories from high-resolution model reanalysis. This method allowed the rate of change in biomass to be evaluated along trajectories and related to finescale inputs. A major drawback is that the method is strongly limited by the amount of synchronous chlorophyll data available along trajectories. Zhang et al. (2019) circumvented this problem by averaging properties over 2° grids, using global-scale datasets of surface drifters, satellite altimetry and ocean colour data. Their global analysis revealed a positive correlation between the strain rate of the flow and phytoplankton growth, consistent with the hypothesis that this growth is sustained by upwelling along sharp fronts. Guo & Chai (2019) focused on sorting the mesoscale and submesoscale structures associated with elevated patches of chlorophyll over subtropical gyres of the global ocean, and were able to estimate that both contributed equally.

3.1.3. Evaluating vertical inputs. Liu & Levine (2016) used satellite sea surface temperature data to detect the location of spatial heterogeneities at the scale of $\sim 10km$ in the north Pacific subtropical gyre and quantified the median chlorophyll overload associated with them. They evaluated that chlorophyll enhancement over fronts was $\sim$ 20%. Haeck et al. (2023) applied the same approach to the northwest Atlantic, and showed that the strength of the enhancement was stronger in regions that are naturally more productive, and varied from 7 to nearly 40% (red bars in Figure 2). Importantly, Haeck et al. (2023) also evaluated the chlorophyll surplus due to fronts at the scale of bio-provinces. The large-scale surplus accounts both for the local enhancement over fronts and for the surface area covered by fronts. It varies between 1 and 20% (blue bars in Figure 2). Importantly, the comparison between the three different estimates in Figure 2 highlights that focusing on variability, or on local effects systematically leads to a strong overestimation of the global impact of finescales on phytoplankton abundance.

3.2. Eddy fluxes of carbon, oxygen and nutrients

3.2.1. Eddy-pump of carbon. To illustrate current uncertainty in the global assessment of eddy fluxes, we compare independent estimates of the eddy-pump of carbon. Using glider observations of anomalous features of elevated Particulate Organic Carbon (POC) at depth, Omand et al. (2015) explored the subduction of POC by submesoscale features, in a calibrated process-study ocean model of a small ocean slice (100 km width) integrated for four months, which they then used to scale-up the impact of finescales. This led to the estimate that the eddy-pump contributes to half of the total export of POC in the North Atlantic, Kuroshio extension, and the Southern Ocean. Using Biogeochemical Argo floats data across the Southern ocean, Llort et al. (2018) detected subduction events from oxygen anomalies, and associated them with the POC anomalies also measured by the floats; they estimated that the eddy-pump contributes to about 20% of the total POC export in the

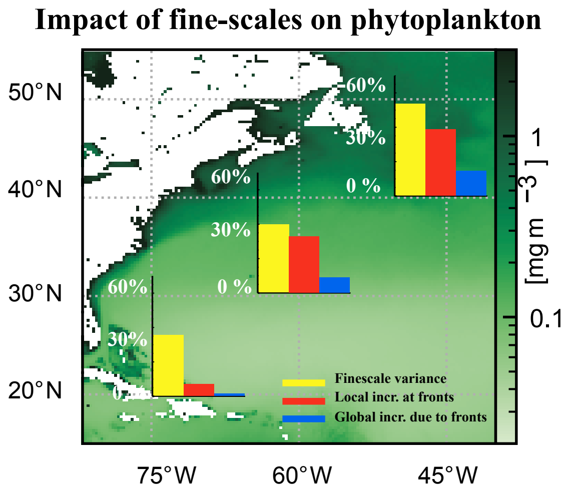

Figure 2

Contribution of finescales to mean phytoplankton abundance in the northwest Atlantic, quantified from 20 years of ocean color data, and using chlorophyll as a proxy for phytoplankton. The background (green color) is the chlorophyll climatology. The bar plots show three % estimates of finescale contributions to chlorophyll by latitudinal bands (20-30°N, 30-40°N, and 40-50°N). Finescale variance (yellow bars) represents the part of the chlorophyll variance associated to subseasonal time scales, and mostly represents the effect of stirring (adapted from Keerthi et al. 2022). Local increase at fronts (red bars) represents the local increase in chlorophyll over fronts due to finescales (adapted from Liu & Levine 2016). Global increase due to fronts (blue bars) represents the large-scale contribution of finescales to chlorophyll in each latitudinal bands (adapted from Haeck et al. 2023).

Southern Ocean. Erickson & Thompson (2018) also evidenced subductive events over a full seasonal cycle in the Northeast Atlantic using data collected from gliders, and find that they did not contribute significantly to carbon export. Finally, Resplandy et al. (2019) used 5 years of an eddy-resolving simulation in an equilibrated, idealized model of the North Atlantic and evaluated, in agreement with Erickson & Thompson (2018), that the contribution of the eddy-pump to the total export was less than 5%, although the magnitude of the local anomalies in the POC vertical profiles were comparable to those of Omand et al. (2015). This large range between estimates of the eddy pump (50%, 20%, 5%) can partially be explained from strong compensation between upward and downward fluxes, which were accounted for in the longer model integration but not in all data-based estimates (Claustre et al. 2021).

3.2.2. Oxygen eddy-fluxes. A second illustration concerns how finescales are primary players in controlling the volume of OMZs (see review by Lévy et al. 2022). Resplandy et al. (2012), with a model at 1/12° resolution, demonstrated that oxygen eddy fluxes contributed to more than 90% of oxygen ventilation of the Arabian Sea OMZ. Brandt et al. (2015) used in-situ data from an extended observational program to derive the oxygen budget of the eastern tropical north Atlantic OMZ. They found that mixing by finescales contributed to about 50% of the oxygen ventilation at the top of the OMZ, and about 80% in its core.

These two examples agree on the primordial role of finescales on ventilating low oxygen environments. This is not surprising given that OMZs are located in regions poorly ventilated by the large-scale circulation. A direct consequence is that oxygen eddy-fluxes are critical in constraining the volume of OMZs. This was further illustrated by Lachkar et al. (2016) who compared the volume of Arabian Sea OMZ in a suite of regional models of increasing resolution. They showed that the modeled OMZ volume decreased and got closer to observations as finescales were better resolved, due to stronger eddy-fluxes.

3.2.3. Nutrient vertical eddy-fluxes. A third illustration concerns the uncertainty in the contribution of finescales to vertical nutrient eddy fluxes. Under nutrient-starved conditions, with a submesoscale resolving regional model of the Kerguelen plateau, Rosso et al. (2016) estimated a vertical flux of iron in the Kerguelen plume nearly twice as large as that derived from direct observations (Bowie et al. 2015). With an idealized model configured to represent the Antarctic Circumpolar Current region away from topographic features, Uchida et al. (2019) emphasized that the eddy iron transport in their model far exceeds the transport by vertical diffusion; this time, the modeled iron supply is more consistent with observations during winter, but is too low during summer. With a realistic submesoscale resolving model of the California Current System, Kessouri et al. (2020) highlighted an intensification of the nutrient supplies by submesoscale of 20% in the offshore oligotrophic North Pacific. In the same study, but under nutrient-replete conditions, they estimated that the subduction of excess nutrients by fine scales in the coastal upwelling region off California is responsible for an attenuation in net primary production of -10%, while Hauschildt et al. (2021) find larger numbers (up to -40%) with a submesoscale resolving model of the upwelling off Peru.

These different estimates are difficult to compare because the changes are not all estimated relatively to the same terms in the nutrient budget equation, and also because the strength and even sign of the nutrient eddy flux depends primarily on the biogeochemical province and varies seasonally. Nevertheless, a common feature to these modeling studies is a high sensitivity (up to a factor of two) of the eddy nutrient flux to model resolution when varied in the mesoscale to submesoscale range. Also, the comparison between model and data estimates is tricky, as the model estimates turn out to be either larger or smaller than the observations also by a factor of two.

3.2.4. Lateral eddy fluxes. The impact of horizontal and/or along isopycnal eddy fluxes is beginning to be better assessed. This is first illustrated by the improved understanding of the nutrient balance of subtropical oligotrophic gyres. With a global eddy-resolving model, Yamamoto et al. (2018) found that the supply of nutrients to subtropical gyres is primarily set by an horizontal eddy transport across the gyre boundaries. In addition to cross-boundary exchanges, and based on a field program at the center of the north Atlantic subtropical gyre, Spingys et al. (2021) evaluated the respective contributions of vertical and isopycnal eddy fluxes in replenishing nutrients to the euphotic zone. Their results confirmed that both acted in conjunction, with the lateral eddy flux about twice as large as the vertical eddy flux. The two fluxes added together could explain about 30% of the measured export.

Lateral eddy transport may also be particularly important close to continental margins, and complement or oppose the mean cross-shore transport. In a modeling study of the U.S. West coast shelf, Damien et al. (2023) estimated the mean and eddy fluxes of oxygen, inorganic nitrogen, and dissolved inorganic carbon in three different regions across the shelf break. They find that both mean and eddy fluxes contributed to off-shore transport at the surface, with respective contributions which depended largely on the region, from equal contribution to negligible contribution of the eddy flux. In contrast at subsurface, the eddy flux was in the opposite direction to the mean offshore transport, and often dominated.

3.3. Upscale feedback

The upscale feedback is seen from integrating a model with increasing grid resolution, and over a period long enough for the circulation to equilibrate. The coordinated development of higher resolution ESMs with resolutions at least 50 km in the atmosphere and 0.25° to 0.1° in the ocean, is improving the representation of the mean state of the ocean, including boundary currents and volume transports through narrow straits (Haarsma et al. 2016, Chang et al. 2020). Chassignet et al. (2020) showed with a suite of low-resolution (1°) and eddy-resolution (1/10°) pairs of models integrated for 60 years that the position, strength, and variability of western boundary currents, equatorial currents, and the Antarctic Circumpolar Current was strongly resolution dependent. This change in model circulation implies changes in the biogeochemical adjustment of the ocean, which were quantified in a separate study by Harrison et al. (2018). They found that while the global export was not significantly affected by the change in resolution from 1° to 1/10°, there were large compensating effects between different ocean basins (up to ± 50 %), due to changes in the mean route taken by nutrients.

A second example is provided by Busecke et al. (2019), who showed that the equatorial Pacific OMZ was poorly represented with a coarse resolution model (1°), due to an unrealistic behavior of the equatorial undercurrent. With finer resolution (1/10°), the undercurrent was better represented, leading to a modeled OMZ in better agreement with observations, with in particular the flat shape of its upper boundary that was better represented thanks to the correction of the mean large-scale advection of oxygen at the equator.

The changes associated with increased model resolution were also estimated and compared over a higher resolution range, in the modeling experiments of Lévy et al. (2012a), after a 100-year spin-up at 1/54° and 1/9° resolution. In these experiments, the vertical eddy fluxes of nutrients in an oligotrophic gyre were counter-intuitively lower at higher resolution, despite stronger vertical velocities. This was due a deeper nutricline at higher resolution, which resulted from a change in the mean advective fluxes of nutrients.

4. IMPACT OF FINESCALES ON THE NATURAL LOW FREQUENCY VARIABILITY OF BIOGEOCHEMICAL CYCLES

There are large, natural variations in marine biogeochemical cycles at interannual to decadal time scales (i.e. Rodenbeck et al. 2015, Landschützer et al. 2016), and the scientific consensus is that they are driven by the natural low-frequency variability of the coupled ocean-atmosphere system. This is supported by a large literature where biogeochemical low-frequency variability is related with climate indices such as the El Nino Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD), the North Atlantic Oscillation (NOA), the Southern Annular Mode (SAM) or the Pacific Decadal Oscillation (PDO) (Feucher et al. 2022, Ma et al. 2022, Poupon et al. 2022, Lim et al. 2022). For example, regarding phytoplankton, ENSO and the IOD have been shown to explain most of phytoplankton variability in the tropical Pacific (Racault et al. 2017) and tropical Indian Ocean (Resplandy et al.

2009), respectively. But at higher latitudes, only modest correlations have been found between year-to-year phytoplankton anomalies and the NAO (Martinez et al. 2016) or the SAM (Lovenduski & Gruber 2005). A growing number of studies, discussed below, suggest that this could be related to the projection of high-frequency, finescale fluctuations onto the variability at interannual and decadal timescales. Recent literature suggest different lines of evidence: the fact that the intensity of eddy fluxes may exhibit fluctuations at low frequency; the fact that eddy fluxes occur randomly over the seasonal cycle, resulting in year-to-year differences; and the intrinsic low-frequency variability that emerges from the large-scale feedback.

4.1. Low frequency variability in the intensity of eddy fluxes

The first line of evidence is that the eddy field and submesoscale motions respond to external atmospheric forcing, and that the external forcing varies at interannual to decadal timescales. An illustration is provided by Busecke & Abernathey (2019), who used 25 years of geostrophic surface velocities derived from altimetry data to compute surface eddy diffusivities at the scale of the global ocean. They find interannual variability throughout the global ocean, regionally correlated with climate indices. Outputs from submesoscale permitting hindcast simulations of the North Pacific (Sasaki et al. 2020, 2022) further revealed that both mesoscale and submesoscale motions showed low-frequency variability, in an interconnected way, and in relation with ENSO and the PDO. This implies that the amplitude of eddy fluxes of nutrients, oxygen or carbon should also vary at low frequencies, in response to low frequency variations in the forcing.

4.2. Annual variability related with intermittent eddy fluxes

The second line of evidence comes from the analysis of ocean color data, which allow both the effect of finescales to be seen and changes in phytoplankton from year-to-year to be measured. In order to examine interannual variations in phytoplankton in the Southern Ocean, Prend et al. (2022) decomposed phytoplankton variations into three components, sub-seasonal ($< 3 months$), seasonal, and multi-annual ($> 1 year$). The low-frequency component (multi-annual) represented only a small fraction ($\sim 20\%$) of the total variance (Figure 3a), but was the only one that showed significant correlations with the SAM index (Figure 3b). In addition, Prend et al. (2022) showed that fast variations (sub-seasonal) represented a large part of the total variance ($\sim 50\%$), and also contributed to year-to-year changes in phytoplankton biomass over vast areas of the Southern Ocean (Figure 3c). Indeed, subseasonal events, which are often associated with fronts and eddies, perturb the seasonal cycle of phytoplankton productivity in a random manner that varies from one year to the next, generating inter-annual variability. That implies that annual changes in phytoplankton are related both to low-frequency climate variability operating at large-scale (and captured by the multi-annual component), and to intermittent forcing at finescales (captured by the sub-seasonal component) which does not remain correlated over large regions.

4.3. Upscale feedback: intrinsic variability

The third line of evidence is that intrinsic low-frequency variability emerges from oceanic non-linearities which are particularly strong at finescales. High frequency eddy variability

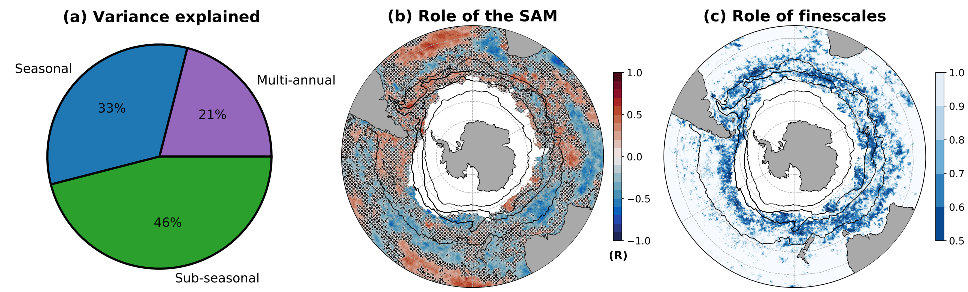

Figure 3

Contribution of ocean finescales versus contribution of Southern Annular Mode (SAM) to phytoplankton interannual variability in the Southern Ocean (SO), evaluated from 20 years (1999-2018) of satellite chlorophyll data. a) % of total chlorophyll variance associated with its sub-seasonal, seasonal and multi-annual components, averaged over the SO. b) Role of the SAM in the low-frequency variation of phytoplankton, quantified by the correlation between the SAM index and the multi-annual component (hashed when non significant) (adapted from Prend et al. 2022); the correlation between the SAM and the seasonal and sub-seasonal components is not significant and is not shown. c) Role of finescales in the low-frequency variation of phytoplankton, highlighted by the correlation square between annual mean chlorophyll, and annual mean of the multi-annual component of chlorophyll. Dark blue regions (when the correlation drops) indicate where finescales contribute most to changes in the amount of phytoplankton from year-to-year (adapted from Keerthi et al. 2022).

is random and chaotic, but can cascade toward multi-annual time scales and basin scales (Sérazin et al. 2017). Results from an ensemble of eddy-permitting (1/4°) simulations revealed that chaotic processes, which start to emerge at this resolution, lead to significant low-frequency variability in the ocean heat content (Penduff et al. 2018), currents (Cravatte et al. 2021), and meridional heat transport (Zanna et al. 2018). With a coupled model at 1/10°, Jüling et al. (2021) showed that the strength of multidecadal variability increases compared to lower resolution simulations.

Using an ensemble of three ocean biogeochemical eddy permitting global model simulations, Gehlen et al. (2020) evidenced that intrinsic variability propagated from physical properties to the air-sea flux of CO_2 in areas of high mesoscale activity, accounting for nearly a third of the interannual variability of the annual air-sea CO_2 flux in the mid latitude Southern Ocean. Using a sub-mesoscale permitting (1/54°) idealized model of the North Atlantic, Levy et al. (2014) quantified the impact of intrinsic variability on phytoplankton production. They found that intrinsic variability was responsible for up to 20% of the large-scale interannual fluctuations of phytoplankton growth in the subtropics. Importantly, the amplitude of the phytoplankton response to this emergent intrinsic variability decreased when the model resolution decreased from 1/54° to 1/3°, suggesting that the estimates of Gehlen et al. (2020), obtained with a 1/4° model, might be strongly underestimated.

5. IMPACT OF FINESCALES ON THE BIOGEOCHEMICAL RESPONSE TO CLIMATE CHANGE

Climate change over the 21st century is expected to alter biogeochemical cycles, but the magnitude, and sometimes even the sign of the response predicted by Earth System Models (ESM) used for climate projections remain highly uncertain (Bahl et al. 2019, Kwiatkowski et al. 2020, Henson et al. 2022). One of the consequences of global warming is the intensification of ocean stratification, which inhibits both the transport of nutrients to the euphotic layer through turbulent mixing and the penetration of oxygen. Thus, climate change is likely to slow down biogeochemical cycles, with serious subsequent threats such as reduced ocean productivity, reduced carbon uptake and deoxygenation (Bopp et al. 2013, Kwiatkowski et al. 2020). In an increasingly stratified ocean, finescales could potentially counteract this general trend and help to limit these threats. But is it really the case ? The exploration of this question is in its infancy due to methodological limitation, and we present here different lines of research that begin to draw a general picture. First, there is indirect evidence that finescales play a role in the response of biogeochemical cycling to climate change that come from ESMs. Second, the intensity of eddy fluxes might change in the future. And third, the rate of change of certain properties under warming scenarios strongly depends on the mean state, making our projections sensitive to upscale feedbacks.

5.1. Evidence from Earth system model projections for the 21st century

ESMs suggest that finescales may be important in the response of biogeochemical cycling to future warming. As mentioned before, the horizontal grid resolution of ESMs is not sufficient to capture eddies and fronts, which are thus parametrized; and interestingly, modifications of biogeochemical cycles with climate change show different sensitivities to the mixing parameters used in these parameterizations. For instance the rates of primary production and export are weakly sensitive (Bahl et al. 2020), the total oceanic carbon content can change by up to 30% (Löptien & Dietze 2019), the sign of the tropical oxygen trend under climate warming can reverse (Ito et al. 2022), OMZs may shrink or expand (Bahl et al. 2019). Moreover, for typical values of the mixing coefficient, there is a breakdown of linearity in the change of OMZ volume against radiative forcing, further highlighting that the sensitivity to finescale parameterization is particularly critical for oxygen (Löptien & Dietze 2019, Bahl et al. 2020).

5.2. Trends in eddy fluxes

There is evidence that trends are emerging in the frequency and intensity of fronts and eddies. For example, the ocean eddy activity has increased in eddy-rich regions over the satellite altimetry record (Martínez-Moreno et al. 2022, Li et al. 2022) and the frequency of fronts in the California Current upwelling system has increased slightly over the past 30 years (Kahru et al. 2018).

The future evolution of this trend is a complex issue because of the wide variety of forcings involved, including global warming but also changes in winds or upwelling intensity. Some characteristics are nevertheless emerging from model projections. Submesoscale activity is projected to be reduced both in nested projections in the Northeast Atlantic, due to the intensification of stratification (Richards et al. 2021), and in the central and eastern equatorial Pacific in a long-term high-resolution (1/10° in the ocean) climate simulation under a high carbon emission scenario (Wang et al. 2022). In these two cases, this leads to reduction in the upward heat flux close to 50%. The reduced vertical submesoscale eddy heat flux implies biogeochemical eddy fluxes may also be reduced.

But on the other hand, eddy activity is projected to intensify around a western boundary current with climate change, as shown by a regional eddy resolving model (Matear et al. 2013). In this model, this leads to a projected increase in primary projection of 10%, while at coarse-resolution primary production is projected to decrease. Eddy-kinetic energy intensification around boundary currents, also noted by (Oliver et al. 2015) in the east Australia current, is confirmed in global climate models with nested high-resolution regions (Beech et al. 2022), particularly around the Kuroshio current and Antarctic Circumpolar Current, but may not around the Gulf Stream. An increase in eddy kinetic energy was also projected in the California Current System from downscaled climate projections (Cordero Quiros et al. 2022).

5.3. Upscale feedback

Estimating the impact of improved model resolution on climate projections of biogeochemical cycles is difficult due to the high computational requirements. Couespel et al. (2021) focused on one piece of the complicated response of the ocean nutrient cycle to climate change. Namely, they examined the resolution dependence of the projected decline of primary production in an idealized model configuration forced with a prescribed warming, under an increasing horizontal resolution (1° to 1/27°) and under a range of parameter values for the eddy parameterization employed in the 1 resolution simulation. The model represented a double gyre circulation at mid-latitudes, where primary production depended on convective nutrient supplies on the one hand, and on mean advective nutrient supplies from the western boundary current (the nutrient stream) on the other, in a manner similar to that highlighted with the Community Earth System Model by Whitt (2019). They found that while the decline in primary production was only weakly sensitive to the eddy parameters in the eddy-parameterized coarse resolution simulations, the simulated decline in the subpolar gyre was halved at the finest eddy-resolving resolution (-12% at 1/27° vs. -26% at 1°) at the end of the 70-year-long global warming simulations (Figure 4a). This difference stemmed from the high sensitivity of the nutrient stream to resolution, and not, rather counter-intuitively, to increased stratification or changes in eddy fluxes of nutrient. Brett (2022) conducted similar twin experiments to examine how the decline in primary production was sensitive to resolution in the Porcupine Abyssal Plain. They found that resolving the submesoscale did not strongly impact the projected reduction; the difference from the two studies may be due to the more regional configuration used in Brett (2022), which may have not allowed for full upscaling.

Here, we extend the model results of Couespel et al. (2021) to examine other aspects of biogeochemical cycles. We illustrate that deoxygenation in the twilight zone (Figure 4b) is reduced with increasing model resolution because of a weaker reduction in ventilation (mostly through vertical mixing), albeit partly compensated by an smaller decline in oxygen consumption related to the weaker decline in surface primary production described above. We also illustrate that the CO_2 uptake is increased (Figure 4c), due to a stronger overturning circulation at high resolution storing more carbon at depth, and also to a weaker negative feedback in response to warming at higher resolution.

While the processes driving this sensitivity remain to be fully investigated, these new

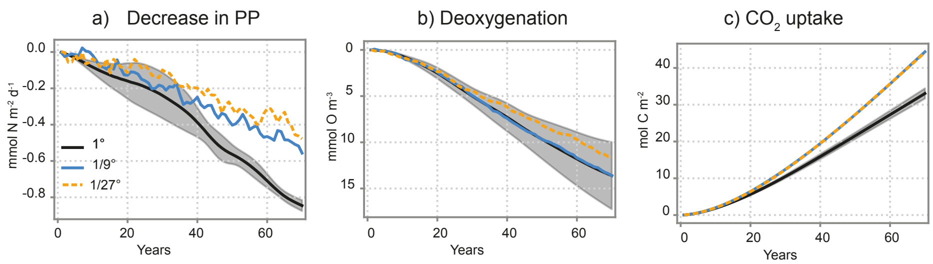

Figure 4

Impact of model grid resolution on projected response of biogeochemical indicators under climate change. Simulated a) decrease in Primary Production (PP) in the subpolar gyre (adapted from Couespel et al. 2021), b) deoxygenation between 400 and 1000 meter depth, and c) cumulated uptake of CO_2 in a 2000 km x 3000 km double-gyre model with closed boundaries, forced by an linearly increasing atmospheric temperature and increasing levels of atmospheric pCO_2, equivalent to the RCP8.5 scenario. The model is run at three different grid resolutions, 1° (black line), 1/9° (blue line) and 1/27° (orange dashed line). At 1° resolution, subgrid processes are parametrized (Gent & McWilliams 1990) and sensitivity to a large range of parameters is performed; the black line shows the mean and gray shading is the standard deviation of this set of simulations. With increasing model resolution, the projected decrease in PP and deoxygenation are not as severe as projected at coarse resolution, and the increase in CO_2 uptake is larger.

results show that model resolution affects all aspects of marine biogeochemical cycles, and strongly suggests that finescales need to be taken into account when assessing the impact of global warming on ocean biogeochemical cycles. This calls for accelerated interdisciplinary coordinated efforts to incorporate the role of finescale ocean processes on large-scale climate and biogeochemistry, particularly given that biogeochemical tracers may require specific parameterizations (Prend et al. 2021).

SUMMARY POINTS

1. Quantifying the overall impact of finescales on global biogeochemical cycling is challenging from both an observational and modeling perspective due to the need to solve both small-scales and large-scales.
2. Finescales contribute to large-scale biogeochemical cycles both through local eddy-fluxes and through upscale feedbacks of finescales on the large-scale circulation. Separating these effects is necessary to meaningfully compare observational and model-based results.
3. There is significant uncertainty in the contribution of eddy-fluxes to the mean state of biogeochemical cycles, and the overall importance depends on the tracer and region (Table 1).
4. There is large uncertainty in the contribution of eddy-fluxes to the variability and future state of biogeochemical cycles (Table 1).
5. Upscale feedbacks significantly modulate the mean state, the natural low-frequency variability of biogeochemical fluxes and their response to climate change (Table 1). This poses a great challenge for climate projections that do not resolve these scale transfers accurately.

Table 1 Summary of the reported small (< 10%), medium (> 10% and < 50%) and large (> 50%) impacts of finescales on the mean state, low-frequency variability and response to climate change of marine biogeochemical cycles.

	Mean state	Low frequency variability	Climate change
Eddy fluxes	• Phytoplankton : **medium** local increase, **small** regional surplus; **large** effect on temporal variability • Carbon export : **small to large** • Nutrient fluxes (vertical and lateral) : **small to large** • Oxygen ventilation : **large**	• Low frequency variability of intensity • Random occurrence leading to **medium** interannual variations in phytoplankton	• Large uncertainties in future evolution of intensity • **Small** impacts on PP
Upscale feedback	• **Medium** changes in large scale nutrient routes • **Medium** changes in location of export • **Large** changes and more realistic OMZs • **Medium** changes in nutricline depth	• Intrinsic chaotic variability drives **medium** variability in air-sea CO_2 fluxes and PP	• Changes in the large-scale circulation leads to **medium** attenuation of climate change impacts (less PP decline, less deoxygenation, more C uptake)

FUTURE ISSUES

1. How can we best extrapolate observations which are local in space and time to derive quantitative estimates of eddy-fluxes at the scale of bio-provinces and over the annual cycle ?
2. What are the impacts of downscale feedbacks from finescales on vertical mixing ?
3. What are the mechanisms by which finescale variability of biogeochemical tracers contributes to lower frequency variability, and how can they be estimated from observations?
4. How do finescales respond to anthropogenic forcing and how does this influence climate feedbacks related to biogeochemical cycling?
5. How does the parameterization of finescale processes in coarse resolution models contribute to uncertainty in future climate projections of biogeochemical cycles?
6. Should specific parameterizations for biogeochemical tracers be developed and incorporated into ocean and climate models ?

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