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Competition between phytoplankton and mixotrophs leads to metabolic character displacement

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ABSTRACT

While plankton are often characterized by metabolism as either phototrophic primary producers or heterotrophic consumers, many actually combine photosynthesis and phagotrophy within a single cell. These "mixotrophic" plankton, which play an important biogeochemical role in marine food webs, exhibit diverse metabolic strategies with varied contributions from photosynthesis and phagotrophy. Mixotrophs co-exist with specialist phototrophs and heterotrophs, competing for shared resources; yet we do not know how this competition alters a mixotroph's metabolic strategy or impacts biogeochemistry. We constructed a mathematical model to simulate the dynamics of a planktonic community which consists of mixotrophs and their specialist phototrophic competitor, phytoplankton. Our simulation demonstrates how the presence of competing phytoplankton causes metabolic character displacement, shifting mixotrophs to a more heterotrophic niche. We find that the displacement is affected by various environmental and physiological factors. For example, this displacement effect is temperature dependent, suggesting a link between community-level competitive mechanisms and global climate change. The proposed model therefore may be used to develop a more comprehensive analysis of the competition between constitutive mixotrophs and specialist phototrophs or heterotrophs. Our model also provides a mathematical framework for predicting constitutive mixotroph survival in the context of global warming.

1. Introduction

Biologists often characterize life by metabolism, broadly categorizing organisms into two classes: autotrophs (that generate organic material from chemical or light energy) and heterotrophs (that obtain organic matter from other species through, e.g., predation). However, a metabolic strategy that combines photosynthesis and heterotrophy, known as mixotrophy, is actually widespread (Sanders, 1991; Flynn et al., 2013; Selosse et al., 2017), particularly in planktonic ecosystems (Burkholder et al., 2008; Stoecker et al., 2017). Indeed, mixotrophy is the default lifestyle of many single-celled plankton (Ward, 2019), and microbial mixotrophs can dominate marine communities as key grazers of bacteria (Zubkov and Tarran, 2008; Unrein et al., 2014).

Mixotrophic species can exhibit diverse metabolic strategies. Amongst the constitutive mixotrophs (i.e., mixotrophs that contain a permanent plastid but still engage in phagotrophy; Stoecker et al., 2017), species vary in the degree to which they are obligately photosynthetic (i.e., will die without light) or phagotrophic (i.e., will die without prey) and in the degree to which they combine the two forms of metabolism. For example, under combined light and prey limitation, two mixotrophic chrysophytes can exhibit very different metabolic strategies (Wilken et al., 2020): One *Ochromonas* strain was able to adjust its nutrition from complete phagotrophy to mixotrophy as a function of light and therefore is characterized as a facultative mixotroph. A different strain was identified as an obligate phototroph because it could not survive phagotrophically in darkness (Lie et al., 2018). Li et al. (2022) also illustrated in their study a spectrum of mixotrophic strategies by the variation in grazing abilities.

Where mixotrophs fall on the phototrophy–phagotrophy spectrum can have significant consequences for ecosystem-level biogeochemical characteristics. Since mixotrophs compete with both phototrophs and heterotrophs for resources, their metabolic strategy contributes to community composition and the relative abundance of primary and secondary producers (Stickney et al., 2000), particularly when a trade-off between specialization and generalization is considered (Våge et al., 2013). It has also been hypothesized that nutrient cycling and trophic transfer efficiency likely depend on the predominant mixotroph metabolic strategy within the ecosystem (Li et al., 2022), and that a mixotroph-dominated structure has a potentially more efficient cycle between remineralization and primary production (Mitra et al., 2014).

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What strategy, then, should a mixotroph adopt? The answer depends on environmental conditions. Stoecker (1998) constructed conceptual models for six physiological types of mixotrophs, comparing their maximum growth rates under different metabolic strategies, and demonstrating that the growth optimizing strategy of mixotrophs is affected by the availability of dissolved inorganic nutrients, light, and prey. Chakraborty et al. (2017) developed a trait-based model to analyze how the optimal metabolic strategies of mixotrophs are dependent on their cell size under various environmental conditions. Their study showed how environmental conditions affect mixotroph metabolic strategies in a controlled setting where mixotrophs are the only species present.

While these studies considered mixotrophs in isolation, in reality it is rare to find a single species of plankton living by themselves in marine ecosystems. Mixotrophs often co-occur with similarly sized phototrophs and heterotrophs (Edwards, 2019). This coexistence of species that have similar metabolic strategies leads to competition for limited resources, such as inorganic nutrients and light (Decelle, 2013). As a result, mixotroph metabolic strategies are likely shaped not only by the supply of resources (e.g., light, inorganic nutrients, and prey), but also by competition with other species. Compared to their specialist competitors, mixotrophs invest extra energy into maintaining cellular machinery for both photosynthesis as well as prey uptake and digestion, which may lead to lowered resource use efficiency (Tittel et al., 2003; Raven, 2003). As a result, it has been suggested that mixotrophs should be less successful in competition compared to specialist phototrophs or heterotrophs (Rothhaupt, 1996; Thingstad et al., 1996; Tittel et al., 2003; Jost et al., 2004; Flynn and Mitra, 2009). However, other studies have shown that mixotrophy in fact provides advantages in certain environments (Nygaard and Tobiesen, 1993; Flynn and Mitra, 2009). For example, in a controlled environment with characteristics conventionally associated with oligotrophic lakes, mixotrophs were found to sustain positive net growth while their specialist competitors, zooflagellates, were eliminated almost everywhere. (Crane and Grover, 2010). Clearly, competition affects the ecological constraints that mixotrophs are subjected to, which raises the question of what specific environmental conditions favor mixotrophs over their specialized competitors.

Competitive effects may be modulated by abiotic environmental conditions, including temperature. Warming treatments have been shown to have a positive effect on phytoplankton biomass and a negative effect on nutrient flux (as a result of increased water column stratification), leading to potentially more intense competition among primary producers (Lewandowska et al., 2014). Experimental results have not been entirely conclusive, however. For example, Princiotta et al. (2016) examined the role of temperature on grazing and photosynthesis of a mixotrophic alga, identifying an increase in both ingestion and photosynthesis rates. However, Wilken et al. (2013) showed that warming can lead to differences in the increase of mixotroph metabolic rates, proposing that it would be more beneficial for mixotrophs to become more phagotrophic with rising temperature. The relationship between mixotroph metabolism and temperature appears complex and may incorporate ecological feedbacks, making prediction of warming's effect on competitive trait displacement difficult.

Here, we model the effects of a specialized phototrophic competitor on the optimal metabolic strategy of a constitutive mixotroph. In our model, mixotrophic growth (as well as competition with a specialized primary producer) depends on a single nutrient resource. Phototrophy and phagotrophy are treated as completely substitutable methods for obtaining this resource and fueling subsequent growth. These simplifying assumptions help abstract mixotrophs' complex interactions as both producers and consumers (Stickney et al., 2000) into mathematical terms. By varying input parameters, we simulate a variety of interesting, real-life and theoretical scenarios. Specifically, we ask (1) how different investments of resources into phagotrophy and phototrophy affect resource availability in the environment, (2) what effects competition between phytoplankton and mixotrophs has on mixotroph metabolic strategies, (3) what factors contribute to these effects, and (4) how temperature alters outcomes.

2. Methods

To simulate the dynamics between specialized phototrophic phytoplankton (P) and mixotrophs (M), we used a box model of a marine microbial food web in a well-mixed water column (Fig. 1). In our model, mixotrophs graze on bacteria (B) and compete with phytoplankton for inorganic nutrients (N) needed for photosynthetic growth. Mixotroph and phytoplankton mortality contributes to a pool of organic matter (O) that is remineralized by bacteria. In our model, all biotic and abiotic state variables are measured in units of nutrients per volume (Table 1).

Nutrients in our model come from two sources: vertical mixing and remineralization of organic matter. Mixing occurs at a dilution rate (D) with an external nutrient concentration N_0. Nutrients are consumed by phytoplankton and mixotrophs, which have maximum growth rates u_P and u_M, respectively. Bacteria contribute to the nutrient pool by remineralization of organic matter with an efficiency parameter c. (All symbols, their meanings and typical units, and parameter values used in this study are listed in Table 1.)

$$\frac{dN}{dt} = -u_P PN - u_M MN + D(N_0 - N) + cu_B BO; \tag{1}$$

Nutrient uptake by phytoplankton supports growth. Phytoplankton mortality (m_P) is proportional to P^2 and represents the death of phytoplankton from outside predators and natural causes. Phytoplankton are also diluted out of the system at the dilution rate D.

$$\frac{dP}{dt} = u_P PN - m_P P^2 - DP; \tag{2}$$

Like phytoplankton, mixotrophs experience photosynthetic growth, density-dependent mortality, and dilution, but also feed on bacteria with an attack rate a. The mixotroph nutrient uptake rate is given by u_M, and the mixotroph mortality rate is given by m_M.

$$\frac{dM}{dt} = u_M MN - m_M M^2 + aMB - DM. \tag{3}$$

The proportion of mixotroph investment in phototrophy is denoted by θ. The nutrient uptake rate of mixotroph (u_M) is proportional to θ and reaches its theoretical maximum value ($\hat{u}_M$) when mixotrophs are fully phototrophic (i.e. when $\theta = 1$):

$$u_M = \theta \hat{u}_M. \tag{4}$$

We assume that mixotrophs experience a trade-off between metabolic investments, such that increasing investments in phototrophy cause decreasing investments in phagotrophy. Following Gonzalez et al. (2022), we model the attack rate a as a decreasing function of θ that is scaled by the shape parameter z:

$$a = \left(1 - \theta^{2^z}\right)^{2^{-z}} \hat{a}, \tag{5}$$

where $\hat{a}$ is the maximum achievable attack rate when $\theta = 0$. When $z = 0$, the mixotroph experiences a linear tradeoff. In the supplementary material, we consider two additional cases: $z = 1$, representing a "generalist" tradeoff in which the mixotroph can simultaneously maintain high rates of phototrophy and phagotrophy at intermediate θ values, and $z = -1$, representing a "specialist" tradeoff in which only one metabolic rate can be high at a time (Figure S1).

Phytoplankton, mixotroph, and bacteria mortality terms all contribute to the pool of organic matter, which is then remineralized by bacteria with a rate of u_B and remineralization efficiency c. Bacteria are grazed by mixotrophs with the attack rate $(1-\theta)\hat{a}$ and have a mortality rate m_B. Both bacteria and organic matter are removed from the system at the dilution rate D.

$$\frac{dB}{dt} = (1-c)u_B BO - (1-\theta)\hat{a}MB - m_B B^2 - DB; \tag{6}$$

Table 1
Model symbols and their meanings.

Symbol	Description	Typical units	Simulation values (Without Phytoplankton)	Simulation values (With Phytoplankton)
Variables:				
N	Inorgantic nutrients	μmol m^{-3}	$N_0 = 1$	$N_0 = 1$
P	Phytoplankton	μmol m^{-3}	$P_0 = 0$	$P_0 = 1$
M	Mixotroph	μmol m^{-3}	$M_0 = 1$	$M_0 = 1$
B	Bacteria	μmol m^{-3}	$B_0 = 1$	$B_0 = 1$
O	Organic matters	μmol m^{-3}	$O_0 = 1$	$B_0 = 1$
t	Time	days		
Parameters:				
θ	Percentage of resource mixotroph invest in phototrophy		$(0, 1)$	$(0, 1)$
u_P	Growth rate, phytoplankter	day^{-1}	0	1
u_M	Growth rate, mixotroph	day^{-1}	$\hat{u}_M\theta$	$\hat{u}_M\theta$
$\hat{u}_M$	Maximum growth rate, mixotroph	day^{-1}	0.5	0.5
u_B	Growth rate, bacteria	day^{-1}	1	1
m_P	Mortality rate of phytoplankter	day^{-1}	0.01	0.01
m_M	Mortality rate of mixotroph	day^{-1}	0.01	0.01
m_B	Mortality rate of bacteria	day^{-1}	0.01	0.01
D	Dilution rate	day^{-1}	0.01	0.01
a	Attack rate of mixotroph on bacteria	m^3 day^{-1} $\mu\mathrm{mol}^{-1}$	$\hat{a}(1-\theta)$	
$\hat{a}$	Maximum attack rate of mixotroph on bacteria	m^3 day^{-1} $\mu\mathrm{mol}^{-1}$	0.5	0.5
N_0	External nutrient concentration	μmol m^{-3}	1	1
Q_h	Temperature coefficient Q_{10} for any phagotrophic process		2.70	2.70
Q_p	Temperature coefficient Q_{10} for any phototrophic process		1.88	1.88
c	Efficiency of bacteria remineralization		0.5	0.5

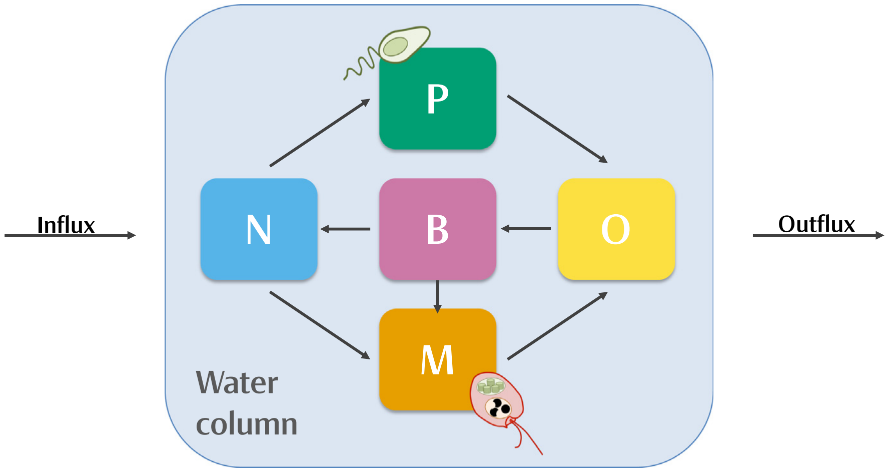

Fig. 1. The dynamics among specialized phototrophic phytoplankton (P), mixotrophs (M) and bacteria (B) using nutrients (N) and organic matter (O) are represented using a box model. Vertical mixing and remineralization of organic matter performed by bacteria provide nutrients to the system, which are taken up by both phytoplankton and mixotrophs for photosynthesis. Mixotrophs also graze on bacteria, which provide an additional means of nutrient acquisition. Both phytoplankton and mixotrophs produce organic matter, supporting the internal cycling of nutrients.

$$\frac{dO}{dt} = m_P P^2 + m_M M^2 + m_B B^2 - u_B BO - DO. \tag{7}$$

To study the effects of mixotroph investment in phototrophy on ecosystem dynamics, we simulated the model for $\theta \in (0, 1)$ while setting other parameters as constants (Table 1). We define the "optimal" mixotroph investment strategy (θ_{opt}) as the value of θ that minimizes the steady-state nutrient concentration. Because competition between mixotrophs and phytoplankton is mediated through the shared nutrient resource, minimizing the nutrient concentration maximizes mixotroph competitive ability (Tilman, 1977, 1990).

We also consider temperature dependency in this model by defining rate parameters as a function of temperature (T). This is done by introducing the temperature coefficient, Q_{10}, such that:

$$X^{temperature\ dependent} = XQ_{10}^{(T-20)/10}, \tag{8}$$

where X represents the uptake rates (u_P, u_M, u_B), mortality rates (m_P, m_M, m_B), and the mixotroph attack rate (a). Importantly, the phagotrophic parameter (mixotroph attack rate a) may either take the same or a different Q_{10} value from the phototrophic uptake and mortality rates (Wilken et al., 2013; Archibald et al., 2022). We simulated the temperature-dependent model under these two Q_{10} assumptions and compared the model's asymptotic behavior in each.

We considered two competition scenarios (Table 1): (1) a baseline case in which only mixotrophs are present ($P = 0$), and (2) a competition case in which $P > 0$. The first case established a baseline for the

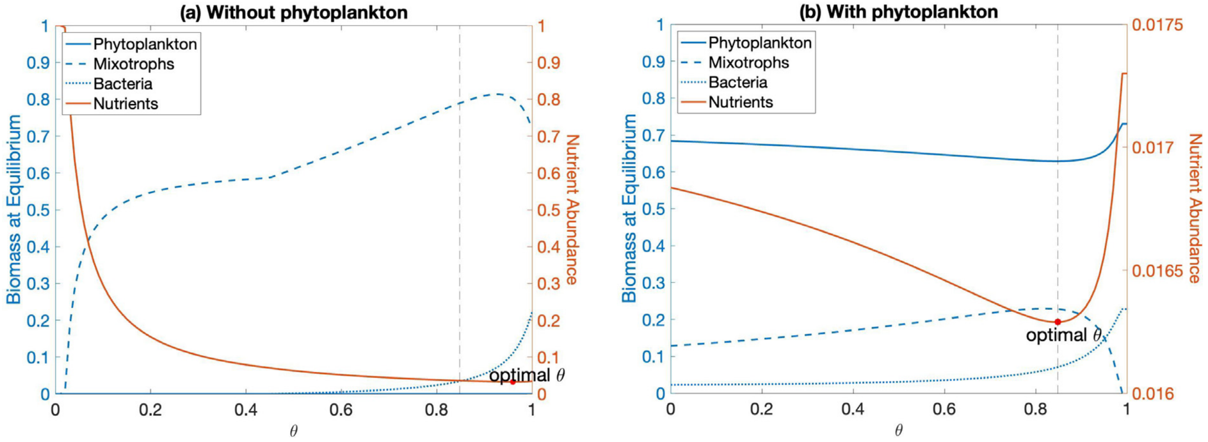

Fig. 2. Variable mixotroph metabolic strategy affects the equilibrium ecosystem state. The optimal mixotroph strategy is defined as the value of θ that minimizes the nutrient concentration (denoted as θ_{opt}). The competition brought by the presence of phytoplankton leads to a decrease in θ_{opt} from 0.96 to 0.85, signifying a trait displacement effect as a result of the competition that pushes mixotrophs away from phototrophic niche.

optimal mixotroph metabolic strategy in the absence of competition, and the second case allowed us to measure character displacement due to competition.

3. Results

The equilibrium ecosystem state depends on the mixotroph's metabolic strategy (θ). Mixotroph and phytoplankton biomass at equilibrium change as mixotrophs move from entirely phagotrophic to entirely phototrophic strategies (Fig. 2). Even in the absence of phytoplankton, the optimal mixotroph strategy occurs at a θ value between zero and one, indicating that some degree of mixotrophy is favored, instead of complete phototrophy or phagotrophy. When the mixotroph is entirely phagotrophic ($\theta = 0$) and phytoplankton are absent, there are no primary producers in the system and therefore no source of new organic matter. As a result, both mixotrophs and bacteria are extinct at equilibrium.

As θ initially increases, mixotrophs are able to exploit abundant inorganic nutrients via photosynthesis, supporting higher mixotroph biomass (Fig. 2a). However, the high attack rates maintained at small values of θ ensure that bacteria are near extinction at equilibrium. Eventually, as mixotrophs invest more into phototrophy (and consequently less into phagotrophy), attack rates drop and bacterial populations increase. This increased bacterial biomass contributes to further increases in mixotroph biomass in two ways: (1) by accelerating remineralization of inorganic nutrients that support photosynthesis, and (2) by directly supporting phagotrophic growth. As θ continues to grow, nutrients become scarcer in the environment due to mixotroph consumption while bacteria accumulate, and phototrophy gradually becomes less favorable for mixotrophs because of the opportunity cost of not utilizing the bacterial prey pool. Maximum mixotrophic biomass corresponds very closely to θ_{opt}, where the mixotroph is exploiting both nutrients and bacteria pools to some degree (Fig. 2a).

When phytoplankton are present in the ecosystem, mixotrophs have overall lower biomass and an optimal metabolic strategy that is more phagotrophic compared to when phytoplankton are absent (Fig. 2b). The presence of phytoplankton competitively displaces mixotrophs from a highly photosynthetic ($\theta_{opt} > 0.95$) niche towards a greater reliance on bacteria (that are being supported by photosynthetically produced organic matter). Importantly, mixotrophs that are entirely phagotrophic are able to persist when phytoplankton are present because there is a primary producer to convert inorganic nutrients into organic matter that can be utilized by the rest of the ecosystem.

The mixotroph's optimal metabolic strategy (θ_{opt}) is sensitive to a number of model parameters, often in opposite directions (Fig. 3). For example, as the growth rate of phytoplankton (u_P) increases, the competition between mixotrophs and phytoplankton is more intense. This leads mixotrophs to shift towards a more phagotrophic metabolic strategy to mitigate the competition effect (lower θ_{opt}; Fig. 3a). On the other hand, as the maximum uptake rate of the mixotroph ($\hat{u}_M$) increases, photosynthesis becomes more efficient and θ_{opt} becomes more phototrophic (Fig. 3b). Similarly, as the attack rate ($\hat{a}$) of mixotrophs increases, the bacterial prey pool may become depleted, leading mixotrophs to rely more on photosynthesis (Fig. 3c). In general, an increase in parameters such as $m_P, \hat{a}$ and $\hat{u}_M$ would give mixotrophs more advantages in competition with phytoplankton. This would in turn lead to an increase in θ_{opt}, encouraging the optimal metabolic strategy of mixotrophs to become more phototrophic. An increase in parameters such as u_P (increasing phytoplankton photosynthetic rates) and m_M (increasing mixotroph mortality), on the contrary, make the mixotroph a weaker competitor. Alternatively, an increase in u_B provides more prey for phagotrophy. Therefore, increases in all of these parameters lead to a decrease in θ_{opt}, encouraging mixotrophs' metabolic strategy to become more phagotrophic.

Our results were sensitive to the trade-off that the mixotroph experienced between investment strategies. Mixotrophs with generalist trade-off curves tended to maintain relatively higher investments in photosynthesis (greater θ_{opt} values) even in the presence of phytoplankton because they experience weaker reductions in attack rate compared to mixotrophs with linear trade-offs (Fig. S2–S3). In contrast, mixotrophs with specialist trade-offs can only achieve high rates of one metabolic process at a time. As a result, our analysis predicts that these mixotrophs will tend to specialize as either phototrophs ($\theta_{opt} = 0$, in the absence of phytoplankton competition) or phagotrophs ($\theta_{opt} = 1$, in the presence of phytoplankton competition) (Fig. S4–S5). Note that a phagotrophic strategy ($\theta_{opt} = 0$) can still be resource-minimizing due to feedbacks between mixotroph grazing, bacterial abundance, and nutrient remineralization (Fig. S4).

Temperature and the phagotrophic Q_{10} value of mixotrophs also affect the optimal strategy of mixotrophs and the corresponding biomass of phytoplankton, mixotroph, and bacteria (Fig. 4). With rising temperatures, multiple metabolic rates increase, including both mixotroph and phytoplankton growth rates. These increasing metabolic rates have contradicting effects on θ_{opt} (Fig. 3). As a result, the overall displacement effect of temperature depends on the integrated effects of multiple, sometimes opposing, factors. We examined the competition effect both as a function of temperature and the Q_{10} of mixotroph grazing. When phytoplankton are absent, warming temperatures allow the accumulation of both mixotroph and bacteria biomass as internal cycling becomes more efficient. The growing number of bacteria in

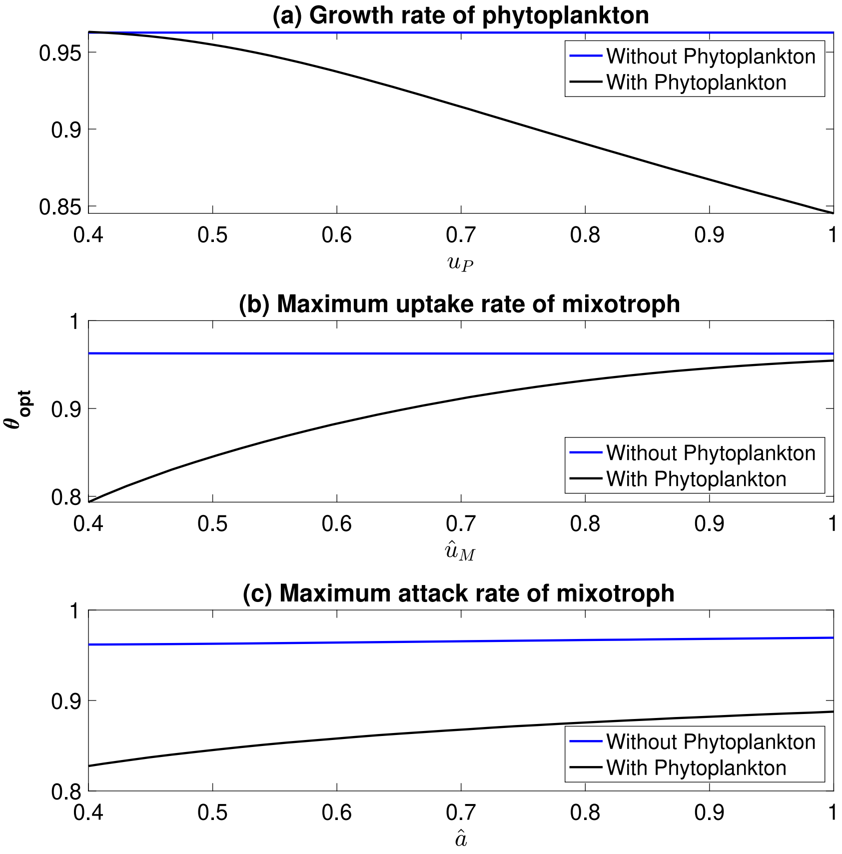

Fig. 3. θ_{opt} is a function of model parameters. Parameters that cause θ_{opt} to increase, such as $\hat{u}_M$ and $\hat{a}$, are considered phototrophy-encouraging parameters (Fig. 3b&c); parameters that cause θ_{opt} to decrease, such as u_P, are considered phagotrophy-encouraging parameters (Fig. 3a). When phytoplankton are absent from the system, θ_{opt} is less sensitive to the change in the model parameters.

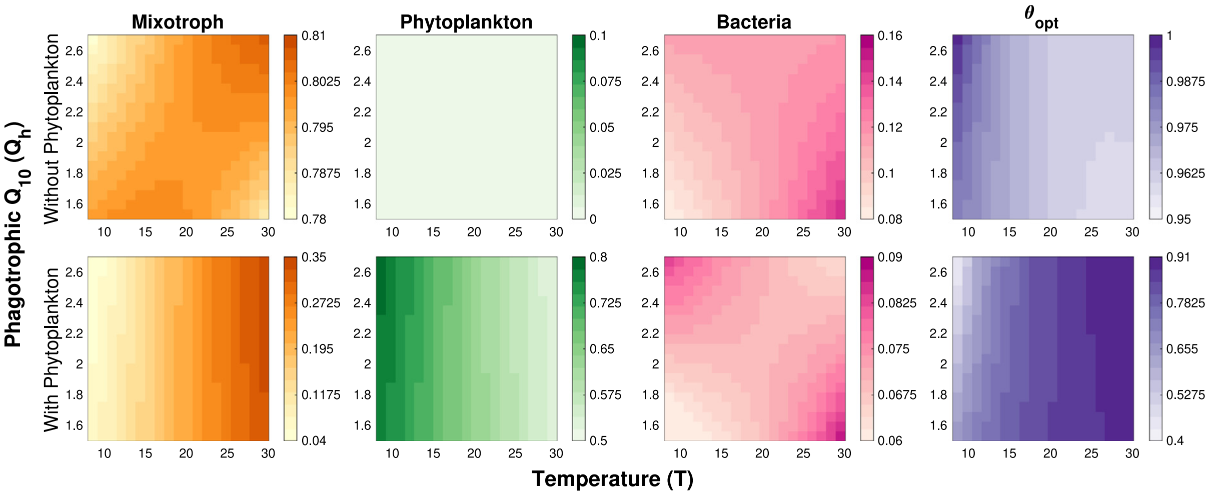

Fig. 4. Response of mixotroph (left column), phytoplankton (2nd column), and bacterial (3rd column) biomass and the mixotroph's optimal strategy (θ_{opt}) as a function of temperature, phagotrophic Q_{10}, and competition. Note the use of different color bars between subplots, which have been chosen to highlight the temperature-dependent patterns. In the absence of phytoplankton (top row), an increase in temperature (along the x-axis) accelerates metabolism, which leads to increases in mixotroph and bacteria biomass. The increase in bacteria selects for increased phagotrophy (lower values of θ_{opt}) in the mixotroph. Even so, at low Q_{10} values, mixotroph's accelerated metabolism is not efficient enough to mitigate the increased respiratory losses brought by high temperatures, and mixotroph biomass begins to decrease as temperature goes above 20 degrees. Bacteria biomass, on the other hand, is able to increase much faster with fewer predators. In the presence of phytoplankton (bottom row), competition causes competitive displacement of mixotrophs towards a more phagotrophic niche, and θ_{opt} is overall lower compared to the top row. However, as mixotrophs' phagotrophic efficiency increases (along the y-axis), their competitive dominance increases, driving decreases in phytoplankton biomass and opening the opportunity for higher mixotroph θ_{opt} values.

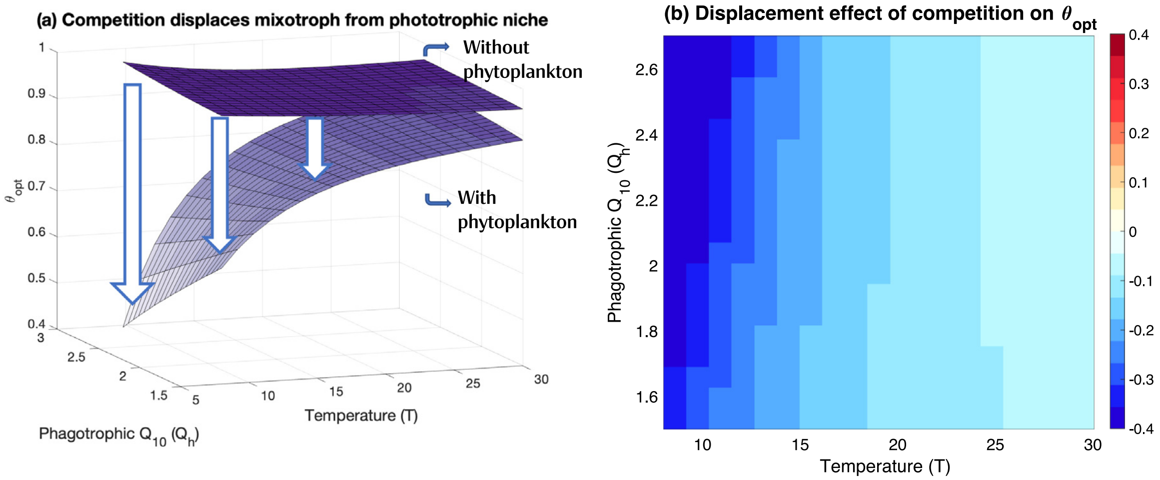

Fig. 5. Response of the mixotroph's optimal strategy, θ_{opt}, as a function of temperature and phagotropic Q_{10}. In the absence of phytoplankton, mixotroph's optimal strategy is more phototrophic and the mixotroph has a higher θ_{opt} value. In the presence of phytoplankton, the competition displaces mixotroph from its phototrophic niche, causing the θ_{opt} value to decrease (left). Furthermore, at higher temperatures, mixotrophs with a lower phagotropic Q_{10} are able to sustain enough bacteria for more efficient internal cycling, which in turn supports mixotroph phagotrophy. In this scenario, mixotroph is more sensitive to the competition as phagotrophy quickly outweighs phototrophy.

turn supports mixotroph phagotrophy, leading to a decrease in θ_{opt} (recall that $\theta_{opt} = 0$ means fully phagotrophic). In the meantime, the increasing respiratory losses at higher temperatures cause a decrease in mixotroph biomass when Q_{10} is low, since mixotroph phagotrophy is not efficient enough to mitigate the losses. At a higher phagotrophic Q_{10} level, however, the grazing term of the mixotroph becomes too large as temperature increases, such that the consumption eventually starts to damage bacterial growth, leading to a much slower accumulation in bacteria biomass. Mixotrophs are thus forced to decrease their shift towards phagotrophy. The balance between these contrasting mechanisms means that the relationship between θ_{opt} and temperature depends in part on the Q_{10} value for mixotroph grazing.

When phytoplankton are present, they compete with mixotrophs for nutrients. As phagotrophic efficiency increases, mixotrophs become competitively dominant over phytoplankton, whose biomass begins to decrease. Fewer competitors open the opportunity for mixotrophs to perform more phototrophy, leading to an increase in θ_{opt}. However, the competition with phytoplankton still displaces mixotrophs from their phototrophic niche, as θ_{opt} is generally lower in values after competition is introduced (Fig. 5a). This displacement effect is subject to the change in temperature and Q_{10}. Overall, the displacement effect of competition is larger at lower temperatures and higher Q_{10} values (Fig. 5b).

4. Discussion

This study examines the effects of competition between mixotrophs and a specialized phytoplankton competitor on mixotroph metabolic strategy. Previous modeling studies have shown that the combination of phototrophy and heterotrophy can grant mixotrophs a competitive edge (Flynn and Mitra, 2009; Leles et al., 2018; Ward, 2019). In experimental studies, mixotrophs are often found to prefer one metabolic strategy over another (Sanders et al., 1990; Lie et al., 2018). These diverse metabolic strategies mixotrophs can exhibit have been shown to be affected by the availability of both nutrients and prey resources (Jones, 2000; Wilken et al., 2020; Livanou et al., 2020). The results of our model simulations agree with the theory that mixotroph's optimal metabolic strategy is to utilize both photosynthesis and phagotrophy, even without the presence of competitors. Furthermore, our study suggests that the choice of metabolic strategy is also affected by the competition brought by phytoplankton, which displaces mixotrophs away from the photosynthetic niche to adopt a more phagotrophic metabolism. The presence (or absence) of phytoplankton creates ecological feedbacks that affect the supply rate of resources needed for mixotroph growth, shifting abiotic conditions previously demonstrated to influence mixotroph metabolic strategy (Chakraborty et al., 2017; Decelle, 2013). The magnitude of this trait-displacement is subject to changes in temperature and the thermal sensitivity (Q_{10}) of phagotrophic metabolic processes. We found that the competitive displacement effect is larger at lower temperatures, and that mixotrophs with relatively high phagotrophic Q_{10} values are more sensitive to this effect.

As both predators and primary producers, mixotrophic microorganisms are increasingly recognized for their significant contribution to carbon cycling. Mixotrophs' biogeochemical niche is often quite complex, as their photosynthetic energy acquisition compensates (at least in part) for their respiratory losses (Worden et al., 2015; Wilken et al., 2020). As a result, mixotrophy itself can make the transfer of biomass up the food chain more efficient, leading to an increase in vertical carbon flux (Ward and Follows, 2016). However, the exact magnitude of this effect likely depends on the degree of mixotrophy expressed (i.e. the mixotroph's nutritional strategy; Wilken et al., 2014), thus highlighting the importance of understanding the link between a mixotroph's metabolic strategy and its biogeochemical niche. Here, we have explored the influence of competition on mixotrophy's role in carbon cycling: As mixotrophs are shifted out of the phototrophic niche by competition with specialist phototrophs, there would be less carbon capture in the marine ecosystem and increased overall respiration by plankton communities. The presence of temperature dependence in our results suggests that the relationship between competition and mixotrophic biogeochemical niche in marine ecosystems may indeed shift as a result of global climate change. Other studies (e.g. Jassey et al., 2015) have found that mixotrophs play a key role in the response of ecosystem carbon cycling to climate change, which makes it even more important to understand the thermal response of these organisms.

Previous competition models have examined the competitive advantages and disadvantages of mixotrophs, but contrasting theories exist (Stickney et al., 2000). Although some expected that the potential evolutionary costs of maintaining both phototrophic and heterotrophic machinery may give mixotrophs disadvantages (Stickney et al., 2000; Raven, 2003), others argue that, even with relatively higher costs, the combined use of phototrophy and phagotrophy could give mixotrophs advantages under certain environmental conditions (Bockstahler and Coats, 1993; Katechakis and Stibor, 2006). In reality, it has also been suggested that the metabolic costs for photosynthesis and prey uptake are multidimensional and that, within different ranges of costs, mixotrophs may have higher or lower overall costs than specialized competitors (Raven, 2003). This idea further complicates the evaluation of mixotrophy's competitiveness. Our model examines the case where mixotrophs are less competitive compared to their specialized phototroph competitor (see Fig. 2b) and concludes that they are also forced out of their phototrophic niche when competing with phytoplankton for a single limited nutrient source. What would happen if we consider other cases where mixotrophs are more than or equally competitive as specialized phototrophs? This suggests a future direction for similar studies.

In our study, we examine mixotroph strategies that minimize nutrients, on the principle that this strategy maximizes the mixotroph's competitive ability. Indeed, our test simulations show that mixotrophs with optimal strategies achieve higher biomass than mixotrophs with suboptimal strategies, although competitive exclusion does not always occur. Thus, our model suggests that, if an evolutionary analysis were undertaken, evolutionary branching leading to coexistence of different mixotroph types could occur. This is consistent with other modeling studies of mixotroph evolution (e.g., Troost et al., 2005a,b). Further, other optimality conditions, such as maximization of growth rates, could be considered.

The model we used in our study accounts for the interactions between a small number of plankton types (mixotrophs, phytoplankton, and bacteria) under a single inorganic nutrient source. The relative simplicity of this structure allows for a rigorous exploration of mechanisms and model parameters. However, real marine ecosystems include many more axes of complexity that could be adapted to investigate effects of specific ecological phenomenon on mixotroph optimal metabolic strategy. For example, competition often occurs for multiple resources simultaneously, so the effects of competition are likely more complex than those presented here. Co-limitation of light (Huisman and Weissing, 1994) or phosphorus (Codeço and Grover, 2001) would provide interesting avenues for future investigation. On the other hand, competition with not just phototrophs but also heterotrophs has been widely discussed. By combining light, inorganic nutrients, and prey as substitutable resources, mixotrophs are found to be able to reduce prey abundance below the critical food concentration of competing specialist heterotrophs and thus outcompete them in the competition (Rothhaupt, 1996; Tittel et al., 2003). This strategy has a potential effect on character displacement and the actual direction of such displacement calls for future research.

Furthermore, the mixotrophs in our model are assumed to use phototrophy and phagotrophy interchangeably for growth, even when they experience different trade-offs between metabolic investments (Figures S1–S5). In this way, our model parallels other representations of mixotrophs such as those used in large-scale upper ocean ecosystem models (Ward and Follows, 2016) However, there is a wide array of mixotrophs that exist in nature, and our model does not capture the nuances of mixotrophs with different resource requirements. For example, inducible mixotrophs (e.g., *Prorocentrum minimum*, Johnson, 2014) prefer phototrophy and feed only when nutrients are limiting. Other mixotrophs are obligate phagotrophs or phototrophs (Lie et al., 2018; Wilken et al., 2020; Moeller et al., 2019). Incorporating these mixotroph strategies would require alternative model formulations that account for the different types of resources mixotrophs obtain through phototrophy and phagotrophy (e.g., that accounts for both carbon and nutrients; Flynn and Mitra, 2009). Such models have used quota-based approaches, where growth depends on internal rather than environmental concentration of nutrients (Ward et al., 2011; Leles et al., 2018; Edwards, 2019). Future work could expand on our model to include multiple resource types in order to better account for other mixotroph metabolic strategies.

Knowing that mixotrophs may be either more or less competitive than their specialized competitors as environmental factors are altered, raises the question of what types of environments would generally favor mixotrophy over specialized phototrophy or phagotrophy. Hansson et al. (2019) identified variables driving the success of mixotrophs using data collected from North American lakes. They found that the success of mixotrophy was positively related to the concentration of colored dissolved organic matter (cDOM) and dissolved CO_2. They also pointed out that while water temperature and food abundance have a positive effect on mixotroph productivity as well, these factors also favor specialized phototrophic phytoplanktons in the same way. Competition, then, may influence not only the optimal strategy of mixotrophic plankton, but play a role in maintaining mixotrophy as a trophic strategy in general.

Mixotrophs play a vital role in establishing the biogeochemical character of marine ecosystems. Here, we have used a simple model of competition between a mixotroph and a specialized phototrophic phytoplankton to explore competitive trait-displacement in mixotrophic metabolic strategy. Our results suggest that, in the presence of phytoplankton, mixotrophs should experience "competitive displacement" of their metabolic investment traits. Specifically, mixotrophs should shift towards more phagotrophic investments to reduce niche overlap with strict phototrophs. Thus, mixotrophs' role in carbon cycling will depend upon the presence or absence of competitors. This effect on mixotroph nutritional strategy is also temperature dependent, suggesting a link between community-level competitive mechanisms and global climate change. Given the unique biogeochemical nature of marine mixotrophs, understanding this link is an important building block in constructing a comprehensive theory of how mixotrophs' ecological role changes in the context of global warming.

CRediT authorship contribution statement

Tianyi Chu: Model analysis, Writing – original draft, Writing – review & editing. **Holly V. Moeller:** Writing – review & editing. **Kevin M. Archibald:** Model analysis, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Holly Moeller reports financial support was provided by Simons Foundation. Holly Moeller reports financial support was provided by National Science Foundation. Holly Moeller reports financial support was provided by US Army Research Laboratory.

Data availability

All data can be simulated from the equations provided in the paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecolmodel.2023.110331.

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