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Key Points:

- Mesoscale eddy stirring and diapycnal mixing supply nutrients to the world ocean's subtropical gyres
- Mesoscale eddy stirring supply dominates over diapycnal mixing in the thermocline and plays a crucial role in recharging nutrients
- Mesoscale eddy stirring supply intensifies along the flanks of the subtropical gyres

Supporting Information:

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

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The Role of Mesoscale Eddy Stirring and Microscale Turbulence in Sustaining Biological Production in the Subtropical Gyres

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Abstract Sustaining phytoplankton primary production and organic carbon export requires the physical supply of nutrients to the sunlit ocean. In the extensive downwelling regions of the subtropical gyres, the pathways of this nutrient supply remain unclear. Vertical sinking of organic matter from the sunlit layer and its remineralization below cause net downward nutrient transfer in the upper subtropical ocean. Microscale mixing of nutrients across density surfaces and upwelling by mesoscale eddies and submesoscale fronts have been invoked to re-supply nutrients from the thermocline to the sunlit layer. However, a physical mechanism is required to replenish nutrients exported across the thermocline base and sustain a quasi-steady state upper-ocean nutrient budget on inter-annual timescales. Stirring along density surfaces by mesoscale eddies has emerged as a possible supply mechanism to close this nutrient budget. Here, we quantify the relative importance of mesoscale stirring and microscale mixing in supplying nutrients to the oligotrophic regions of the upper subtropical oceans, using global observationally based data sets for nutrients and diapycnal and isopycnal diffusivities. Mesoscale stirring dominates nutrient replenishment in the thermocline of subtropical gyres over microscale turbulence, contributing to 70%–90% of combined supply by the two processes. The stirring supply is most important along gyre flanks, where boundary currents and upwelling zones promote sharp nutrient gradients and vigorous mesoscale activity. Mesoscale fluxes provide sufficient nutrients to offset depletion in the thermocline due to upward microscale mixing into the sunlit layer. This analysis suggests that eddy stirring is significant in maintaining organic carbon export within subtropical gyres.

Plain Language Summary Phytoplankton growth requires a supply of nutrients to the sunlit layer of the ocean. This supply is difficult to achieve in the vast subtropical gyres—central regions of the ocean basins where water moves downward on large scales. In this study, we use global ocean observational data to examine how two small-scale physical processes help move nutrients upward in these nutrient-poor areas. We find that large swirling features in the ocean, called eddies, play a key role in stirring and replenishing nutrients just below the sunlit layer. This supply may be enough to fuel even smaller-scale processes that move nutrients upward, ultimately supporting phytoplankton growth in the sunlit zone. Because phytoplankton form the base of the marine food web and influence how much carbon the ocean absorbs from the atmosphere, these processes have important implications for both marine ecosystems and Earth's climate.

1. Introduction

The export of organic carbon from the sunlit euphotic zone to the deep ocean, mediated by phytoplankton primary production and particle remineralization, is a major control on atmospheric CO₂ (Field et al., 1998). The vertical sinking of organic matter from the euphotic zone and subsequent remineralization depletes the euphotic zone and enriches the thermocline with inorganic nutrients. The long-term maintenance of export production relies on the physical re-supply of inorganic nutrients to the euphotic zone (Dugdale & Goering, 1967). This supply is easily achieved in regions of wind-induced upwelling, but is more difficult in the ocean's subtropical gyres, where large-scale downwelling removes nutrients from the euphotic zone.

Traditionally, the transfer of nutrients upward into the subtropical euphotic zone has been attributed to diapycnal mixing driven by microscale turbulence, typically acting on 1 cm to O(10 m) scales (Lewis et al., 1986; Williams & Follows, 2003). Estimates of the nutrient supply by diapycnal mixing to the euphotic zone of the North Atlantic subtropical gyre typically range from 0.002 to 0.05 mol N m^{−2} yr^{−1} (Dietze et al., 2004; Fernández-Castro

et al., 2015; Ledwell et al., 1993; Mourinho-Carballido et al., 2011; Painter et al., 2013; Spingys et al., 2021). This diapycnal supply increases over ridge systems, due to internal wave generation at, and interaction with, topography (Spingys et al., 2021; Tuerena et al., 2019); and in the presence of double-diffusive instabilities (Fernández-Castro et al., 2015) and winter convective mixing (Michaels et al., 1994). However, such diapycnal supply still falls short of tracer-based estimates of nutrient demand in the euphotic zone, which range from 0.42 to 0.65 mol N m⁻² yr⁻¹ in the subtropical North Atlantic (Jenkins, 1986; Jenkins & Wallace, 1992; Stanley et al., 2015), by at least one order of magnitude. As such, diapycnal mixing cannot by itself explain how subtropical biological production is sustained.

Vertical nutrient transfer by mesoscale (10–100 km) and submesoscale (1–10 km) eddies has since been invoked to transfer nutrients upward into the euphotic zone (Williams & Follows, 2011). Cyclonic and mode-water eddies involve doming isopycnals, which expose nutrients to the euphotic zone (D. McGillicuddy & Robinson, 1997; McGillicuddy et al., 2003). This process typically operates in the top ~150 m, yet can lift nutrients from as deep as 200–300 m (Cianca et al., 2007; D. McGillicuddy & Robinson, 1997; McGillicuddy et al., 2003). Estimates of the resultant euphotic layer supply typically range from 0.07 to 0.19 mol N m⁻² yr⁻¹ in the North Atlantic subtropical gyre (Cianca et al., 2007; Martin & Pondaven, 2003; McGillicuddy et al., 2003; Siegel et al., 1999). Interactions between wind stress and eddies can also upwell nutrient-rich waters into the euphotic zone, depending on the wind direction and eddy vorticity (Dewar & Flierl, 1987; Gaube et al., 2015; D. J. McGillicuddy, 2016). Generation of large submesoscale vertical velocities due to the intensification of surface fronts is also suggested to inject nutrients into the euphotic zone (Calil & Richards, 2010; Haëck et al., 2023; Lévy et al., 2001, 2012; Tandon & Nagai, 2019; Williams & Follows, 2003). While the rectified supply of nutrients by mesoscale and submesoscale circulations is an appealing solution to the maintenance of biological production, this supply relies on the rapid replenishment of nutrients below the sub-euphotic layer. This replenishment raises a second conundrum: how are the nutrients of the thermocline sustained? Although the remineralization of organic matter sinking from the euphotic zone enriches the thermocline with nutrients (Beckmann & Hense, 2009; Gupta et al., 2022), remineralization is only partial, such that vertical export of organic matter persists beyond the base of the thermocline. As such, there is a net nutrient deficit in the upper ocean, including the euphotic zone and thermocline, of the subtropical gyres, and a physical mechanism is required to sustain a quasi-steady state upper-ocean nutrient budget (Figure 1).

Lateral transfer of nutrients by the large-scale background flow may supplement thermocline and euphotic layer nutrient levels (Lee & Williams, 2000; Letscher et al., 2016; Williams & Follows, 1998). Isopycnal slopes and euphotic layer nutrients are enhanced at the flanks of the subtropical gyres, due to wind-driven upwelling in the subpolar and equatorial regions. Western boundary currents also form well-defined nutrient streams along northern and western gyre boundaries (Pelegrí & Csanady, 1991; Williams et al., 2011). The wind-driven, meridional Ekman convergence over the subtropical gyres laterally transfers nutrients from these nutrient-rich flanks, thus adding to diapycnal transfer and time-dependent upwelling (Lee & Williams, 2000; Letscher et al., 2016; Williams & Follows, 1998). However, this lateral nutrient contribution tapers out toward the center of the subtropical gyres due to biological consumption (Williams & Follows, 1998). As such, the maintenance of nutrients in the thermocline over much of the subtropical gyres remains unclear.

Isopycnal stirring of nutrients by mesoscale eddies, hereafter termed eddy stirring, may provide the missing puzzle piece in the nutrient supply mechanism of subtropical gyres. A recent field study of the nitrate budget in the interior of the North Atlantic subtropical gyre provided strong indications of eddy stirring sustaining the nutrient supply to the thermocline (Spingys et al., 2021). The study invoked a relay-race supply mechanism to sustain biological production, whereby nutrients are delivered to the thermocline by eddy stirring and then passed on to the euphotic zone by diapycnal mixing and further eddy stirring. This relay-race supply mechanism is supported by a model study of the North Pacific phosphate budget (Gupta et al., 2022), which revealed that biological production is maintained in the subtropical gyre by the isopycnal eddy transfer of nutrients to the thermocline, particle remineralization within the thermocline, and the vertical transfer of nutrients to the euphotic zone via a combination of diapycnal mixing and time-dependent upwelling. A model investigation of the Southern Ocean tracer metal budget (Uchida et al., 2020) also endorses the maintenance of thermocline nutrients by mesoscale eddy stirring.

However, further work is required to assess the eddy stirring role in the upper-ocean nutrient budget of the subtropical gyres. In Spingys et al. (2021), supply estimates were based on observations from a central region of

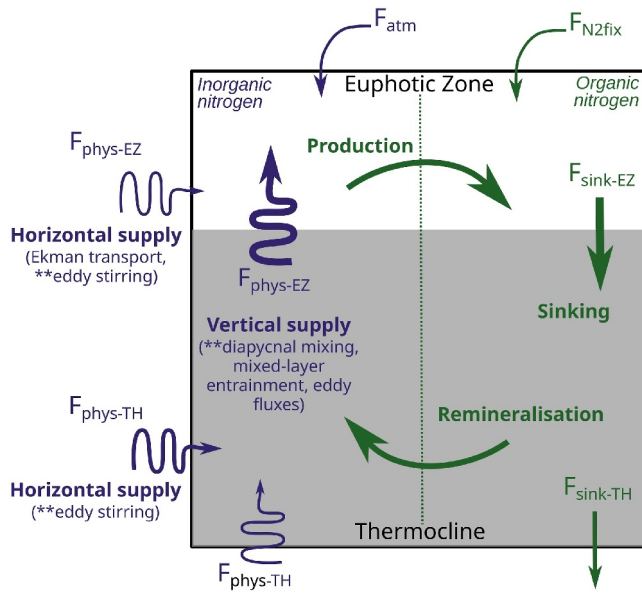


Figure 1. Schematic of the inorganic (purple) and organic (green) nutrient fluxes comprising the upper-ocean nutrient budget of the subtropical gyres, inspired by Beckmann and Hense (2009) and Gupta et al. (2022). Fluxes quantified in this study are marked by **. Vertical sinking of organic matter from the euphotic zone and subsequent remineralization transfer nutrients downwards, depleting the euphotic zone and enriching the thermocline with nutrients. The euphotic zone is re-supplied with nutrients by (i) near-surface processes: atmospheric deposition, F_{atm} , and nitrogen fixation, F_{N2fix} , and (ii) a range of horizontal and vertical physical supply mechanisms, $F_{phys-EZ}$, such as diapycnal mixing, time-dependent eddy and frontal fluxes, winter convection, eddy stirring, and Ekman transports. Vertical export of organic matter beyond the base of the thermocline, $F_{sink-TH}$, persists because remineralization in the thermocline is only partial. To balance $F_{sink-TH}$, a physical nutrient flux to the thermocline, $F_{phys-TH}$, is required, for which eddy stirring is invoked (Gupta et al., 2022; Spingys et al., 2021).

the North Atlantic subtropical gyre, far from gyre boundaries. Spingys et al. (2021) hypothesize that the nutrient supply role of eddy stirring would be larger outside the central study area, toward the flanks of the North Atlantic subtropical gyre, where isopycnal nutrient gradients are larger. In addition, only the vertical convergence of the isopycnal eddy nitrate fluxes was used to estimate supply rates, due to data sparsity, yet the horizontal convergence is expected to be important (Williams & Follows, 2003).

Here, we use observationally based climatological data sets to quantify the nutrient supply by mesoscale eddy stirring and microscale diapycnal mixing over the entire North Atlantic subtropical gyre, including the western boundary current, and the world's four other subtropical gyres. In doing so, we test and build upon the hypothesis of Spingys et al. (2021) and Gupta et al. (2022) that the isopycnal eddy stirring contribution intensifies at the gyre margins and in the thermocline, and contributes more nutrients to the upper subtropical oceans than traditionally invoked diapycnal processes. By using climatological data instead of field observations, we provide a global picture of how this nutrient supply process operates across each subtropical gyre. Convergences in isopycnal and diapycnal directions encompass both the horizontal and vertical contributions of stirring and mixing to nutrient supply. As such, the observational limitations of the previous field study are addressed. Our ultimate aim is to constrain and contextualize the role played by eddy stirring and diapycnal mixing in supplying nutrients to the upper layers of the subtropical gyres.

2. Methods and Data

2.1. Methods

Using climatological data, we compare the magnitude of the supply of nutrients to the upper layers of the subtropical gyres. Specifically, we estimate nutrient flux convergences to the winter mixed layer and thermocline by mesoscale eddy stirring and microscale turbulence. For the winter mixed layer, the nutrient flux convergences are relevant in sustaining both near-surface production and subsurface production in the seasonal thermocline.

Any nutrients supplied to the base of the winter mixed layer are assumed to be transferred to phytoplankton in the euphotic layer via winter convective mixing prior to the spring bloom. For the thermocline, the nutrient flux convergences are relevant for closing the nutrient budget that sustains carbon export across the base of the thermocline. Next, we introduce the nutrient budget equation used in this study, and then describe the closures applied to estimate each budget term.

2.2. Nutrient Budget for a Density Layer

The budget for a nutrient between two density surfaces can be written as Bleck (1998), Spingys et al. (2021)

$$\underbrace{\frac{\partial}{\partial t}(\overline{N})}_{\text{tendency}} + \underbrace{\nabla_{iso} \cdot (\overline{\mathbf{u}N})}_{\text{isopycnal advection}} + \underbrace{\left(\frac{\partial}{\partial z} (w^* N) \right)}_{\text{diapycnal advection}} = \underbrace{\nabla_{iso} \cdot (\overline{K_{iso} \nabla_{iso} N})}_{\text{isopycnal diffusion}} + \underbrace{\frac{\partial}{\partial z} \left(-K_{dia} \frac{\partial \overline{N}}{\partial z} \right)}_{\text{diapycnal diffusion}} + \underbrace{\overline{S}}_{\text{biological source}}, \quad (1)$$

where N is the nutrient concentration, $\mathbf{u}$ is the along density surface velocity, ∇_{iso} is the along density surface gradient, w^* is the velocity across density surfaces, K_{iso} is the isopycnal diffusivity, K_{dia} is the diapycnal diffusivity, S is the biological source, and z is the vertical position of a density surface. $\partial N / \partial z$ is the vertical nitrate gradient between density surfaces which is used as an approximation of the diapycnal nitrate gradient, because isopycnals are quasi-horizontal. In this budget, the changes in the nutrient concentration within a layer stem from a balance between the convergence of isopycnal and diapycnal advective and diffusive fluxes, and biological

sources or sinks. The along-isopycnal terms includes longitudinal and a latitudinal components. The overbar represents a climatological time average, which integrates the effects of many eddies. The negative sign in the diapycnal diffusive flux reflects the use of a down-gradient closure.

2.2.1. Diffusive Nutrient Supply

The focus of this paper is on the convergences of the isopycnal diffusive and diapycnal terms in Equation 1, which represent the supply of nutrients by mesoscale eddy stirring and microscale turbulence, respectively. This focus enables us to address the knowledge gap of the relative importance of mesoscale eddy stirring in supplying nutrients to the global subtropical oceans—a process that has only recently received attention (Gupta et al., 2022; Spingys et al., 2021)—in contrast to the traditionally invoked role of diapycnal processes in sustaining nutrient supply. The isopycnal diffusion by microscale turbulence is ignored because it is several orders of magnitude smaller than the isopycnal diffusion by mesoscale eddies (Tennekes & Lumley, 1972).

Over the different subtropical gyres of the global ocean, we compare the relative magnitude of the diapycnal diffusion, diapycnal advection and mesoscale isopycnal diffusion of nutrients, which are evaluated over an isopycnal layer of thickness h , as

$$\underbrace{(\overline{F_{dia}}|_{bot} - \overline{F_{dia}}|_{top})/\overline{h}}_{\text{diapycnal diffusion}}, \underbrace{((w^*N)|_{bot} - (w^*N)|_{top})/\overline{h}}_{\text{diapycnal advection}}, \underbrace{\overline{\nabla_{iso} \cdot F_{iso}}}_{\text{isopycnal diffusion}} \quad (2)$$

There are additional processes that affect the nutrient budget of the upper subtropical ocean (Figure 1), including the gyre circulation involving the Ekman and geostrophic time-mean circulations (Letscher et al., 2016; Williams & Follows, 1998, 2003; Williams et al., 2006), boundary current transport (Pelegri & Csanady, 1991; Williams et al., 2011), time-varying transport by mesoscale eddies (Doddridge et al., 2016; Lee & Williams, 2000), time-varying sub-mesoscale frontal circulations (Lévy et al., 2001, 2012), winter convective entrainment (Williams et al., 2000), and remineralization (Beckmann & Hense, 2009; Gupta et al., 2022).

2.2.2. Closure for the Supply Terms

The diapycnal diffusive tracer flux, F_{dia} , and isopycnal diffusive tracer flux, F_{iso} , are parameterized by the downgradient closures:

$$F_{dia} = -K_{dia} \frac{\partial \overline{N}}{\partial z}, \quad (3)$$

$$F_{iso} = -K_{iso} \nabla_{iso} \cdot \overline{N}, \quad (4)$$

where K_{dia} is a diapycnal diffusivity, K_{iso} is an isopycnal diffusivity assumed isotropic in the longitudinal and latitudinal directions, $\frac{\partial \overline{N}}{\partial z}$ is a diapycnal nutrient gradient across bounding isopycnals, and $\nabla_{iso} \cdot \overline{N}$ is an isopycnal nutrient gradient made up of longitudinal and latitudinal components. Positive directions are defined as northward, eastward and toward lighter density classes, as the focus of this study is on upward nutrient fluxes.

The diapycnal velocity, w^* , associated with the diapycnal advective tracer flux, w^*N , is generated from the diapycnal contrasts in the diapycnal density flux (Nurser et al., 1999; Spingys et al., 2021), as follows:

$$w^* = \frac{\partial}{\partial \gamma}(F_{dia, \gamma}) = \frac{\partial}{\partial \gamma} \left(-K_{dia} \frac{\partial \gamma}{\partial z} \right), \quad (5)$$

where $F_{dia, \gamma}$ is the diapycnal diffusive density flux, and γ is neutral density calculated using the routines of Jackett and McDougall (1997). Here the sign convention is such that a positive $F_{dia, \gamma}$ and w^* are directed toward lighter neutral surfaces. The w^* can be interpreted as the effective transport across a density surface as the surface is moved by turbulent mixing (de Lavergne et al., 2016; Nurser et al., 1999).

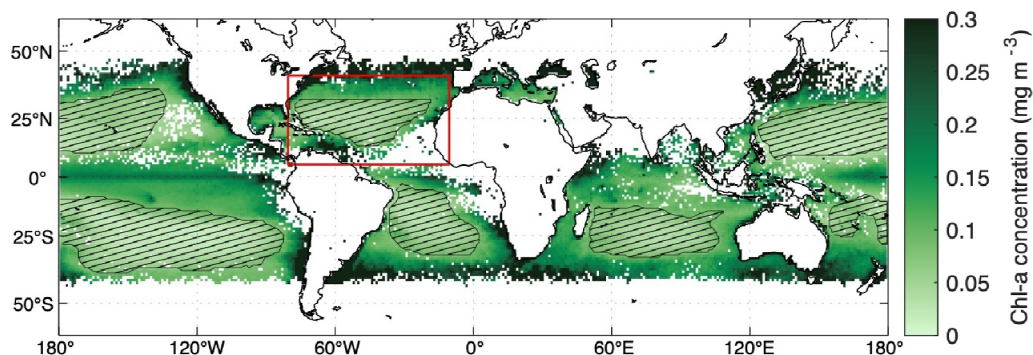


Figure 2. Spatial extent of the oligotrophic regions of the subtropical gyres (hatching) defined by chlorophyll-*a* (chl-*a*) concentration $<0.1 \text{ mg m}^{-3}$ overlaying average surface chl-*a* concentration in 2021, obtained from satellite-derived measurements of ocean color (Hu et al., 2012). Red box marks the focus area of analysis of nutrient supply in this study, encompassing the subtropical North Atlantic and bounding oceanic regions.

2.2.3. Layer-Integrated Supply

The magnitudes of the nutrient supply by mesoscale eddies and microscale turbulence to the winter mixed layer and thermocline are obtained by integrating the supply terms (Equation 2) over the thickness of the two layers.

In our study, the depth of the base of the winter mixed layer is taken from the maximum winter value in the climatological mixed layer depth data set of the World Ocean Atlas (WOA) 2018 (Figure 2a). The depth of the mixed layer of WOA is defined by the change in the potential density of 0.03 kg m^{-3} from the depth of 10 m (National Centers for Environmental Information, 2024). The depth of the base of the thermocline is taken as the depth of the 27 kg m^{-3} neutral density surface, which is approximately the upper bound of the nitrate-rich intermediate waters in the subtropical gyres. See Text S1 in Supporting Information S1 for details of the calculation. See Figure S1 in Supporting Information S1 for the supply layers plotted on meridional sections across the subtropical gyres.

Given that the base of the winter mixed layer is notably deeper than the euphotic zone and summer mixed layer (Figure S3 in Supporting Information S1), the nutrient convergences within the winter mixed layer are relevant for sustaining both near-surface production and subsurface production in the seasonal thermocline (Jenkins & Goldman, 1985).

Our treatment of eddy stirring as transferring nutrients exclusively along isopycnals introduces a limitation in this study. In winter, isopycnals within the mixed layer become vertical, causing eddy stirring to potentially act laterally and diapycnally across these isopycnals, unlike the along-isopycnal stirring below the mixed layer (Ferrari et al., 2008). Seasonal transition in eddy behavior at the base of the winter mixed layer are not included in our calculations, because we use an annual-mean climatological density and nutrient structure where both stratified summer and mixed winter conditions are represented, and thus isopycnals remain inclined.

2.3. Data

The rates of nutrient supply by eddy stirring and microscale turbulence are derived from global estimates of isopycnal and diapycnal diffusivities and climatological nutrient distributions, following Equations 3–5. Given the global and near full-depth coverage of data in this study, both the vertical and horizontal convergences of nitrate fluxes are used to estimate supply rates. This choice is more complete than the Spingys et al. (2021) field study, where only the vertical convergences of nitrate fluxes are used to estimate supply rates. However, there is a caveat with our climatological analysis that the isopycnal and diapycnal diffusivities, and the climatological nutrients, are taken from independent data sets, each with their own uncertainties (see Section 2.3.4), and may not be internally consistent.

2.3.1. Climatological Diffusivity Estimates

Isopycnal diffusivity, relevant to mesoscale eddy stirring, is taken from Groeskamp et al. (2020), where isopycnal diffusivity is estimated from observation-based climatological data sets of salinity, temperature, pressure, and

eddy kinetic energy, following mixing length and flow suppression theory (Ferrari & Nikurashin, 2010; Klocker et al., 2012). The resolution of the isopycnal diffusivity data set is 1° in longitude and latitude, and variable in depth. Groeskamp et al. (2020) use annual-mean fields of salinity, temperature and pressure from the WOA 2018 (Garcia et al., 2018), and eddy kinetic energy from Copernicus Marine Environment Monitoring Service (CMEMS) geostrophic velocity anomalies derived from satellite altimetry.

Diapycnal diffusivity with resolution of 1.5° in longitude and latitude, and 200 m in depth, is taken from Whalen et al. (2012). This estimate is from the rate of internal wave-driven diapycnal mixing based on the strain information in Argo float density profiles. Two modifications to the diffusivity estimates are applied prior to analysis: (a) a refinement of the longitude and latitude resolutions from 1.5° to 1.0° is applied via linear interpolation, in order to match the resolution of other data used in this study; and (b) missing upper-ocean diffusivities between the base of the winter mixed layer and 300 m are set to be the same as diffusivities at 300 m. Missing diffusivities within the winter mixed layer stay set to NaN because of large uncertainties involved, but are likely orders of magnitude higher than at 300 m due to surface forcing. Modification (b) highlights a limitation of this study: diapycnal diffusivity may be underestimated between 300 m and the base of the winter mixed layer. There are also missing diffusivities over considerable parts of the subtropical gyres, due to deficient Argo sampling coverage. In those locations, nutrient supplies are not estimated; see Figure S2 in Supporting Information S1.

Temperature and salinity are taken from observation-based mean fields from the WOA 2018 (Locarnini et al., 2018; Zweng et al., 2019) with resolution of 1° in longitude and latitude, and variable in depth. These data are used to estimate neutral density with the routines from the Gibbs Seawater (GSW) Oceanographic Toolbox of Jackett and McDougall (1997). Neutral density is used in the calculation of diapycnal velocity associated with microscale turbulence, and to define the density grid with a spacing of 0.02 kg m^{-3} on which calculations are performed.

2.3.2. Nutrient Distribution

Nitrate data with resolution of 1° in longitude and latitude, and variable in depth, are assessed in this study, because nitrate is typically the limiting nutrient in subtropical gyres (Moore et al., 2013). The data are taken from observation-based mean fields from the WOA 2018 (Garcia et al., 2018).

2.3.3. Spatial Definitions

The spatial extents of the oligotrophic regions of the subtropical gyres (Figure 2b) are defined following a biological criterion: annual-mean surface chlorophyll-*a* (chl-*a*) concentrations must be $<0.1 \text{ mg m}^{-3}$. These concentrations are taken directly from the Hu et al. (2012) chl-*a* product, which derives monthly chl-*a* values from satellite-observed ocean color data from 2002 to present. To apply this criterion, gyre region masks were manually constructed by tracing the 0.1 mg m^{-3} contour in the 2021 annual-mean chl-*a* field. This approach ensured spatial coherent gyre masks and avoided the inclusion of scattered low-chl-*a* grid cells. The resulting mask is publicly available via the project's GitHub repository: https://github.com/KateOglethorpe/Nutrients_mixing_subtropics. The spatial distribution of chl-*a* $<0.1 \text{ mg m}^{-3}$ regions in 2021 is broadly consistent with those observed across the period 1997–2022 (Figure S4 in Supporting Information S1). Given that (a) chl-*a* concentration is a common metric of phytoplankton abundance (Siegel et al., 2013), (b) the subtropical gyres exhibit low phytoplankton abundance (Williams & Follows, 1998), and (c) the physical characteristics of subtropical gyres vary considerably between gyres (McClain et al., 2004), this biological condition of low chl-*a* is appropriate for an objective global definition. These oligotrophic regions lie within a dynamical definition of subtropical gyres using dynamic height or wind-driven Ekman upwelling (Williams & Follows, 2011).

2.3.4. Data Limitations

The uncertainties associated with each global climatological data set are provided by each respective data sources (Garcia et al., 2018; Groeskamp et al., 2020; Locarnini et al., 2018; Whalen et al., 2012; Zweng et al., 2019). The primary source of uncertainty across all data sets arises from the uneven data coverage in time and space. This limitation forces the annual cycle to be examined by compositing all data regardless of the year of observation and varying sample sizes to contribute to each average. For the diapycnal diffusivity data set, notable uncertainty also arises from the indirect estimation of diffusivities from the strain in density profiles (Whalen et al., 2012). This

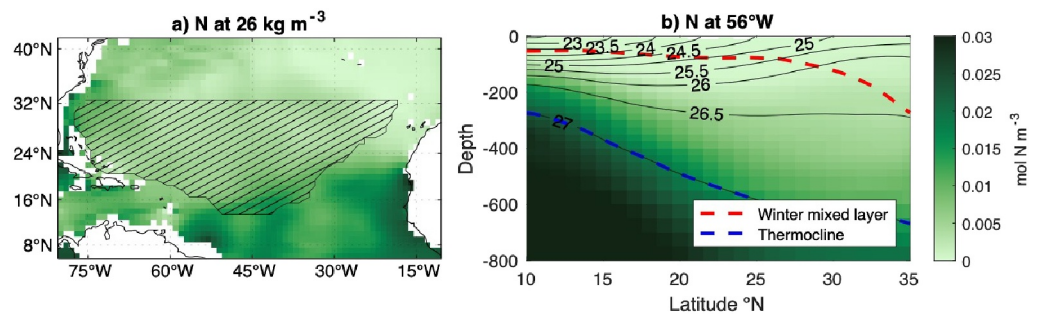


Figure 3. Spatial distribution of nitrate, N , in the North Atlantic subtropical gyre: (a) Horizontal map of N at 26.5 kg m^{-3} , and (b) meridional section of N along 56°W . Hatching on the horizontal map indicates the oligotrophic domain of the gyre, defined as regions with surface chlorophyll- a concentration $< 0.1 \text{ mg m}^{-3}$. Black lines in the meridional section represent annual-mean neutral density surfaces. The red and blue dashed lines denote the base depths of the winter mixed layer and the thermocline, respectively.

method assumes that all diapycnal mixing is driven by internal waves, while other mechanisms such as double diffusion, may also contribute. Another source of uncertainty in our study stems from infilling missing thermocline diffusivity values (300 m to the winter mixed layer base), which potentially underestimates diffusivity in this range. Furthermore, our linear interpolation of the diapycnal diffusivity estimates from 1.5° to 1.0° resolution adds uncertainty. See Section 3.5 and Figure S7 in Supporting Information S1 for a comparison of climatological data sets and derived nitrate fluxes in our analysis with the field estimates of Spingys et al. (2021).

3. Nutrient Supply to the Oligotrophic Region of the North Atlantic Subtropical Gyre

3.1. Nutrient Distribution

The oligotrophic region of the North Atlantic subtropical gyre, like the oligotrophic regions of the other subtropical gyres in the world's oceans, is nitrate-poor by definition as compared to the high latitudes and tropics. However, nitrate variation within the North Atlantic oligotrophic region is still considerable (Figure 3). Nitrate, N , increases with depth, peaking in the deep waters of the south-east where N exceeds $0.03 \text{ mol N m}^{-3}$ below 400 m. In contrast, the lowest N is found in the surface waters. These spatial variations result in substantial nitrate gradients along and across density surfaces over the North Atlantic oligotrophic region. Diapycnal nitrate gradients, $\frac{\partial N}{\partial z^*}$, are negative over the large majority of the region, peaking in the south where the increase in N with depth is greatest (Figures S5a and S5b in Supporting Information S1). Isopycnal nitrate gradients, $\nabla_{iso} N$, are generally elevated along the gyre flanks as compared to the center (Figures S5c and S5f in Supporting Information S1).

3.2. Rates of Mixing

The isopycnal diffusivity, K_{iso} , associated with eddy stirring, and diapycnal diffusivity, K_{dia} , and diapycnal velocity, w^* , associated with microscale turbulence, also vary considerably over the oligotrophic region of the North Atlantic subtropical gyre (Figure 4). Large K_{iso} is found along the western and north-western boundaries, reaching a maximum of $4,600 \text{ m}^2 \text{ s}^{-1}$ in the surface waters in the north-western corner. Low K_{iso} of $< 1000 \text{ m}^2 \text{ s}^{-1}$ is found in the east and south-east, broadly decreasing with depth. There are considerable missing values of K_{dia} and w^* due to gaps in the data set. Elevated K_{dia} occurs along the southern boundary and in the eastern half of the gyre. The K_{dia} data is modified due to missing diffusivities at 0–300 m, with vertically homogeneous K_{dia} from 300 m to the base of the mixed layer. w^* is generally positive over the thermocline where the density stratification increases with depth, representing diapycnal upwelling. For clarification of this spatial pattern, see diagnostics of the w^* calculation at two representative sites in the gyre in Text S2 and Figure S6 in Supporting Information S1.

3.3. Nutrient Fluxes

Variations in nitrate distribution (Figure 3) and mixing rates (Figure 4) control the pattern of nitrate fluxes to varying degrees (Figure 5). The isopycnal diffusive nitrate flux, F_{iso} , associated with eddy stirring, is strongest along the flanks of the North Atlantic oligotrophic region. Specifically: strong northward F_{iso} of $> 200 \text{ mol}$

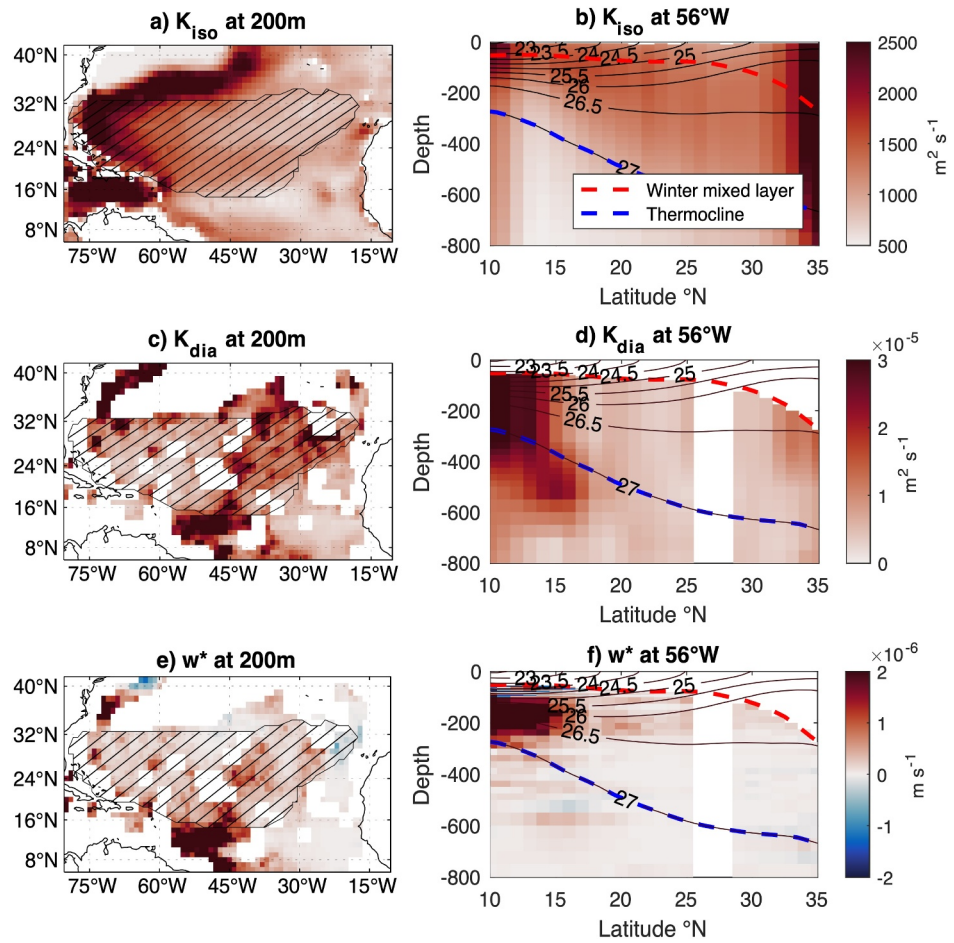


Figure 4. Spatial distributions of isopycnal diffusivity, K_{iso} (a, b), diapycnal diffusivity, K_{dia} (c, d), and diapycnal velocity, w^* (e, f). In the North Atlantic subtropical gyre: horizontal maps at 200 m (left column) and meridional sections at 56°W (right column). Positive w^* is directed to lighter density surfaces. Hatching on the horizontal map indicates the oligotrophic domain of the gyre, defined as regions with surface chlorophyll- a concentration $<0.1 \text{ mg m}^{-3}$. Black lines in the meridional section represent annual-mean neutral density surfaces. The red and blue dashed lines denote the base depths of the winter mixed layer and the thermocline, respectively.

$\text{N m}^{-2} \text{ yr}^{-1}$ along the southern flank, strong southward F_{iso} of $<-200 \text{ mol N m}^{-2} \text{ yr}^{-1}$ along the north-western flank, and moderate eastward F_{iso} of $>150 \text{ mol N m}^{-2} \text{ yr}^{-1}$ along the north-western flank. The intense northward F_{iso} along the southern flank, coinciding with peak northward $\nabla_{iso} \bar{N}$, suggests that nitrate gradients are a key driver of F_{iso} in this area. In contrast, the strong southward and eastward F_{iso} of the north-western flank, which align with peak K_{iso} values, indicate that K_{iso} predominately controls F_{iso} in these areas.

For the microscale turbulence-driven nitrate fluxes of F_{dia} and w^*N , their spatial variations resemble both those of diapycnal nitrate gradient and mixing rates. Maximum F_{dia} of $0.12 \text{ mol N m}^{-2} \text{ yr}^{-1}$ along the mid-southern flank coincides with high K_{dia} and $\frac{\partial \bar{N}}{\partial z}$. As such, both K_{dia} and $\frac{\partial \bar{N}}{\partial z}$ are important drivers of F_{dia} . The pattern of w^*N largely follows that of w^* , where w^*N fluxes nutrients downwards in waters shallower than the maximum density stratification over the majority of the oligotrophic region of the gyre and upwards in deeper waters. These fluxes reach a maximum of $1.2 \text{ mol N m}^{-2} \text{ yr}^{-1}$ along the southern flank, where both large N and w^* are found as compared to the rest of the oligotrophic region.

3.4. Nutrient Supply

Nutrient supply by eddy stirring, generated by the convergence of F_{iso} , is largely concentrated along the north-western and eastern flanks of the oligotrophic domain of the North Atlantic subtropical gyre (Figure 6a).

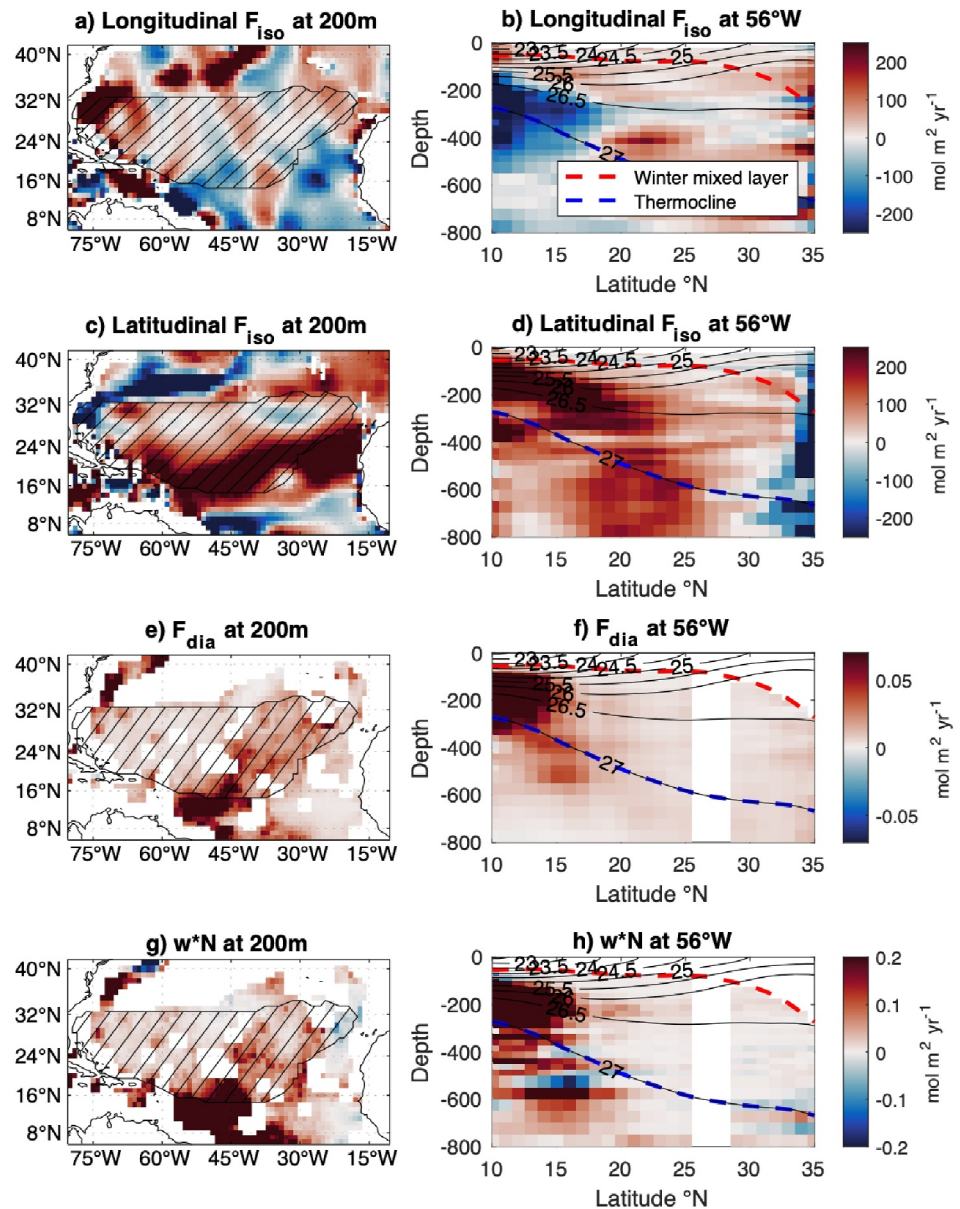


Figure 5. Spatial distributions of the longitudinal isopycnal diffusive nitrate flux, F_{iso} , (a, b), latitudinal F_{iso} , (c, d), diapycnal diffusive nitrate flux, F_{dia} , (e, f), and diapycnal advective nitrate flux, $w*N$ (g, h) in the North Atlantic subtropical gyre: horizontal maps at 200 m (left column) and meridional sections at 56°W (right column). Hatching on the horizontal map indicates the oligotrophic domain of the gyre, defined as regions with surface chlorophyll-*a* concentration $<0.1 \text{ mg m}^{-3}$. Black lines in the meridional section represent annual-mean neutral density surfaces. The red and blue dashed lines denote the base depths of the winter mixed layer and the thermocline, respectively.

Maxima occur at approximately the core of the Gulf Stream along the north-western flank, with a supply of $0.58 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the mixed layer and $3.3 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the thermocline. There is also notable N supply to the thermocline layer of the low-chlorophyll core of the North Atlantic subtropical gyre, strengthening toward the east. Patches of relatively weak nitrate loss (i.e., negative N supply) by mesoscale eddy stirring are also found in some areas of the domain flanks. From the mixed layer, nutrient loss peaks in magnitude south of the elevated nutrient supply along the north-western flank, centered at $29.5^\circ\text{N } 77.5^\circ\text{W}$, with a rate of $-0.062 \text{ mol N m}^{-2} \text{ yr}^{-1}$. From the thermocline, nutrient loss peaks further south along the western flank, centered at $22.5^\circ\text{N } 70.5^\circ\text{W}$, with a rate of $-0.76 \text{ mol N m}^{-2} \text{ yr}^{-1}$. Like the nitrate supply, the nitrate loss is greater from the thermocline than from the

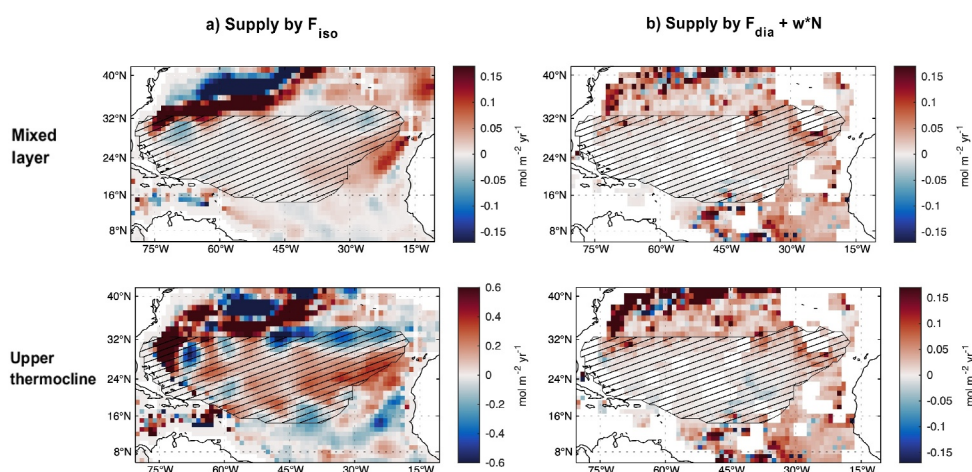


Figure 6. Distribution of estimates of nitrate supply to the winter mixed layer (top row) and the thermocline (bottom row) of the subtropical North Atlantic by (a) the isopycnal diffusive nitrate flux, F_{iso} , due to mesoscale stirring, and (b) diapycnal diffusive nitrate flux, F_{dia} , and diapycnal advective nitrate flux, w^*N , due to microscale turbulence. Hatching indicates the oligotrophic domain of the North Atlantic subtropical gyre, defined by surface chlorophyll- a concentration $<0.1 \text{ mg m}^{-3}$. See Figure 2 for plots of the base depths of the mixed layer and the thermocline, defined as the maximum climatological winter mixed layer depth and the depth of the 27 kg m^{-3} neutral density surface, respectively (Section 2.2.3).

mixed layer. From the thermocline, there is also considerable nitrate loss on the northern flank in the east and southern flank in the center of the oligotrophic domain.

Nutrient supply by microscale turbulence, generated by convergences of F_{dia} and w^*N , is generally lower than that by eddy stirring (Figure 6b). Diapycnal nutrient supply contributes to less than $0.05 \text{ mol N m}^{-2} \text{ yr}^{-1}$ over the majority of the North Atlantic oligotrophic region and increases toward its southern, eastern and northern boundaries. Maximum turbulence-driven supply rates of $0.26 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the mixed layer and $0.29 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the thermocline, both found along the northern flank, are smaller than those of the eddy stirring-driven supply rates by factors of 2 and 11, respectively. Nutrient loss by microscale turbulence is considerably weaker than the eddy stirring-driven loss from the thermocline.

The oligotrophic part of the North Atlantic subtropical gyre receives combined supplies by mesoscale eddies and microscale turbulence of $0.023 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the winter mixed layer and $0.11 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the thermocline (Figure 7). Eddy stirring contributes 60% and 90% to these mixed layer and thermocline supplies, respectively. The smaller time-mean supply by microscale turbulence contributions is dominated by F_{dia} , which drives over 70% of the winter mixed layer diapycnal supply and 60% of the thermocline diapycnal supply.

3.5. Comparison With Field Estimates of Nitrate Fluxes

The global climatological estimates of diffusivities, nitrate, and nitrate fluxes in this study are compared with historical field estimates of Spingys et al. (2021) at 24 sites in the central subtropical North Atlantic (Figure S7 in Supporting Information S1). Overall, the two approaches show reasonable agreement, with diffusivities exhibiting larger discrepancies than nitrate. Excluding the mixed layer, K_{iso} and K_{dia} estimates are of the same order of magnitude for the two approaches, differing by factors of 0.3–1.3 and 0.4–2.4, respectively. For nitrate concentration, the climatological estimates are closely constrained to the field measurements, differing by factors of 1–1.4 excluding near-zero values. Nitrate fluxes are similarly of the same order of magnitude for both approaches, generally differing by factors of less than 2, with the exception of a few data points, such as w^*N at $>27.6 \text{ kg m}^{-3}$; the full climatological-field comparison is provided in Figure S7 in Supporting Information S1. In general, climatological values are distributed around the corresponding field-based values, with neither consistently greater than the other. Potential sources of these discrepancies are discussed in Section 5.

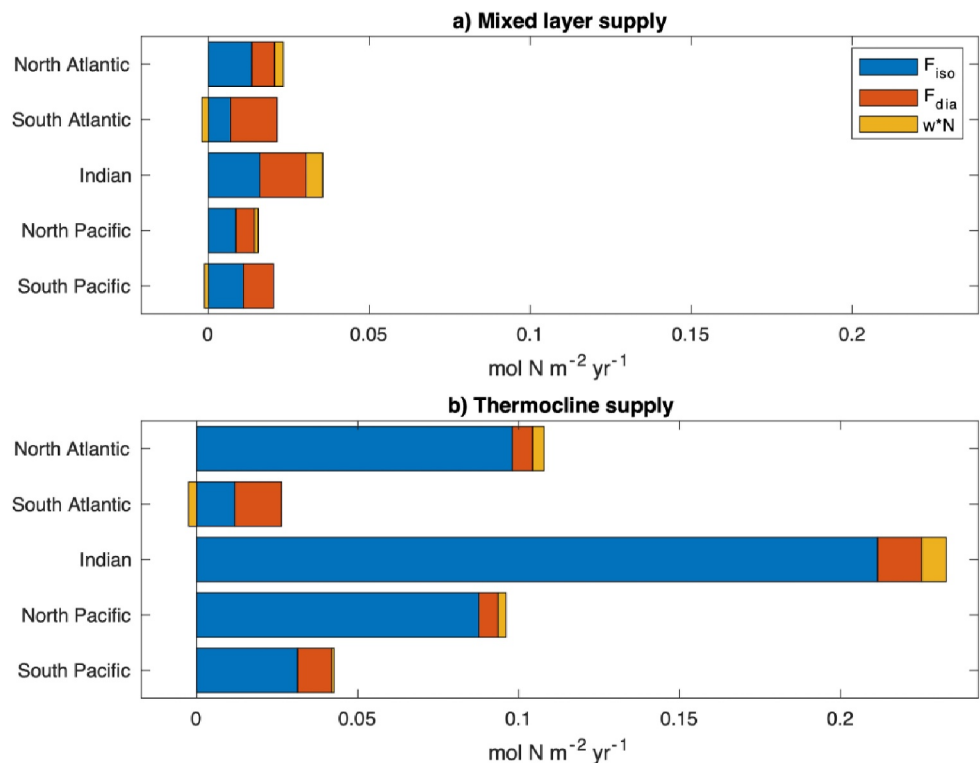


Figure 7. Compilation of the integrated averages of estimates of nitrate supply to (a) the winter mixed layer and (b) the thermocline by the isopycnal diffusive nitrate flux, F_{iso} , due to mesoscale eddies (blue), and the diapycnal diffusive nitrate flux, F_{dia} (orange) and diapycnal advective nitrate flux, $w*N$ (yellow), both due to microscale turbulence, over the world's subtropical gyres. Nitrate supply by other physical mechanisms and particle remineralization, which are components of the nutrient budget of the upper subtropical ocean, are not represented by this compilation.

4. Global Assessment of Nutrient Supply to the Oligotrophic Regions of Subtropical Gyres

The estimation of nitrate fluxes and supply from the North Atlantic is now extended to the world's four other subtropical gyres to assess the role of eddy stirring and microscale turbulence in sustaining nutrient levels.

4.1. Overview of Global Results

The oligotrophic region of the Indian Ocean subtropical gyre receives the largest amount of nitrate, with a combined supply by mesoscale eddies and microscale turbulence of $0.036 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the winter mixed layer and $0.23 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the thermocline, considerably greater than in the oligotrophic regions of the other four subtropical gyres (Figure 7). For the thermocline, where the nitrate supply to the Indian Ocean oligotrophic region is greatest, eddy stirring dominates the supply over microscale turbulence, contributing up to 90% of the combined supply. For the winter mixed layer of the Indian Ocean oligotrophic region, eddy stirring and microscale turbulence contribute approximately equal nitrate supplies.

Like in the Indian Ocean subtropical gyre, the oligotrophic regions of the world ocean's four other subtropical gyres receive notably more nitrate to the thermocline than to the winter mixed layer (Figure 7). The thermocline nitrate supplies of $0.11 \text{ mol N m}^{-2} \text{ yr}^{-1}$ for the North Atlantic, $0.097 \text{ mol N m}^{-2} \text{ yr}^{-1}$ for the North Pacific, $0.043 \text{ mol N m}^{-2} \text{ yr}^{-1}$ for the South Pacific, and $0.024 \text{ mol N m}^{-2} \text{ yr}^{-1}$ for the South Atlantic are greater than their corresponding winter mixed layer supplies by factors of 4.6, 6.2, 2, and 1.2, respectively. In the North Atlantic, North Pacific, and South Pacific oligotrophic regions, where the thermocline nitrate supplies are largest, eddy stirring dominates over microscale turbulence in supplying nutrients. Eddy stirring makes up 55%–60% and 70%–90% of their mixed layer and thermocline combined nitrate supplies, respectively. In contrast, in the South Atlantic oligotrophic region, where the thermocline supply is smallest, microscale turbulence dominates the

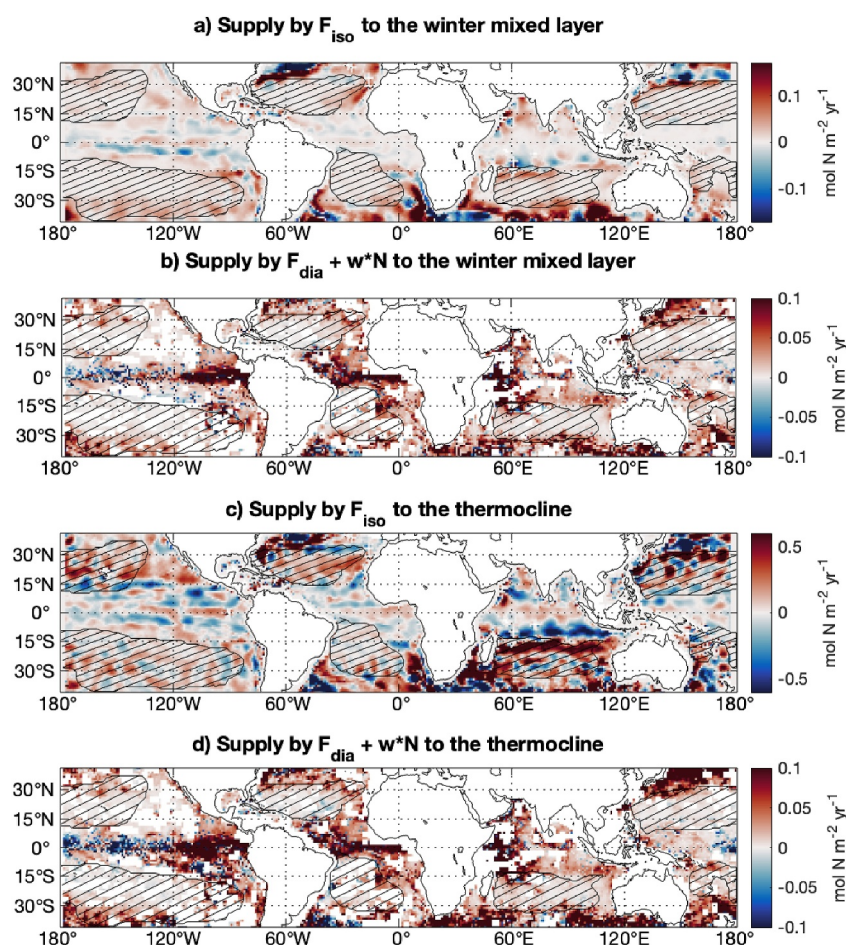


Figure 8. Distribution of estimates of nitrate supply to the winter mixed layer and thermocline of the global oceans by (a) + (c) the isopycnal diffusive nitrate flux, F_{iso} , due to mesoscale eddies, and (b) + (d) the diapycnal diffusive nitrate flux, F_{dia} , and diapycnal advective nitrate flux, w^*N , due to microscale turbulence. Hatching indicates the spatial extent of the oligotrophic domain of the subtropical gyres, defined by surface chlorophyll- a concentration $<0.1 \text{ mg m}^{-3}$.

supply over eddy stirring, making up 65% of the combined thermocline supply. Microscale turbulence and eddy stirring make approximately equal contributions to the mixed layer supply of the South Atlantic oligotrophic region. For all oligotrophic regions of the subtropical gyres, F_{dia} dominates the microscale turbulence-driven nitrate supply, making up 65%–100% of the combined diapycnal supplies. w^*N contributes to nitrate loss from the mixed layer and thermocline of the South Atlantic oligotrophic region and mixed layer of the South Pacific oligotrophic region.

To gauge the uncertainty and robustness of these gyre-scale estimates of supply rates, we perform a sensitivity analysis (Figure S8 and Table S1 in Supporting Information S1 for method details). Perturbing the size of the oligotrophic regions of the subtropical gyres by 15%–20% has minimal impact on the estimated relative roles of eddy stirring and microscale turbulence in supplying nitrate, with the exception of the South Atlantic oligotrophic region. In the North Atlantic, Indian, and North and South Pacific, the contributions of F_{iso} to the mixed layer and thermocline change by less than 5% for a 15%–20% change in region size. However, in the South Atlantic, the same change in region size significantly reduces the role of eddy stirring in nitrate supply to the thermocline, decreasing it from 50% to 20%. Therefore, while spatial extent of the oligotrophic domain introduces notable uncertainty in our results for the South Atlantic, it has little effect on the domains for the other subtropical gyres 7.

These gyre-scale estimates of supply rates may be small because of the partial cancellation of substantial positive and negative local supply rates during spatial integration. However, these local processes are not negligible; and

their spatial patterns remain critical for understanding the maintenance of nutrient distributions within the different gyres, as shown in Figure 8 and described in the following section.

4.2. Comparative Assessment Between Different Subtropical Gyres

There is a similarity between the North Atlantic and North Pacific supply regimes (Figure 8), which is most evident in the intensification of eddy stirring-driven nitrate supply along the western-poleward flanks of their oligotrophic regions. Along the north-western boundary of the North Pacific region, south of the Kuroshio Current, eddy stirring-driven winter mixed layer and thermocline supplies reach their maxima of $0.23 \text{ mol N m}^{-2} \text{ yr}^{-1}$ and $2.0 \text{ mol N m}^{-2} \text{ yr}^{-1}$, respectively. Although the approximate locations of the North Pacific maxima match those in the North Atlantic, their magnitudes differ notably where the North Pacific supply falls short of North Atlantic supply by over half for the mixed layer and over one quarter for the thermocline. High eddy stirring-driven supply along the eastern flank, which is considerable for the North Atlantic oligotrophic region, is less prominent in the North Pacific oligotrophic region and only important in the thermocline. Nitrate loss from the thermocline along the equatorward flank is more extensive for the North Pacific than the North Atlantic supply regimes, where a zonal band of nitrate loss from the thermocline extends close to the entirety of the southern flank of the North Pacific oligotrophic region. For the turbulence-driven supply, there is also notable resemblance between the two Northern Hemisphere oligotrophic regions. Like the North Atlantic, microscale turbulence in the North Pacific contributes to less than $0.05 \text{ mol N m}^{-2} \text{ yr}^{-1}$ over the majority of the oligotrophic region and intensifies along the poleward flank, where this supply reaches a maximum of $0.27 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the mixed layer and $0.35 \text{ mol N m}^{-2} \text{ yr}^{-1}$ to the thermocline. As in the North Atlantic, nitrate loss by turbulent mixing from the North Pacific is considerably smaller in extent and magnitude as compared to that by eddy stirring over the majority of the oligotrophic region.

In the oligotrophic domains of the Southern Hemisphere gyres, there is a broad resemblance to that of the North Atlantic gyre in terms of the patterns of eddy stirring and turbulence-driven nitrate supplies, while some clear differences also exist (Figure 8). For the South Atlantic oligotrophic region, the peak of eddy stirring-driven supply along the western poleward flank as seen in the North Atlantic and North Pacific oligotrophic regions is not present. Instead, this maximum supply is located poleward and westward of the oligotrophic region (Figure 8). The eddy stirring-driven supply along the eastern flank is elevated as seen in the Northern Hemisphere regions. In the South Atlantic oligotrophic region, the eddy stirring-driven nitrate supplies to the winter mixed layer and thermocline peak in the south-eastern corner, with values of $0.08 \text{ mol N m}^{-2} \text{ yr}^{-1}$ and $0.40 \text{ mol N m}^{-2} \text{ yr}^{-1}$, respectively, close to regions of eastern boundary upwelling. Like the Northern Hemisphere oligotrophic regions, high eddy stirring-driven supply in the east is accompanied by small patches of marked nitrate loss. Due to substantial gaps in K_{dia} , the turbulence-driven supply regime over the South Atlantic is difficult to characterize. As in the North Atlantic, the diapycnal nutrient supply may intensify along the equatorward flank, where the turbulence-driven mixed layer and thermocline supply maxima of 1.1 and $1.2 \text{ mol N m}^{-2} \text{ yr}^{-1}$ are found, and along the poleward flank.

Like in the other subtropical gyres, the oligotrophic regions of the South Pacific and Indian Ocean receive most of their mixed layer supply across their flanks (Figure 8). For the mixed layer of the South Pacific region, there is an intensification of eddy stirring-driven supply along the western-poleward flank, although less prominent than in the Northern Hemisphere. The winter mixed layer and thermocline eddy stirring-driven supply maxima of $0.10 \text{ mol N m}^{-2} \text{ yr}^{-1}$ and $1.6 \text{ mol N m}^{-2} \text{ yr}^{-1}$, respectively, occur along the western flank off the Australian coast. Eddy stirring-driven supply to the winter mixed layer is also intensified in the poleward half of the South Pacific oligotrophic region. Eddy-stirring supply to the thermocline is notably higher than winter mixed layer supply. As in the South Atlantic, substantial missing K_{dia} data over the South Pacific limits the description of its turbulence-driven supply. However, there is an intensification along the poleward flank, where the mixed layer turbulence-driven supply reaches a maximum of $0.24 \text{ mol N m}^{-2} \text{ yr}^{-1}$, and in the eastern half, where the turbulence-driven supply to the thermocline reaches a maximum of $0.30 \text{ mol N m}^{-2} \text{ yr}^{-1}$.

For the oligotrophic region of the Indian Ocean subtropical gyre, the greatest enhancement of nutrient supply occurs along the equatorward flank, rather than the western-poleward flank as seen in the North Atlantic, North Pacific, and South Pacific subtropical gyres. This equatorward enhancement is most notable in the thermocline, where eddy stirring-driven supply reaches $>0.50 \text{ mol N m}^{-2} \text{ yr}^{-1}$ (Figure 8). The mixed layer and thermocline supply by eddy stirring attain their maxima of 0.12 and $1.6 \text{ mol N m}^{-2} \text{ yr}^{-1}$, respectively, along the western half of

the equatorward flank. Eddy stirring-driven supply also intensifies considerably along the poleward flank and along the western and eastern flanks. The most prominent spatial features of turbulence-driven supply are intensification in the north-west corner of the oligotrophic region and the poleward flank, where the mixed layer and thermocline supply maxima reach 0.93 and 0.99 mol N m² yr⁻¹.

5. Discussion and Conclusions

In the extensive downwelling regions of the subtropical gyres, there is a long-standing question of how the biological production and vertical export of organic matter are sustained. Vertical sinking of organic matter and subsequent remineralization result in a downward nutrient transfer, depleting the euphotic zone and enriching the upper thermocline with nutrients. Thermocline nutrients are returned to the euphotic zone by a combination of vertical transport processes such as small-scale diapycnal mixing (Spingys et al., 2021; Tuerena et al., 2019), deep winter mixing (Mouriño-Carballido et al., 2021), time-dependent eddy and frontal pumping (Lévy et al., 2012; McGillicuddy et al., 2003; Oschlies, 2002), or eddy-wind interactions (Gaube et al., 2015; D. J. McGillicuddy, 2016). However, remineralization of the sinking organic matter is only partial, such that vertical export of organic matter persists beyond the base of the thermocline, resulting in a net nutrient deficit in the upper subtropical ocean above ~1,000 m (Beckmann & Hense, 2009). Nutrients are replenished by allochthonous and biological sources such as atmospheric deposition (Michaels et al., 1996), biological nitrogen fixation (Painter et al., 2013), and by lateral transport processes such as horizontal Ekman transfers (Williams & Follows, 1998). Nutrient stirring by mesoscale eddies has recently been invoked as a key player in the nutrient budget in subtropical gyres (Gupta et al., 2022; Spingys et al., 2021). Eddy stirring may be involved in a relay mechanism (Gupta et al., 2022; Spingys et al., 2021) by which nutrients are supplied to the thermocline by mesoscale eddy stirring and passed on to a variety of physical processes, such as diapycnal mixing, deep winter mixing, and time-dependent eddy and frontal pumping, which supply nutrients to the euphotic layer. Ocean model studies also show that this stirring-induced diffusive transfer of tracers provides the dominant contribution to tracer ventilation in a wide range of scenarios (Bopp et al., 2015). However, the role of eddy stirring in supplying nutrients to the subtropical gyres of the global oceans has not been previously assessed.

Here, a nutrient supply analysis for oligotrophic regions of all the subtropical gyres is conducted using climatological data sets to quantify the diffusive, isopycnal and diapycnal supply of nutrients in the upper subtropical gyres and assess the significance of isopycnal stirring. The climatological analysis supports the view that eddy stirring provides an important nutrient pathway in the subtropical gyres: eddy stirring along isopycnals is elevated along the flanks of the world's subtropical gyres and largely dominates over small-scale turbulence across isopycnals in supplying nutrients to the thermocline. The analysis builds upon the hypotheses of Spingys et al. (2021) based on field data over the central region of the North Atlantic subtropical gyre. Like Spingys et al. (2021), only two physical nutrient pathways are investigated, despite the possible importance of other physical pathways and particle remineralization sustaining the upper subtropical ocean with nutrients. The peak rate of winter mixed layer supply by eddy stirring of 0.58 mol N m⁻² yr⁻¹, which is found along the western-poleward flank of the North Atlantic oligotrophic region, is over 10 times the rate of nitrate supply by eddy stirring estimated by the field study of Spingys et al. (2021), which was assessed at 300 m (approximately the base of the winter mixed layer) from field data in the center of the North Atlantic subtropical gyre. This mis-match in supply rates is expected, given that the field site is far away from the gyre boundaries where most of the nutrient exchange happens. Similarly, the peak rate of thermocline nitrate supply by eddy stirring in this study of 3.3 mol N m⁻² yr⁻¹, which is found along the western-poleward flank of the North Atlantic oligotrophic region, is substantially larger than thermocline supply rates at the region's center. Since the intensification of eddy stirring-induced nitrate supply along gyre boundaries is also marked in the world's other subtropical gyres, with examples in the western-poleward flank in the North Pacific, the equatorward flank in the Indian Ocean, and the eastern flanks in the Atlantic, the first component of the relay race mechanism hypothesis—that the supply is initiated by intensified lateral eddy stirring at gyre margins—is supported by this study.

The second element of the hypothesis—that isopycnal eddy stirring is an important process for replenishing the thermocline nutrient levels—is also supported. For oligotrophic regions of the North Atlantic, North Pacific, South Pacific, and Indian Ocean subtropical gyres, eddy stirring contributes 70%–90% of the combined thermocline supplies by eddy stirring and microscale turbulence, whilst eddy stirring and microscale turbulence make comparable nutrient contributions to the winter mixed layer. As such, the supply of nutrients by isopycnal eddy

stirring strengthens in the thermocline inventory as compared to the winter mixed layer. An exception is the oligotrophic region of the South Atlantic subtropical gyre, where microscale turbulence dominates both the winter mixed layer and thermocline supplies. This difference may be attributed to the relatively more restricted oligotrophic domain of the South Atlantic compared to other subtropical gyres.

To understand the order-of-magnitude importance of eddy stirring compared to other physical terms in fluxing nutrients within the upper subtropical ocean, our estimates of eddy stirring-driven nutrient supply to the thermocline are compared to previous estimates of euphotic layer supply driven by a variety of other physical processes. Our comparison differs in terms of spatial and temporal scales, since we estimate gyre-scale supply rates on climatological timescales whilst the majority of past studies estimate local supply rates on much shorter, typically sub-seasonal, timescales. For the North Atlantic subtropical gyre, estimates of euphotic layer nitrate supply by diapycnal mixing and time-dependent eddy pumping, ranging from 0.002 to 0.05 mol N m⁻² yr⁻¹ (Dietze et al., 2004; Fernández-Castro et al., 2015; Ledwell et al., 1993; Mouriño-Carballido et al., 2011; Painter et al., 2013; Spingys et al., 2021) and 0.07–0.19 mol N m⁻² yr⁻¹ (Cianca et al., 2007; Martin & Pondaven, 2003; McGillicuddy et al., 2003; Siegel et al., 1999), respectively, are comparable to our averaged estimate of eddy stirring-driven thermocline supply over the North Atlantic oligotrophic region of 0.10 mol N m⁻² yr⁻¹. These euphotic layer supplies are substantially weaker than the intensified eddy stirring-driven thermocline supplies along the flanks of the oligotrophic regions, peaking at 3.3 mol N m⁻² yr⁻¹. As such, we propose that the thermocline is replenished by eddy stirring over considerable portions of the subtropical gyres.

Eddy stirring is potentially most relevant in replenishing nutrients to the upper subtropical ocean as a whole, along the vertical extent of the winter mixed layer and thermocline, balancing the vertical sinking of organic matter below the thermocline (Figure 3). In this context, the relevance of eddy stirring can be gauged by comparing with other external sources of reactive nitrogen to the upper ocean, such as biological nitrogen fixation and atmospheric deposition (Beckmann & Hense, 2009). In two recent global compilations, average nitrogen fixation rates in mid- and low-latitude ocean basins ranged from 0.01 to 0.2 mol N m⁻² yr⁻¹ (mean: 0.05 mol N m⁻² yr⁻¹) (Shao et al., 2023; Wang et al., 2019), with similar numbers ~0.05 mol N m⁻² yr⁻¹ reported for the average deposition flux of reactive nitrogen (Jickells et al., 2017). Eddy stirring fluxes are similar, if not larger, than such surface fluxes, highlighting their relevance in sustaining carbon export in the subtropics.

The extension of our climatological analysis from a central part of the North Atlantic subtropical gyre to the oligotrophic regions of the North Atlantic subtropical gyre and the world ocean's other four subtropical gyres reveals key physical drivers sustaining nutrients in the gyres. Consistent with Gupta et al. (2022), large intensification of nutrient supply by eddy stirring along the western-poleward flanks of the North Atlantic and North Pacific subtropical gyres points to the energetic eddy fields of the western boundary currents of the Gulf Stream and Kuroshio Current, respectively, as being crucial agents of nutrient supply to the subtropical gyres. Intensified cross-frontal nutrient gradients and isopycnal diffusivities along these flanks support the vigorous stirring of nutrient-rich waters into the gyres (Gupta et al., 2022; Lee & Williams, 2000; Mackas et al., 1985; Olson, 1991; Yamamoto et al., 2018; Yu et al., 2019). Similarly, the intensification of eddy stirring-induced nutrient supply along the western-poleward flanks of the Indian Ocean and South Pacific subtropical gyres, which coincides with large isopycnal diffusivities, points to the energetic mesoscale eddy fields of the western boundary currents of the Agulhas Current and East Australian Current, respectively (Groeskamp et al., 2020; Yu et al., 2019), as playing important roles in sustaining supply. Absence of intensification of the eddy stirring nutrient supply along the western-poleward rim of the South Atlantic subtropical gyre suggests that its western boundary current, the Brazil Current, may play a less important role in sustaining nutrient levels than in the other subtropical gyres. This result may be explained by the weaker and shallower flow of the Brazil Current compared to other western boundary currents (da Silveira et al., 2020; Marsh & Seville, 2021), contributing to lack of nutrients and mesoscale eddy activity. In addition, our spatial extent of the oligotrophic region of the South Atlantic subtropical gyre may not encompass the mixing and nutrient characteristics of the Brazil Current, as this current extends southward of the oligotrophic subtropical region (Marsh & Seville, 2021). Our sensitivity analysis further supports this conclusion by showing that nutrient supply area integral estimates for the South Atlantic region are notably more sensitive to size of the oligotrophic region compared to other subtropical gyres. The noisiness in the eddy stirring-driven supply in these oligotrophic regions is similar to that of the eddy flux convergences over the North Pacific subtropical gyre in the model study by Gupta et al. (2022).

Our analysis also shows that eastern boundary upwelling regions are important in sustaining nutrient levels in the subtropical gyres (Gupta et al., 2022; Long et al., 2022). The nutrient supply to the winter mixed layer and/or the thermocline by mesoscale eddy stirring notably intensifies along the eastern flanks of all oligotrophic regions of the subtropical gyres. For the Atlantic subtropical gyres, this intensification is the result of elevated eastward nutrient gradients along their eastern flanks involving nutrient-rich waters in the Canary and Benguela coastal upwelling regions, respectively, to the east of the gyres (Fernández-Castro et al., 2019; Hutchings et al., 2009; Long et al., 2022; Marsh & Seville, 2021; Pelegrí & Peña-Izquierdo, 2015). Similarly, for the South Pacific subtropical gyre, where equatorward nutrient gradients strengthen toward the eastern rim, the intensification of eddy stirring supply may be explained by the upwelling of nutrients in the Peruvian upwelling region, found on the equatorial flank of the gyre's eastern rim. For the Indian Ocean subtropical gyre, where isopycnal diffusivity intensifies along the gyre's eastern flank relative to the gyre center, mesoscale eddies associated with the eastern boundary current of the Leeuwin Current (Morrow et al., 2003; Waite et al., 2007) may drive enhanced eddy stirring-induced nutrient supply. For the North Pacific subtropical gyre, although a patch of enhanced eddy stirring-induced supply is notable along the gyre's mid-eastern flank, isopycnal diffusivity and nutrient supply do not increase toward the eastern boundary current and coastal upwelling region (Marsh & Seville, 2021). As such, the gyre's eastern boundary processes may not be responsible for enhanced supply. The greater ocean basin width of the Pacific, relative to the Indian and Atlantic, may partly underpin this diminished role for eastern boundary upwelling.

Additional basin-specific physical processes may contribute to explaining the spatial patterns of nutrient supply over the subtropical gyres. First, the oxygen-poor, nutrient-rich shadow zone of the eastern tropical Atlantic may play a key role in setting up the steep northward nutrient gradients across the eastern portion of the North Atlantic subtropical gyre (Brandt et al., 2015; Karstensen et al., 2008). These strong gradients appear largely responsible for the substantial eddy stirring-driven supply of nutrients to the thermocline layer in the core and eastern parts of the gyre. Basin-specific processes appear important for the Indian Ocean, where its equatorward gyre flanks receive substantially more nutrients via eddy stirring than the other subtropical gyres. Unlike the Atlantic and Pacific Oceans, where easterly trade winds drive equatorial upwelling, the monsoon-dominated Indian Ocean has off-equator upwelling extending as far south as 15°S (Kang et al., 2021). This process may intensify the equatorward nutrient gradients and nutrient supply along the gyre's equatorward flank. Moving to the western-equatorward corner of the gyre, the vigorous mesoscale eddy field associated with the impingement of the westward South Equatorial Current onto Madagascar's east coast (Palastanga et al., 2006) may further enhance the eddy stirring-driven nutrient supply. Along the poleward flank of the Indian Ocean subtropical gyre, elevated nutrient supply by mesoscale eddies may be explained by the equatorward propagation of nutrient-rich waters from the Southern Ocean (Castro et al., 2022).

Our study reveals clear signals of the important role of mesoscale eddy stirring in sustaining thermocline nutrient levels in the oligotrophic regions of the subtropical gyres, and on the underlying oceanographic drivers of supply. The broad agreement between our estimates of diffusivity, nitrate, and nitrate fluxes and the field estimates of Spingys et al. (2021) supports the validity of using global climatologies to estimate nitrate fluxes and supply rates (Section 3.5; Figure S7 in Supporting Information S1). The greater disparity between climatological and field estimates for diffusivities, compared to nitrate, is expected given that: (a) diffusivities vary over several orders of magnitude, in contrast to much smaller variations in nitrate concentration; and (b) the climatological nutrient field is constrained by many decades of observations, providing a more robust representation of large-scale structure, whereas the global diffusivity data sets remain relatively recent, with more limited observational coverage to constrain uncertainties.

Nonetheless, notable uncertainties persist in these climatological data sets. Primarily, estimates of diapycnal nutrient supply are sparse over considerable portions of the subtropical gyres including the winter mixed layer due to missing K_{dia} estimates. For areas where K_{dia} is available, K_{dia} estimates also only consider internal wave-driven diapycnal mixing. As such, the roles of other diapycnal mixing processes, such as diapycnal diffusion by salt fingers and wintertime convective entrainment, which both supply significant nitrate to phytoplankton in the North Atlantic subtropical gyre (Fernández-Castro et al., 2015; Michaels et al., 1994), are not considered. Additionally, uncertainty in our nitrate supply estimates arise from uneven spatial and temporal coverage of the data used to estimate global climatological averages of K_{iso} , N , T , and S (Garcia et al., 2018; Groeskamp et al., 2020; Locarnini et al., 2018). To address this source of uncertainty, future work should seek to obtain

spatio-temporally concurrent nutrient measurements and direct estimates of mixing rates from key nutrient supply areas, such as those at gyre boundaries identified by our analysis.

In conclusion, the transport of nutrients along density surfaces by mesoscale eddies is important in replenishing the thermocline nutrient deficit in the oligotrophic parts of the subtropical gyres for four of the world's five subtropical gyres. This mechanism is thus significant for sustaining surface biological production and deep carbon export. The eddy-driven supply to the thermocline is consistently intensified along the subtropical gyre flanks, where a variety of physical ocean processes, most notably western boundary currents, generate steep nutrient gradients and vigorous eddies. The eddy-driven supply to the mixed layer is weaker than that to the thermocline, yet is expected to work with a host of other physical processes—including the diapycnal transfer by internal wave-driven mixing that we quantify, as well as deep winter mixing and time-dependent eddy and frontal circulations that we do not quantify—to replenish the euphotic layer with nutrients. Our analysis of climatological data sets over the global ocean supports the viewpoints of Spingys et al. (2021), where eddy stirring was found to replenish the thermocline in the center of the North Atlantic subtropical gyre, and Gupta et al. (2022), where an interplay between lateral and vertical transfers was found to sustain the biological productivity of the North Pacific subtropical gyre. Overall, our analysis supports the view that nutrient delivery to oligotrophic parts of the global subtropical gyres is underpinned by a “relay race” of multiple biological and physical processes in which mesoscale eddy stirring emerges as a key component.

Data Availability Statement

The data used in this study are publicly available. The WOA 2018 data are available at Garcia et al. (2018), Locarnini et al. (2018), Zweng et al. (2019). Global estimates of isopycnal diffusivity by Groeskamp et al. (2020) are available through Figshare at Groeskamp (2020). The Gibbs Seawater Oceanographic Toolbox can be found online at Jackett and McDougall (1997). The nutrient supply estimates and code used in this study are available through Zenodo at Oglethorpe (2025).

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