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Biophysical Aspects of Resource Acquisition and Competition in Algal Mixotrophs

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ABSTRACT: Mixotrophic organisms combine autotrophic and heterotrophic nutrition and are abundant in both freshwater and marine environments. Recent observations indicate that mixotrophs constitute a large fraction of the biomass, bacterivory, and primary production in oligotrophic environments. While mixotrophy allows greater flexibility in terms of resource acquisition, any advantage must be traded off against an associated increase in metabolic costs, which appear to make mixotrophs uncompetitive relative to obligate autotrophs and heterotrophs. Using an idealized model of cell physiology and community competition, we identify one mechanism by which mixotrophs can effectively outcompete specialists for nutrient elements. At low resource concentrations, when the uptake of nutrients is limited by diffusion toward the cell, the investment in cell membrane transporters can be minimized. In this situation, mixotrophs can acquire limiting elements in both organic and inorganic forms, outcompeting their specialist competitors that can utilize only one of these forms. This advantage can be enough to offset as much as a twofold increase in additional metabolic costs incurred by mixotrophs. This mechanism is particularly relevant for the maintenance of mixotrophic populations and productivity in the highly oligotrophic subtropical oceans.

Keywords: mixotroph, plankton, diffusion, resource acquisition, resource competition, mechanistic.

Introduction

Aquatic protists are often classified as either autotrophic phytoplankton or heterotrophic zooplankton. This dichotomy underpins most conceptual and mathematical models of marine ecosystems (e.g., Azam et al. 1983; Fasham et al. 1990), but in reality the boundary is often blurred by the existence of mixotrophs: organisms that combine both autotrophic and heterotrophic nutrition (Nygaard and Tobiesen 1993; Stoecker 1998). Mixotrophs are found in all aquatic environments (Stoecker 1998), and they may play an important role in determining ecological and biogeochemical dynamics. In coastal and subpolar waters, for example, mixotrophy provides dinoflagellates with the flexibility to endure large environmental changes during tidal and seasonal cycles (Li et al. 2000; Litchman 2007). However, in the low-seasonality subtropical oceans, where such nonequilibrium dynamics are presumably much less important, mixotrophy remains a prevalent strategy. Zubkov and Tarran (2008) recently found that photosynthetic protist species, which account for more than 80% of the total chlorophyll in regions of the North Atlantic, were also responsible for 40%–95% of the total bacterivory. Small mixotrophs have been shown to be of similar importance in coastal oligotrophic waters (Havskum and Riemann 1996).

Why are mixotrophs so ubiquitous? The ability to draw on multiple resources clearly allows mixotrophs to reduce their reliance on any single resource (e.g., Nygaard and Tobiesen 1993; Rothhaupt 1996; Tittel et al. 2003), but there are also certain physiological trade-offs that must be considered. Dinoflagellates, for example, frequently combine photosynthesis and grazing (Stoecker 1999), but they are typically less efficient in terms of resource acquisition and growth than their specialist competitors (Tang 1995; Litchman et al. 2007). Similarly, growth and grazing rates are lower in some mixotrophic protists relative to those in obligate heterotrophs (Perez et al. 1997; Zubkov and Tarran 2008). The low and apparently uncompetitive values of these traits can be interpreted in terms of key physiological constraints. Cells have a limited surface area, and mixotrophs must partition it to accommodate transporter sites for both inorganic and organic resources (Litchman et al. 2007). In addition, they must incorporate and maintain the internal cellular components required for both autotrophy and heterotrophy (Raven 1997), leading to increased metabolic costs.

How do these trade-offs play out in the ocean? Mathematical and numerical models provide a platform to consider the costs and benefits of different trophic strategies. An idealized model of a marine ecosystem (Thingstad et al. 1996) revealed that the strategy of "eating your competitor" may be an effective way for mixotrophs to out-

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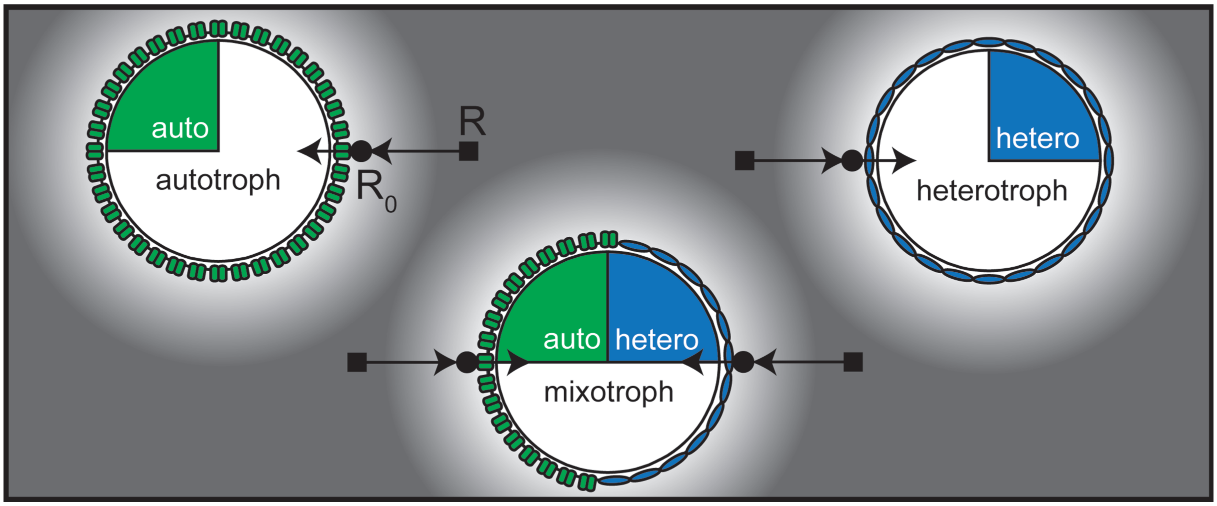

Figure 1: Resource acquisition is a two-stage process: squared arrows represent encounters, circled arrows represent handling. The symbols covering the cell surface represent handling sites for nitrate (*green*) and bacteria (*blue*). The filled areas within each cell represent the metabolic costs of autotrophy (*green*) and heterotrophy (*blue*). Mixotrophs must divide their surface area between uptake sites and must accommodate and maintain cellular machinery for both trophic strategies. The generic resource concentration in the bulk medium is given by R, while the concentration at the cell surface is given by R_0.

compete more efficient autotrophic specialists. Troost et al. (2005*a*, 2005*b*) showed that mixotrophy can be a successful strategy if autotrophic and heterotrophic traits are combined so that there is no intrinsic physiological cost to mixotrophy, although it is not clear that such a trade-off is realistic. More physiologically demanding constraints were placed on mixotrophs by Crane and Grover (2010), who showed that mixotrophs may be able to coexist with specialists in a model ecosystem with a diverse range of resource- and grazer-driven controls. Such controls were also shown to be important by Stickney et al. (2000), who demonstrated that mixotrophs could coexist with specialist species in oligotrophic environments.

Here we complement these earlier studies by developing a simplified physiological description of planktonic cells in which we represent some of the important trade-offs among different trophic strategies. These concern the allocation of cell surface area to transporters for inorganic and organic resources, as well as the additional metabolic costs of maintaining both autotrophic and heterotrophic machinery. We first recapitulate some theory regarding the acquisition of resources by diffusion toward and transport across the cell membrane. We then develop an idealized model of a plankton community and outline some key trade-offs concerning resource acquisition and metabolism. Numerical and analytical solutions to the model are then used to show how mixotrophs can outcompete specialists in stable environments, if resources are drawn down to such low levels that physical constraints begin to override biological trade-offs at the cell surface.

Resource Acquisition: Theoretical Background

Acquisition of some generic resource R (e.g., inorganic nutrients, organic matter, or bacteria) can be described as a two-stage process comprising resource encounters and cross-membrane transport. This is shown schematically in figures 1 and 2, as a flux toward the cell is followed by transport across the cell membrane at individual uptake sites.

Resource Encounters

We describe resource encounters as a diffusive flux toward the cell (fig. 2*A*), as this has been shown to be an appropriate model for both inorganic nutrients (Pasciak and Gavis 1974) and bacteria (Kiørboe et al. 2002). If R (mmol R m^{-3}) is the resource concentration in the bulk medium, and R_0 (mmol R m^{-3}) is the resource concentration at the cell surface, then the total rate of diffusive flux (mmol R cell^{-1} day^{-1}) toward the cell (Berg and Purcell 1977; Jumars et al. 1993; Yoshiyama and Klausmeier 2008) is given by

$$\phi_{\text{diff}} = 4\pi r S_h \Phi \kappa (R - R_0), \tag{1}$$

where r is the cell radius (m), κ is the resource diffusivity

($\mathrm{m^2\ day^{-1}}$), S_h is the dimensionless Sherwood number that accounts for the effects of sinking and advection, and Φ is another dimensionless number accounting for the enhancement of the diffusive flux toward nonspherical cells (Armstrong 2008).

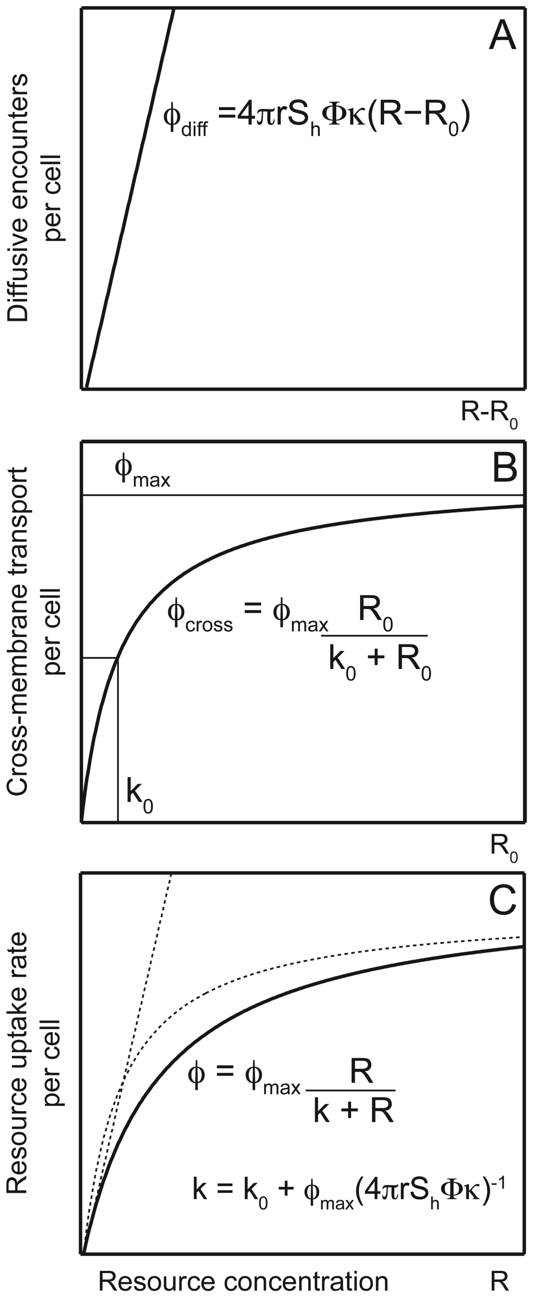

Figure 2: Schematic diagram showing rates of diffusive resource encounter and cross-membrane transport. The rate of diffusion toward the cell (*A*) is set by the difference between the resource concentration at the cell surface (R_0) and the concentration in the bulk medium (R). The rate of cross-membrane transport (*B*) is given by a Michaelis-Menten function of the concentration at the cell surface (R_0). The Michaelis-Menten-like approximation (bold line in *C*; after Armstrong 2008) accounts for both these processes (*dotted lines*). Here uptake is a function of the concentration in the bulk medium (R). Uptake at low resource concentrations is mostly limited by diffusion, while uptake at high resource concentrations is mostly limited by cross-membrane transport.

Cross-Membrane Transport

Following Aksnes and Egge (1991), we calculate the rate of cross-membrane transport (fig. 2*B*) as

$$\phi_{\text{cross}} = \phi^{\max}\frac{R_0}{k_0+R_0} = nh^{-1}\frac{R_0}{(ah)^{-1}+R_0}, \tag{2}$$

where $\phi^{\max} = nh^{-1}$ is the maximum uptake rate for resource R, $k_0 = (ah)^{-1}$ is the half-saturation constant, n is the number of cross-membrane transport sites ($\mathrm{cell^{-1}}$), h is the handling time per unit of resource ($\mathrm{s\ (mmol\ N)^{-1}}$), and a is the resource clearance rate for a single unoccupied uptake site ($\mathrm{m^3\ day^{-1}}$).

A General Model of Resource Acquisition

The two models of resource acquisition were combined by Pasciak and Gavis (1974) to give a general quadratic equation for two-stage resource uptake. This was later approximated in a simpler Michaelis-Menten-like form by Armstrong (2008; fig. 2*C*), who combined equations (1) and (2) into the following expression:

$$\begin{aligned}\phi &= nh^{-1}\frac{R}{[(ah)^{-1}+nh^{-1}(4\pi r\Phi S_h\kappa)^{-1}]+R}\\ &= \phi^{\max}\frac{R}{k+R},\end{aligned} \tag{3}$$

where k is a half-saturation constant accounting for the effects of both diffusion and cross-membrane transport,

$$k = (ah)^{-1} + \frac{nh^{-1}}{4\pi r\Phi S_h\kappa}. \tag{4}$$

Note that at high resource concentrations (i.e., $R \gg k$), equation (3) reduces to

$$\phi = \phi^{\max}. \tag{5}$$

This is independent of R, which indicates that resource uptake saturates at a maximum value $\phi^{\max}$ ($\mathrm{mmol\ N\ cell^{-1}\ day^{-1}}$). Conversely, at very low resource concentrations (i.e., $R \ll k$), equation (3) reduces to

$$\phi = \phi^{\max}k^{-1}R, \tag{6}$$

and uptake at low concentrations becomes a near linear function of the resource affinity, or clearance rate, $\alpha = \phi^{\max}k^{-1}$ ($\mathrm{m^{-3}\ cell^{-1}\ day^{-1}}$).

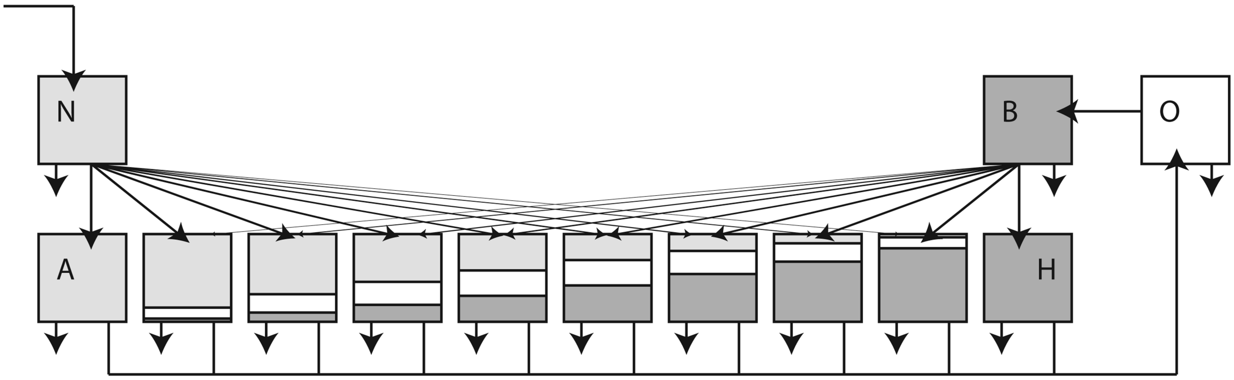

Figure 3: Model of a microbial community with plankton occupying a range of strategies between autotrophy and heterotrophy. Autotrophic protists (*A*) consume inorganic nitrogen (*N*). Heterotrophs (*H*) consume bacteria (*B*). Bacteria consume organic nitrogen (*O*). Nitrogen fluxes between state variables are indicated by arrows; arrows not leading into another box indicate outflow from the chemostat. Each plankton box is schematically divided between uptake of inorganic matter (*light gray*) and uptake of bacteria (*dark gray*). The white areas represent an inefficiency in combining trophic strategies.

The functional form given in equation (3) is used in the next section to develop a model community of autotrophs, mixotrophs, and heterotrophs. The new form of k will allow analysis of the relative importance of resource encounters and cross-membrane transport under a number of scenarios relating to resource availability and cell size.

A Model Community of Autotrophs, Mixotrophs, and Heterotrophs

We now develop an idealized model of a marine ecosystem. To explore the competitive advantages and disadvantages of mixotrophy in relation to pure autotrophy and heterotrophy, we model the community as a number of discrete plankton types occupying a range of resource acquisition strategies (e.g., Myers and Graham 1954; Caron 2000). Within this framework, nutrients may be acquired in dissolved inorganic form, through grazing on bacteria, or via some combination of both. Focusing on this particular form of mixotrophy allows a relatively simple model structure and corresponds to the bacterivorous feeding strategy that has been shown to be important in a range of aquatic ecosystems (Nygaard and Tobiesen 1993; Havskum and Riemann 1996; Zubkov and Tarran 2008). The model solutions can, however, be generalized to describe mixotrophic consumption of any combination of inorganic and organic resources, including dissolved organic matter (Bruggeman 2009) or other eukaryotes (Stoecker 1999).

We adopt a quota-based approach, where growth is a function of internal, rather than environmental, nutrient concentrations (Caperon 1968; Droop 1968). As well as being more realistic, this allows resolution of key physiological trade-offs in resource acquisition and growth. Nitrogen was selected as the model currency because it is believed to be the most limiting nutrient in many marine environments, but the results may be generalized to apply to any other macro- or micronutrient.

Growth of each generic plankton cell of type j is determined by the size of its internal nitrogen quota, Q_j (mmol N cell^{-1}), above a minimum value, $Q_j^{\min}$, such that

$$\mu_j = \mu_j^{\infty}\left(\frac{Q_j - Q_j^{\min}}{Q_j}\right). \tag{7}$$

Here μ_j^{∞} is the theoretical maximum growth rate (day^{-1}) at infinite quota. The size of the nitrogen quota is determined by the balance of nutrient uptake, grazing, and growth, where $\phi_j^{N_{\max}}$ and $\phi_j^{B_{\max}}$ are the maximum uptake rates (mmol N cell^{-1} day^{-1}) for inorganic nitrogen N and bacteria B (mmol N m^{-3}), respectively, while k_{N} and k_{B} are the respective half-saturation constants (mmol N m^{-3}). As discussed in the previous section, these account for the limiting effects of both diffusive resource encounters and cross-membrane transport:

$$\frac{dQ_j}{dt} = \phi_j^{N_{\max}}\frac{N}{N + k_{\mathrm{N}_j}} + \phi_j^{B_{\max}}\frac{B^2}{B^2 + k_{\mathrm{B}_j}^2} - \mu_j Q_j. \tag{8}$$

The model structure, shown schematically in figure 3, includes state variables for inorganic and organic nitrogen, bacteria, and several (J) plankton types. The model is set up to mimic a laboratory chemostat, where nutrient medium is fed into a well-lit, well-mixed vessel of fixed volume. Although idealized, the chemostat model is analogous to a simple two-layer ocean model with no light limitation and instant remineralization of exported matter beneath the mixed layer (Thingstad et al. 1996). The model state variables and parameters are listed with their corresponding units in table 1.

Inorganic nitrogen solution enters the system at a fixed rate (D) and concentration (N_0), and an equal outflow acts to dilute inorganic nutrient N (mmol N m^{-3}), organic detritus O (mmol N m^{-3}), and population densities X (cells m^{-3}). Organic nitrogen is generated through a constant plankton mortality (m, equal for all plankton) and is consumed by bacteria. The biomass of bacteria and plankton types, although not explicit in the model equations, can be calculated as the product of cell density and cell quota.

$$\frac{dN}{dt} = D(N_0 - N) - \sum_{j=1}^{J} \phi_j^{N_{\max}} \frac{N}{N + k_{N_j}} X_j, \tag{9}$$

$$\frac{dO}{dt} = \sum_{j=1}^{J} mQ_j X_j - \phi_B^{O_{\max}} \frac{O}{O + k_O} X_B - DO, \tag{10}$$

$$\frac{dX_j}{dt} = \mu_j X_j - (D + m)X_j. \tag{11}$$

Bacteria are modeled in a similar fashion, but they consume only organic detritus, with maximum uptake rate $\phi_B^{O_{\max}}$ and half-saturation constant k_O. They have explicit state variables for population density X_B (cells m^{-3}) and nitrogen quota Q_B (mmol N cell^{-1}):

$$\mu_B = \mu_B^{\infty}\left(\frac{Q_B - Q_B^{\min}}{Q_B}\right), \tag{12}$$

$$\frac{dQ_B}{dt} = \phi_B^{O_{\max}} \frac{O}{O + k_O} - \mu_B Q_B, \tag{13}$$

$$\frac{dX_B}{dt} = \mu_B X_B - \sum_{j=1}^{J} \phi_j^{B_{\max}} \frac{B^2}{B^2 + k_{B_j}^2} X_j - DX_B. \tag{14}$$

Grazing is parameterized with a Holling type III function, as this was a necessary condition for stability in the numerical model (see Gentleman and Neuheimer 2008), but we note that the analytical solutions outlined later in the article are equally valid if a Holling type II response is used instead. Light limitation is not considered in this study (but see Rothhaupt 1996).

Parameterization and Trade-Offs

Here we identify some key trade-offs between autotrophic and heterotrophic strategies that will define competition within the model community. In terms of resource acquisition, modeled plankton types are assumed to be identical in terms of size, shape, and motility and to have an equal cell surface area available to accommodate the han-

Table 1: Model variables and parameters

	Definition	Values	Units	Source for value
State and auxiliary variables:				
N	Inorganic nitrogen		mmol N m^{-3}	
O	Organic nitrogen		mmol N m^{-3}	
Q_B	Bacterial N quota		mmol N cell^{-1}	
Q_j	Plankton j N quota		mmol N cell^{-1}	
X_B	Bacterial cell density		cells m^{-3}	
X_j	Plankton j cell density		cells m^{-3}	
$B_B = Q_B X_B$	Bacterial N biomass		mmol N m^{-3}	
$B_j = Q_j X_j$	Plankton j N biomass		mmol N m^{-3}	
Parameters:				
D	Chemostat dilution rate	.1	day^{-1}	
N_0	Incoming N concentration	8.0	mmol N m^{-3}	
$Q_B^{\min}$	Minimum quota	$.16 \times 10^{-1}$	mmol N cell^{-12}	Thingstad 1987
μ_B^{∞}	Growth rate at infinite quota	6.0[a]	day^{-1}	Thingstad 1987
$\phi_B^{O_{\max}}$	Maximum O uptake rate	9.6×10^{-12}[a]	mmol N cell^{-1} day^{-1}	Thingstad 1987
k_O	Half-saturation O concentration	.1	mmol N m^{-3}	Thingstad 1987
$Q^{\min}$	Minimum quota	5.0×10^{-11}	mmol N cell^{-1}	Tozzi et al. 2004
μ^{∞}	Growth rate at infinite quota	2.0	day^{-1}	Tozzi et al. 2004
$\phi^{N_{\max}}$	Maximum N uptake rate	1.5×10^{-10}	mmol N cell^{-1} day^{-1}	Tozzi et al. 2004
$\phi^{B_{\max}}$	Maximum B grazing rate	3.84×10^{-10}	mmol N cell^{-1} day^{-1}	Zubkov and Tarran 2008
k_N	Half-saturation N concentration	.5	mmol N m^{-3}	Tozzi et al. 2004
k_B	Half-saturation B concentration	1.25	mmol N m^{-3}	Rothhaupt 1996
m	Mortality	.2	day^{-1}	

[a] Value adjusted from Thingstad (1987).

dling sites needed for cross-membrane transport of resources.

Given that ion-specific uptake sites for just one resource may take up as much as 10% of the cell surface area (Aksnes and Egge 1991) and the fact that cells may require as many as 50 macro- and micronutrients (Litchman et al. 2007), it seems likely that there is a trade-off with regard to how much surface area is assigned to uptake of any one resource (Litchman et al. 2007). This trade-off is framed in the model in terms of the number of uptake sites n assigned to either inorganic nutrient uptake n^{N} or grazing on bacteria n^{B}. The superscripts N and B correspond to the inorganic nutrients and bacterial resources, respectively. The subscripts s and m will denote specialists (i.e., autotrophs and heterotrophs) and mixotrophs, respectively.

To account for the limited space available on the cell surface, we allow specialist cells to assign all of the available area to handling sites for either inorganic nutrient uptake or grazing, so that each cell can accommodate the maximum number of sites for either resource ($n_{\mathrm{s}}^{\mathrm{N}} = n_{\max}^{\mathrm{N}}$ or $n_{\mathrm{s}}^{\mathrm{B}} = n_{\max}^{\mathrm{B}}$). Mixotrophic cells must allocate space between the two resources, and this reduces the number of handling sites that can be accommodated for each resource. If β is the fraction of the available area assigned to autotrophy, then $n_{\mathrm{m}}^{\mathrm{N}} \leq \beta n_{\max}^{\mathrm{N}}$ and $n_{\mathrm{m}}^{\mathrm{B}} \leq (1-\beta) n_{\max}^{\mathrm{B}}$.

Recalling from equation (3) the general function for uptake of resource R,

$$\phi = nh^{-1}\frac{R}{[(ah)^{-1} + nh^{-1}(4\pi r\Phi S_{\mathrm{h}}\kappa)^{-1}] + R} = \phi^{\max}\frac{R}{k+R},$$

the trade-off in the number of cell surface uptake sites n appears in the maximum uptake rate $\phi^{\max}$ and in the half-saturation constant k. The maximum uptake rate ($\phi^{\max} = nh^{-1}$) is always dependent on n, but the contribution of n toward the half-saturation constant k varies with the relative importance of diffusion and cross-membrane transport,

$$k = (ah)^{-1} + \frac{nh^{-1}}{4\pi r\Phi S_{\mathrm{h}}\kappa}.$$

This balance is critically dependent on cell size (Armstrong 2008), because the number of uptake sites n on the cell surface scales with the square of the cell radius, r^2. As the ratio n/r ($\propto$ surface area/radius) increases with cell size, the size of the second term in equation (4) also increases. Below some critical cell radius, k is dominated by cross-membrane transport limitation (i.e., $(ah)^{-1} \gg nh^{-1}/4\pi r\Phi S_{\mathrm{h}}\kappa$), so that k is independent of n, and the affinity ($\alpha = \phi^{\max}k^{-1}$) is linearly proportional to n:

$$k = (ah)^{-1},$$
$$\alpha = na. \tag{15}$$

In larger cells, by contrast, k is set primarily by the slow rate of diffusion (i.e., $(ah)^{-1} \ll nh^{-1}/4\pi r\Phi S_{\mathrm{h}}\kappa$) and k is linearly proportional to n, while the affinity is independent:

$$k = \frac{nh^{-1}}{4\pi r\Phi S_{\mathrm{h}}\kappa},$$
$$\alpha = 4\pi r\Phi S_{\mathrm{h}}\kappa. \tag{16}$$

From this standpoint, we can define k as being sensitive to the trade-off in n in the limit of diffusion-limited uptake and insensitive to the trade-off in the limit of cross-membrane transport–limited uptake, with the converse true for the resource affinity, as illustrated in figure 4 and table 2.

Although the critical size at which diffusion takes over from cross-membrane transport limitation is not well known, budgeting constraints suggest that even the smallest eukaryotes will be limited by diffusion at very low resource concentrations, such as those seen in the oligotrophic gyres (Chisholm 1992).

To account for an assumed inefficiency in division of the cell surface between uptake of two resources (sensu Troost et al. 2005*b*), the number of uptake sites n for each resource is subject to an additional reduction of up to 20% in mixotrophs. This penalty manifests in the maximum uptake rate and in either the half-saturation constant or the resource affinity, as outlined above and in table 2. In addition to this trade-off in surface transport sites, metabolic costs associated with maintaining two trophic strategies are also considered in the model: μ^{∞} is constrained to be up to 20% lower in mixotrophs than in specialists, while the minimum quota $Q^{\min}$ is constrained to be as much as 20% larger (following Crane and Grover 2010). Although these costs are consistent with previous theoretical work, they are nonetheless poorly constrained by data. The results were, however, qualitatively insensitive to changes of ±99%. We otherwise assume that autotrophs and heterotrophs have identical values for the minimum quota $Q^{\min}$ and the theoretical maximum growth rate μ^{∞}. Model symbols and units within the two limits are outlined in greater detail in table 2.

Model Analysis

In this section, we examine competition among autotrophs, mixotrophs, and heterotrophs within the limits of

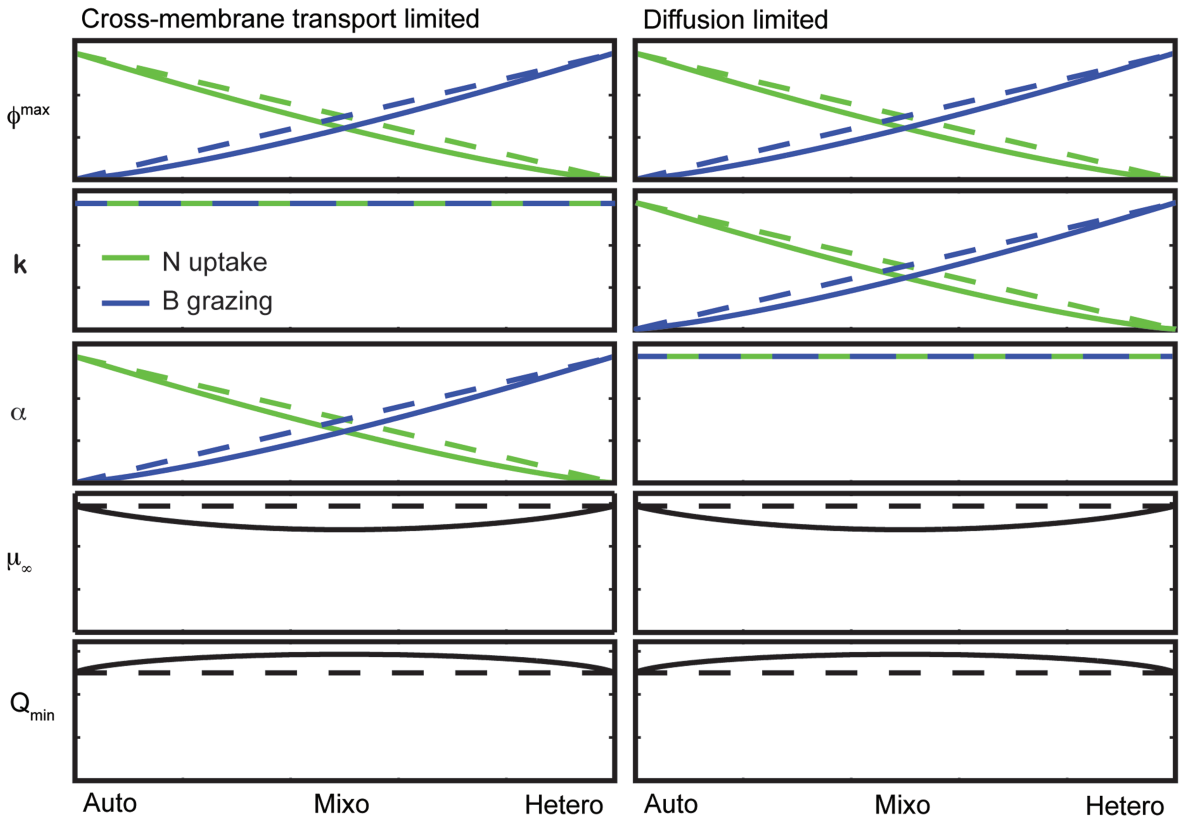

Figure 4: Trade-offs from autotrophy to heterotrophy in the limits of cross-membrane transport–limited uptake (*left*) and diffusion-limited uptake (*right*). The affinity curves are calculated as $\alpha = \phi^{max}k^{-1}$. The dashed lines represent the trade-offs in the absence of the extra inefficiency terms (see table 3).

diffusion-limited and cross-membrane transport–limited uptake. The model is evaluated at equilibrium, both numerically and analytically, as we try to explain the presence of mixotrophs under relatively stable conditions (e.g., Nygaard and Tobiesen 1993; Havskum and Riemann 1996; Zubkov and Tarran 2008). Given the short timescales of plankton growth and mortality, the assumption of equilibrium is appropriate for ecosystems within the strongly stratified subtropical gyres and also for summer stratification in more temperate regions, where growth and losses are tightly coupled. The ecology of mixotrophs in environments with strong seasonal or tidal cycles is beyond the scope of this work (but see Li et al. 2000; Litchman 2007; Bruggeman 2009).

Numerical Experiments

Figure 5 shows output from the numerical model as it was run to equilibrium with a time step of 10 minutes. The model parameter values are listed in table 1. When the model was parameterized with the assumption of cross-membrane transport–limited uptake (i.e., k was independent of n), the autotroph and heterotroph specialists quickly outcompeted the mixotrophs and settled into a two-species equilibrium (fig. 5*A*). Conversely, when the model was configured so that planktonic resource uptake was limited by diffusion (i.e., k was proportional to n), mixotrophs quickly outcompeted the specialists (fig. 5*B*), in spite of the extra physiological costs outlined above.

Mathematical Analysis

The numerical results suggest that mixotrophs gain an advantage when diffusion limitation dominates uptake at low resource concentrations. In this section, we examine this idea more fully, using analytical solutions derived through the application of resource competition theory (Tilman 1982).

The model equations can be solved by setting the time rate of change for all state variables to 0 and considering each plankton species in the absence of any other plankton types (i.e., $J = 1$, and bacteria are still present). These

Table 2: Biophysical parameters determining the resource uptake traits, within the limits of cross-membrane transport and diffusion limited uptake

	Symbol	Units	Transport	Diffusion
Trait:				
Uptake	ϕ		$nh^{-1}\{R/[(ah)^{-1} + R]\}$	$nh^{-1}\{R/[n(h4\pi rD\Phi S_\mathrm{h})^{-1} + R]\}$
Maximum uptake	$\phi^{\max}$		nh^{-1}	nh^{-1}
Half-saturation constant	k		$(ah)^{-1}$	$n(h4\pi r\kappa S_\mathrm{h}\Phi)^{-1}$
Affinity	$\alpha = \phi^{\max}k^{-1}$		na	$4\pi r\kappa S_\mathrm{h}\Phi$
Parameter:				
Resource concentration	R	mmol N m^{-3}		
Transport site encounter rate	a	m^3 day^{-1}		
Resource handling time	h	s $(\mathrm{mmol\ N})^{-1}$		
Transport sites per cell	n	cell^{-1}		
Resource diffusivity	κ	m^2 day^{-1}		
Sherwood number	S_h	...		
Cell shape parameter	Φ	...		

Note: Note that n is the only one of the listed biophysical parameters that varies among the modeled plankton types.

solutions are outlined in the appendix and are shown graphically in figure 6. The equilibrium solutions for autotrophic, heterotrophic, and mixotrophic plankton are plotted in the plane of ambient inorganic nitrogen and bacterial concentrations (Tilman 1982; Rothhaupt 1996). The dashed lines represent points in the nutrient plane where the specialists exhibit zero net growth. These "zero-net-growth isoclines" (ZNGI; Tilman 1982) run parallel to the *X*- and *Y*-axes, because the net growth rates of the autotroph and heterotroph are independent of the environmental concentrations of bacteria and inorganic nitrogen, respectively. The curved lines represent the ZNGIs of three different mixotrophs. At any point along one of these lines, the mixotrophs' overall nitrogen demand is satisfied by a combination of bacterial and inorganic nitrogen, as specified by the distance along the *X*- and *Y*-axes, respectively. These lines always have a negative gradient, as increasing amounts of one resource will decrease the demand for the other resource. The gradient gradually decreases to 0 at the *Y*-axis, as low bacterial biomasses are not heavily exploited when using the Holling type III grazing function.

Resource-competition theory states that in the presence of excess resources, populations of each plankton type will acquire resources and grow, reducing the ambient resource concentrations to a level where uptake and growth balance losses. If an organism is able to persist at ambient resource concentrations at which other organisms are not able to grow, those latter organisms will be competitively excluded. In figure 6, the autotroph and the heterotroph are able to survive at ambient resource concentrations of $\overline{N}_\mathrm{s}$ and $\overline{B}_\mathrm{s}$, respectively. When ambient resources reach these levels, both organisms are able to satisfy their resource requirements, and they coexist.

The resource requirements of a mixotroph can be satisfied through any combination of resources that falls on the ZNGI. In the case of mixotroph m_a, at every point along its ZNGI, it is outcompeted for resources by either the autotroph, the heterotroph, or both. This mixotroph will never be able to satisfy its nutrient requirements at equilibrium and will be competitively excluded. In the case of mixotroph m_b, although it is outcompeted for resources in almost all situations, it is able to maintain a steady population when ambient resource concentrations are at $\overline{N}_\mathrm{s}$ and $\overline{B}_\mathrm{s}$ (black dot in fig. 6). These are the exact levels that would be reached in the presence of the autotroph and heterotroph, and so mixotroph m_b is able to coexist with these two species. Finally, although mixotroph m_c is outcompeted when either inorganic or organic matter are very scarce, if the balance is favorable, it is able to survive at resource levels that exclude both the autotroph and the heterotroph (bold line in fig. 6).

Figure 6 reveals two conditions that must be satisfied if mixotrophs are to survive at equilibrium. Mixotrophs

Table 3: Formulas defining the parameter trade-offs

Parameter	Formula
μ_j^∞	$\mu^\infty[\beta^{1.3} + (1 - \beta)^{1.3}]$
$Q_j^{\min}$	$Q^{\min}[\beta^{0.77} + (1 - \beta)^{0.77}]$
$\phi_j^{N_{\max}}$	$\phi^{N_{\max}}\beta^{1.3}$
$\phi_j^{B_{\max}}$	$\phi^{B_{\max}}(1 - \beta)^{1.3}$
k_{N_j}	$k_\mathrm{B}\beta^{1.3}$
k_{B_j}	$k_\mathrm{N}(1 - \beta)^{1.3}$

Note: The 10 plankton types evaluated in the numerical model (i.e., $j = 1, 2, \ldots, 10$) vary linearly in their trophic strategy between purely autotrophic ($\beta = 1$) and purely heterotrophic ($\beta = 0$). Their parameter values are adjusted from the values given in table 1, using the formulas outlined above. Note that the half-saturation constants k_N and k_B are subject to these trade-offs only if uptake is diffusion limited.

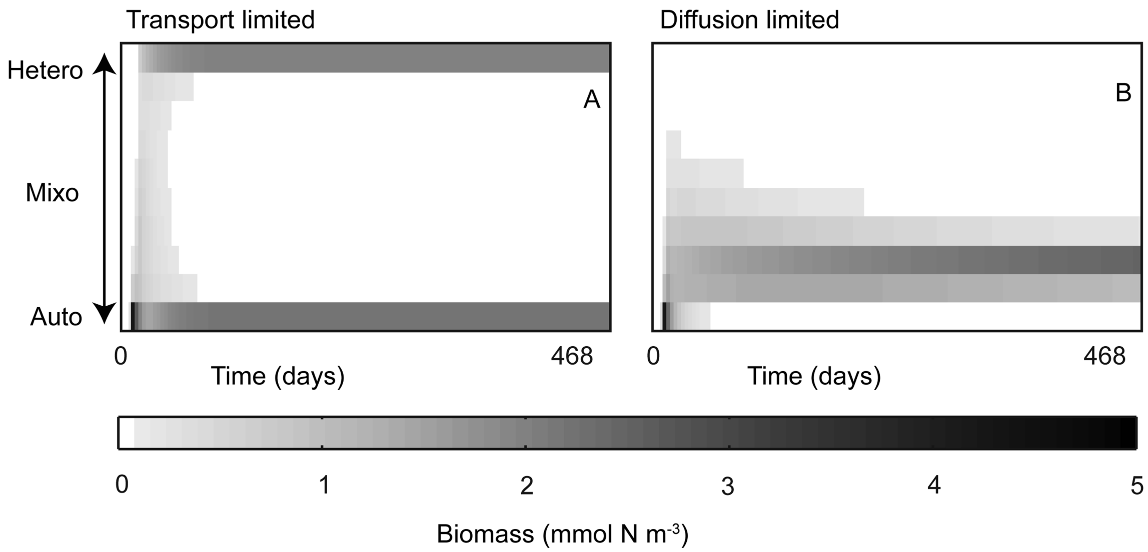

Figure 5: Biomass as a function of time: transport-limited results (*A*) and diffusion-limited results (*B*). The biomass of each modeled plankton class is represented by one row in each panel (autotrophs at the bottom, mixotrophs in the middle, heterotrophs at the top).

can survive at steady state only if they simultaneously avoid (1) being outcompeted for inorganic nitrogen by autotrophs (i.e., $\overline{N}_s \geq \overline{N}_m$) and (2) being outcompeted for bacterial prey by heterotrophs (i.e., $\overline{B}_s \geq \overline{B}_m$). Writing these two conditions using the full solutions derived in the appendix, we gain two simultaneous inequalities:

$$\frac{\bar{\mu}\overline{Q}_s k_{Ns}}{\phi_s^{N_{max}} - \bar{\mu}\overline{Q}_s} \geq \frac{\bar{\mu}\overline{Q}_m k_{Nm}(\overline{B}_m^2 + k_{Bm}^2) - \phi_m^{B_{max}}\overline{B}_m k_{Nm}}{\phi_m^{B_{max}}\overline{B}_m + \phi_m^{N_{max}}(\overline{B}_m^2 + k_{Bm}^2) - \bar{\mu}\overline{Q}_m(\overline{B}_m^2 + k_{Bm}^2)}, \tag{17}$$

$$\frac{\bar{\mu}\overline{Q}_s k_{Bs}^2}{\phi_s^{B_{max}} - \bar{\mu}\overline{Q}_s} \geq \frac{\bar{\mu}\overline{Q}_m k_{Bm}^2(\overline{N}_m + k_{Nm}) - \phi_m^{N_{max}}\overline{N}_m k_{Bm}^2}{\phi_m^{N_{max}}\overline{N}_m + G_m^{max}(\overline{N}_m + k_{Nm}) - \bar{\mu}\overline{Q}_m(\overline{N}_m + k_{Nm})}, \tag{18}$$

where an overbar denotes the equilibrium value for a variable. The inequalities can be rearranged (see appendix) to give the following general condition for mixotroph survival at equilibrium:

$$\frac{\overline{Q}_s}{\overline{Q}_m}\left[\overbrace{\frac{\alpha_m^N}{\alpha_s^N}}^{1} + \overbrace{\frac{\alpha_m^B}{\alpha_s^B}}^{2} - \overbrace{\frac{\phi_m^{N_{max}}}{\phi_s^{N_{max}}}\left(\frac{k_{Ns}}{k_{Nm}} - 1\right)\frac{\overline{N}_m}{\overline{N}_m + k_{Nm}}}^{3} \right. \tag{19}$$

$$\left. - \overbrace{\frac{\phi_m^{B_{max}}}{\phi_s^{B_{max}}}\left(\frac{k_{Bs}^2}{k_{Bm}^2} - 1\right)\frac{\overline{B}_m^2}{\overline{B}_m^2 + k_{Bm}^2}}^{4}\right] \geq 1,$$

where $\phi^{max}k^{-1}$ has been replaced with the generic resource affinity α (m^3 $cell^{-1}$ day^{-1}), and the quota size required for equilibrium growth is given by

$$\overline{Q} = \frac{Q^{min}}{1 - \bar{\mu}/\mu^{\infty}}. \tag{20}$$

We have already seen that Q^{min} is always larger in mixotrophs than in specialists, because the former must incorporate the cellular machinery required for both autotrophy and heterotrophy (Raven 1997). In addition, empirical observations suggest that μ^{∞} is smaller in mixotrophs, and hence equation (20) tells us that $\overline{Q}$ is always larger in mixotrophs. Although equation (19) is somewhat complicated, it can be greatly simplified by substituting for k and α within the limits of cross-membrane transport and diffusion limited uptake.

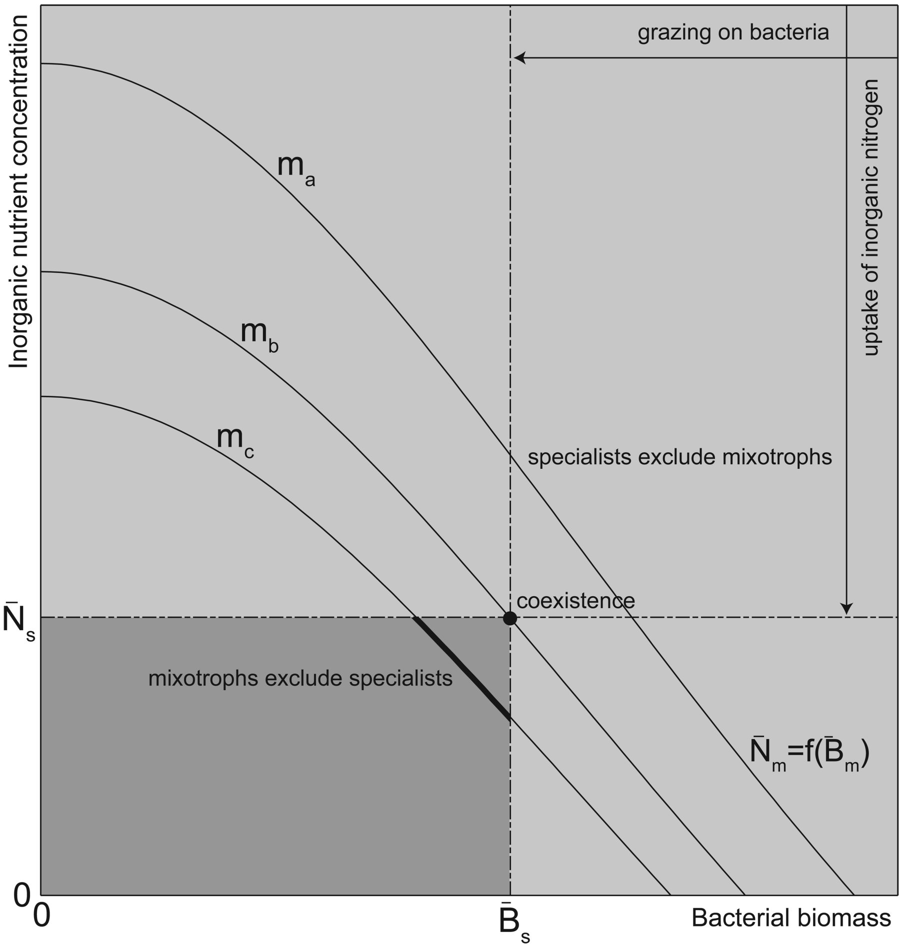

Figure 6: Zero net growth isoclines for an autotroph, a heterotroph, and three different mixotrophs (m_a, m_b, and m_c) as functions of ambient concentrations of inorganic nitrogen and bacteria. See text for further description.

Cross-Membrane Transport–Limited Uptake

The relative importance of diffusion and cross-membrane transport varies with environmental conditions and a number of morphological and physiological factors (Pasciak and Gavis 1974; Aksnes and Egge 1991). Cross-membrane transport limitation predominates at high resource concentrations and is most important in very small cells (Chisholm 1992; Armstrong 2008). In this limit, the half-saturation constants k_N and k_B take the general form $k = (ah)^{-1}$, and the maximum possible uptake rate is given by $\phi^{max} = nh^{-1}$. The affinity in this case is given by $\alpha = \phi^{max}k^{-1} = na$, and this is proportional to n in the same way as ϕ^{max} is. This means that uptake is affected by the trade-off in n at both high and low resource concentrations.

Recalling that k is independent of trophic strategy, terms 3 and 4 drop out of equation (19) (the terms in parentheses approach 0), and the condition for mixotroph survival simplifies to

$$\frac{\overline{Q}_s}{\overline{Q}_m}\left(\frac{\alpha_m^N}{\alpha_s^N}+\frac{\alpha_m^B}{\alpha_s^B}\right)=\frac{\overline{Q}_s}{\overline{Q}_m}\left(\frac{n_m^N}{n_s^N}+\frac{n_m^B}{n_s^B}\right)\geq 1. \qquad (21)$$

This is similar to equation (8) in Thingstad et al. (1996) but accounts for the more realistic saturating-uptake functions, as well as differences in the growth rates and minimum quotas. Given our assumptions regarding the physiological trade-offs, the condition cannot be satisfied. The ratio $\overline{Q}_s/\overline{Q}_m$ is always <1 on account of our assumption that mixotrophs have larger equilibrium quotas than specialists, and the bracketed terms cannot be >1 because the number of uptake sites for each resource is limited by the partitioning of the cell surface.

In summary, the two specialist plankton species may use all of their available surface area to acquire resources, but mixotrophs must partition their surface area for the handling of two resources. The total mixotroph uptake rate is effectively a weighted average of the two specialist uptake rates. As long as cross-membrane transport remains limiting, mixotrophs cannot simultaneously outcompete both specialists in terms of total resource acquisition, and because they also have the highest metabolic costs, they will always be outcompeted at equilibrium.

Diffusion- or Encounter-Limited Uptake

Although diffusion limitation is most important in large cells and at low resource concentrations, it is likely that it controls uptake in all eukaryotes at very low resource concentrations (Chisholm 1992). Cross-membrane transport limitation will, however, always take over at some higher resource concentration. In this limit, the half-saturation constants take the general form $k = n(h4\pi r\Phi S_{\mathrm{h}}\kappa)^{-1}$, and because the maximum possible uptake rate is still given by $\phi^{\max} = nh^{-1}$, the affinity is now independent of n, with $\alpha = 4\pi rD\Phi S_{\mathrm{h}}$. The number of cross-membrane transport sites remains important at high resource concentrations but becomes much less important as resource concentrations decrease and diffusion takes over as a limiting factor.

As the resource affinities are now independent of n, the first and second terms in equation (19) each reduce to 1. Although the half-saturation constants are now given by $k = n(h4\pi r\Phi S_{\mathrm{h}}\kappa)^{-1}$, the third and fourth terms also simplify because the invariant biophysical parameters all drop out:

$$\frac{\overline{Q}_{\mathrm{s}}}{\overline{Q}_{\mathrm{m}}}\Bigg[1 + 1 + \left(\frac{n_{\mathrm{m}}}{n_{\mathrm{s}}} - 1\right)\overbrace{\frac{\overline{N}_{\mathrm{m}}}{\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}}}^{\mathrm{A}} + \left(\frac{n_{\mathrm{m}}}{n_{\mathrm{s}}} - 1\right)\overbrace{\frac{\overline{B}^2_{\mathrm{m}}}{\overline{B}^2_{\mathrm{m}} + k^2_{\mathrm{Bm}}}}^{\mathrm{B}}\Bigg] \geq 1. \tag{22}$$

If resource concentrations are large relative to the half-saturation constants (i.e., $N \gg k_{\mathrm{Nm}}$ and $B \gg k_{\mathrm{Bm}}$), then terms A and B in equation (22) approach 1, and the condition simplifies to

$$\frac{\overline{Q}_{\mathrm{s}}}{\overline{Q}_{\mathrm{m}}}\left[\frac{n^N_{\mathrm{m}}}{n^N_{\mathrm{s}}} + \frac{n^B_{\mathrm{m}}}{n^B_{\mathrm{s}}}\right] \geq 1. \tag{23}$$

This is the same as equation (21), indicating that if resource uptake is saturated at high resource concentrations, then the trade-off in the cell surface area is important and mixotrophs cannot outcompete specialists. However, as the system approaches equilibrium, resource are drawn down to the relatively low concentrations at which the resource supply is balanced by uptake. As resources become scarce (i.e., $N \ll k_{\mathrm{Nm}}$ and $B \ll k_{\mathrm{Bm}}$), terms A and B in equation (22) both approach 0, and the condition simplifies to

$$\frac{\overline{Q}_{\mathrm{s}}}{\overline{Q}_{\mathrm{m}}} \geq \frac{1}{2}. \tag{24}$$

As resource concentrations diminish, the biological trade-off in n becomes less important, and mixotrophs gain an uptake advantage as they are able to simultaneously match the uptake rates of both the autotrophs and the heterotrophs. This advantage is large enough to compensate for as much as a twofold increase in other physiological costs (i.e., the equilibrium quota $\overline{Q}_{\mathrm{m}}$) relative to the specialists (eq. [24]). This is possible because uptake becomes less dependent on the trade-off in cell surface area as resources are drawn down to a point where diffusion is slow relative to the resource-handling time. Handling sites are unoccupied for most of the time, and the total number of sites becomes less important. Mixotrophs can effectively acquire inorganic nitrogen at the same rate as the autotroph and can graze bacteria at the same rate as the heterotroph. For the parameters applied here, mixotrophs gain enough resources to offset their higher metabolic costs and can therefore exclude the specialists. Generalizing beyond these limits, at resource concentrations between zero and saturation, mixotrophs will have a larger uptake advantage at lower resource concentrations.

Discussion

Mixotrophic plankton combine autotrophic and heterotrophic traits, but this generality represents a compromise between the two trophic strategies. It could be argued that the slow uptake and growth rates of mixotrophs should make these organisms less competitive, but we have shown that the onset of physical uptake limitation can diminish the effects of certain biological trade-offs. When diffusion sets the rate of resource acquisition, mixotrophs can simultaneously match the uptake rates of specialist autotrophs and specialist heterotrophs. This ability to efficiently combine two resources allows mixotrophs to compensate for the slower growth rates and larger minimum quotas that are associated with their generalist strategy.

Generalism gives mixotrophic plankton an advantage when the resource encounter rate is low. Although mixotrophs cannot exploit resources at the same high rates as the specialists, this is irrelevant if there is time to process each encountered resource unit before the next one arrives. In the most oligotrophic aquatic environments, mixotrophs may acquire almost as many resources as both the specialists combined, and for the model presented here, this advantage is more than enough to cover the extra metabolic costs of mixotrophy. Conversely, specialism becomes a good strategy whenever resources are encountered more frequently than they can be assimilated. When resources are abundant, such as in phytoplankton blooms, autotroph and heterotroph specialists lose nothing by being selective but gain advantage from their higher growth rates and lower metabolic costs.

Although the diffusion-limited encounter rate is most important in large phytoplankton (Armstrong 2008) and in bacterivorous grazers (Dolan and Pérez 2000), even the smallest protists will be diffusion limited under strongly oligotrophic conditions (Chisholm 1992). As a result, small mixotrophic protists are able to thrive in the stratified oligotrophic waters of both temperate and subtropical oceans (Havskum and Riemann 1996; Zubkov and Tarran 2008).

Unmanipulated field observations (Andersson et al. 1996; Hajdu et al. 1996) and nutrient enrichment experiments (Samuelsson et al. 2002) have shown that mixotrophic *Chrysochromulina* species are more abundant under oligotrophic conditions than when nutrients are replete. A community shift from mixotrophic to specialist species has also been observed upon nutrient addition in mesocosm experiments (Havskum and Hansen 1997; Baretta-Bekker et al. 1998) and field studies (Arenovski et al. 1995). Further experimental support is provided by Katechakis and Stibor (2006), who found that oligotrophic conditions were required for the survival of the mixotrophic nanoflagellate *Ochromonas tuberculata* in a community of specialist photo- and phagotrophic plankton. The observation that mixotrophic flagellates may relieve iron limitation via the ingestion of bacteria (Barbeau et al. 1996) is also consistent with the conclusion that mixotrophs may combine scarce resources in order to outcompete specialists.

A similar niche has been noted for the mixotrophic consumption of inorganic nutrients and light (e.g., Rothhaupt 1996; Tittel et al. 2003), and the ability of mixotrophs to combine inorganic nutrients, photosynthesis, and organic resources may help to explain the persistence of unexpectedly high concentrations of chlorophyll *a* in both postbloom, nutrient-limited waters (Tittel et al. 2003) and extremely low-light, deep-winter mixed layers (e.g., Backhaus et al. 2003; Ward and Waniek 2007).

The size composition of the planktonic community may also be affected by the higher efficiency of diffusion-limited mixotrophs. Observations show that phytoplankton communities generally respond to increases in nutrient availability with a broadening of the plankton-size spectrum to include larger cells (Chisholm 1992). It is hypothesized that larger cells benefit from a combination of reduced grazing pressure (Moloney and Field 1989; Armstrong 1994) and cellular-loss processes (Kriest and Oschlies 2007) but cannot grow at low resource concentrations, because they are strongly limited by diffusion (Armstrong 2008). If plankton can use mixotrophy to overcome moderate diffusion limitation, this constraint on the community-size distribution may be relaxed, and mixotrophs may be able to reduce their grazing and exudation losses by growing to larger sizes. We speculate that under stable conditions, mixotrophs will survive at the upper end of the observed community-size spectrum, at the transition between cross-membrane transport and diffusion limitation. This would lead to a preponderance of larger mixotrophs in eutrophic systems such as coastal and upwelling regions (e.g., Jeong et al. 2005; Johnson and Stoecker 2005; Yoo et al. 2009), with smaller mixotrophs restricted to oligotrophic regions (e.g., Havskum and Riemann 1996; Zubkov and Tarran 2008). Further observational and modeling work will, however, be required to confirm or refute this prediction.

We have used an idealized model to show how mixotrophs can take advantage of the physical limits of resource acquisition in order to compete with specialist autotrophic and heterotrophic plankton. Mixotrophy is undoubtedly a complex phenomenon, and we seek not to reproduce all of this complexity but rather to capture essential aspects of the process in the simplest and most general description possible. This particular model does not account for such processes as kleptoplastidity (Stoecker 2009), toxin production (Sheng et al. 2010), or nonequilibrium dynamics (Litchman 2007), and the effects of size were not fully explored in this study. The model also lacks the level of detail included in a number of conceptual models (Jones 1997, 2000; Stoecker 1998), but the formulation may be sufficiently general to be applied, with certain caveats, to many of the different mixotrophic "groups or "types" that have been qualitatively outlined in the literature. In the future, the insights gained from simple models such as this one and others (e.g., Thingstad et al. 1996; Troost 2005*b*; Bruggeman 2009; Crane and Grover 2010) could be combined with more realistic physiology (e.g., Flynn and Mitra 2009) and a more detailed representation of the ecosystem structure and ocean physics, so that the diverse range of mixotrophic behavior might be reproduced and better understood in a single mechanistic model.

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APPENDIX

Resource Competition

The ecosystem model equations can be solved by setting the time rate of change for all state variables to 0 and considering each plankton species in the absence of any other plankton types (i.e., $J = 1$, and bacteria are still present). In this way, the equilibrium resource requirements for each plankton type can be evaluated and used to predict the results of resource competition (Tilman 1982).

In this analysis, the subscript j is dropped from all parameters and state variables. An overbar indicates an equilibrium value, with subscript s denoting parameters specific to specialists and subscript m indicating parameters specific to mixotrophs.

All plankton. For all populations of cells at steady state, growth is balanced by dilution and mortality (eq. [11]):

$$\bar{\mu} = D + m. \tag{A1}$$

As D and m are independent of trophic strategy, $\bar{\mu}$ is identical for all cells.

Specialists. Steady state solutions can be found for the quota size at equilibrium and the resource requirements of the specialists:

$$\overline{Q}_{\mathrm{s}} = \frac{Q_{\mathrm{s}}^{\min}}{1 - \bar{\mu}/\mu_{\mathrm{s}}^{\infty}}, \tag{A2}$$

$$\overline{N}_{\mathrm{s}} = \frac{\bar{\mu}\overline{Q}_{\mathrm{s}}k_{\mathrm{Ns}}}{\phi_{\mathrm{s}}^{N_{\max}} - \bar{\mu}\overline{Q}_{\mathrm{s}}}, \tag{A3}$$

$$\overline{B}_{\mathrm{s}} = \sqrt{\frac{\bar{\mu}\overline{Q}_{\mathrm{s}}k_{\mathrm{Bs}}^2}{\phi_{\mathrm{s}}^{B_{\max}} - \bar{\mu}\overline{Q}_{\mathrm{s}}}}. \tag{A4}$$

For purely autotrophic and heterotrophic cells, the quota is in balance between growth and the uptake of inorganic nitrogen N or bacteria B. The N requirement of the specialist autotroph is independent of B, and the converse is true for the specialist heterotroph.

Mixotrophs. Similar solutions can be found for mixotrophic plankton, but in this case the quota is in balance between growth and the uptake of both inorganic nitrogen and bacteria. Inorganic and organic resources are broadly substitutable (Tilman 1982), and thus increasing the supply of one will decrease the demand for the other. For this reason, there is not one steady state value for $\overline{N}$ and $\overline{B}$ but rather a set of correlated solutions:

$$\overline{Q}_{\mathrm{m}} = \frac{Q_{\mathrm{m}}^{\min}}{1 - (\bar{\mu}/\mu_{\mathrm{m}}^{\infty})}, \tag{A5}$$

$$\overline{N}_{\mathrm{m}} = \frac{\bar{\mu}\overline{Q}_{\mathrm{m}}k_{\mathrm{Nm}}(\overline{B}_{\mathrm{m}}^2 + k_{\mathrm{Bm}}^2) - \phi_{\mathrm{m}}^{B_{\max}}\overline{B}_{\mathrm{m}}^2k_{\mathrm{Nm}}}{\phi_{\mathrm{m}}^{B_{\max}}\overline{B}_{\mathrm{m}}^2 + \phi_{\mathrm{m}}^{N_{\max}}(\overline{B}_{\mathrm{m}}^2 + k_{\mathrm{Bm}}^2) - \bar{\mu}\overline{Q}_{\mathrm{m}}(\overline{B}_{\mathrm{m}}^2 + k_{\mathrm{Bm}}^2)}, \tag{A6}$$

$$\overline{B}_{\mathrm{m}} = \sqrt{\frac{\bar{\mu}\overline{Q}_{\mathrm{m}}k_{\mathrm{B}}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}) - \phi_{\mathrm{m}}^{N_{\max}}\overline{N}_{\mathrm{m}}k_{\mathrm{Bm}}^2}{\phi_{\mathrm{m}}^{N_{\max}}\overline{N}_{\mathrm{m}} + \phi_{\mathrm{m}}^{B_{\max}}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}) - \bar{\mu}\overline{Q}_{\mathrm{m}}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}})}}. \tag{A7}$$

Competition. Two conditions must be satisfied if mixotrophs are to survive at equilibrium. Mixotrophs must be able to find a balance between consumption of inorganic nitrogen and bacteria where, through utilization of these two resources, they simultaneously avoid (1) being outcompeted for inorganic nitrogen by autotrophs (i.e., $\overline{N}_{\mathrm{s}} \geq \overline{N}_{\mathrm{m}}$) and (2) being outcompeted for bacterial prey by heterotrophs (i.e., $\overline{B}_{\mathrm{s}} \geq \overline{B}_{\mathrm{m}}$). These two conditions can be expressed mathematically as a pair of simultaneous inequalities combining equations (A3), (A4), (A6), and (A7) (note that the second inequality is actually $\overline{B}_{\mathrm{s}}^2 \geq \overline{B}_{\mathrm{m}}^2$, which is equivalent because biomass cannot be <0):

$$\frac{\bar{\mu}\overline{Q}_{\mathrm{s}}k_{\mathrm{Ns}}}{\phi_{\mathrm{s}}^{N_{\max}} - \bar{\mu}\overline{Q}_{\mathrm{s}}} \geq \frac{\bar{\mu}\overline{Q}_{\mathrm{m}}k_{\mathrm{Nm}}(\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2}) - \phi_{\mathrm{m}}^{B_{\max}}\overline{B}_{\mathrm{m}}k_{\mathrm{Nm}}}{\phi_{\mathrm{m}}^{B_{\max}}\overline{B}_{\mathrm{m}} + \phi_{\mathrm{m}}^{N_{\max}}(\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2}) - \bar{\mu}\overline{Q}_{\mathrm{m}}(\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2})}, \tag{A8}$$

$$\frac{\bar{\mu}\overline{Q}_{\mathrm{s}}k_{\mathrm{Bs}}^{2}}{\phi_{\mathrm{s}}^{B_{\max}} - \bar{\mu}\overline{Q}_{\mathrm{s}}} \geq \frac{\bar{\mu}\overline{Q}_{\mathrm{m}}k_{\mathrm{Bm}}^{2}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}) - \phi_{\mathrm{m}}^{N_{\max}}\overline{N}_{\mathrm{m}}k_{\mathrm{Bm}}^{2}}{\phi_{\mathrm{m}}^{N_{\max}}\overline{N}_{\mathrm{m}} + G_{\mathrm{m}}^{\max}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}) - \bar{\mu}\overline{Q}_{\mathrm{m}}(\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}})}. \tag{A9}$$

Multiplying out the fractions and dividing through by $\bar{\mu}$, Q_{m}, $\phi_{\mathrm{s}}^{N_{\max}}$, k_{Nm}, and $(\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2})$ in the first inequality and by equivalent terms in the second and using equation (8) to substitute for

$$\bar{\mu}\overline{Q}_{\mathrm{m}} = \phi_{\mathrm{m}}^{N_{\max}}\frac{\overline{N}_{\mathrm{m}}}{\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}} + \phi_{\mathrm{m}}^{B_{\max}}\frac{\overline{B}_{\mathrm{m}}^{2}}{\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2}},$$

the following can be obtained by adding the two simultaneous equations:

$$\frac{\overline{Q}_{\mathrm{s}}}{\overline{Q}_{\mathrm{m}}}\left[\overbrace{\frac{\alpha_{\mathrm{m}}^{N}}{\alpha_{\mathrm{s}}^{N}}}^{1} + \overbrace{\frac{\alpha_{\mathrm{m}}^{B}}{\alpha_{\mathrm{s}}^{B}}}^{2} - \overbrace{\frac{\phi_{\mathrm{m}}^{N_{\max}}}{\phi_{\mathrm{s}}^{N_{\max}}}\left(\frac{k_{\mathrm{Ns}}}{k_{\mathrm{Nm}}} - 1\right)\frac{\overline{N}_{\mathrm{m}}}{\overline{N}_{\mathrm{m}} + k_{\mathrm{Nm}}}}^{3} - \overbrace{\frac{\phi_{\mathrm{m}}^{B_{\max}}}{\phi_{\mathrm{s}}^{B_{\max}}}\left(\frac{k_{\mathrm{Bs}}^{2}}{k_{\mathrm{Bm}}^{2}} - 1\right)\frac{\overline{B}_{\mathrm{m}}^{2}}{\overline{B}_{\mathrm{m}}^{2} + k_{\mathrm{Bm}}^{2}}}^{4}\right] \geq 1. \tag{A10}$$

In order for mixotrophs to be viable at steady state, this condition must be satisfied (note that the generic resource affinity $\alpha = \phi^{\max}k^{-1}$).

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