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Resource limitation determines temperature response of unicellular plankton communities

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A warmer ocean will change plankton physiological rates, alter plankton community composition, and in turn affect ecosystem functions, such as primary production, recycling, and carbon export. To predict how temperature changes affect plankton community dynamics and function, we developed a mechanistic trait-based model of unicellular plankton (auto-hetero-mixotrophic protists and bacteria). Temperature dependencies are specifically implemented on cellular process rather than at the species level. Since the uptake of resources and metabolic processes have different temperature dependencies, changes in the thermal environment will favour organisms with different investments in processes such as photosynthesis and biosynthesis. The precise level of investments, however, is conditional on the limiting process and is ultimately determined dynamically by competition and predation within the emergent community of the water column. We show how an increase in temperature can intensify nutrient limitation by altering organisms’ interactions, and reduce relative cell-size in the community. Further, we anticipate that a combination of temperature and resource limitation reduces ecosystem efficiency at capturing carbon due to strengthening of the microbial loop. By explicitly representing the effects of temperature on traits responsible for growth, we demonstrate how changes on the individual level can be scaled up to trends at the ecosystem level, helping to discern direct from indirect effects of temperature on natural plankton communities.
INTRODUCTION

Climate change is expected to alter the functioning of marine microbial communities and associated ecosystem processes, such as primary production, trophic transfer to higher trophic levels, and carbon sequestration. The impacts occur through changes in the physical environment and through the direct effect of temperature on physiological processes within the cell. Until recently, the focus has been on how changes in the physical environment alter the resource availability for plankton (Doney 2006). For example, rising global temperatures can lead to a stronger stratification of the water column, limiting the mixing of nutrients into the photic zone (Behrenfeld et al. 2006). Conversely, sea ice thawing can increase light availability, triggering blooms earlier in the year and prolonging its duration (Kahru et al. 2011). Taken together, the changes in ecosystem function are the result of a delicate balance between positive and negative effects driven by changes in the physical environment.

Despite temperature being the key component of global change, attention has only recently turned to the direct effects of temperature on individual plankton cells and associated ecosystem processes (Allen et al. 2005; López-Urrutia and Morán 2007; Toseland et al. 2013; Edwards et al. 2016; Thomas et al. 2017; Sommer et al. 2017). Temperature affects most metabolic processes by accelerating enzyme activity (Eppley 1972; Raven and Geider 1988). Cellular processes such as biosynthetic and respiration rates tend to double with a temperature increase of 10 degrees ($Q_{10} \approx 2$), also leading to an increase of the maximum potential growth rate with temperature with a $Q_{10} \approx 2$ (Eppley 1972). Yet, in nature, growth tends to be restricted not only by metabolic functions, but also by the availability of resources (Clarke 2003; Marañón et al. 2018; Morán et al. 2018). Therefore, the temperature dependence of resource uptake rates also matters (Shuter 1979). For example, the affinity for light (slope of the photosynthetic rate at low light levels) is fairly insensitive to temperature, and mainly depends on the concentration of chlorophyll and chloroplasts (Raven and Geider 1988). Hence, in light-limited environments, growth will be almost independent of temperature. Uptake of dissolved compounds, e.g. nutrients or dissolved organic matter, is limited by the diffusive rate (Munk and Riley 1952; Kiørboe 2008); therefore, the response
to temperature in nutrient-limited environments would be controlled by the scaling of diffusivity, which is weak, and not by enzymatic activity. Taken together, the temperature response of a cell could vary between being neutral (no change) to varying a factor 2 over a 10 degree change, depending upon whether growth is limited by light, resource uptake, or biosynthesis.

However, the response of a community not only depends on the cellular-level response, but also on how the community composition changes. Species have adapted their physiology to maximize growth in a given environment, resulting in a left skewed unimodal curve (reaction norm), which peaks at the optimal temperature (Thomas et al. 2012). This curve has been shown to vary according to the level of resources (Thomas et al. 2017), due to a balance between protein investments into various functions, with a steep drop at high temperature as increasing investment in chaperones to assist protein folding limits growth (Chen and Laws 2017). On the other hand, species are able to modify their optimal temperature through adaptations, where an increase in the photosynthetic capacity of cells has been observed in warmer conditions (Schaum et al. 2017). The community response to a temperature change emerges when the curves from all species are added. Therefore, when a resource is limiting, the growth rate of the overall community might stay the same, but the community composition can change due to the different temperature optima of each species (see Edwards et al. 2016 for a good example). Therefore, an understanding of the community level temperature responses must account for the changes in the community composition, as new winners can emerge under changed temperature conditions (Dutkiewicz et al. 2013).

To assess how the direct effects of temperature alter the fitness of individual cells, and potentially scale to ecosystem processes, we developed a trait-based model of the plankton community. A cell is described by two traits: its size and its investments in phototrophy vs. biomass synthesis (biosynthesis). All processes in the model are affected by temperature: light harvesting, resource uptake, predation, and metabolism; however, the emergent population-level temperature response depends on which processes are limiting. The trait-based formulation makes it possible to reduce model complexity dramatically while at the same time resolving the adaptive nature of the plankton community under changing temperatures. We use the model to address the question of how...
community structure and function changes with temperature. We focus on three central aspects of ecosystem function: primary production (the amount of carbon fixed), carbon flow towards higher trophic levels, and export to depth and dissolved pathways (such as refractory dissolved organic matter, rDOM). The exploration is done by embedding the cell-model into a physical 1-D water column model.

**METHODS**

We consider a minimal food-web model of marine unicellular organisms that represents heterotrophic bacteria, and mixotrophic flagellates and/or ciliates. The cell model is later embedded in a planktonic bio-geochemical food-web framework. In the following we first describe the biological compartments (generalists and bacteria), then the temperature scaling of vital rates, and finally the planktonic food-web and the coupling to the physical environment.

**Generalists**

The cell model has a simple physiology which captures the main processes for uptake of resources, biosynthetic rate, and respiration. How temperature affects each process is introduced further down. A cell can acquire carbon by phototrophy, nitrogen by diffusive uptake, and a mix of nitrogen and carbon by phagotrophy (Fig. 1). Cells have three functional compartments: photosynthetic machinery, biosynthetic machinery, and structural material, into which the cell invests various proportions of its carbon mass. The photosynthetic mass (e.g. chloroplasts and pigments) fixes carbon. Biosynthetic mass (e.g. mitochondria and ribosomes), converts fixed carbon to functional cellular material. Finally, structural mass is associated with those structures essential for the cell integrity, such as cell walls and membranes, but that are not directly responsible for cell growth. It is assumed that cells do not have a storage compartment, such that they grow directly in pace with the uptake of resources and the activity of the biosynthetic apparatus. Finally, for simplicity, cells have a fixed C:N ratio.

Total mass of the cell $V$ ($\mu$gC cell$^{-1}$) is divided between structural mass, photosynthetic machinery $\phi_L V$ ($\mu$gC cell$^{-1}$) and biosynthetic machinery $\phi_B V$ ($\mu$gC cell$^{-1}$). We assume that cells invest half of the acquired mass on structure, and the rest of acquired mass can be invested
either in the photosynthetic or biosynthetic apparatus (fig. 1), with the consequent trade-off that $\phi_L + \phi_B = 1/2$. Hence, total mass of a cell becomes $V = V(\phi_L + \phi_B + 1/2)$, allowing the resource uptake strategy of a cell to be described by a single trait, $\phi_L = \phi_B - 1/2$.

Uptake rates of resources – light, nutrients, and food – and biosynthesis are represented by Monod kinetics (Monod 1949). Carbon fixation $J_L$ ($\mu$gC d$^{-1}$) inside a cell is:

$$J_L = M \frac{A_L L}{A_L L + M},$$

where $L$ is irradiance (W m$^{-2}$), $A_L$ is affinity for light ($\mu$gC d$^{-1}$ (W m$^{-2}$)$^{-1}$) which depends on the investments, and $M$ is the maximum biosynthetic rate ($\mu$gC d$^{-1}$ cell$^{-1}$). All fluxes $J$ are per cell, and thus given in units of $\mu$gC d$^{-1}$ cell$^{-1}$.

The affinity for light absorption depends on the investment in the photosynthetic apparatus $\phi_L$. However, absorption is also limited by the cell surface area, proportional to $V^{2/3}$. Considering both effects, the affinity for light becomes (Chakraborty et al. 2017):

$$A_L = c_L V^{2/3} \frac{a_L \phi_L V}{a_L \phi_L V + c_L V^{2/3}},$$

where $c_L$ is the maximum photosynthetic affinity ($\mu$gC d$^{-1}$ (W m$^{-2}$)$^{-1}$), and $a_L$ the affinity per investment in photosynthesis ($\mu$gC d$^{-1}$ (W m$^{-2}$)$^{-1}$ ($\mu$gC$^{2/3}$)$^{-1}$). At very high investments or under optimal light levels, the affinity is dominated by the first term of the right hand side, i.e., proportional to $V^{2/3}$, while at low investment the affinity is proportional to cell volume $V$.

Nitrogen uptake ($J_N$) by a cell is:

$$J_N = M \frac{Q_{C:N} A_N N}{Q_{C:N} A_N N + M},$$

where $N$ is dissolved nitrogen ($\mu$gN L$^{-1}$), and $A_N$ nitrogen affinity (L d$^{-1}$ cell$^{-1}$). $J_N$ is in units of carbon whereas $N$ in nitrogen; the conversion is implemented through the fixed C:N ratio $Q_{C:N}$ ($\mu$gC $\mu$gN$^{-1}$). Nutrient uptake is considered diffusion-limited, scaling with the radius of the cell.
rather than by the surface area (Munk and Riley 1952). Hence, affinity for nutrients becomes:

\[ A_N = \alpha_N V^{1/3}, \]  

(4)

where \(\alpha_N\) is nutrient affinity per biomass (L d\(^{-1}\) (\(\mu\)gC\(^{1/3}\))\(^{-1}\)).

Food uptake \(J_F\), that is, consumption of prey with concentration \(F\) (\(\mu\)gC L\(^{-1}\)) is:

\[ J_F = M \frac{A_F F}{A_F F + M}. \]  

(5)

In the model, a large generalist \((G_2)\) can eat a smaller generalist \((G_1)\), which at its turn, \(G_1\) can predate on bacteria \((B)\).

The clearance rate of active prey encounter scales in average linearly with cell volume (Kiørboe 2011), and so affinity \(A_F\) (L d\(^{-1}\) cell\(^{-1}\)):

\[ A_F = \alpha_F V, \]  

(6)

where \(\alpha_F\) is the specific affinity for food (L d\(^{-1}\) (\(\mu\)gC\(^{-1}\))\(^{-1}\)).

The maximum uptake rate of each process is determined by the maximum biomass synthesis rate, which is proportional to the mass of the biosynthetic apparatus:

\[ M = \mu_{max} \phi_B V, \]  

(7)

where \(\mu_{max}\) is the specific maximum biosynthesis rate per investment (d\(^{-1}\)).

Respiration rate associated with cell maintenance are assumed to be the same for all machinery, and approximately scale with body mass (Kiørboe and Hirst 2014):

\[ J_R = k V. \]  

(8)

where \(k\) is the maintenance cost (d\(^{-1}\)).
Since growth requires both carbon and nutrients, Liebig’s law of the minimum is applied. The total carbon flux is then:

\[ J_{\text{tot}} = \min [J_L + J_F - J_R, \ J_N + J_F]. \] (9)

Note that the nutrient flux is measured in units of carbon through the assumption of a fixed C:N ratio, which is implemented in equation 3. Finally, the carbon-specific population division rate \( \mu \) (d\(^{-1}\)) is defined by the increase in mass:

\[ \mu = \frac{J_{\text{tot}}}{V}. \] (10)

Leakage of either carbon or nitrogen occurs when these are in excess inside the cell. Therefore, the leakage of carbon is:

\[ J_{\text{Cleak}} = \max [0, \ J_L - J_R - J_N] \] (11)

and the leakage of N is the inverse of the carbon leakage:

\[ J_{\text{NLeak}} = \max [0, \ -J_L + J_R + J_N]. \] (12)

**Temperature dependencies**

We consider temperature dependencies on: carbon fixation, diffusive uptake, respiration, and biosynthetic processes. All dependencies are described by multiplying the processes with a \( Q_{10} \) factor, and therefore the rate \( R \) at a given temperature \( T \) becomes:

\[ R = R_{\text{ref}} Q_{10}^{(T-T_{\text{ref}})/10}. \] (13)

The reference rate \( R_{\text{ref}} \) is defined as the rate at temperature \( T_{\text{ref}} = 18^\circ \text{C} \) (table 1) and the value of \( Q_{10} \) represents the factorial increase when the temperature is increased by 10\(^\circ\)C. We use the \( Q_{10} \) factor to describe temperature dependencies as this factor is much more intuitive than the Arrhenius equation and the corresponding activation energy. When \( Q_{10} = 1 \) there is no change
with temperature; \( Q_{10} > 1 \) is an increase of a rate with temperature; and the opposite effect for \( Q_{10} < 1 \). Recall that here we focus on the response of the overall community, which is the upper envelope of the temperature response of all species together (Eppley 1972; Edwards et al. 2016). Therefore, the shape of the community curve is not unimodal (as the species-specific response) but exponential within the range of temperatures where biological rates are functional. Carbon fixation at low light levels is temperature independent (Raven and Geider 1988; Clarke 2017), therefore we use a \( Q_{10} = 1 \) for the light affinity \( \alpha_L \) (table 1). The temperature dependency of nutrient affinity is governed by the temperature scaling of molecular diffusivity, which is proportional to viscosity. The viscosity of sea water doubles over a 20°C temperature increase from 2°C to 22°C, implying that diffusivity has \( Q_{10} = 1.5 \) approximately (Jumars et al. 1993; Thingstad and Aksnes 2018). Active encounters with prey are described by the clearance rate (Andersen et al. 2016). The clearance rate has a complicated response to temperature as it depends on the physical environment and the motility of the organisms. Consequently, the response might vary depending on whether the prey, the predator, or both are motile. Assuming the latter case, we could consider that encounter rates increase, but also escape rates increase, with the approximate result that both effects cancel one another. In the absence of an empirically justified temperature scaling we assume a \( Q_{10} = 1 \). Respiration and maximum potential growth rate scale with a \( Q_{10} \) close to 2 (Eppley 1972; Clarke 2003). Under resource limitation, all the temperature scalings are below 2 because respiration has a \( Q_{10} \) of 2. Since the \( Q_{10} \) of respiration is larger than any resource limited uptake process, the growth efficiency of a cell (anabolic processes – catabolic processes) decreases when resources are limiting (López-Urrutia and Morán 2007).

**Bacteria**

Bacteria are similar to the generalists, but they are smaller and they do not photosynthesize or engage in phagotrophy. Instead, they acquire \( N \) and dissolved organic carbon (DOC) by diffusive uptake, and so the functional responses for these resources are the same form as for nutrients in the generalist model (Eq. 3), with different affinity values for \( DOC \) (Table 1). Additionally, we assume that bacteria are able to hydrolyze particulate organic matter (POM), which is then transferred to
the dissolved N and C pools. POM hydrolysis is represented by a saturating response (Anderson and Williams 1998a):

\[ J_{\text{POM}} = \mu_{\text{POM}} \frac{\alpha_{\text{POM}} P}{\alpha_{\text{POM}} P + \mu_{\text{POM}}} \] (14)

where \( P \) is the concentration of POM, \( \mu_{\text{POM}} \) is the maximum specific hydrolysis rate of POM (\( \mu_{\text{gC}} \text{d}^{-1} \text{cell}^{-1} \)), and \( \alpha_{\text{POM}} \) the initial slope of the functional response for hydrolysis (L d\(^{-1}\) cell\(^{-1}\)). The flux of the limiting resource determines the total biomass synthesis rate:

\[ J_{\text{tot}} = \min(J_{\text{DOC}} - J_R, J_N). \] (15)

The specific division rate of the population is the same as in equation 10, and leakage of C and N as equations 11 and 12 replacing \( J_L \) by \( J_{\text{DOC}} \).

**Microbial community model**

The generalist model is embedded in a bio-geochemical food-web with six main compartments (Fig. 2): bacteria (\( B \)), small generalist (\( G_1 \)), large generalist (\( G_2 \)), nitrogen (\( N \)) including both organic and inorganic, dissolved organic carbon (\( D \)) and particulate organic matter (\( P \)), the latter including both nitrogen and carbon. Parameters and variables are listed in table 1. The key structural elements are the two generalist groups. To allow adaptation of the composition and function of the generalists we describe them as a system of infinite diversity (SID, Bruggeman and Kooijman 2007), i.e., as a distribution of biomass along the trait-axis \( \phi_L \).

The currency of the model is \( \mu_{\text{gC}} \text{L}^{-1} \), with the exception of the nitrogen pool which is given in \( \mu_{\text{gN}} \text{L}^{-1} \), hence the conversion factor \( Q_{\text{C:N}} \) in the corresponding equations. Pools containing both carbon and nitrogen possess the same stoichiometry, \( Q_{\text{C:N}} \). All organisms take nutrients from the \( N \) pool, bacteria also rely on DOC and hydrolyse POM, which goes to the DOC pool and to nutrients. Generalists perform both photosynthesis and phagotrophy: small generalists eat bacteria (\( J_{F_1} \)), and large generalists eat small generalists (\( J_{F_2} \)). Natural mortality (\( \gamma \)) is represented by a quadratic term, allowing to impose a control when concentrations are too high. In the natural environment such could represent viral lysis when prey density is high. Still the value of \( \gamma \) was
taken small enough as not to rule model dynamics. A fraction $\delta$ of dead matter goes to the dissolved pools, and $(1 - \delta)$ to the POM pool. Excess carbon and nitrogen in the cells is leaked ($J_{C, \text{leak}}$ and $J_{N, \text{leak}}$ respectively), going to the corresponding dissolved pools. We assume that dead material from bacteria is recalcitrant dissolved organic matter, rDOM (Jiao et al. 2010), which is removed from the system due to its low turnover rate. The modelled system, its compartments, and fluxes, are illustrated in figure (2), and the governing equations are:

$$\frac{dG_{1,i}}{dt} = \mu_{1,i} G_{1,i} - \gamma G_{1,i}^2 - \frac{G_{1,i}}{\sum_{i=1}^{n} G_{1,i}} \left( \sum_{j=1}^{n} \frac{J_{F2,j}}{V_2} G_{2,j} \right)$$

$$\frac{dG_{2,i}}{dt} = \mu_{2,i} G_{2,i} - \gamma G_{2,i}^2 - m_{\text{htl}} G_{2,i}$$

$$\frac{dB}{dt} = \mu_B B - \gamma B^2 - \frac{\sum_{i=1}^{n} J_{F1,i} G_{1,i}}{V_1}$$

$$\frac{dN}{dt} = \frac{1}{Q_{\text{CN}}} \left( - \sum_{i=1}^{n} \left( \frac{J_{N1,i}}{V_1} G_{1,i} + \frac{J_{N2,i}}{V_2} G_{2,i} \right) - \frac{J_{Nb}}{V_B} B \right)$$

$$\frac{J_{leak,1,i}}{V_1} G_{1,i} + \frac{J_{leak,2,i}}{V_2} G_{2,i} \right) + \frac{J_{Nleak} B}{V_B} + \frac{J_{\text{POM}}}{V_B} B + \delta \sum_{i=1}^{n} \gamma (G_{1,i}^2 + G_{2,i}^2) \right)$$

$$\frac{dP}{dt} = (1 - \delta) \sum_{i=1}^{n} \gamma (G_{1,i}^2 + G_{2,i}^2) - \frac{J_{\text{POM}}}{V_B} B$$

$$\frac{dD}{dt} = \sum_{i=1}^{n} \left( \frac{J_{\text{leak,1},i}}{V_1} G_{1,i} + \frac{J_{\text{leak,2},i}}{V_2} G_{2,i} \right) + \frac{J_{\text{leak,B}}}{V_B} B - \frac{J_{\text{DOC}}}{V_B} B + \frac{J_{\text{POM}}}{V_B} B + \delta \sum_{i=1}^{n} \gamma (G_{1,i}^2 + G_{2,i}^2)$$

The last term in the large generalist equation corresponds to losses to higher trophic levels $m_{\text{htl}}$ (d$^{-1}$).

The trait-distributions of the two generalist groups are discretized with $n = 20$ trait groups representing cells with investments in light harvesting $\phi_L$ varying from 0 to 1/2 (and, correspondingly, investments in biosynthesis varying from 1/2 to 0).

**Physical set-up**

We used the Framework for Aquatic Biogeochemical Models (FABM; Bruggeman and Bolding 2014), which allows the coupling of custom biochemical models with different ocean models. Here
we used the 1D water column model General Ocean Turbulence Model (GOTM, Burchard et al. 1999). The model simulates the upper 50 m of a water column of a temperate region (seasonal). Physical data from the L4 station (50°N, 4°W; in the English Channel) was used as a model setup, and later some modifications were introduced (we therefore did not intend to explicitly model the L4 station). For the L4 station water-column setup refer to the ERSEM source codes explained in Butenschön et al. 2016. In our case, we set an open bottom boundary, allowing the entrance of nutrients and the export of detrital matter. The input rate of nutrients is defined as 

\[ V_{N,\text{bottom}} = \nu(N_b - N) \]

where \( \nu \) is the exchange rate equivalent to 1 d\(^{-1} \), \( N_b \) a fixed concentration (140 \( \mu \)gN L\(^{-1} \)). Sinking POM leaves through the bottom boundary at a rate equivalent to the sinking velocity, set at 10 m d\(^{-1} \). The simulation time was 9 years, and by the end of the simulations solutions had converged to a periodic solution. The FABM-GOTM code of the model can be found in GitHub.

Since we seek to observe the direct effects of temperature on organisms (without the physical environment being altered), an increase in temperature was not forced in the physical environment itself, but only in the biological system, so only biological processes are affected by the increase in temperature. We exposed the system to a +3°C rear in temperature, expecting a linear response in ecosystem functions. Additionally, a 3°C increase falls within the estimated range of temperature rise due to climate change in the next 100 years (Stocker et al. 2013).

**Ecosystem function**

As indicators of ecosystem function we consider carbon flux into the ecosystem (gross primary production), carbon cycling within the ecosystem (carbon transfer to higher trophic levels), and carbon flux out of the ecosystem (respiration, carbon export, and \( rDOM \) production). Gross primary production \( GPP \), the total amount of carbon fixed by photosynthesis, can be directed either to population growth if enough nutrients are available, or leaked and transferred to the dissolved pool. Redistribution inside the ecosystem occurs through the net production to higher trophic levels \( HTL \) as the amount of carbon lost from the \( m_{HTL} \) term. The main losses are export to depth, as the flux of \( POM \) across 50 m, and the formation of refractory dissolved organic matter \( rDOM \) through
alysis of bacteria. We characterize the efficiencies of these fluxes as the ratio between them and gross primary production: the higher trophic level efficiency $\epsilon_{HTL}$ as the ratio between losses and gross primary production ($\epsilon_{HTL} = m_{HTL} G_2 / GPP$). The ratio of resired to fixed carbon in the ecosystem (also referred to in the literature as metabolic balance) is $\epsilon_{\text{resp}} = (J_{R,G_1} + J_{R,G_2} + J_{R,B}) / GPP$, where values that surpass unity mean that the system is completely heterotrophic, i.e., more carbon is being respired than fixed, which can happen if there has been an accumulation of dissolved or particulate organic matter over time. The export efficiency is the ratio between export flux at a given depth and integrated $GPP$ over that depth horizon ($\epsilon_{\text{exp}} = C_{\text{exported}} / GPP$). A higher $\epsilon_{\text{exp}}$ indicates an ecosystem more effective in exporting carbon. Finally, the $rDOM$ produced relative to GPP is $\epsilon_{\text{rDOM}} = \gamma B^2 / GPP$, where higher values indicate a strengthening of the microbial loop and pump.

**RESULTS**

We first perform a simple optimization analysis of the cell model to find the investments that maximize cell division rate under various resource and temperature combinations ("resources" include light). Next we embed the cell model in the biological-physical model and explore the response of the system to a rise in temperature.

**Optimization of the cell-model**

The optimal investment $\phi*_{L}$ maximizes division rate (Eq.10) in an environment of light ($L$), nutrients ($N$), and food ($F$):

$$\phi*_{L}(L, N, F) = \text{argmax}_{\phi_{L}} \{ \mu(\phi_{L}; L, N, F) \},$$

(17)

By assuming that the plankton species with the highest division rate dominates a given environment, we can use the traits of the optimal cells as representatives of the overall community. Fig. 3 shows the temperature response of division rate for the optimal cells, $\mu(\phi*_{L}; L, N, F)$. Depending on the environment there are clear variations in the cells’ investment in light harvesting vs. biomass synthesis and in their trophic strategy.
Investments in photo harvesting increases as light decreases when food availability is low (shaded areas in Fig. 3). In low light conditions, cells are light limited and will prioritize light harvesting by increasing investments in light uptake $\phi_L$. Conversely, under high light, the cells are limited by their capacity to synthesize biomass ($\phi_B$), and consequently lower their investment in $\phi_L$ to maximize their capacity for synthesis. When food is abundant, investments in photo harvesting stay constant across light gradients. In this case, cells are limited by nutrients, and therefore, light investments will be reduced as much as possible as to maximize synthesis. This reduction in light investments should however not make the cell carbon-limited. All in all, investments are adjusted to lessen the constraint from the limiting process.

All cells are mixotrophic, but there are clear differences in the degree of mixotrophy between small and large cells (dashed lines in Fig. 3). Small cells are primarily autotrophic and obtain most of their carbon and nutrients from photo harvesting and nutrient uptake, while large cells get the majority of their resources from phagotrophy. Nevertheless, large cells are not purely heterotrophic, they do phototrophy to at least cover their respiratory costs. In that way, the large cells can use all the carbon and nutrients gained from phagotrophy for synthesis of new biomass. Still, larger cells invest less in light harvesting than small cells (see Chakraborty et al. (2017)).

Exposing the cells to a rise in temperature elicits changed investments and division rates. First, investments in photo harvesting increase with temperature. This is a response to biosynthesis becoming faster with temperature ($Q_{10} = 2$), while photosynthesis does not ($Q_{10} = 1$). Therefore increasing temperature shifts the limiting factor for growth from biosynthesis towards photo harvesting, everything else being equal.

Temperature response is highest in resource unlimited conditions and weakest in resource limited conditions, particularly under carbon (light and food) limitation (Fig. 4). The differences in temperature responses mainly reflect whether resource uptake or synthesis is limiting growth: when resources are limiting the temperature response is small, but it increases to a $Q_{10} \approx 2$ in the resource replete condition. To a lesser degree the response is determined by the temperature response of the uptake pathway, because only nutrient uptake has a $Q_{10} > 1$. Large cells in general
have slower division rates than small cells, which indicates that they are in general more limited by resource uptake than synthesis. It is possible for $Q_{10} < 1$ at low concentrations of carbon resources (light and food). This results from respiration increasing at a higher rate with temperature than resource uptakes at limiting conditions ($Q_{10} = 2$ for respiration vs. $Q_{10} = 1$ for affinity for food and light). And therefore, when resources are low, an increase in temperature results in a reduced growth, because the relative loss of carbon due to respiration outweighs the relative gain in carbon fixation. This effect no longer applies when resource levels are higher since temperature has a greater effect on biosynthesis, which has the same $Q_{10}$ as respiration, than on affinity. Overall, the temperature response of the optimal cells varies with the resource environment, being strongest under unlimited resources and weakest under limiting conditions.

**Biological and physical model**

The optimization analysis was made for fixed resource concentrations; however, in reality resource concentrations change with time and depth (in particular light), and are emergent outcomes of competition and predation (nutrients and food). The resource environment will determine which process limits growth, and the limitation (carbon, nutrients, or biosynthesis) will ultimately shape the community’s temperature response. We thus explore a dynamic resource environment in a temperate system. The following will focus on identifying the limiting process: carbon (photosynthesis), nutrients (nutrient uptake), or synthesis. Knowing the limiting process gives insight into the community temperature response.

The modelled seasonal succession well represents typical observed successions (Fig. 5): an early spring bloom of mainly phototrophic small cells is grazed by larger mainly phagotrophic cells. The summer production is limited in the upper mixed layer. A small autumn bloom is triggered by inorganic nitrogen mixed up from the deeper layer. The small cells are predominantly phototrophic, though they still obtain up to 30% of their carbon from food. The larger cells change their trophic strategy throughout the season. In the early summer they are mainly heterotrophic, feeding on the smaller cells, while in the summer they become increasingly mixotrophic. Phagotrophy is the main source of nutrients during summer for both small and large cells.
The optimization model showed how the temperature response of cells is largely determined by whether the limiting factor is resource uptake (weak response) or synthesis (strong response) (Fig. 3). In the dynamic environment, the small generalists are predominantly limited by carbon (light), except in the late summer where they are nutrient limited and their growth rate is low (Fig. 5). As synthesis has the highest $Q_{10}$ we expect that the small cells will show a strong response to increasing temperatures, since they tend to be less limited by resources (Fig. 6). On the other hand, large generalists are predominantly limited by resources and their growth is not controlled by the biosynthetic rate, due to their need for much larger resources concentrations (Fig. 4). In summary: we expect smaller cells to have a stronger temperature response than larger cells.

How the division rate changes with temperature is only one part of understanding how a community responds to temperature changes. Other important factors are changes in resource availability (prey) and predation rates. Fig. 7 shows water column integrated dynamical variables over a seasonal cycle in the base-line scenario and in a scenario in which temperature was raised +3°C, illustrating how temperature changes biomass and resulting resource availability. As suggested by the analysis of limitation above, the small generalists responds positively to the temperature increase, while overall the biomass of the larger cells remain largely unchanged. However, the overall picture is more nuanced. Increased carbon leakage increases DOC to the benefit of the bacteria population leading to increased overall bacteria respiration. Further, at higher temperature, cells are able to drive nutrients to lower concentrations enabling a higher net primary production.

The overall functions of the ecosystem in terms of its yearly carbon budget is shown in Fig. 8. The system fixes about 80 g of carbon per m$^2$ per year. Most is lost as refractory DOM and respiration, and only about 3 gC are exported as particulate carbon, either to the deep ocean or to higher trophic levels. The average response of these fluxes to the 3°C temperature increase is an increase of about 20%, corresponding to a $Q_{10}$ of about 1.8. The responses of the ecosystem efficiencies are more modest, with a lower fraction of GPP being exported ($Q_{10} \approx 1.5$), unchanged efficiency of DOM production and trophic transfer, and an increased fraction of GPP being respired ($Q_{10} \approx 1.4$). All in all, in absolute terms all rates increase, yet, in relative terms, we have a more
heterotrophic system (higher metabolic balance) and a system less efficient at exporting carbon to depth.

**DISCUSSION**

We have developed a trait-based model of the temperature dependency of the primary mass flows in a pelagic protist community. The model is mechanistic and based on temperature responses of fundamental processes and on general rules for how resource uptakes scale with cell size. There is a growing realization of the need for a better representation of the temperature dependence of primary producers in the ocean, and in particular the need to understand how these temperature dependencies are tempered by the availability of various resources (Thomas et al. 2017; Schaum et al. 2017; Marañón et al. 2018). The trait-based formulation of our model makes it possible to go beyond the responses of single cells and to simulate how an entire community adapts to environmental conditions of light, nutrients, food, and temperature. As an example, we have simulated the seasonal succession in a temperate system and its response to a temperature increase. Despite the conceptual simplicity of the model, the community response to a temperature increase is complex.

The temperature response of the cells depends upon which process is limiting. Limitation by biosynthesis leads to a strong temperature response, while resource limitation leads to weak temperature responses. On the level of individual cells, we find that small cells are typically limited by their ability to perform biosynthesis, while larger cells are limited by resource uptake. This difference makes small cells more sensitive to changes in temperature than large cells, as the biosynthesis rate changes faster with temperature than resource uptake rates. This low temperature response under nutrient limitation has also been observed experimentally (Marañón et al. 2018) and in meta analysis (Thomas et al. 2017). Others observed different effects of temperature depending on whether the system was bottom-up or top-down controlled (Chen et al. 2012; Peter and Sommer 2013; Morán et al. 2017), and López-Urrutia and Morán (2007) observed a decrease in bacterial growth efficiency with temperature when resource-limited. Here we show that not only does nutrient limitation play a role, but any resource uptake limitation will tend to weaken the
temperature responses. We observe a broad range of temperature response, from flat (no response) towards a $Q_{10}$ of around 2, depending on the the degree of resources limitation. Light limitation in particular will give a particularly weak response due to photosynthesis at non-saturating levels of light being temperature independent (Raven and Geider 1988; Clarke 2017).

The insight regarding the key role of resource limitation was made possible by explicitly separating the process of assimilation and synthesis in the functional response in the model. If these two processes are considered together the role of limitation becomes opaque. For instance, functional responses are usually formulated with the half-saturation constant, which is the ratio between maximum uptake and substrate affinity. Hence, this formulation mixes the processes of assimilation and enzymatic activity, which makes it unsuitable for mechanistically describing the limiting process and temperature responses (see Thingstad and Aksnes (2018)).

When cells are exposed to resource competition in a water column, they drive down the concentration of the limiting resource (except light for which they do not compete appreciably). The lowered resource concentration leads to resource limitation, and thereby weak temperature responses. The example we used to explore resource competition was of a temperate seasonal succession. In this example, the early bloom period will not be resource limited, while the summer is. If we instead consider a low latitude oligotrophic ocean, resource limitation will be stronger throughout the year, and we expect the temperature response to be even weaker. In any case, the diversity of temperature responses makes it difficult to apply a single $Q_{10}$ or Arrhenius temperature function to protist growth rates in ecosystem models. Even assuming differential temperature effects between autotrophs and heterotrophs (Brown et al. 2004) is insufficient (Chen and Laws 2017).

Measures of ecosystem function increase overall with a $Q_{10}$ around 1.8; a warmer ocean fixes more carbon, creates more DOM and rDOM, sends more carbon to higher trophic levels, and respires more carbon. Nevertheless, the warmer ecosystem is less efficient at retaining carbon, as more of it is respired. We also find a negative relationship between ef-ratio (export relative to GPP) and temperature, in agreement with the literature (Pomeroy and Deibel 1986; Laws et al. 2000; Laws et al. 2011; Cael and Follows 2016; Cael et al. 2017). There is a reduction in relative cell size.
of the community, due to higher competition for nutrients during the stratified period (even without
the thermal effect on water column stability), and the better performance of bacteria due to higher
biosynthetic rate and DOC concentrations. Overall there is an enhancement in the importance of
the microbial loop and the microbial pump.

The model is based on simplifications, particularly in the values of $Q_{10}$, in the role of
dissolved organic matter, in the choice of a fixed stoichiometry, and in the physics. Regarding
$Q_{10}$, more knowledge is needed on the temperature of predator-prey interactions and the uptake
of dissolved compounds. If, for example, the $Q_{10}$ of predator-prey interaction is larger than
1, the overall community $Q_{10}$ will increase. Production and degradation of dissolved organic
matter (DOM; labile, semi-labile, refractory DOM, etc.) is sketchily represented. An example is the
production of refractory DOM, which we assume is created by viral lysis of bacteria, represented by
a quadratic mortality. The assumption of fixed stoichiometry is a rough simplification, particularly
in autotrophs, which have variable C:N:P ratios due to luxury uptake (Droop 1974), and to differing
investments in chloroplast, ribosomes, and cell walls in response to resource conditions (Toseland
et al. 2013). As temperature affects competition for resources and investments in biosynthesis, it
will also affect stoichiometry and thus macro-nutrients cycling prediction under climate change
scenarios (Yvon-Durocher et al. 2017). We have now resolved the direct effects of temperature on
organisms and the overall community, but left open the question of the relative strength of indirect
(effects due to changes in the physical environment) vs. direct effects of climate change on the
planktonic community. Overall, incorporation of the considerations previously mentioned will
refine the results, however, they are not expected to fundamentally alter the general conclusion that
the community-level temperature response is smaller than expected from metabolic considerations.

CONCLUSION

Effects of temperature on physiological processes have been studied for over a century, never-
theless, we argue that interpretation of data related to global warming could have been mislead by
effects of resource limitation (López-Urrutia and Morán 2007; Behrenfeld et al. 2016). Here, by
explicitly representing effects of temperature on processes responsible for growth in a mechanistic
model, we show that patterns in the individual level can be scaled to observed trends in the ecosystem level, and that species interactions can actually exacerbate nutrient limitation by increasing competition just by temperature effects *per se*. We anticipate an strengthening of the microbial activity and the increasing importance of the dissolved pathway and the microbial pump for carbon sequestration in the oceans, at least when it comes to direct effects of temperature in the microbial food-web.

**ACKNOWLEDGEMENTS**

A. Visser, K.H. Andersen, and C. Serra-Pompei acknowledge support from the Gordon & Betty Moore Foundation through award 5479, and the Centre for Ocean Life, a Villum Kahn Rasmussen Centre of Excellence funded by the Villum Foundation. G.I. Hagstrom acknowledges support from the Simons Foundation grant 395890, NSF Award OCE-1848576, and the Center for Ocean Life at DTU Aqua.

**CONFLICTS OF INTEREST**

The authors declare that they have no conflict of interests.

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Serra-Pompei, January 18, 2019


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### TABLE 1. Variables and parameters

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<th>Description</th>
<th>Units</th>
<th>value</th>
<th>$Q_{10}$</th>
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<tbody>
<tr>
<td>$G_1, G_2, B$</td>
<td>Concentration of $G_1, G_2$ and $B$ in the system</td>
<td>$\mu gC L^{-1}$</td>
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<td></td>
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<tr>
<td>$V_B$</td>
<td>Cell mass of $B$</td>
<td>$\mu gC Cell^{-1}$</td>
<td>$10^{-8}$</td>
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</tr>
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<td>$V_1$</td>
<td>Cell mass of $G_1$</td>
<td>$\mu gC Cell^{-1}$</td>
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<tr>
<td>$V_2$</td>
<td>Cell mass of $G_2$</td>
<td>$\mu gC Cell^{-1}$</td>
<td>$10^{-2}$</td>
<td></td>
</tr>
<tr>
<td>$\phi_L$</td>
<td>Investment in photosynthesis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\phi_B$</td>
<td>Investment in biosynthesis</td>
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<td></td>
</tr>
<tr>
<td>$\alpha_L$</td>
<td>Affinity per investment in photosynthesis</td>
<td>$\mu gC d^{-1} (W m^{-2})^{-1} \mu gC^{-1}$</td>
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<td>$1$</td>
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<tr>
<td>$c_L$</td>
<td>Maximum light affinity</td>
<td>$\mu gC d^{-1} (W m^{-2})^{-1} (\mu gC^{2/3})^{-1}$</td>
<td>$0.005$</td>
<td>$1$</td>
</tr>
<tr>
<td>$\alpha_N$</td>
<td>Nutrient affinity</td>
<td>$L d^{-1} (\mu gC^{1/3})^{-1}$</td>
<td>$3.7 \times 10^{-5}$</td>
<td>$1.5$</td>
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<tr>
<td>$\alpha_F$</td>
<td>Food affinity</td>
<td>$L d^{-1} (\mu gC)^{-1}$</td>
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<tr>
<td>$\alpha_{DOC}$</td>
<td>Affinity for DOC</td>
<td>$L \mu gC^{-1} d^{-1}$</td>
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<td>$K_{POM}$</td>
<td>Half saturation constant for POM hydrolysis</td>
<td>$\mu gC L^{-1}$</td>
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<tr>
<td>$\mu_{POM}$</td>
<td>Maximum POM hydrolysis rate</td>
<td>$\mu gC d^{-1} cell^{-1}$</td>
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<td>$\mu_{max}$</td>
<td>Maximum specific growth rate</td>
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<td>$2$</td>
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<tr>
<td>$k$</td>
<td>Metabolic cost</td>
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<td>$Q_{C:N}$</td>
<td>C:N ratio</td>
<td>$\mu gC \mu gN^{-1}$</td>
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<tr>
<td>$\delta$</td>
<td>Fraction of dead matter going to N and DOM</td>
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<tr>
<td>$\gamma$</td>
<td>Background mortality</td>
<td>$L (\mu gC d)^{-1}$</td>
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<tr>
<td>$m_{hl}$</td>
<td>Loss rate to predation of HTL</td>
<td>$d^{-1}$</td>
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<tr>
<td>$N$</td>
<td>Nutrients concentration</td>
<td>$\mu gN L^{-1}$</td>
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</tr>
<tr>
<td>$L$</td>
<td>Irradiance</td>
<td>$W m^{-2}$</td>
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<td></td>
</tr>
<tr>
<td>$D$</td>
<td>Dissolved organic carbon (DOC) concentration</td>
<td>$\mu gC L^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$P$</td>
<td>Particulate organic matter (POM) concentration</td>
<td>$\mu gC L^{-1}$</td>
<td></td>
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<tr>
<td>$F$</td>
<td>Food: concentration of prey perceived by a predator</td>
<td>$\mu gC L^{-1}$</td>
<td></td>
<td></td>
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</table>

* All parameters were obtained from the literature. Parameters of generalist except for biosynthetic rate, come from Chakraborty et al. (2017), who obtained those by inferring from observations. Note that in Chakraborty et al. (2017) they use structural biomass and we use total biomass, so all the parameters that are multiplied by the structural biomass have here been divided by 2 (considering our assumption of structural biomass being half the total biomass). Affinity for light was derived from Daines et al. 2014. Parameters from generalists that could be extended to bacteria by allometric laws were maintained (affinity for nitrogen ($\alpha_N$) and maximum growth rate). Affinity for DOC was derived from Thingstad et al. (2007). Degradation rates of POM from bacteria were obtained from Anderson and Williams (1998b). Mortality rate was left as a free parameter. Loss to higher trophic levels was derived from Chakraborty et al. (2017).
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Fig. 1. Schematic representation of the generalist cell model. Total mass of the cell $(V)$ is divided in 3 compartments: structural mass $(\frac{1}{2}V)$, photosynthetic machinery $(\phi_LV)$, and biosynthetic machinery $(\phi_BV)$. Acquired carbon from photosynthesis $(J_L)$, nitrogen from diffusive uptake $(J_N)$, and carbon and nitrogen from food $(J_F)$, are synthesized in the biosynthetic apparatus following Liebig’s law of the minimum. Newly produced biomass is then allocated to either the photosynthetic apparatus, the biosynthetic apparatus, or to structural biomass according to the partitioning of investments in photosynthesis $(\phi_L)$ and biosynthesis $(\phi_B)$ (hourglass symbols show the positive feed-backs of these allocations). Part of the cellular carbon is respired $(J_R)$. Excess $N$ or $C$ resulting from Liebig’s minimum are excreted back to the environments $(J_{N,\text{leak}}$ and $J_{C,\text{leak}}$ respectively).
Fig. 2. Biological system of the microbial community. The system contains six carbon and nitrogen pools: bacteria ($B$), small generalists ($G_1$), large generalists ($G_2$), dissolved organic carbon ($DOC$), particulate organic matter ($POM$), and a dissolved nitrogen pool ($N$) which includes both organic and inorganic $N$. Fluxes ($J$) are explained in section 2. Dashed lines represent leakage of carbon and nitrogen. The pointed line in $J_{POM}$ is the action of bacteria degrading $POM$ which then goes to the $N$ and $DOC$ pools.
Fig. 3. Temperature dependency of division rate, light investments, and fraction of carbon and nutrients derived from phagotrophy for small and large generalists (left and right column respectively) under various resource conditions. The upper block of panels is at low food levels (F=5µgC L⁻¹) and the lower at high food levels (F=5µgC L⁻¹). Each row of small panels is under a given condition of light (L in W m⁻²), and each column a given concentration of nutrients (N in µgN L⁻¹).
Fig. 4. $Q_{10}$ values of the temperature response of cell division rate as a function of resource conditions, as determined by fits to the actual response (see Fig. 3) for $G_1$ (A) and $G_2$ (B). The x-axis represents changes in light (W m$^{-2}$), nutrients ($\mu$gN L$^{-1}$), and food ($\mu$gC L$^{-1}$), from 0 to 1000. To plot the nitrogen ($N$) curve we fixed the values for light and food (I=1000, F=0). For the light curve ($I$) we fixed N=1000 and F=0. Finally for the food curve $F$ both light and nutrients were fixed to 0. The $Q_{10}$ was fitted for the optimal growth obtained for each condition; therefore investments might also be different. Only effects on positive growth are shown. The $Q_{10}$ for each combination of light, food and nutrients was calculated by linear regression between temperature and log of the growth rate.
Fig. 5. Seasonal succession in a temperate water column. Note varying ranges on the concentrations of carbon. Mean investments are calculated as biomass weighted mean: $\bar{\phi}_L = \sum_i \phi_{L,i} B_i / n$, where $n = 20$ is the number of trait groups. The two lowest panels show the relative gains of nutrients coming from phagotrophy ($J_F:J_N$).
Fig. 6. Illustration of the limiting process for small (A) and large generalists (B). We only considered the trait group with the highest biomass at each time and depth. The colors show whether growth rate is ruled by biosynthetic rate or by uptake of resources, and in the latter case, whether they are limited by carbon or nitrogen. Carbon limitation occurs if leaks of nitrogen overcome carbon leaks, and the other way around for N limitation. Synthesis limitation occurs where mean limiting resources/$K$) is larger than 1, being $K$ the half saturation constant for that given resource and equivalent to $M/A_X$. White regions indicate biomass concentrations below 5$\mu$gC L$^{-1}$. 
Fig. 7. Dynamical variables integrated over the upper 30m of the water column. Black line is the base-line scenario, red is the +3°C scenario (left y axis). Everything is in units of mgC m$^{-2}$, except the nitrogen pool which is in mgN m$^{-2}$. Upper Shaded areas are the fraction of concentration changed relative to the base-line scenario (right y axis), negative values mean a decrease while positive an increase. The high anomaly values in the DOC plot are an artefact of the rapid change in DOC concentration over time, and have therefore been left out.
Fig. 8. Ecosystem functions and their response to a $3^\circ$C increase in temperature. Panel A shows total GPP over a year and its further fate. The functions are: Gross primary production (GPP), production of refractory dissolved organic matter (rDOM), respiration, losses to export, and losses to higher trophic levels (HTL). Panel B shows the total change in percent for each rate in response to the $3^\circ$C increase in temperature. Panel C shows the percent change relative to GPP in response to the temperature increase. Carbon flows relative to GPP are: export efficiency ($\epsilon_{Cexp} = C_{exported}/GPP$), rDOM production efficiency ($\epsilon_{rDOM} = \gamma B^2/GPP$), trophic transfer efficiency ($\epsilon_{HTL} = m_{HTL}G_2/GPP$), and respiration ($\epsilon_{resp} = (J_{R,G1} + J_{R,G2} + J_{R,B})/GPP$).