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## HORIZONS

# Modelling emergent trophic strategies in plankton

KEN H. ANDERSEN<sup>1\*</sup>, DAG L. AKSNES<sup>2</sup>, TERJE BERGE<sup>3</sup>, ØYVIND FIKSEN<sup>2</sup> AND ANDRÉ VISSER<sup>1</sup>

<sup>1</sup>VKR CENTRE FOR OCEAN LIFE, INSTITUTE FOR AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, JÆGERSBORG ALLÉ 1, 2920 CHARLOTTENLUND, DENMARK, <sup>2</sup>DEPARTMENT OF BIOLOGY, UNIVERSITY OF BERGEN AND HJORT CENTRE FOR MARINE ECOSYSTEM DYNAMICS, THORMØHLENSGT. 53 A/B, N-5020 BERGEN AND <sup>3</sup>VKR CENTRE FOR OCEAN LIFE, MARINE BIOLOGICAL SECTION, UNIVERSITY OF COPENHAGEN, STRANDPROMENADEN 5, 3000 HELSINGØR, DENMARK

\*CORRESPONDING AUTHOR: kha@aqua.dtu.dk

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Plankton are typically divided into phytoplankton and zooplankton in marine ecosystem models. Yet, most protists in the photic zone engage in some degree of phagotrophy, and it has been suggested that trophic strategy is really a continuum between pure phototrophs (phytoplankton) and pure phagotrophs (unicellular zooplankton). Such a continuum of trophic strategies is well represented by trait-based modelling techniques. A key model ingredient is the size of individual cells, as size constrains affinities for nutrient uptake, photosynthesis and active encounter with other cells. We outline a general trait-based model of a unicellular planktonic organism where size is a central trait and where nutrient uptake, photosynthesis and phagotrophy are determined by investments into these functions and by the physical constraints imposed by organism size. This framework provides simple predictions of how trophic strategy correlates with size.

**KEYWORDS:** trade-off; optimization; mixotrophy

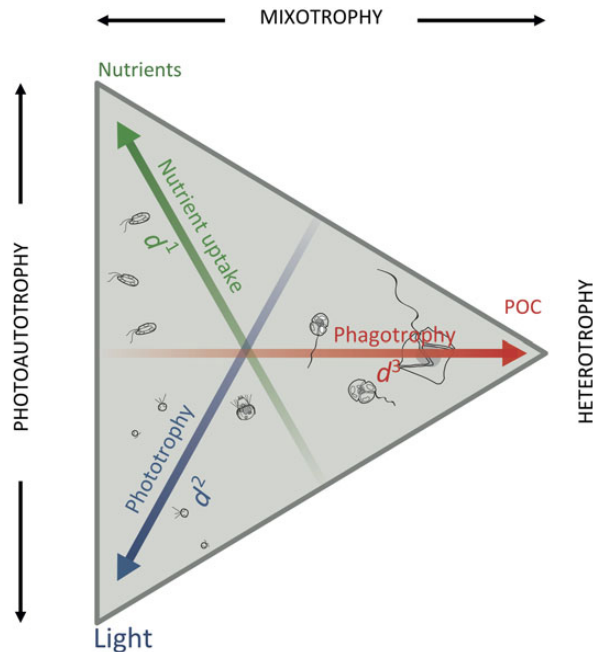
## INTRODUCTION

There is a central distinction in unicellular plankton models between phytoplankton (phototrophs) and zooplankton (heterotrophs). This is particularly evident in NPZ type models (Fasham *et al.*, 1990; Franks, 2002; Flynn *et al.*, 2013) where functional groups are divided between phytoplankton and zooplankton state variables. This division into two discrete trophic groups is challenged

by evidence showing that large groups of organisms, in particular flagellates and ciliates, are mixotrophic and simultaneously prey upon other organisms (phagotrophy), photosynthesize and take up dissolved inorganic nutrients (Raven, 1996; Stoecker, 1998; Barton *et al.*, 2013; Flynn *et al.*, 2013). Such mixotrophs dominate grazing on bacteria in vast open ocean areas (Hartmann

et al., 2012; Mitra et al., 2014) and constitute the majority of bloom forming “harmful algae” in coastal areas (Burkholder et al., 2008). Mixotrophy occurs in several different forms and individual organisms are mixotrophic to varying degrees (Stoecker, 1998). In general, one can define the trophic strategy along a “mixotrophic axis” ranging between a pure photoautotroph and a pure heterotroph (Jones, 1994; Flynn et al., 2013).

At the phototrophic end of the mixotrophic continuum, photoautotrophs (i.e. cyanobacteria and diatoms) also invest to varying degrees into photosynthesis and nutrient uptake (Shuter, 1979; Raven, 1984). Photoautotrophs can therefore be characterized along another continuum defined by the relative investment in photosynthesis and nutrient uptake (Bruggeman and Kooijman, 2007). Taken together the trophic strategy, from photoautotrophy to heterotrophy, may be defined within the continuum spanned by the three axes defining the uptake of fundamental elements: the two axes spanning the space between uptakes of carbon from photosynthesis combined with dissolved inorganic nutrients and an axis representing uptake of both carbon and nutrients from phagotrophy (Fig. 1).



**Fig. 1.** Conceptual illustration of the trophic continuum from photosynthesis over mixotrophy to pure heterotrophy. The trophic continuum is defined by the allocation into three harvesting traits: nutrient uptake, photosynthesis and phagotrophy, each leading to uptake of dissolved inorganic nutrients,  $\text{CO}_2$  and particulate organic matter. A specific organisms’ trophic strategy is defined as a point within the triangle: an organism in the middle will invest equally into all three traits, an organism somewhere along the left side will be a pure phototroph and an organism at the right tip would be a pure heterotroph. On each arrow depicting the traits is indicated how the affinity towards the trait scales with organism size  $d$ .

Here, we synthesize current ideas on modelling the trophic continuum of plankton by focusing on organism size and allocation of energy to three central resource-harvesting traits: allocations to inorganic nutrient uptake, to photosynthesis (carbon uptake) and to phagotrophy (carbon and nutrient uptake). Because the total investment in all three traits is limited by total cell resources (here carbon and nutrients), high investment in one trait occurs at the expense of allocation to the other traits; the three dimensional trait space can be projected onto the two-dimensional trophic strategy continuum. An organism’s trophic strategy may therefore be defined as a point within the triangle spanned by the three traits (Fig. 1): An organism at the vertex associated with allocating all resource to phagotrophy is a classic unicellular zooplankton; an organism on the side defined by allocation to both nutrient uptake and photosynthesis is a pure photoautotroph (e.g. diatoms and cyanobacteria) and an organism somewhere between these two extremes is a mixotroph (e.g. most dinoflagellates with chloroplasts). We sketch the building blocks for a trait-based modelling framework where trophic strategy is an emergent property and not specified *a priori* and make general conjectures of the correlations between organism size and resource-harvesting traits.

## SIZE AS A MASTER TRAIT

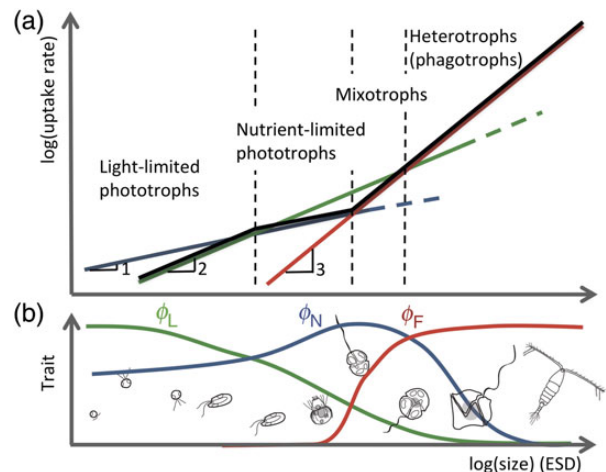
Cell size has been used as a “master trait” to structure plankton community models (Litchman and Klausmeier, 2008; Finkel et al., 2009), either conceptually in zero-dimensional models (Fuchs and Franks, 2010; Banas, 2011), within a water column (Terseleer et al., 2014) or within a global circulation model (Ward et al., 2012). Size affects all aspect of unicellular organisms. It is recognized as a key regulator of uptakes: affinities of nutrient uptake (Munk and Riley, 1952; reviewed by Fiksen et al., 2013), photosynthesis through the “packaging effect” (Morel and Bricaud, 1981), clearance rates of phagotrophy (Kjørboe, 2011) and preferred predator-prey size ratios (Hansen et al., 1994). Further, size affects losses through size-dependent mortality risk (Hirst and Kjørboe, 2002) and size-dependent sinking rates (Aldredge and Gotschalk, 1989). Such size-based relationships have been used to argue that larger cells are more likely to be mixotrophic, whereas smaller ones take up inorganic nutrients directly (Ward et al., 2011; Barton et al., 2013; Våge et al., 2013a,b).

The influences of organism size on uptake of nutrients, photosynthesis and phagotrophy are known from theory and meta-analyses of experiments. The potential for uptake is conveniently described by the organism’s affinity towards nutrients, light or other organisms. The

affinity is the slope of the functional response at the origin, referred to as the “clearance rate” when encounter with other organisms is concerned. The affinity towards dissolved nutrients is limited by speed of diffusion towards the cell surface (Munk and Riley, 1952). This theory predicts that affinity scales proportionally to the linear dimension of the cell (reviewed by Fiksen *et al.*, 2013), i.e. as  $\propto d^1$ , where  $d$  is the equivalent spherical diameter. The affinity towards light is limited by self-shading of photons (the “package effect”) (Morel and Bricaud, 1981) and possibly by diffusion of CO<sub>2</sub> within the cell (Wirtz, 2011). Both effects predict that the photosynthetic rate is limited by surface area and thus that the affinity is  $\propto d^2$ . Finally, the affinity towards other organisms is determined by how effectively it can find and ingest prey. Empirical data show that the clearance rate is proportional to organism volume, or  $\propto d^3$  (Kiorboe, 2011). Disregarding other limiting effects, the affinities can be used to determine the scope for growth, from the specific affinity, i.e. the affinity divided by organism volume  $\propto d^3$ . The specific affinities of organisms towards nutrients, light or prey are therefore expected to change systematically with size: smaller organisms will have a higher specific affinity towards nutrients than larger ones, whereas larger organisms will have a higher specific affinity towards prey organisms than small organisms.

Using affinity as a proxy for competitive ability, we can make simple predictions about how the trophic strategy scales with size. The uptake rate is the affinity multiplied by the resource concentration (nutrients, light or food) (Fig. 2a). A dominant trophic strategy among organisms of a given size is the one that yields the highest uptake rate. It is clear, then, why larger organisms are heterotrophs: phagotrophy yields by far the highest resource encounter rate for large organisms. Phototrophs need special care because they must combine two mechanisms, nutrient uptake and photosynthesis, and will be limited by the one which gives the lowest yield. This leads to the prediction that smaller organisms are light limited photoautotrophs, whereas intermediate size organisms are nutrient limited. There is a particular range where photosynthesis will provide more carbon than phagotrophic uptake, but where phagotrophy provides more nutrients than uptake of dissolved nutrients. In this size range, a mixotrophic strategy is profitable, i.e. using photosynthesis to provide carbon for metabolism and using active feeding to assimilate nutrients and carbon for biomass synthesis.

These predictions of the size ranges where one trophic strategy dominates over others depend on the concentrations of the resources. If, in the sketch in Fig. 2a, the nutrient concentrations are lowered and light increased, such as in an oligotrophic situation, the size range of



**Fig. 2.** Scaling of resource uptake and allocation traits as a function of organism size. (a) Uptake rates (carbon or nutrients per time) through different strategies: uptake of diffusing nutrients (blue), photosynthetic fixing of carbon (green) and phagotrophic uptake of food containing both nutrient and carbon (red). The trophic strategy with the highest uptake rate of carbon and nutrients is highlighted with a black line. Because phototrophs have to combine carbon from photosynthesis with uptake of dissolved nutrients, Liebig’s law means that their effective uptake rate is limited by either light (for small phototrophs) or nutrients (large phototrophs). (b) Expected investments into harvesting traits.

nutrient limited photoautotrophs and mixotrophs would increase to include smaller organisms. This pattern fits with the classical interpretation of the seasonal succession of cell size in temperate coastal systems (Kiorboe, 1993): large photoautotrophic cells (diatoms) dominate during nutrient-rich spring conditions that are overtaken by smaller cells (dinoflagellates and cryptophytes), often with a mixotrophic strategy, during the nutrient-depleted summer condition (Barton *et al.*, 2013; Mitra *et al.*, 2014). On spatial scales, larger species (10–200  $\mu\text{m}$ ) are associated with coastal waters with high nutrient input, whereas small species dominate open ocean oligotrophic waters (Hartmann *et al.*, 2012). Here, the food web generally consists of small photosynthetic cyanobacteria (e.g. *Synechococcus* (<1  $\mu\text{m}$ )) that are grazed by small mixotrophic picoflagellates ( $\sim 2\text{--}5 \mu\text{m}$ ) (Hartmann *et al.*, 2012).

## RESOURCE-HARVESTING TRAITS

The trophic strategy lends itself naturally to modelling within a trait-based paradigm (Wirtz and Eckhardt, 1996; Norberg *et al.*, 2001; Litchman and Klausmeier, 2008; Follows and Dutkiewicz, 2011). Centred on the concept of functional traits, i.e. those that have a fundamental importance for fitness, the trait-based approach is essentially a marriage between a classic NPZ model

(Fasham *et al.*, 1990; Franks, 2002) and “cost-benefit” models (Shuter, 1979; Raven, 1984; Geider *et al.*, 2009). As an example, consider the allocation to chloroplast as a trait. Investing in chloroplasts leads to a higher photosynthetic rate. This investment has a cost in terms of resources (nutrients, carbon) needed to synthesize the chloroplasts and fuel their maintenance, resources that may otherwise have been invested in other traits (e.g. nutrient affinity). The advantage (higher light affinity) and the costs (investment, maintenance and reduced function elsewhere) constitute the trade-off associated with the trait. Similar considerations can be made for traits related to dissolved nutrient uptake (Klausmeier *et al.*, 2004; Bruggeman and Kooijman, 2007), phagotrophy (Bruggeman, 2009), investment into defence (Wirtz and Eckhardt, 1996; Merico *et al.*, 2009), cell size (Clark *et al.*, 2013), temperature (Shuter, 1979; Toseland *et al.*, 2013) and resistance to pathogens (Våge *et al.*, 2013a,b). If the trade-off can be parameterized, it provides a mechanistic approach to derive the parameters of the vital rates of the individual cell.

Trait-based descriptions have been developed of both the mixotrophic and the phototrophic continuums. Trait-based descriptions of mixotrophs have described unicellular plankton by a single trait describing the degree of heterotrophy (Troost *et al.*, 2005; Bruggeman, 2009; Ward *et al.*, 2011; Våge *et al.*, 2013a,b). Such models view mixotrophy as a means of dealing with situations with depletion of dissolved nutrients by acquiring nutrients through phagotrophy as an alternative or supplement to uptake of dissolved inorganic nutrients. To describe the phototrophic continuum, trait-based models have used allocation between nutrient harvesting and photosynthesis as a trait (Bruggeman and Kooijman, 2007) or simply considered the nutrient allocation as constant and considered investment into phototrophy as the variable trait (Shuter, 1979; Raven, 1984). Here, we propose a marriage between those two kinds of approaches.

## TROPHIC STRATEGY EMERGING FROM INVESTMENTS

A trait-based model of a unicellular organism can be formulated once the trade-off involved in each trait is known. Here, we sketch a model with three “resource-harvesting traits” that represent how an individual unicellular organism prioritizes functions through investments in organelles such as chloroplasts and cell membranes with uptake sites containing transporter proteins (e.g. ATPases). The costs are defined in terms of construction and maintenance of these machineries as well as other costs such as increased mortality risk. Additionally, there

are respiratory costs associated with the actual functions proportional to the uptakes of carbon, nutrients and other organisms. A central “alternative cost” is that allocation to one trait comes at the expense of allocation to other, represented by the allocation-triangle in Fig. 1. The trade-offs (benefits and costs) related to allocation between harvesting traits are as follows:

- (i) Nutrient uptake,  $\phi_N$ , represents uptake machinery, including transporter proteins (ATPases) and enzymes for reducing substrates (e.g. nitrate reductase) for dissolved nutrients. Since uptake sites are substrate-specific and some groups of organisms have specific elemental needs, this trait may be divided into several (Klausmeier *et al.*, 2004). The benefit of increased allocation to uptake sites is higher affinity and maximum uptake rate although with a saturating effect as site number increases (Aksnes and Cao, 2011). But uptake sites might also be costly since these are potential entry points for viral attack (Menge and Weitz, 2009), and it has been proposed that resistance against viral attack will slow the growth of abundant and cosmopolitan picoplanktonic prokaryotes (Yooseph *et al.*, 2010).
- (ii) Light harvesting,  $\phi_L$ , represents investment in pigments present in the chloroplasts leading to higher affinities and maximum uptake rates for light. The investment costs are rather well known (Raven, 1984) as well as the respiratory costs (Falkowski and Raven, 1997).
- (iii) Phagotrophy,  $\phi_F$ , represents affinity (clearance rate) for prey or other particulate organic material. Phagotrophy involves prey capture, engulfment, digestion, assimilation and egestion. The costs for synthesizing the full machinery involved in phagotrophy have not been quantified experimentally; however, the biochemical pathways are well known. Calculations of potential energetic costs of synthesis of the phagotrophic machinery show that the investment costs of a typical phagotrophic apparatus are <10% of the cells carbon or nutrient currency (Raven, 1996). Phagotrophy might also have an additional cost in terms of increased susceptibility to predators due to increased encounters (Raven, 1996, 1997).

The budgeting of limiting chemical elements through the trade-offs leads to a formulation of population growth rate of cells as a function of their traits:

$$r(\boldsymbol{\phi}, X) = \mu(\boldsymbol{\phi}, X) - m(\boldsymbol{\phi}, X) \text{ with } \boldsymbol{\phi} = \{\phi_N, \phi_L, \phi_F, d\}, \quad (1)$$

with  $\mu$  being the birth or doubling rate and  $m$  the mortality rate.  $X$  represents environment (light, nutrients, food, temperature, prey, predators, etc.) as a function of space and time and  $\phi$  the set of all traits, including size  $d$ . This equation allows for the evaluation of the fitness of different trait combinations and would form the basis for inclusion in a conceptual model of the entire trait distribution, for adaptive dynamics, or for moment closure techniques (Wirtz and Eckhardt, 1996; Norberg *et al.*, 2001; Bruggeman and Kooijman, 2007). We conjecture that the harvesting traits will vary systematically with size (Fig. 2b): small organisms will invest primarily in photosynthesis and secondly in nutrient uptake, intermediate sized cells will invest in all three harvesting traits and large cells will invest exclusively in phagotrophy. The predicted balance between investments in harvesting traits will depend on the exact quantification of the trade-offs.

## SUMMARY

We have synthesized a sketch of trait-based modelling principles for unicellular planktonic organisms. We propose that a combination of harvesting traits and organism size will yield important insights into how the emergent trophic strategy depends on environmental conditions. The insights outlined provide hypotheses for testing, which, if not borne out by data, should prompt a re-evaluation of the currently well-established relationships between affinities and organism size. In accordance with the central idea in trait-based modelling, functional groups can be abandoned, to the extent that the traditional distinction between photoautotrophs (phytoplankton) and heterotrophs (zooplankton) is discarded. That is, the model predicts the optimal allocation, and thereby the emerging trophic strategy, between photosynthesis, nutrient uptake and phagotrophy. In principle, this scheme can be extended to include other forms of heterotrophy where the carbon source is dissolved organic carbon to include heterotrophic bacteria. Though conceptually appealing, applications face a number of issues.

In accordance with the assumption of diffusion limitation, we considered that the affinity towards nutrient uptake scales linearly with organism diameter. This prediction is, however, not consistent with recent meta-analyses of experimental data (Edwards *et al.*, 2012), which predict that the affinity rather scales with surface area, i.e. diameter squared. On the other hand, experimental analysis from a single group done under comparable protocols, but with much fewer data points, is consistent with linear scaling (Tambi *et al.*, 2009). Why is there an apparent mismatch between some observations and theory? Could it be that the density of uptake sites increases with size such that the linear scaling of affinity

with size is modified? This question can be addressed by trait-based models as outlined earlier.

An organism is characterized by other traits than just the three resource-harvesting traits considered here. A trait representing biomass synthesis would represent investments in nucleus (DNA), mitochondria, RNA and ribosomes (protein synthesis) and endoplasmic reticulum. A central trait not explicitly considered here is defence, representing investments in defences against grazers, parasites and pathogens (Winter *et al.*, 2010). An example is the silica frustule that diatoms construct for protection against predation (Hamm *et al.*, 2003) and viral attack (Raven, 2006) and for facilitation of a metabolically inert vacuole that increases volume (Raven, 1997; Thingstad *et al.*, 2005). The cost is in building the frustule, which creates a reliance on silicate and the rapid loss of competitive ability under low environmental silicate concentrations (Egge and Aksnes, 1992). Building defences into trait-based models requires quantification of defence costs as well as the associated mortality reductions, which are currently unavailable.

Mechanistic trait-based frameworks, such as those sketched here, can mature into plankton models for global circulation models. Realization of that vision requires establishment of trade-offs, analyses of model behaviour and development of the technical basis required for implementation in circulation models. Some of this is under way, e.g. trade-offs related to organism size have been amply analysed by meta-analyses. There is a need, however, to reduce the large uncertainty inherent in such meta-analyses by high quality data from large experimental efforts with harmonized protocols (Tambi *et al.*, 2009; Marañón *et al.*, 2013). Further, there is a need for targeted laboratory analyses aimed directly at quantifying trade-offs through simultaneous measurements of benefits (affinities and maximum uptake rates) and costs (metabolic and investments) for traits other than photosynthesis such as nutrient uptake, phagotrophy, defence, etc. This could be realized by comparing strains in species with large trait variation between strains. Molecular techniques enable studies of gene expression, which will certainly be useful in trait characterization (Toseland *et al.*, 2013). An alternative means of quantifying trade-offs is to exploit extant knowledge of the energetics of basic chemical transformations (e.g. Froelich *et al.*, 1979).

Implementation of multi-dimensional trait-based models in global circulation simulations calls for dimension reduction of the model, discretizing the four trait axes proposed here (three harvesting traits and size) with just 10 bins each would require  $10^4$  state variables, which is currently not feasible. Moment closure techniques (Wirtz and Eckhardt, 1996; Norberg *et al.*, 2001; Bruggeman and Kooijman,



2007) are a promising direction that needs to be developed within a circulation model context. Moment closure may not work well for size distributions because they tend to become multi-modal (Banas, 2011), so the size axis must either be discretized or other techniques developed. Efforts on all three fronts (establishment of trade-offs, analyses of models and technical implementation) are well under way, and the continued progress through the concerted effort of theoretical ecology, data analyses, laboratory work and global circulation modelling will pave the way for practical implementations.

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