Diversity of Growth Rates Maximizes Phytoplankton Productivity in an Eddying Ocean

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Abstract In the subtropical gyres, phytoplankton rely on eddies for transporting nutrients from depth to the euphotic zone. But, what controls the rate of nutrient supply for new production? We show that vertical nutrient flux both depends on the vertical motion within the eddying flow and varies nonlinearly with the phytoplankton growth rate. Flux is maximized when the growth rate matches the inverse of the decorrelation timescale for vertical motion. Using a three-dimensional ocean model and a linear nutrient uptake model, we find that phytoplankton productivity is maximized for a growth rate of 1/3 day$^{-1}$, which corresponds to the timescale of submesoscale dynamics. Variability in the frequency of vertical motion across different physical features of the flow favors phytoplankton production with different growth rates. Such a growth-transport feedback can generate diversity in the phytoplankton community structure at submesoscales and higher net productivity in the presence of community diversity.

Plain Language Summary The productivity of phytoplankton is the result of a two-way coupling between the rate of phytoplankton growth and nutrient supply by physical mechanisms. A three-dimensional model of an oceanic eddy flow field maximizes its nutrient flux to the sunlit surface layer when the average phytoplankton growth rate is approximately 1/3 day$^{-1}$, which is consistent with observations. Different features of the flow field experience variable frequencies in the up/down motion and favor different phytoplankton growth rates to maximize new production, providing a way to generate diversity in the community composition of phytoplankton. Since changing the grid resolution of ocean models alters the vertical velocities, the biological growth rates also ought to be altered to represent the appropriate physical-biological coupling.

1. Introduction

The diverse community of phytoplankton and the heterotrophic ecosystem that it supplies affects the depth and efficacy of ocean primary production, as well as the cycling of carbon and other elements. Most of the world’s ocean is depleted of nutrients (oligotrophic) in the sunlit (euphotic) layer where nutrients are taken up by phytoplankton, but nutrient concentration increases with depth below the euphotic layer. In such regions, the production of phytoplankton relies on the physical transport of nutrient-enriched water from depth to the euphotic zone where light enables photosynthesis (McGillicuddy et al., 1998). Over long spatial and temporal scales, the system is balanced such that the rate of export of organic matter is determined by the rate of nutrient input that contributes to photosynthetic carbon fixation (Ducklow et al., 2001; Falkowski et al., 1998).

The upward transport of nutrient-rich water occurs via a range of mechanisms, including surface boundary layer-turbulence, wind-driven upwelling, coastal upwelling, eddy uplift, and frontal instabilities (Denman & Garrett, 1983; Lipschultz et al., 2002). In the pelagic ocean, the physical supply of nutrients induced by vertical advection associated with fronts and eddies (Jenkins & Goldman, 1985) is thought to limit the rate of new production, which is the rate of phytoplankton production fueled by a fresh supply of macronutrients from outside the euphotic layer. Vertical velocities are typically $10^{-3}$–$10^{-4}$ times smaller than the horizontal velocities associated with ocean currents and eddies on scales of 1–100 km. But, submesoscale dynamics, associated with strong vertical vorticity (of the order of the planetary vorticity $f$) can result in vertical velocities of $O(100)$ m/day on spatial scales $O(1)$ km. These rapid vertical motions are thought to be particularly influential for phytoplankton growth (Mahadevan, 2016).

Besides physical processes, the gradient in the mean nutrient distribution and the anomalies in concentration from the mean distribution also affect nutrient transport. Physical transport, as well as biological and chemical processes that create sinks (or sources) for nutrients, affect nutrient distribution. The spatial heterogeneity of...
reactive (biogeochemical) tracers in the ocean is dependent on the ratio of advection to reaction timescales, which is quantified with the Damköhler number, Da, a nondimensional parameter (Abraham, 1998; López et al., 2001; Mahadevan & Archer, 2000). This ratio controls the nonlinear relationship between reaction products and physical decorrelation timescales and affects the efficiency of transport (Mahadevan & Campbell, 2002; Pasquero et al., 2005; Prend et al., 2021; Smith et al., 2016). Transport is optimized when reaction and physical timescales are of the same order of magnitude \((Da = O(1))\).

Hence, the nutrient supply rate cannot be assessed from physics alone; it also depends on the rate of nutrient uptake by phytoplankton, which is closely related to the growth rate, a physiological characteristic that depends on the kind of phytoplankton, its size, the ambient temperature, light, and nutrient availability. Ocean ecosystems are highly heterogeneous with phytoplankton cell sizes and growth rates varying by orders of magnitude (Laws, 2013). This diversity of phytoplankton has a wide range of growth rates that are both affected by and affect the nutrient supply rate.

In this article, we begin by introducing a bio-physical model (Section 2) which we first analyze in a conceptual example to examine the interplay between nutrient flux and nutrient uptake by phytoplankton (Section 2.1). We then demonstrate that varying biological uptake rate affects the nutrient flux and spatial distribution of nutrient in a realistic ocean model (Section 2.2). We generalize the quantitative prediction of the nutrient flux dependence on vertical velocity and nutrient uptake on Lagrangian trajectories and evaluate the implications of this relationship for biogeochemistry and biodiversity (Section 3). We then discuss the implications of these findings for both modeling and observations (Section 4) before concluding (Section 5).

2. Nutrient Supply and Uptake

Oceanic biogeochemical tracers typically have a strong depth dependence, with relatively weak lateral variability. This is due to the dependence of phytoplankton growth on sunlight, and due to the ocean’s density stratification and the Earth’s rotation, which inhibit vertical movement of water. In the oligotrophic, subtropical oceans, the area- and time-averaged vertical profile of nutrient \(N(z)\) is depleted in the near-surface euphotic layer (upper 100 m), and has a strong vertical gradient (nutricline) in the region of strong density stratification (pycnocline) approximately between 100 and 500 m (Figure S1 in Supporting Information S1). The nutrient concentration is altered by advection and nutrient uptake (or resupply), which we model as a linearized resource-limited source/sink function \(f(N) = -\lambda(N - N_0(z))\) (Abraham, 1998; López et al., 2001). This function is a linearization of a nonlinear nutrient-phytoplankton model near carrying capacity (Text S2 in Supporting Information S1). See also Section 4 for more discussion of the limitations of a linear model. Our simple model for nutrient

\[
\frac{\partial N}{\partial t} + \nabla \cdot (uN) = -\lambda(N - N_0(z))
\]

accounts for transport by the ocean velocity field \(u = (u, v, w)\) and the uptake (and resupply) of nutrients (Mahadevan & Archer, 2000). It averages over several aspects of the ecosystem and the interactions of its components due to grazing, mortality, detritus production, and bacterial remineralization. Here, \(\lambda\) is the rate of uptake or resupply (per unit time). For practical purposes, we take \(\lambda\) to be depth-independent in our model and encode all the depth dependence in \(N_0(z)\), but in a general model, \(\lambda\) could vary in space and time, or be a function of temperature. By defining the nutrient anomaly \(N'(x,y,z,t) = N(x,y,z,t) - N_0(z)\) and taking the horizontal area-average, denoted by \(\langle \rangle\) of Equation 1, over a region with no large-scale horizontal gradients in \(N\), we are left with a balance between vertical transport and nutrient uptake or resupply, because the spatial average of the vertical velocity \(\langle w \rangle\) vanishes, \(\langle w \rangle = 0\) and \(\langle uw' \rangle = \langle vN' \rangle = 0\), such that

\[
(\partial_x N') + (\partial_z (wN')) = -\langle \lambda N' \rangle.
\]

Nutrient anomalies are generated by the vertical advection of nutrient and restored to the equilibrium profile at a rate \(\lambda\). Where \(N' > 0\), nutrient is consumed, as by the new production of phytoplankton. Where \(N' < 0\), nutrient is restored to its equilibrium profile, and the resupply represents remineralization. Time-averaged over a long period (several months) we expect a steady state in which the nutrient flux at the base of the euphotic layer \((z = -z_e)\) is balanced by the nutrient consumption above it \((\langle uw' \rangle)_{z_e} = -\int_{z_e}^0 \langle \lambda N' \rangle dz\). In a time- and area-averaged sense, the net uptake (resupply) is equivalent to the net community production (NCP), which over the long term, is balanced
Dependence of Flux on the Frequency of Vertical Velocity and Uptake Rate

The dependence of the nutrient flux on the covariance between $w$ and $N'$ can be demonstrated conceptually (Figure 1) by using an oscillating, sinusoidal vertical velocity $w = w_0 \sin(2\pi \tau t)$ with period $\tau$ and angular frequency $\omega = 2\pi \tau^{-1}$. When the uptake rate $\lambda \gg \tau^{-1}$ (fast uptake), the nutrient anomaly is in phase with the vertical velocity, but its magnitude is small because nutrients are consumed immediately (Figure 1b). Consequently, the magnitude of the flux is small. By contrast, when $\lambda \ll \tau^{-1}$ (slow uptake), nutrients remain unconsumed and the nutrient anomaly is large, but out of phase with the vertical velocity (Figure 1d). Because the nutrient anomaly and vertical velocity are out of phase, there are times of positive and negative flux, which, when averaged in time (and denoted by an overbar), results in a small net vertical flux $\bar{w}N'$. The net nutrient flux is maximized between those two extremes, when $\omega/\lambda = 1$ in this case, the nutrient anomalies have a larger magnitude relative to the fast growth case and a $45^\circ$ phase shift relative to the vertical velocity (Figure 1c). As a consequence, the net positive flux is maximal when averaged over a time period $\tau$ (Text S2 in Supporting Information S1).

Figure 1. (a) Phase and amplitude relationships on a water parcel advected by an idealized, oscillatory vertical velocity, with the nutrient anomaly ($N'$ in purple) and nutrient flux ($wN'$ in green (positive) and blue (negative)) over one time period $\tau$. (b–d) show $N'$ and $wN'$ for three different values of uptake rate $\lambda$. The time-integrated flux $\bar{w}N'$ is maximized when $\lambda = 2\pi \tau$ (c) as described in Section 2.1.
2.2. Nutrient Fluxes in an Oligotrophic Eddy Field

Vertical motions occurring on a wide range of spatial and temporal scales contribute to biological tracer fluxes, resulting in more complex patterns of eddy correlation than in a simple oscillatory flow field (Freilich & Mahadevan, 2019; Uchida et al., 2019; Yang et al., 2021). We use a nonhydrostatic numerical ocean model to examine the dependence of the vertical nutrient flux on the uptake rate \( \lambda \) in the fully developed, nonlinear oceanic regime. In such a flow field, we consider the characteristic timescale \( \tau \) of the vertical velocity to be the decorrelation timescale of Lagrangian water parcels as they move up and down across the nutricline. A three-dimensional (3-D), high-resolution (1 km horizontal and variable vertical resolution) numerical ocean model is used to simulate a midlatitude eddy field that is based on hydrography from the western North Atlantic subtropical gyre. The model is a periodic channel 256 km × 320 km in extent and 1 km deep. The developed flow field represents characteristics of the subtropical eddy field as described in Freilich and Mahadevan (2019). The strongest vertical velocities are at horizontal spatial scales of a few kilometers and occur on the edges of \( \sim 100 \) km scale mesoscale eddies (Figure 2a). We couple this physical model to the simplified nutrient model (Equation 1) and use a representative regional mean as the equilibrium nutrient profile \( N_0(z) \) with the nutricline centered at 115 m (Figure S10 in Supporting Information S1). The maximum new production in the model is centered at 115 m depth, the location of the maximum gradient in the nutrient profile. We vary the uptake rate \( \lambda \) between 0.005 and 50 day\(^{-1} \), which encompasses the observed range of phytoplankton growth rates in nutrient-limited midlatitude subtropical gyres (Laws, 2013).

On average, water parcels ascending through the nutricline into the euphotic zone will carry a positive nutrient anomaly compared to surrounding water, while those descending will be nutrient-depleted. When \( \lambda \gg \tau^{-1} \) (fast uptake), the nutrient anomaly is small (Figure 2b; \( \lambda = 1.5 \) day\(^{-1} \)) and in phase with \( w \) (Figure 2a). The vertical nutrient flux \( w'N' \) at a depth of 115 m (shown in blue-green shades above the cube in Figure 2b) is small, but positive everywhere, because upward (downward) velocity is correlated with positive (negative) nutrient anomaly. Conversely, for \( \lambda \ll \tau^{-1} \) (slow uptake), the nutrient anomaly is large (Figure 2c; \( \lambda = 0.015 \) day\(^{-1} \)) and spatially decorrelated with \( w \) (Figure 2a), resulting in a filamentous distribution of the nutrient as unconsumed nutrient is stirred by the flow. In this case, the vertical flux of nutrient (shown in blue-green shades in Figure 2c) has large values due to the relatively large nutrient anomalies being advected vertically, but the vertical flux is both positive and negative. A negative (downward) flux of nutrient occurs when a positive nutrient anomaly is advected.

Figure 2. Snapshots of vertical velocity, nutrient anomaly, and vertical nutrient fluxes on model day 135. (a) Vertical velocity at \( z = -117 \) m. (b, c) Lower cube is nutrient anomaly, the upper panel is the vertical nutrient flux at \( z = -117 \) m with uptake rates (b) \( \lambda = 0.015 \) day\(^{-1} \) and (c) \( \lambda = 1.5 \) day\(^{-1} \). Black contours are density.
downward before it can be taken up by the slowly growing phytoplankton, or a negative nutrient anomaly is transported upward before it is equilibrated to \( N_0(z) \). The net flux integrated over the domain is small, as the positive and negative nutrient fluxes cancel each other. The two cases (Figures 2b and 2c) have a similar net nutrient flux: in one case the local fluxes are small, and in the other, the fluxes are bi-directional and cancel out. The maximum net nutrient flux is achieved (but not shown in the figure) for a value of \( \lambda \) that is intermediate between Figures 2b and 2c.

The spatial distribution of the fluxes depends on the nutrient uptake timescale (Figure S8 in Supporting Information S1). With a slow uptake rate (\( \lambda \ll r^{-1} \)), the spatial distribution of the nutrient anomaly is heavily influenced by stirring in the horizontal and the cascade to small scales driven by lateral stirring (Abraham, 1998). With a fast uptake rate (\( \lambda \gg r^{-1} \)), the nutrient anomaly is present at small spatial scales because the vertical velocity, especially the high frequency component of the vertical velocity, has relatively more small scale variability than the horizontal velocity (Freilich & Mahadevan, 2021; Mahadevan & Campbell, 2002).

3. Lagrangian Description of Nutrient Flux

In a nonlinear, eddying oceanic flow field, each water parcel has a unique trajectory. As a water parcel moves upward and downward by 1–100 m on timescales of days, it simultaneously moves 1–100 km horizontally. We isolate the effect of vertical motion in our 3-D flow field by following water parcels in the Lagrangian frame while tracking their nutrient concentration and nutrient flux by solving \( \frac{dN}{dt} = -\lambda N \) according to Equation 1 on each water parcel trajectory. We examine 14 different values of \( \lambda \) in the range 0.005–50 day\(^{-1} \). The time-integrated vertical nutrient flux \( wN^\tau \) along water parcel trajectories is calculated over 30 days as water parcels move up and down through the nutricline.

3.1. Theoretical Dependence of Flux on Biological Rate

Theoretically, we can estimate the time-averaged flux \( \bar{wN}^\tau \) from \( \frac{\partial N'}{\partial t} + w \frac{\partial}{\partial z}(N_0(z) + N') = -\lambda N' \), if we assume that the mean free path of water mass trajectories, meaning the average magnitude of depth variation, is small relative to variations in the slope of the background nutrient concentration \( \frac{\partial N_0}{\partial z} \). This assumption may introduce errors in some situations, but is valid near equilibrium and for small amplitude perturbations (Text S2 in Supporting Information S1). We solve for the nutrient anomaly \( N' \) using the integrating factor method (see Text S2 in Supporting Information S1 for details). The vertical flux of nutrient (time averaged over time \( t \)) is the covariance between the nutrient anomaly and vertical velocity along a given trajectory. It is given by the auto-covariance of \( w \) weighted by \( \lambda \) as

\[
\overline{wN'} = \frac{dN_0}{dz} \int_0^t e^{-\lambda(t-s)} w(s) \nu(t) ds. \tag{3}
\]

Vertical motion transports nutrient due to the gradient \( dN_0/dz \) and creates an anomaly in nutrient concentration, which contains a memory of vertical motion for the uptake time (\( \lambda^{-1} \)) (Flierl & McGillicuddy, 2002). The vertical velocity auto-covariance matters for a longer period of time for smaller (as compared to larger) values of \( \lambda \).

3.2. Vertical Velocity Characteristics and Biophysical Fluxes

For each model trajectory, we identify the value of \( \lambda \) that maximizes the flux \( \bar{wN}^\tau \). We denote this value as \( \lambda_0 \).

Each water parcel trajectory has a full spectrum of vertical velocity frequencies, but the relative contribution of different vertical velocity frequencies is variable across the domain. The Lagrangian frequency spectrum (Figure 3a) averaged over all those trajectories on which nutrient flux is maximized for \( \lambda = 0.075 \text{ day}^{-1} \) (slow uptake) has more power at low frequencies, as compared to the frequency spectrum of trajectories on which nutrient flux is maximized for \( \lambda = 0.75 \text{ day}^{-1} \) (fast uptake). All trajectories have a peak at the inertial frequency, but the near-inertial oscillations contribute relatively little to the vertical fluxes (Figure S8 in Supporting Information S1).

When we average across all water parcel trajectories in the 3-D model, we obtain a maximum in the average Lagrangian nutrient flux as a function of the uptake rate \( \lambda \) (Figure 3c, orange curve), despite the wide range in the shapes of the vertical kinetic energy spectra of the Lagrangian time series (e.g., Figure 3a). The uniform uptake rate that on average maximizes the time-averaged flux in the 3-D model is 1/3 day\(^{-1} \) (peak of the histogram in
Figure 3b). A timescale of 3 days is shorter than the turnover timescale of mesoscale eddies in the subtropical gyres and corresponds to length scales of $O(10 \text{ km})$ in the vertical kinetic energy (Figure S8a in Supporting Information S1). This falls in the range of subinertial submesoscale dynamics (Callies et al., 2020; Cao et al., 2021; McWilliams, 2016; Torres et al., 2018).

As a comparison, we calculate the along-trajectory nutrient flux on the full suite of water parcel trajectories (Equation 3), which is based on the vertical velocity autocovariance. For any given $\lambda$, the range in the nutrient flux on the different individual trajectories is due to the difference in the vertical velocity frequency characteristics on those trajectories. Along each trajectory, the theoretical expectation of the flux and the flux obtained from the 3-D model are consistent (Figure 3c, Figure S2 in Supporting Information S1).

In the absence of biological uptake, the eddy-driven nutrient flux is given by Equation 3 with $\lambda = 0$ and can be expressed as a diffusive flux according to to Taylor (1921) (indicated in Figure 3c by the gray bar). On average, biological uptake at the rate $\lambda = 1/3 \text{ day}^{-1}$ results in an enhancement of the vertical nutrient flux to three times the flux with no biological uptake. If the community has a uniform uptake rate of 0.3 day$^{-1}$, the median flux is 0.177 $\mu$mol m$^{-2}$ day$^{-1}$. However, the extreme values of the flux are even larger. If the rate is such that it maximizes the flux locally on each trajectory (Figure 4), the median flux is 0.193 $\mu$mol m$^{-2}$ day$^{-1}$, which is 10% higher than with uniform $\lambda$.

The biological rate that maximizes the flux depends on the local dynamics (Figure 3a). In different regions and with different model resolution, we would expect these principles to hold but to be quantitatively different.

A spatial distribution of $\lambda_0$ plotted at the origin of each trajectory (Figure 4) shows variability that corresponds with the physical features of the flow field. The nutrient flux is maximized by small $\lambda$ (slow uptake) on Lagrangian trajectories that originate in relatively stable regions of the flow, while large values of $\lambda$ (fast uptake) maximize the nutrient flux on trajectories that are in unstable regions or where eddies interact. The process described here is a mechanism for coexistence of distinct biological communities over short spatial scales due to differential growth that is attributable to small scale variability in the vertical velocity (Perruche et al., 2011). This mechanism differs from lateral stirring of distinct phytoplankton communities, which also results in finescale spatial variability of the community composition (d’Ovidio et al., 2010; Lévy et al., 2015).
4. Discussion

Observations show that fronts and eddies affect the rate of primary production and the community composition (Letelier et al., 2000; McGillicuddy, 2016; Rodriguez et al., 2001; Sakamoto et al., 2004; White et al., 2007). At global scales, phytoplankton community structure has also been observed to depend on local rates of resource supply (Marañón, 2015). At a long-term oceanographic timescale series in the subtropical North Pacific, Station Aloha, there is a six-fold variation in the growth rate in the eukyotic zone (Figure 5). However, primary production is not linearly correlated with mesoscale eddy variability (Barone et al., 2019; Ferrón et al., 2021). We observe that the average covariance of nutrient anomalies at the base of the euphotic zone and the carbon specific growth rate (Equation 2) over the 30 year record has a non-linear dependence on the growth rate. This correspondence with our theoretical prediction suggests that physical processes exert a strong control on the overall nutrient flux and that vertical motions with mesoscale timescales contribute the largest integrated nutrient fluxes. It is notable that a similar biological uptake rate that results in the maximum flux in our 3-D model of a subtropical eddy field emerges as the rate with the maximum estimated phytoplankton new production in the North Pacific subtropical gyre. This rate, $\lambda \approx 0.3$ day$^{-1}$, is also approximately the average growth rate in the North Atlantic subtropical gyre (Goericke & Welschmeyer, 1998). It is tempting to think that the growth rates of phytoplankton in the ocean are evolved to match the physical rates of supply.

This theoretical framework that rigorously defines the relationship between vertical transport characteristics and the biological rate helps to resolve long-standing uncertainties in the role of physical processes on biogeochemical fluxes (Gruber et al., 2011; Liu & Levine, 2021). Though several numerical modeling studies (Mahadevan & Archer, 2000) have reported an enhancement in phytoplankton productivity with an increase in vertical velocity, some observational and modeling studies (Gruber et al., 2011; Hernández-Carrasco et al., 2014) have also reported a reduction in productivity due to the export of unconsumed nutrient as in Figure 2c. The inter-relatedness of the phytoplankton uptake rate, nutrient anomaly, vertical velocity and nutrient supply shown in this model system is applicable to other biogeochemical properties and biological processes such as ocean carbon uptake (Kwon et al., 2009; Mignone et al., 2006), light-limited primary production in the surface mixed layer (Dusenberry et al., 2000; Taylor & Ferrari, 2011), and the distribution of oxygen, pollutants, and trace elements.

The model used here neglects the complexity of biological interactions, which are nonlinear and involve multiple timescales. Behaviors such as luxury nutrient uptake among diatoms can also decouple productivity from nutrient uptake. In the case of nonlinear reactions, the theory outlined here will still apply, but analytic solutions are less tractable. In general with a nonlinear biological function $f(N)$ in Equation 1 the magnitude of the biogeochemical anomaly itself will depend nonlinearly on the biological rate and the timescale may be determined by nonlinear processes such as ecologically driven oscillations (Franks, 2001; Neufeld, 2012). Vertical fluxes may also be affected by vertical variations of both biological rates and the vertical velocity magnitude (Kahru, 1983). In a multi-species system, cross-correlations between components will be a source of spatial and temporal variance (Abraham, 1998; Falkowski et al., 1998; Martin & Pondaven, 2003; Morison et al., 2020). Future work could address the implications of the dependence of flux on biological rate for changes in community composition at the submesoscale while keeping in mind that variations in community composition may also be a result of ecological interactions, but may not alter the NCP (Giovannoni & Vergin, 2012; Malone et al., 1993).

A practical implication of this work for modeling studies is the need to give equal importance to resolving and accommodating for similar timescales in both the physics and biology. Studies that compare the effect of enhanced

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**Figure 4.** (a) Uptake rate that maximizes the nutrient flux for each trajectory plotted at the trajectory origin location. (b) Nutrient flux at the uptake rate that maximizes the flux. The dark green points (saturated at the large end of the color scale) are excluded from the analysis in Figure 3 because they leave the nutricline. The contours are density with the dashed contours being lighter densities.
submesoscale dynamics at finer model resolutions on primary productivity while holding the biological rates constant may find that the nutrient flux and biological productivity are sensitive to the biological timescales that are selected due to alterations in the mean nutrient gradient (Balwada et al., 2018; Lévy et al., 2012; Resplandy et al., 2019). If the vertical motions with timescales on the order of the biological timescales are underrepresented, then there may be a mismatch between the biological and physical processes. The biological rate ($\lambda_0$) that maximizes the biogeochemical flux is dependent on the flow field (which is model resolution dependent). This means that both a smaller and larger rate than $\lambda_0$ could generate the same flux, but result in very different behaviors. Furthermore, the change of flux in response to resolving vertical velocities at higher wavenumber and frequency could differ in sign (either increase or decrease). Hence, knowing whether the model's biological rate is less or more than $\lambda_0$ is helpful in interpreting the model results. Moreover, the fine-scale structure that we find in the optimal community-level growth rate ($\lambda_0$) suggests that resolving a diversity of phytoplankton may be advantageous for improving model estimates of biogeochemical fluxes.

There is not a clear separation between the mesoscale and submesoscale, but rather a continuum in which the integral timescale of the vertical velocity is affected by eddies. Nonetheless, the biological uptake timescale that maximizes the nutrient flux in our model is within the range of timescales of up- and down-ward motion associated with sub-inertial submesoscale dynamics, corroborating the importance of its contribution for nutrient supply. Mesoscale and submesoscale fluxes are often parameterized as a turbulent diffusion in global models. However, because the timescale of the diffusion feeds back on the nutrient gradient, the biological rate affects the eddy diffusivity coefficient and a diffusive parameterization may not appropriately represent the fluxes, especially when the physical and biological timescales are similar (Smith et al., 2016). As a consequence, nutrient fluxes and NCP may be underestimated if submesoscale features are not included and the projected changes in ocean biogeochemical cycles may be highly sensitive to the relationship between the biological and physical models (Brett et al., 2021; Löptien & Dietze, 2019). The estimation of a Lagrangian flux as suggested here may aid both analysis and parameterization (Plumb, 1979). Better understanding of the frequency characteristics of

Figure 5. (a) Histogram of carbon-specific growth rate estimated from primary production and cell counts at the Hawaii Ocean Time-series station ALOHA. (b) Temporal average of biological nutrient flux at 120 m as a function of the carbon specific growth rate at 120 m.
submesoscale dynamics (Callies et al., 2020; Torres et al., 2018) could improve diagnosis of biogeochemical fluxes and ecological community composition.

5. Conclusions

The vertical flux of nutrients is modulated by the coupling between phytoplankton growth rate (nutrient uptake rate) and the frequency (inverse of decorrelation time) of the vertical velocity of water parcels moving up and down through the nutrient line. Even linear biological reactions result in a nonlinear dependence of the nutrient flux on the uptake rate $\lambda$, with the maximum flux in a three-dimensional oceanic eddy field for $\lambda = 1/3$ day$^{-1}$ when $\lambda$ is uniform, and an even higher maximum if $\lambda$ varies across water parcels. At the same time, the vertical flux influences the growth and distribution of phytoplankton. The variability in the spectral characteristics of different water parcel trajectories implies that a range of phytoplankton growth rates is favored to maximize the rate of nutrient supply and new production in an oceanic eddy field. This mechanism of bio-physical coupling supports variability in the structuring of phytoplankton communities on meso- and submeso-scales.

Data Availability Statement

The model code for the flow fields and offline tracer advection and reaction is available at http://doi.org/10.5281/zenodo.5799693. Offline particle tracking was performed using the code available at http://doi.org/10.5281/zenodo.3902282. Particle trajectories analyzed in this manuscript are available at http://doi.org/10.5281/zenodo.5800100. Data was obtained from HOT-DOGS application (National Science Foundation Award #175617); University of Hawai‘i at Mānoa.

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