

Mixotroph ecology: More than the sum of its parts

Marine microbial ecosystems represent an important nexus in the Earth system, linking photosynthesis and biological productivity to global nutrient cycles and climate. Each year, marine biota export billions of tons of organic carbon into the deep ocean, maintaining an oceanic reserve that has a profound moderating effect on our climate (1). Our current understanding of these important microbial ecosystems has been shaped to a large extent by the terrestrial macroscopic world we see around us. In particular, the distinction between photosynthetic phytoplankton and heterotrophic zooplankton reflects a very familiar divide between plants and animals. While this distinction is intuitive, a great many species at the base of marine food webs defy such strict classifications (2). These flexible organisms, known as mixotrophs, not only use energy from the sun to take up nutrients and grow but they can also kill and eat other plankton. At present, we know that mixotrophy is the default lifestyle for many single-celled plankton, and we know that they often dominate marine communities (3). However, there remains considerable uncertainty as to how different environmental conditions select for mixotrophy across broad environmental gradients. While a number of hypotheses have been developed to explain the ecological niche of mixotrophs, we do not have a concrete understanding of how environmental factors shape the balance between different sources of nutrition in these communities. As such, it has been difficult to test the validity of hypotheses and to assess how the ecological role of mixotrophs might affect global ecosystem function, biogeochemical cycles, and climate. In PNAS, Edwards (4) presents a new synthesis of field observations and mathematical modeling that helps to address this knowledge gap.

Motivated by the observed prevalence of mixotrophs in marine communities, a number of conceptual models have been developed with the goal of pinning down the ecological constraints and functional consequences of mixotrophic nutrition. Alongside these conceptual models, numerical models embedded within simulated representations of the

oceanic environment have been used to quantitatively assess the likely ecological and biogeochemical role of mixotrophs (5, 6). At the global scale, models suggest that the presence of mixotrophy can enhance trophic transfer efficiency, sustaining larger organisms at higher trophic levels and increasing oceanic carbon sequestration (7). A common theme among many of these conceptual and numerical models is that mixotrophs are frequently at an advantage because they have the ability to overcome mismatches between the environmental supply and physiological demand of key resources. Although, by definition, phytoplankton are tied to the availability of light and inorganic (or at least non-living) sources of nutrients, and zooplankton are subject to constraints placed on them by the quality and quantity of their prey, mixotrophs are able to mix and match, taking what is available from either or both resource pools to achieve a balanced supply of energy and essential compounds (8). Edwards (4) formalizes this hypothesis in a mathematical model, providing clear analytic solutions and confronting them with observations.

The analysis clearly demonstrates how a community co-limited by both nutrients and carbon selects much more strongly for mixotrophy than would a community limited solely by nutrients. In the heavily stratified oligotrophic gyres, an extremely limited supply of nutrients to the euphotic zone is rapidly sequestered within a community of highly competitive bacterioplankton (9). The resultant scarcity of inorganic nutrients restricts the capacity for strictly photoautotrophic growth among larger (and less competitive) phytoplankton. At the other end of the trophic spectrum, heterotrophic zooplankton can feed on the bacterioplankton community but become carbon limited as a consequence of their energetic requirement to respire carbon from their (relatively) nutrient-enriched prey. In the absence of mixotrophy, we would see the coexistence of nutrient-limited phytoplankton (unable to access the nutrient reserves of the prey community) alongside carbon-limited zooplankton

(unable to use light). In this context, the advantages of mixotrophy can be attributed to the complementarity of nutrient-limited autotrophy and carbon-limited heterotrophy (Fig. 1). Edwards's (4) analysis shows that mixotrophy is selected across a much narrower range of physiological parameters if the entire system is limited solely by access to nutrients. In such a case, the benefits of combining trophic strategies is simply additive and must be offset against any additional costs associated with generalism. In contrast, when each strategy is limited by a resource which the other provides in excess, the overall capacity for growth becomes greater than the sum of its parts.

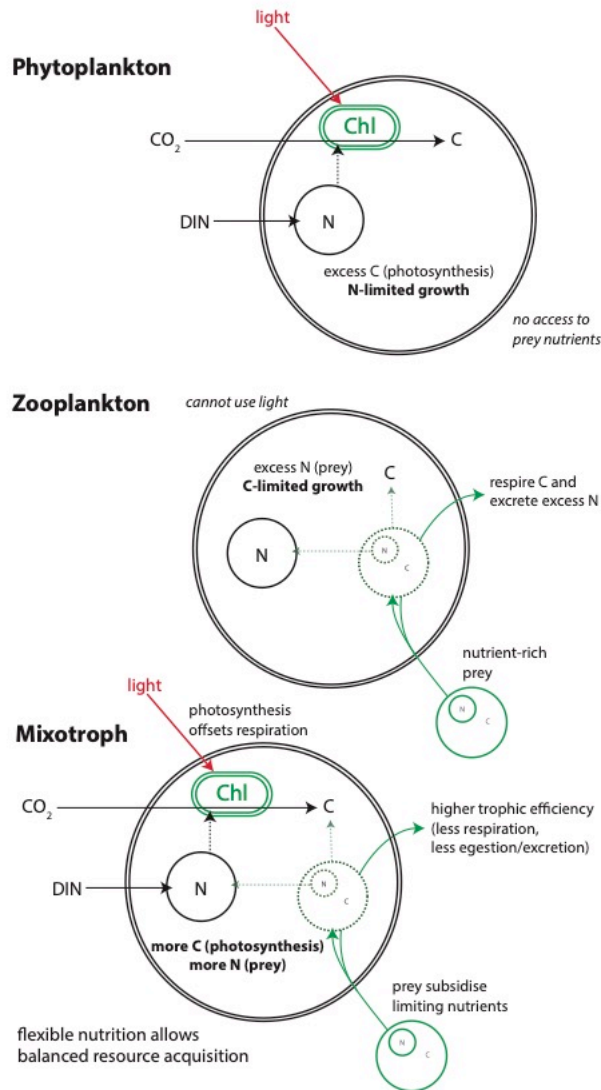


Fig. 1. A schematic view of physiological limitation of phytoplankton, zooplankton, and mixotroph cells within a well-lit, nutrient-impoverished ocean environment. Strictly photoautotrophic phytoplankton are nutrient limited [in this case, dissolved inorganic nitrogen (DIN)], being outcompeted for nutrients by highly competitive bacterioplankton. Strictly heterotrophic zooplankton consume these nutrient-enriched bacterial prey, with the additional demands of respiration leading to carbon limitation. Mixotrophs are selected in this system because ingestion of prey allows them access to more nitrogen than phytoplankton, while photosynthesis allows them access to more carbon than zooplankton. Chl, chlorophyll.

In support of this hypothesis, Edwards (4) presents a compilation of measurements describing the abundance of autotrophic, mixotrophic, and heterotrophic nanoflagellates—an important group of single-celled eukaryotes in the 2- to 20- μm size range. The collated data clearly support the predictions of the model, showing that mixotrophy becomes relatively more abundant both in the brightly lit but nutrient-impooverished subtropical oceans and also in the much more productive waters of the coastal oceans. This supports previous findings that mixotrophy is a particularly dominant strategy within oligotrophic gyres (3, 9), but while previous work has focused on the benefit to mixotrophs of ingested prey nutrients (in competition with specialist phytoplankton), this study emphasizes the simultaneous importance of photosynthetic gains of organic carbon and energy (in competition with specialist zooplankton) (Fig. 1).

One of the challenges of understanding the role and function of mixotrophy in marine communities is that this physiological mechanism is inseparable from its often-complex ecological context. A key achievement of Edwards's (4) work is to simplify this system, focusing on a single taxonomic group at steady state and identifying, in a very general sense, how shifting environmental conditions select for different trophic strategies. Nonetheless, this is a somewhat idealized steady-state perspective on what is undoubtedly a complex and multifaceted phenomenon. Mixotrophy is found in an extremely broad range of species that are distributed throughout the phylogenetic tree of life (10), and there is considerable diversity in how autotrophic and heterotrophic traits are combined (11). Stoecker (12), for example, identified three primarily autotrophic groups that use prey for carbon, nitrogen, or trace compounds, and two primarily heterotrophic groups that use photosynthesis to delay starvation or to increase metabolic efficiency. More recently, an alternative scheme classifies species into a number of groups, contrasting those that are able to synthesize and regulate their own chloroplasts with those that use chloroplasts "stolen" from their prey (13). These schemes have gained empirical support from compilations of taxonomic (14) and genomic (15) field data, with distinct patterns of global biogeography implying a distinct ecological niche for each of the functional groups.

Mixotrophic nutrition has been observed in all marine biomes, of which only a few might reasonably be assumed to approach ecological equilibrium. In addition to their dominance in the stable oligotrophic gyres, mixotrophs are also successful in highly dynamic environments, with trophic flexibility cited as a mechanism to cope with nutrient exhaustion following phytoplankton blooms at temperate latitudes (16, 17) or with the absence of light during the polar winter (18). Alongside the advantages of balancing resource supply and demand, mixotrophs have also been shown to gain an advantage through intraguild predation (19) [or the strategy of "eating your competitor" (20)]. Such mechanisms can only be directly addressed with more complex models, but the insights gained from simplified, yet analytically tractable models will undoubtedly aid in their interpretation. Furthermore, with more data, it should be possible to achieve a clearer global synthesis of ecological trends by developing robust empirical relationships between mixotroph abundance and more readily observed environmental variables such as ocean color and temperature.

In terms of understanding marine biogeochemical cycles and their influence on climate, the synergistic coupling of prey-derived nutrients with photosynthetic carbon fixation highlights the importance not just of mixotrophy, but also of combining multiple-nutrient ocean models with realistic representations of flexible plankton physiology (7). Recent work highlights the value of a quantitative synthesis between conceptual models and field observations: identifying what conditions make mixotrophy a favorable strategy, how environmental and ecological factors affect the balance of autotrophic and heterotrophic traits, and what is the integrated effect on global ecosystem function. In particular, the careful synthesis of models and observations helps to identify the most important factors driving mixotroph ecology while

simultaneously making sure that our intuitive understanding of any observed patterns is self-consistent.

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