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The Impact of Fine-Scale 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 timescale of years remains poorly understood due to the multiscale 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 it is for oxygen ventilation. We highlight the importance of fine scales 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 fine scales on biogeochemical cycles in climate projections.

1. INTRODUCTION

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

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

Euphotic zone: the well-lit upper layer of the ocean (∼0–150 m), where photosynthesis occurs

Twilight zone: the layer below the euphotic zone (∼150–1,000 m), where remineralization prevails

Biogeochemical province: a large-scale ecosystem under coherent physical forcing and environmental conditions

Mesoscale eddy: a coherent rotating vortex with horizontal and temporal scales O(10–100 km, months)

Submesoscale: dynamical features with horizontal and temporal scales just below the mesoscale, O(1–10 km, days)

Rossby number: relative scaling of the inertial and Coriolis terms in the equation of motion

The term marine biogeochemical cycle refers 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, according to the conventional view), 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 is shaped primarily by the ocean general circulation; the exchanges are particularly powerful in regions of convection, subduction, and 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 timescales 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.

In the late 1990s, the idea arose that large-scale exchanges could not fully explain the cycling of elements. This idea 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)], but it later became clear that vertical velocities occurring at the submesoscale also played a role, since they are even more intense at the submesoscale than at the mesoscale [see review by Klein & Lapeyre (2009)].

Ocean mesoscale eddies are in many ways analogous to atmospheric synoptic weather systems but are roughly 10 times smaller in scale; they are ubiquitous in the global ocean, particularly close to western boundary currents, such as the Gulf Stream, where they are generated through the combination of baroclinic and barotropic instabilities. Mesoscale motions, O(10–100 km, months), are characterized by small Rossby numbers, so that the flow is close to geostrophy with a momentum balance involving a primarily horizontal pressure gradient and the Coriolis acceleration. Submesoscale currents, O(1–10 km, days), are flow structures in the form of sharp density fronts and filaments or coherent vortices. They are typically created by mesoscale eddy stirring or emerge spontaneously from baroclinic instability in surface or bottom boundary layers. They are characterized

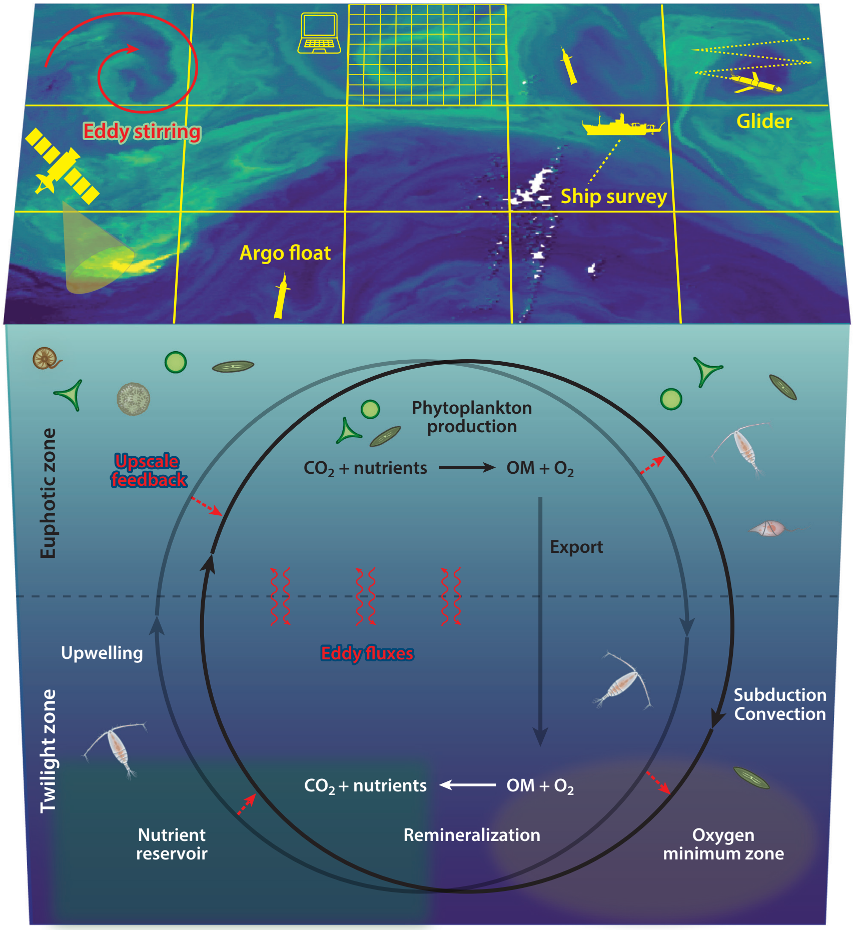

Figure 1

The influence of fine scales (*red*) on marine biogeochemical cycles. (*Top*) Surface view of sea surface chlorophyll on April 22, 2007, from MODIS-Aqua ocean color satellite level-2 data binned on a 1-km grid. Stirring by mesoscale eddies and submesoscale fronts creates fine-scale patterns in the phytoplankton distribution. Overlaid are the model grids used in high-resolution ocean general circulation models and coarse-resolution Earth system models. The scales resolved by monitoring platforms (*yellow*) are also shown. (*Bottom*) Cutaway view showing a schematic representation of ocean biogeochemical cycles driven by the large-scale circulation (*large gray loop*). Fine scales impact these cycles through local eddy fluxes and upscale feedback that modifies the large-scale transport. Abbreviations: MODIS, Moderate Resolution Imaging Spectroradiometer; OM, organic matter.

by a Rossby number on the order of 1 and hence are also significantly influenced by rotation and stratification, but momentum advection is no longer negligible. Other ageostrophic effects can also become important in the balance of forces. Overall, this allows the development of intense submesoscale vertical velocities (McWilliams 2016, 2019; Gula et al. 2022; Taylor & Thompson 2023). Submesoscale and mesoscale circulations are strongly intertwined, each feeding the other (Sasaki et al. 2020, Balwada et al. 2022, Naveira Garabato et al. 2022, Taylor & Thompson 2023), and they often act in conjunction (Freilich & Mahadevan 2019, Uchida et al. 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, partly because there is a continuum rather than a clear cutoff between the two; here, we use the generic term fine scales 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. 2012c, Pietri et al. 2021). But fine scales 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 fine scales must be included through subgrid 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).

Fine scales: dynamical features in the submesoscale to mesoscale range, O(1–100 km, days–months)

Ocean general circulation model (OGCM): computer code that estimates the solution of fluid motions in the ocean on a three-dimensional grid under prescribed atmospheric forcing

Earth system model (ESM): 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 fine-scale transport that complements the gravitational pump

Eddy flux: advective transport of elements by fine-scale currents

Upscale connection: a modification of the ocean circulation through energy transfer from fine scales to large scales

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 these fronts 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 Lévy et al. (2012a, 2018) and Mahadevan (2016)]. 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 CO_2 (Balwada et al. 2018), and to the supply of oxygen at the subsurface (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**).

The previous reviews on biophysical couplings at fine scales (Lévy et al. 2012a, 2018; Mahadevan 2016; McGillicuddy 2016) 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 is the focus of this review, is the extent to which these fine-scale 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 2023), its natural variability (Penduff et al. 2011), and its evolution under climate change (Hewitt et al. 2022). Thus, fine scales may impact biogeochemical cycles both through eddy fluxes at their own scale and through upscale connections (**Figure 1**). These two aspects are discussed below with regard to the mean state, natural variability, and response to climate change of biogeochemical cycles.

In Section 2, we introduce how fine scales may impact marine biogeochemical cycles and how this impact may be quantified. Then we present a review of current estimates of the impact of fine scales 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 (Lévy et al. 2018).

2. EVALUATING THE IMPACTS OF FINE SCALES ON BIOGEOCHEMICAL CYCLES

Evaluating the impacts of fine-scale processes implies measuring how they contribute to the large-scale biogeochemical balance. This poses challenges because fine scales are difficult to observe and model and because the spatiotemporal averaging at which this quantification is meaningful (biogeochemical provinces, >1 year) is much larger than the scales at which eddy 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 and present the different fine-scale impacts conceptually as well as the limitations of the current methods that are used to evaluate them.

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

2.1. Biogeochemical Balance

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

$$\partial_t C = -\nabla \cdot (C\mathbf{v}) + \partial_z(k_z \partial_z C) + B_C. \quad 1.$$

C is the biogeochemical tracer (such as dissolved inorganic carbon, phytoplankton, nitrate, or oxygen, expressed as the mass concentration of carbon, nitrogen, or oxygen), $\mathbf{v}$ is the three-dimensional velocity vector, k_z is the vertical mixing coefficient, and B_C includes the biogeochemical reactions of C, i.e., the mass balance of biogeochemical transformations between C and other tracers; thus, B_C can depend on the concentration of tracers others than C. For instance, in the case of oxygen, B_C will include oxygen production by photosynthesis (which depends on phytoplankton) minus oxygen removal by remineralization (which depends on oxygen); for phytoplankton, B_C will include phytoplankton production by primary production (which depends on phytoplankton and limiting nutrients such as nitrate) minus phytoplankton losses through mortality and predation (which depend on phytoplankton and on their predators). For details on the state variables C and formulation of B_C in biogeochemical models, we refer readers to the recent review by Fennel et al. (2022).

Due to the spatiotemporal decoupling between the different terms in this equation, which is particularly pronounced at fine scales (Estapa et al. 2015, McGillicuddy 2019), this balance is not at equilibrium locally (i.e., $\partial_t C \neq 0$), but an equilibrium may emerge after integrating Equation 1 over sufficiently large spatiotemporal scales—typically the year and over biogeochemical provinces, and over the euphotic or twilight layer (i.e., $\langle \partial_t C \rangle = 0$). The brackets $\langle . \rangle$ represent this large-scale integration. At equilibrium over the euphotic or twilight layer, the amplitude of the biogeochemical reactions $\langle B_C \rangle$ must balance the transport terms, i.e., advection and vertical diffusion. The natural low-frequency variability of these cycles and the response to anthropogenic disturbances manifest 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 and twilight zones, along with the transformation of these elements between organic and inorganic forms in the euphotic and twilight zones (**Figure 1**).

To highlight the importance of fine-scale dynamics in 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:

$$\overline{C\mathbf{v}} = \overline{C}\,\overline{\mathbf{v}} + \overline{C'\mathbf{v}'}. \quad 2.$$

The overbar represents a monthly mean operator and/or a spatial mean operator over boxes larger than the mesoscale (typically 100–200 km wide, which is the size of a coarse-resolution ocean model grid), and the prime is the deviation from this mean. Note that the overbar represents a mean operator over spatiotemporal scales of ∼100 km and 1 month, which are one order of magnitude below those of the brackets (∼1,000 km and 1 year) and that vertical integration is included in the brackets but not in the overbar. We apply the same decomposition to the vertical mixing term. Finally, due to their nonlinear nature, biogeochemical reactions can also be decomposed in a similar manner into eddy ($\overline{B'_C}$) and mean ($\overline{B_C}$) components.

With this decomposition, the large-scale biogeochemical balance becomes

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

2.2. The Different Impacts of Fine Scales

Fine scales naturally enter the large-scale biogeochemical balance (Equation 3) through the eddy advection term $\langle\nabla\cdot(\overline{C'\mathbf{v}'})\rangle$, the eddy vertical mixing term $\langle\partial_z(\overline{k'_z\partial_z C'})\rangle$, and the biogeochemical eddy term $\langle\overline{B'_C}\rangle$. In addition, fine-scale dynamics affects both the large-scale circulation ($\overline{\mathbf{v}}$) and small-scale turbulence ($\overline{k_z}$) by redistributing energy upscale and downscale (Taylor & Thompson 2023); thus, through these scale connections, fine scales enter the balance through the mean advection $\langle\nabla\cdot(\overline{C}\,\overline{\mathbf{v}})\rangle$ and mean vertical diffusion $\langle\partial_z(\overline{k_z}\partial_z\overline{C})\rangle$. This review focuses on the impact of local eddy advective fluxes and upscale connections; for completeness in this section, we also present the other possible pathways, i.e., the impact of fine scales on biogeochemical reactions and on vertical mixing through downscale connection.

2.2.1. Impact of fine scales through local eddy fluxes.

We begin with a description of the impacts of fine scales at the local scale of fine-scale currents. These are decomposed into vertical eddy fluxes and lateral eddy fluxes (also termed stirring).

2.2.1.1. Vertical eddy advective fluxes.

Fine-scale vertical advection associated with mesoscale eddies and submesoscale fronts (Lévy et al. 2012a, 2018; Mahadevan 2016) supplies the euphotic layer with nutrients (Lévy et al. 2001), exports organic carbon [which challenges the view that export essentially results from sinking (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 m d^{-1} (Pietri et al. 2021)] and mesoscale [$w' \sim$ 0.1–10 m d^{-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 m d^{-1} (Liao et al. 2022)], leading to eddy vertical advection fluxes $\overline{C'w'}$ that may greatly 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 (Lévy et al. 2018). Moreover, because vertical eddy fluxes operate at the local scale of eddies and fronts and over relatively short periods of time, while mean vertical transport—either advective or diffusive—operates at much larger spatiotemporal scales, it is not guaranteed that the large-scale contribution of the vertical eddy fluxes, $\langle\overline{C'w'}\rangle$, dominates over those of the other transport fluxes, $\langle\overline{C}\,\overline{w}\rangle$ and $\langle\overline{k_z}\partial_z\overline{C}\rangle$.

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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 (Lévy et al. 2018). But away from the sea surface, the preferential direction for stirring motions is the inclined isopycnal surfaces, leading to an eddy transport along these isopycnals that is often described as isopycnal diffusion (Abernathey et al. 2022). Isopycnal diffusion is important for replenishing subsurface nutrients (Spingys et al. 2021) and for oxygen ventilation (Lachkar et al. 2016).

Isopycnal surface: a surface of constant density along which water parcels can move freely

Mixing layer: an upper layer of up to 1,000-m depth or more characterized by strong vertical mixing

2.2.2. Impact of fine scales through scale connections.

Fine scales also impact biogeochemical cycles at the regional scale through scale connections. Upscale connections connect the fine scales with the large-scale circulation, while downscale connections connect them with vertical mixing.

2.2.2.1. Upscale connection.

The energy transfer from fine scales to the large scale contributes to the dynamical and thermodynamical adjustment of the ocean, and thus to setting $\overline{\mathbf{v}}$; observational evidence of this energy transfer has recently been obtained in the Gulf of Mexico (Balwada et al. 2022). Quantification of the upscale feedback associated with this energy transfer is emerging in recent literature, as the resolution of OGCMs increases. To illustrate this upscale feedback, let us consider two hypothetical simulations of the same model setup, one at high resolution (i.e., with ~1-km grid resolution) and the other at coarse resolution (i.e., with ~100-km or 1° grid resolution). Fine scales are explicitly resolved in the high-resolution simulation but not in the coarse-resolution simulation. Due to scale connections, the mean advection will not be the same in the two simulations, and modeling studies comparing such sets of twin high- and coarse-resolution simulations have shown that $\overline{\mathbf{v}}_{\mathrm{HR}}$ is often closer to observations than $\overline{\mathbf{v}}_{\mathrm{CR}}$ (Busecke et al. 2019, Chassignet et al. 2020). In the above thought experiment, upscale feedback can be estimated as $\langle \nabla \cdot (\overline{C}\,\overline{\mathbf{v}}) \rangle_{\mathrm{HR}} - \langle \nabla \cdot (\overline{C}\,\overline{\mathbf{v}}) \rangle_{\mathrm{CR}}$. Note that coarse-resolution simulations often include parameterizations that capture part of the energy transfer to large scales; in that case, the upscale feedback as estimated above constitutes the part that is not well captured by the parameterization.

upscale connections may partly arise through parameterizations

2.2.2.2. Downscale connection.

Submesoscales play a critical role in multiscale ocean circulation by bridging the gap between rotating and nonrotating flows (Taylor & Thompson 2023). The combined effects of convection, wind stress, and waves near the ocean surface generate boundary-layer turbulence, inducing strong vertical mixing in a vertical region extending from the surface. As they develop, many submesoscale processes increase the vertical density stratification in, or restratify, the upper ocean. Submesoscale restratification limits the depth to which boundary-layer turbulence ($\overline{k_z}$) can penetrate. The seasonal restratification of this mixing layer following the development of submesoscales advances seasonal phytoplankton blooms (Karleskind et al. 2011, Mahadevan et al. 2012). This effect is associated not with changes in the annual fluxes of elements but rather with a time shift of a few weeks (Haëck et al. 2023). OGCMs are not able to capture the full complexity of the downscale connections between submesoscales and boundary-layer turbulence, but these connections can be examined with more complex models, such as large-eddy simulations (Whitt & Taylor 2017). Large-eddy simulation models can only be used in very small domains and do not yet allow meaningful quantification, but nevertheless, using a biogeochemical large-eddy simulation model, Whitt et al. (2019) were able to show that submesoscales could enhance storm-driven vertical mixing of nutrients, $\langle \partial_z(\overline{k_z}\partial_z\overline{C}) \rangle$.

In addition, the fine-scale heterogeneity of vertical mixing $\partial_z\overline{(k_z'\partial_z C')}$ also affects the annual export of carbon, by creating hot spots of export through entrainment (Resplandy et al. 2019) or enhancing the export rate associated with gravitational settling (Taylor et al. 2020). The effects discussed in this paragraph need to be further quantified and are not considered hereafter.

2.2.3. Impact of fine scales on biogeochemical reactions.

Fine scales may impact biogeochemical reactions in various ways. First, eddy transport may directly affect the mean reactive processes $\langle \overline{B_C} \rangle$. For instance, the strength of the eddy nutrient supply affects the structuring of the planktonic ecosystem, with certain plankton species favored and others not (Guo et al. 2022; Mangolte et al. 2022, 2023); the modified structuring may affect, in turn, 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. Second, there is a link between horizontal stirring and phytoplankton biomass accumulation through adjustment of the ecosystem (Lehahn et al. 2017b). And third, fine scales can have effects through the eddy biogeochemical reaction terms $\langle \overline{B'_C} \rangle$. There have been only a few attempts to quantify these terms, which makes it difficult to further discuss their global relevance; the first evaluations (Lévy & Martin 2013, Martin et al. 2015) concluded that they make a negligible contribution to primary production. All of these aspects call for future studies before they can be quantified at a large scale and are not considered further here.

2.3. Methodological Challenges

Classical methods in oceanography are pushed to their limits to evaluate the impact of fine scales on biogeochemical cycles. Here, we discuss the specific challenges associated with each of them.

2.3.1. Local field studies. Much of the recent work on the biogeochemical impacts of submesoscales has relied on local field surveys (Little et al. 2018, Marrec 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 over a few days. Nevertheless, satellite altimetry can be used to guide field surveys and target frontal structures; in one study, for example, four crossings of a frontal structure off California were conducted over a single night, with transects approximately 50 km in length and biogeochemical sampling every 3.5 km along them (de Verneil et al. 2019).

YES, but SWOT

Today, there are no direct observations of fine-scale 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 (Buongiorno Nardelli et al. 2018; D'Asaro et al. 2018; Siegelman et al. 2020; Tarry et al. 2021, 2022; Comby et al. 2022; Cutolo et al. 2022; Garcia-Jove et al. 2022). These local field studies have been useful in providing estimates of $\overline{C'\mathbf{v}'}$ but are difficult to extrapolate to $\langle \overline{C'\mathbf{v}'} \rangle$. Another caveat of these local field studies is that they tend to target strong cases, which may not always be representative of the mean ocean.

2.3.2. Biogeochemical Argo floats. Biogeochemical Argo floats make up a global network of underwater drifting robots that operate autonomously, making relatively high-frequency measurements of a set of biogeochemical variables from the surface down to the twilight zone. They have been used to detect anomalies in the vertical distribution of tracers, which can be related to 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 being deployed, the number of events that they can capture is still very limited. For instance, Wilson (2021) identified a dozen 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 fine scales that emerge at higher resolution feed more eddy fluxes. The general consensus is that models with a grid resolution between 1/3° and 1/6° are eddy permitting, and that the models become eddy resolving at resolutions finer than 1/10°, submesoscale permitting between 1/20° and 1/50°, and submesoscale resolving at 1/100°; this terminology is used here. But in reality, both the mesoscale and the submesoscale become better resolved as the grid is refined (Sasaki et al. 2020), which makes it difficult to properly distinguish between the two kinds of processes on the basis of model experiments of increasing grid resolution.

The fine scales that emerge at higher resolution also feed back 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 becomes more challenging as the grid is refined. Thus, the upscale feedback is often not present in 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 fine scales 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 are limited by clouds. Nevertheless, they are valuable in that they can be used to examine variability in surface phytoplankton across a range of scales. Fine-scale chlorophyll patterns reflect the influence not only of stirring and vertical nutrient eddy fluxes but also of other factors, such as wind bursts (Nicholson et al. 2022) or intrinsic ecological interactions (e.g., 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 analysis of their shape, possibly in relation to preidentified physical features, to the Lagrangian perspective of tracking their formation, where ocean color data have been used alone or in conjunction with other datasets, such as satellite sea surface height or temperature, to relate phytoplankton patchiness to specific physical fine-scale features. In the next section, we discuss how the methods have evolved to allow the extraction of the impact of vertical transport from surface observations.

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3. IMPACT OF FINE SCALES ON THE MEAN STATE OF BIOGEOCHEMICAL CYCLES

Below, we review recent estimates of the impact of fine scales on surface phytoplankton, primary production, carbon export, and oxygen ventilation. These different estimates are summarized in **Table 1**, which illustrates the high degree of uncertainty in our current knowledge.

3.1. Impact of Fine Scales on Surface Phytoplankton

We first review estimates based on ocean color data. This invaluable dataset has motivated the development of innovative approaches to link ocean color spatiotemporal patterns with the stirring of phytoplankton and with nutrient supplies at fine scales, which are presented below.

3.1.1. Stirring of phytoplankton. 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 fine scales through their temporal, rather than spatial, footprint; at each location in the global ocean, the subseasonal component (defined as associated with timescales of <3 months) of phytoplankton was extracted

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

	Mean state	Low-frequency variability	Response to 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 primary production
Upscale feedback	■ **Medium** changes in large-scale nutrient routes ■ **Medium** changes in location of export ■ **Large** changes and more realistic oxygen minimum zones ■ **Medium** changes in nutricline depth	■ Intrinsic chaotic variability driving **medium** variability in air–sea CO_2 fluxes and primary production	■ Changes in the large-scale circulation leading to **medium** attenuation of climate change impacts (less primary production decline, less deoxygenation, and more carbon uptake)

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 example, it varied between 30% and 55% in the Gulf Stream region (yellow bars in **Figure 2**). These results were confirmed by an independent study that used a different approach based on the analysis of the dominant timescale of variability (Jönsson et al. 2023).

3.1.2. Fine-scale inputs of nutrients. To isolate the influence of fine-scale 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 fine-scale 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 color 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.

Quantitative evaluation of the impact of nutrient inputs by fronts was proposed by Liu & Levine (2016), who used satellite sea surface temperature data to detect the location of spatial heterogeneities at the scale of ∼10 km in the North Pacific Subtropical Gyre and measured the median chlorophyll overload associated with them. They estimated that the chlorophyll enhancement over fronts was ∼20%. Haëck et al. (2023) applied the same approach to the northwestern Atlantic and showed that the strength of the enhancement was stronger in regions that are naturally more productive, varying from 7% to nearly 40% (red bars in **Figure 2**). Importantly, Haëck et al. (2023) also evaluated the chlorophyll surplus due to fronts at the scale of bioprovinces. 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**). Comparing the three different estimates in **Figure 2** highlights that focusing on variability, or on

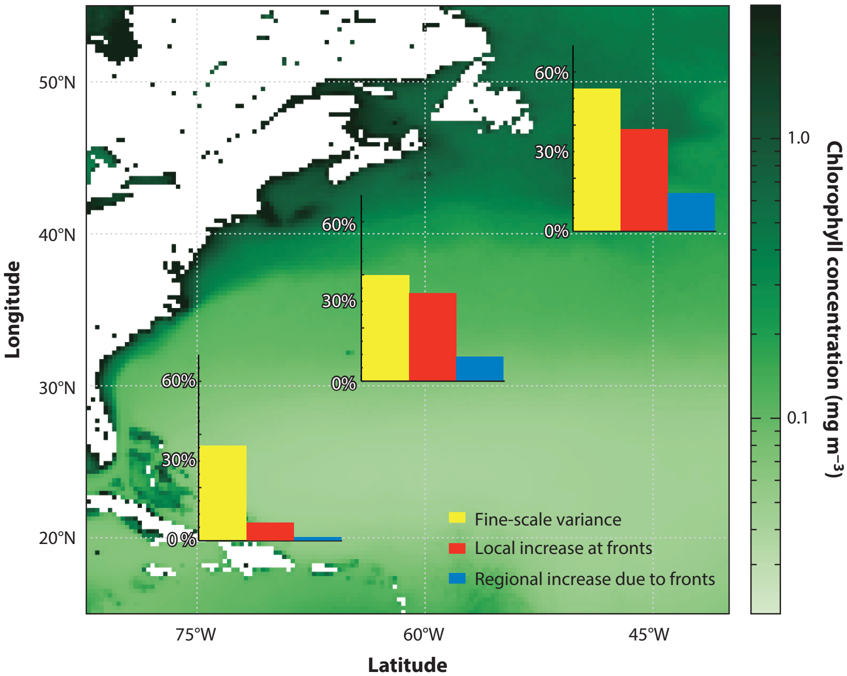

Figure 2

Contribution of fine scales to mean phytoplankton abundance in the northwestern Atlantic, quantified from 20 years of ocean color data, and using chlorophyll as a proxy for phytoplankton. The background (*green*) is the chlorophyll climatology. The bar plots show three percentage estimates of fine-scale contributions to chlorophyll by latitudinal bands (20–30°N, 30–40°N, and 40–50°N). Fine-scale variance (*yellow bars*) represents the part of the chlorophyll variance associated with subseasonal timescales and mostly represents the effect of stirring (data from Keerthi et al. 2022). Local increase at fronts (*red bars*) represents the local increase in chlorophyll over fronts due to fine scales (data from Haëck et al. 2023). Regional increase due to fronts (*blue bars*) represents the large-scale contribution of fine scales to chlorophyll in each latitudinal band (data from Haëck et al. 2023).

local effects systematically, leads to a strong overestimation of the global impact of fine scales on phytoplankton abundance.

3.2. Eddy Fluxes of Carbon, Oxygen, and Nutrients

Here, we review estimates of carbon, nitrogen, and oxygen eddy fluxes derived from both in situ observations and regional model studies.

3.2.1. Eddy pump of carbon. To illustrate current uncertainty in the global assessment of eddy fluxes, we first 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 fine scales. This led to the estimate that the eddy pump contributes to half of the total export of POC in the North Atlantic, the Kuroshio extension, and the Southern Ocean. Using data from Biogeochemical Argo floats across the Southern Ocean, Llort et al. (2018) used positive oxygen anomalies as a physical proxy to detect subduction events and examined the

POC anomalies (also measured by the floats) associated with these events; they estimated that the eddy pump contributes to approximately 20% of the total POC export in the Southern Ocean. By contrast, Erickson & Thompson (2018) identified subductive events over a full seasonal cycle in the northeastern Atlantic using data collected from gliders and found that they did not contribute significantly to carbon export. Finally, Resplandy et al. (2019) used five years of an eddy-resolving simulation in an equilibrated, idealized model of the North Atlantic and determined, in agreement with Erickson & Thompson (2018), that the contribution of the eddy pump to the total export was less than 5%, although the magnitudes 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%, and 5%) can be partially explained by strong compensation between upward and downward fluxes at fine scales, which were accounted for in the longer model integration but not in all data-based estimates (Claustre et al. 2021).

Oxygen minimum zone (OMZ): a region of poorly ventilated hypoxic waters located in the twilight zone, which is crucially important for climate and resources

3.2.2. Oxygen eddy fluxes. A second illustration concerns how fine scales are primary players in controlling the volume of oxygen minimum zones (OMZs) [see review by Lévy et al. (2022)]. Resplandy et al. (2012), with an eddy-resolving 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 fine scales contributed to approximately 50% of the oxygen ventilation at the top of the OMZ and approximately 80% in its core. These two examples agree on the primordial role of fine scales on ventilating low-oxygen environments. This is not surprising given that OMZs are located in regions that are 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 the Arabian Sea OMZ in a suite of regional models of increasing resolution (from eddy permitting to submesoscale permitting, i.e., from 1/3° to 1/24°). They showed that the modeled OMZ volume decreased and became closer to observations as fine scales 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 fine scales to vertical nutrient eddy fluxes. Under nutrient-starved conditions, with a submesoscale-resolving regional model of the Kerguelen plateau (1/80° resolution), 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 at eddy-permitting resolution (2-km resolution), Uchida et al. (2019) emphasized that the eddy iron transport in their model far exceeded the transport by vertical diffusion; this time, the modeled iron supply was more consistent with observations during winter but was too low during summer. With a realistic submesoscale-resolving model (1-km resolution) of the California Current System, Kessouri et al. (2020) highlighted an intensification of the nutrient supplies from the 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) found larger numbers (up to −40%) with a submesoscale-permitting (2.5-km resolution) model of the upwelling off Peru.

These different estimates are difficult to compare because the changes are not all estimated relative to the same terms in the nutrient budget equation and because the strength and even sign of the nutrient eddy flux depend primarily on the biogeochemical province and vary seasonally.

Nevertheless, a common feature of 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 set primarily by a 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 approximately twice as large as the vertical eddy flux. The two fluxes added together could explain approximately 30% of the measured export.

it should be thought as a fully 3D phenomenon

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 US 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 found that both mean and eddy fluxes contributed to off-shore transport at the surface, with the respective contributions depending largely on the region, from equal contributions to negligible contributions of the eddy flux. By contrast, the subsurface 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 of at least 50 km in the atmosphere and 0.25°–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). Using a suite of low-resolution (1°) and eddy-resolution (1/10°) pairs of models integrated for 60 years, Chassignet et al. (2020) showed that the position, strength, and variability of western boundary currents, equatorial currents, and the Antarctic Circumpolar Current were 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). This study showed that although the global carbon 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; in particular, the flat shape of its upper boundary 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. (2012b), after a 100-year spin-up at 1/54° and 1/9° resolutions. In these experiments, the vertical eddy fluxes of nutrients in an oligotrophic gyre were counterintuitively lower at higher resolution, despite stronger vertical velocities. This was due to a deeper nutricline at higher resolution, which resulted from a change in the mean advective fluxes of nutrients.

point:
low lats: clear correlations with plankton and slow-variability cyclic events e.g. El Nino

high lats: no correlations with metrics such as NAO or SAM

hence:
projection of high-frequency, fine-scale fluctuations onto the longer timescales

4. IMPACT OF FINE SCALES ON THE NATURAL LOW-FREQUENCY VARIABILITY OF BIOGEOCHEMICAL CYCLES

There are large natural variations in marine biogeochemical cycles at interannual to decadal timescales [as shown, e.g., in air–sea CO_2 fluxes by Rodenbeck et al. (2015) and 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 associated with climate indices such as the El Niño–Southern Oscillation (ENSO), the Indian Ocean Dipole, the North Atlantic Oscillation, the Southern Annular Mode, or the Pacific Decadal Oscillation (Liao et al. 2020, Feucher et al. 2022, Lim et al. 2022, Ma et al. 2022, Poupon et al. 2022). For example, regarding phytoplankton, ENSO and the Indian Ocean Dipole have been shown to explain most of the 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 North Atlantic Oscillation (Martinez et al. 2016) or the Southern Annular Mode (Lovenduski & Gruber 2005). A growing number of studies, discussed below, suggest that this could be related to the projection of high-frequency, fine-scale fluctuations onto the variability at interannual and decadal timescales. Recent literature suggests 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. These impacts are summarized in **Table 1**.

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 found 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 to ENSO and the Pacific Decadal Oscillation. 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 to Intermittent Eddy Fluxes

The second line of evidence comes from the analysis of ocean color data, which allow both the effect of fine scales to be seen and changes in phytoplankton from year to year to be measured. To examine interannual variations in phytoplankton in the Southern Ocean, Prend et al. (2022) decomposed phytoplankton variations into three components: subseasonal (<3 months), seasonal, and multiannual (>1 year). The low-frequency component (multiannual) represented only a small fraction (~20%) of the total variance (**Figure 3*a***) but was the only one that showed significant correlations with the Southern Annular Mode index (**Figure 3*b***). In addition, Prend et al. (2022)

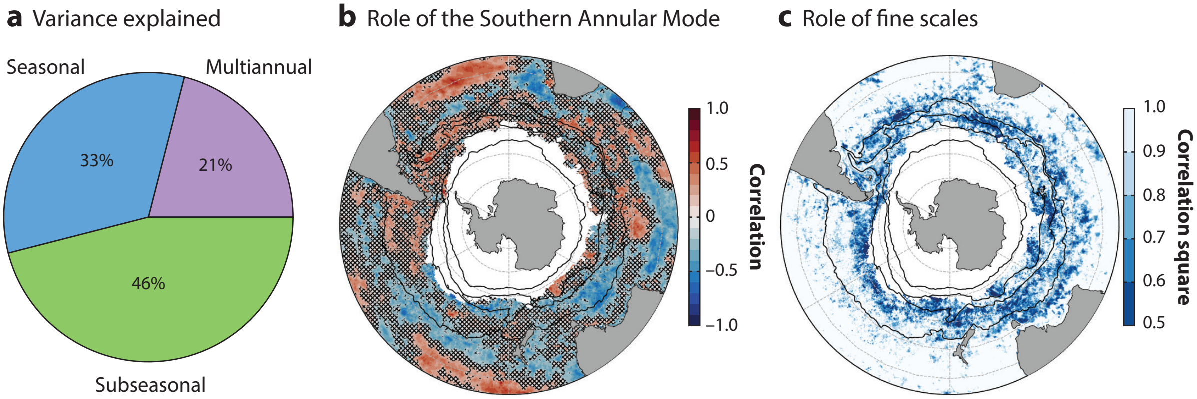

Figure 3

Contribution of ocean fine scales versus contribution of the Southern Annular Mode to phytoplankton interannual variability in the Southern Ocean, evaluated from 20 years (1999–2018) of satellite chlorophyll data. (*a*) Percentage of total chlorophyll variance associated with its subseasonal, seasonal, and multiannual components, averaged over the Southern Ocean. (*b*) Role of the Southern Annular Mode in the low-frequency variation of phytoplankton, quantified by the correlation between the Southern Annular Mode index and the multiannual component (*hatched* when nonsignificant). The correlation between the Southern Annular Mode and the seasonal and subseasonal components is not significant and is not shown. (*c*) Role of fine scales in the low-frequency variation of phytoplankton, highlighted by the correlation square between annual mean chlorophyll and the annual mean of the multiannual component of chlorophyll. Dark blue regions (when the correlation drops) indicate where fine scales contribute most to changes in the amount of phytoplankton from year-to-year. Panel *b* adapted from Prend et al. (2022); panel *c* based on data from Keerthi et al. (2022).

showed that fast variations (subseasonal) represented a large part of the total variance (∼50%) and also contributed to year-to-year changes in phytoplankton biomass over vast areas of the Southern Ocean (**Figure 3*c***). Indeed, subseasonal events, which are often associated with fronts and eddies (Keerthi et al. 2022), perturb the seasonal cycle of phytoplankton productivity in a random manner that varies from one year to the next, generating interannual variability. That implies that annual changes in phytoplankton are related both to low-frequency climate variability operating at a large scale (and captured by the multiannual component) and to intermittent forcing at fine scales (captured by the subseasonal 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 nonlinearities that are particularly strong at fine scales. High-frequency eddy variability is random and chaotic but can cascade toward multiannual timescales 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 with the strength in lower-resolution simulations.

Using an ensemble of three ocean biogeochemical eddy-permitting global model simulations, Gehlen et al. (2020) showed 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 midlatitude Southern Ocean. Using a submesoscale-permitting (1/54°) idealized model of the North Atlantic, Lévy 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 increased when the model resolution increased from 1/3° to 1/54°, suggesting that the estimates of Gehlen et al. (2020), obtained with a 1/4° model, might be strongly underestimated.

5. IMPACT OF FINE SCALES ON THE BIOGEOCHEMICAL RESPONSE TO CLIMATE CHANGE

Climate change over the twenty-first century is expected to alter biogeochemical cycles, but the magnitude and sometimes even the sign of the response predicted by ESMs 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 the physical drivers of 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, fine scales could potentially counteract this general trend and help to limit these threats. But is this really the case? The exploration of this question is in its infancy due to methodological limitations, and we present here different lines of research that begin to draw a general picture (**Table 1**). First, ESMs have provided indirect evidence that fine scales play a role in the response of biogeochemical cycling to climate change. 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.

upscale feedbacks make future projections very sensitive

5.1. Evidence from Earth System Model Projections for the Twenty-First Century

ESMs suggest that fine scales may be important in the response of biogeochemical cycling to future warming. As mentioned above, the horizontal grid resolution of ESMs is not sufficient to capture eddies and fronts, which are thus parameterized, 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), and 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 fine-scale 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 (Li et al. 2022, Martínez-Moreno 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 not only 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 northeastern Atlantic (at 1.25-km resolution), 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 a reduction in the upward heat flux of close to 50%. The reduced vertical submesoscale eddy heat flux implies that biogeochemical eddy fluxes may also be reduced.

On the other hand, however, 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, the intensified eddy activity leads to a projected increase in primary production 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 this intensification may not occur 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. Importance of Upscale Feedback for Climate Projections

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. Specifically, 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 midlatitudes, 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° versus −26% at 1°) at the end of the 70-year-long global warming simulations (**Figure 4*a***). This difference stemmed from the high sensitivity of the nutrient stream to resolution and not, rather counterintuitively, to increased stratification or changes in eddy fluxes of nutrient. Brett et al. (2023) 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 between the two studies may be due to the more regional configuration used by Brett et al. (2023), 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 4*b***) is reduced with increasing model resolution because of a weaker reduction in ventilation (mostly through vertical mixing), although this is partly compensated by a 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 4*c***) due to a stronger overturning circulation at high resolution storing more carbon at depth and a weaker negative feedback in response to warming at higher resolution.

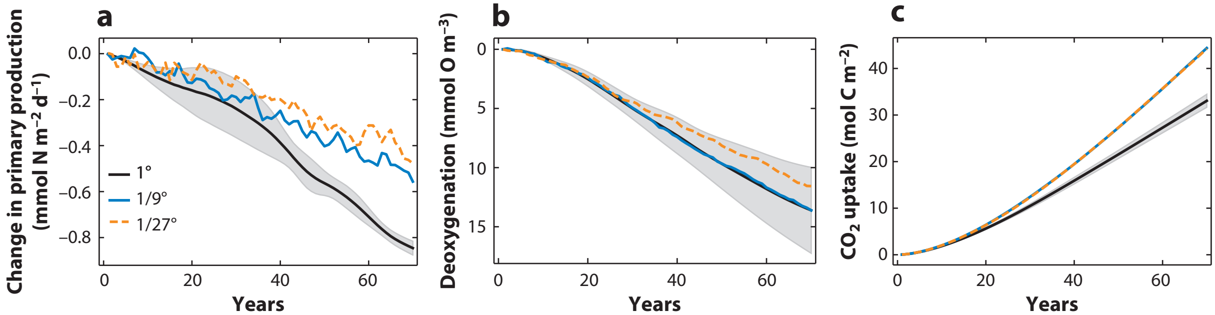

Figure 4

Impact of model grid resolution on the projected response of biogeochemical indicators under climate change. The panels show simulated (*a*) decrease in primary production in the subpolar gyre, (*b*) deoxygenation between 400- and 1,000-m depths, and (*c*) cumulated uptake of CO_2 in a 2,000-km × 3,000-km double-gyre model with closed boundaries, forced by a linearly increasing atmospheric temperature and increasing levels of atmospheric pCO_2, equivalent to the RCP 8.5 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 parameterized (Gent & McWilliams 1990), and sensitivity to a large range of parameters is shown; the black line shows the mean, and gray shading is the standard deviation of the set of sensitivity experiments. With increasing model resolution, the projected decreases in primary production and deoxygenation are not as severe as those projected at coarse resolution, and the increase in CO_2 uptake is larger. Abbreviation: RCP, Representative Concentration Pathway. Panel *a* adapted from Couespel et al. (2021) (CC BY 4.0).

While the processes driving this sensitivity remain to be fully investigated, these new results show that model resolution affects all aspects of marine biogeochemical cycles and strongly suggests that fine scales 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 fine-scale ocean processes in 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 fine scales on global biogeochemical cycling is challenging from both an observational and modeling perspective due to the need to solve both small and large scales.
2. Fine scales contribute to large-scale biogeochemical cycles both through local eddy fluxes and through upscale feedbacks of fine scales 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.
4. There is large uncertainty in the contribution of eddy fluxes to the variability and future state of biogeochemical cycles.
5. Upscale feedbacks significantly modulate the mean state, the natural low-frequency variability of biogeochemical fluxes, and their response to climate change. This poses a great challenge for climate projections that do not resolve these scale transfers accurately.

FUTURE ISSUES

1. How can we best extrapolate observations that are local in space and time to derive quantitative estimates of eddy fluxes at the scale of bioprovinces and over the annual cycle?
2. What are the impacts of downscale feedbacks from fine scales on vertical mixing?
3. What are the mechanisms by which fine-scale variability of biogeochemical tracers contributes to lower-frequency variability, and how can they be estimated from observations?
4. How do fine scales respond to anthropogenic forcing, and how does this influence climate feedbacks related to biogeochemical cycling?
5. How does the parameterization of fine-scale 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?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

M.L. conceived the paper and led the writing. The coauthors, listed in alphabetical order, helped with the clarity of the text and produced **Table 1** and the new material presented in the figures.

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