

Optimality-based modeling of planktonic organisms

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Abstract

On the basis of the assumption that natural selection should tend to produce organisms optimally adapted to their environments, we consider optimality as a guiding concept for abstracting the behavior of aquatic microorganisms (plankton) to develop models to study and predict the behavior of planktonic organisms and communities. This is closely related to trait-based ecology, which considers that traits and functionality can be understood as the result of the optimization inherent in natural selection, subject to constraints imposed by fundamental processes necessary for life. This approach is particularly well suited to plankton because of their long evolutionary history and the ease with which they can be manipulated in experiments. We review recent quantitative modeling studies of planktonic organisms that have been based on the assumption that adaptation of species and acclimation of organisms maximize growth rate. Compared with mechanistic models not formulated in terms of optimality, this approach has in some cases yielded simpler models, and in others models of greater generality. The evolutionary success of any given species must depend on its interactions with both the physical environment and other organisms, which depend on the evolving traits of all organisms concerned. The concept of an evolutionarily stable strategy (ESS) can, at least in principle, constrain the choice of goal functions to be optimized in models. However, the major challenge remains of how to construct models at the level of organisms that can resolve short-term dynamics, e.g., of phytoplankton blooms, in a way consistent with ESS theory, which is formulated in terms of a steady state.

Phytoplankton are an excellent model system for ecological studies because of their small size, short generation times, large population numbers, and ease of manipulation (Litchman and Klausmeier 2008), and the same is true at least to some extent of plankton in general (including bacteria). Furthermore, the long evolutionary histories of phytoplankton (3 billion yr; Hedges et al. 2001), bacteria, and archaea (3–4 billion yr; Battistuzzi et al. 2004) make them particularly suited for examining the concept of optimality. Ecological stability and protection from extinction afforded by high dispersal have permitted planktonic organisms to evolve gradually through millions of years in spite of strong climate variability (Cermeño et al. 2010). Beyond basic ecology, there is much interest in understanding the major roles of plankton in the biogeochemical cycles of carbon and nutrients on Earth and as the foundation of aquatic food webs.

Deterministic modeling is the primary means of expressing and examining quantitatively our understanding of ecological and biogeochemical systems. In an approach that is complementary to trait-based ecology (McGill et al. 2006; Bruggeman and Kooijman 2007; Litchman and Klausmeier 2008), several recent studies have developed improved models of phytoplankton, bacteria, and zooplankton on the basis of some form of the assumption that organisms dynamically rearrange their physiology or alter their behavior to make the most efficient use of their resources (Merico et al. 2009). The basis for the optimality assumption is that through natural

selection only organisms with the most efficient strategies could survive and reproduce in the continual competition for resources. Optimality-based approaches are of course not restricted to plankton but have also been very successful in the analysis of terrestrial systems (Verdolin 2006).

We review recent studies that have applied the concept of optimality to physiological acclimation or behavioral regulation of planktonic organisms or to the dynamics of communities by formulating models to represent the adaptive capacity of life in terms of trade-offs, balancing the benefits vs. costs of competing resource requirements. Rather than organizing our review around the entity (organism or species) considered in each study, we proceed by considering major ecophysiological processes (e.g., uptake, photosynthesis, grazing, Fig. 1) as they affect the fitness of organisms, populations, species, and communities, similar to the process-based view of Wilkinson (2003) for ecosystems and life in general. However, to be as concrete as possible we consider only processes about which extensive studies have yielded detailed information specifically for plankton, which we classify as follows: (1) community dynamics, (2) autotrophic growth (including regulation of multiple physiological processes), and (3) uptake and grazing (considered as a continuum of processes, all of which include both internalization and processing of resources). We frame the review in the context of these classes of processes to transcend the specifics of each organism and process. Thus we aim to give a coherent overview of the concept of optimality as applied to modeling planktonic organisms.

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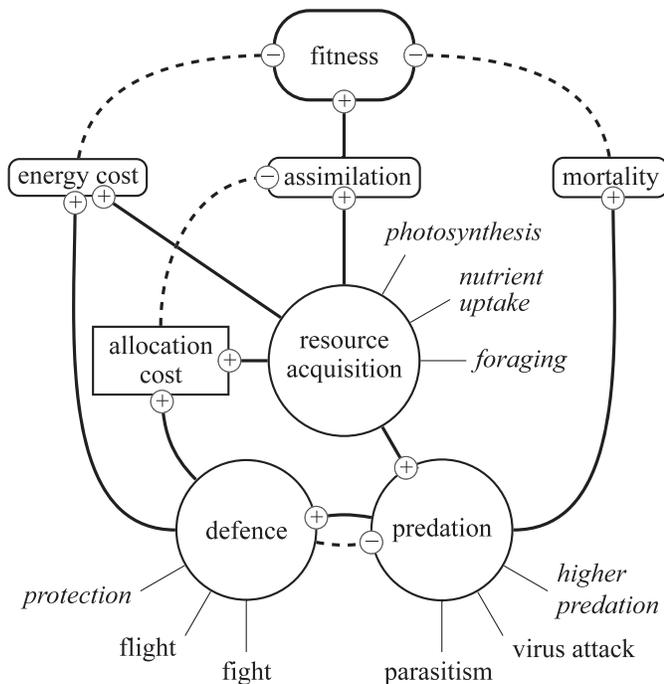


Fig. 1. Major processes and associated trade-offs. Fitness is the balance of gains (assimilation) and losses (energetic cost and mortality). Connecting lines mean “increases” or “induces” (solid with plus symbols), or “reduces” (dashed with minus symbols). Individual processes are categorized into tasks of resource acquisition, predation, and defence. Allocation cost reflects resource utilization for purposes other than growth, as opposed to energy cost and mortality, which are actual loss terms. Resource acquisition, in addition to energy and resource demands, inevitably enhances the risk of predation through interacting with the environment. Processes discussed in the review are italicized.

Optimization, acclimation, and adaptation

The performance of an organism subject to typically fluctuating intra- and interspecific interactions with other organisms and its abiotic environment depends on its traits. Variations in the traits may result from both *acclimation*, i.e., often reversible physiological or behavioral changes not inherited to the next generation, or *adaptation*, i.e., evolutionary change ensuing from natural selection. The ability to acclimate may itself be viewed as an adaptation to cope with a variable environment.

In an optimality-based model, traits of a species are collectively viewed as a manifestation of a solution, whether exact or approximate, to an optimization problem. Modeling optimal acclimation generally comprises two main tasks: defining an appropriate optimization problem or goal function, and determining trade-offs the organisms face in maximizing this goal function. Evolutionary adaptation can be modeled in the same way, although timescales will in most cases be much longer. Competitive displacement among differently adapted species (Bruggeman and Kooijman 2007; Hickman et al. 2010) can be modeled with essentially the same approach (Merico et al. 2009).

Goal functions

Optimality-based modeling approaches define a measure of fitness and assume that the optimization consists of maximizing fitness on some representative timescale for each organism considered. For plankton, an obvious choice is to define fitness (F) as net growth rate, given by the balance between assimilation and loss terms:

$$F = G = A - L, \quad (1)$$

where G is net growth rate, A gross assimilation, and L loss, which may comprise respiration (energetic cost) as well as predation mortality (Fig. 1).

Any goal function geared toward maximizing short-term fitness must also enable the species to survive in the long term for the strategy to be viable on evolutionary timescales; i.e., it must be an evolutionarily stable strategy (ESS) (Maynard Smith and Price 1973; Maynard Smith 1982; Mylius and Diekmann 1995). At least in principle, ESS theory can therefore provide constraints on the choice of goal function. For example, a central condition for an ESS is that it must exclude the possibility of invasion by a competing species, which would require the invader’s net growth rate to exceed that of the resident species. Thus, maximizing net growth rate (G) in Eq. 1 is an obvious choice for the fitness term for an ESS.

However, to resolve short-term dynamics, e.g., phytoplankton blooms and response of grazers, it is necessary to consider the timescales relevant to individual organisms, as opposed to the much longer timescales (or the assumption of steady state) often considered for ESS-centered models in theoretical ecology. In the latter, it is common to solve for the ESS having zero net growth rate, such that any other strategy has negative net growth rate. This ensures that the ESS cannot be invaded. However, it is often not practical to formulate detailed models of short-term processes at the level of organisms in ways that include external loss terms such as grazing by other organisms. Hence many studies at the organism level have taken specific growth rate (excluding external losses), as a goal function to be maximized, to a nonzero value (Fig. 2). Goal functions can also be specified for cellular subsystems relevant to particular processes. For example, the recently developed optimal uptake kinetics considers the goal of maximizing nutrient uptake as an isolated process (Pahlow 2005; Smith and Yamanaka 2007).

We will show below that studies have successfully applied this approach of maximizing specific growth rate to yield improved models. Such goal functions that exclude external loss terms are not sufficient to solve for an ESS. However, neither is the steady-state condition of ESS sufficient to resolve the short-term dynamics of planktonic organisms.

Furthermore, ESS theory rests on the assumption of asexual reproduction, and most models of plankton assume asexual reproduction and constant cell size, in which case growth rate is equivalent to rate of reproduction. However, to model short-term dynamics of sexually reproducing organisms, including zooplankton and some phytoplank-

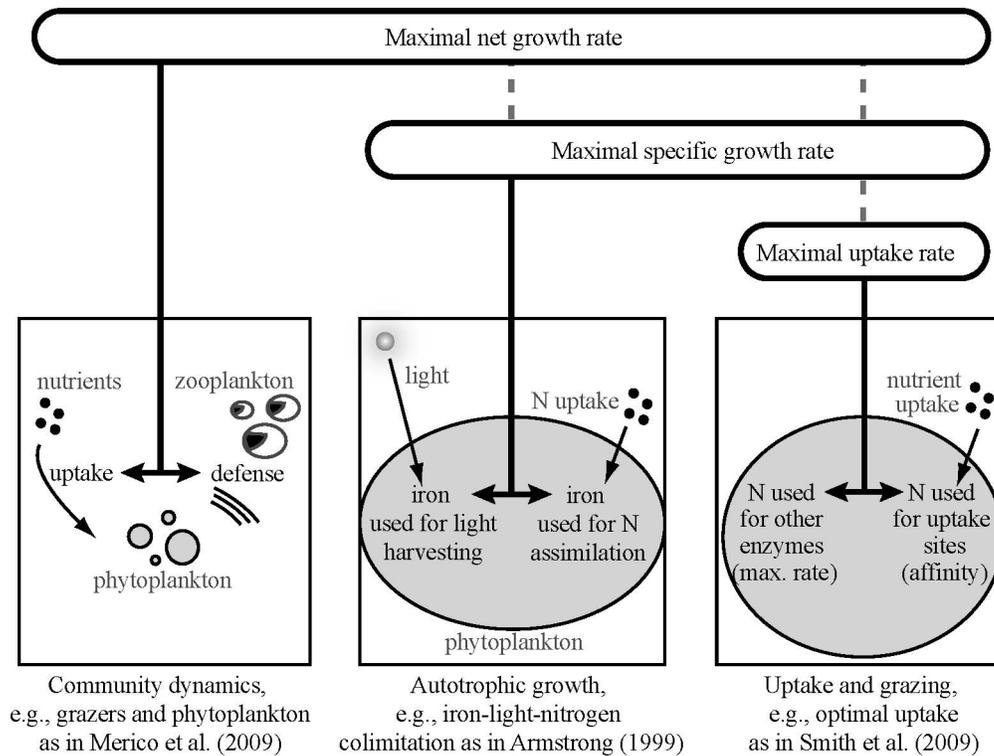


Fig. 2. Diagram showing one example of an optimality-based model for each of the three classes of processes considered in this review. The essential trade-off in each model is indicated by a bold double arrow, connected by a vertical line to the quantity optimized, above. The gray dashed lines indicate that specific growth rate and uptake rate are expected to be positively related to net growth rate, which is the rationale for maximizing them in models that do not explicitly calculate net growth rate.

ton, it may be necessary to consider goal functions that explicitly account for the distinction between rates of reproduction vs. growth.

Trade-offs

The choice of trade-offs (Table 1) and how to represent them is central to optimality-based modeling. To the extent that general trade-offs can be quantified, this strategy provides a basis for constructing models that can predict how organisms acclimate (through physiological or behavioral dynamics), how species evolve, and how species compositions change within communities in response to changing environmental conditions. Thus a model formulated for processes at the level of an organism can also represent the interspecies differences that result from adaptation (Smith et al. 2009), if general trade-offs can be defined for the relevant traits. The biological problems of how best to allocate multiple resources subject to trade-offs have analogs in microeconomics, as Bloom et al. (1985) showed for plants.

The large amount of data compiled for variations in the values of parameters fitted to empirical relationships has been valuable for identifying and quantifying trade-offs for phytoplankton (Litchman et al. 2007) and bacteria (Vallino et al. 1996). Although not defining a trade-off per se, the trait of stoichiometric body composition, together with mass balance, can provide constraints relating resource supply, species composition, and nutrient recycling (Hall

2009). This can play an important role in quantifying trade-offs (Vallino et al. 1996; Bruggeman and Kooijman 2007).

Trade-offs can be incorporated into models with the help of empirical functions or with mechanistically motivated postulates about the processes under consideration. For greater generality, a model must account for opportunity costs and indirect costs of resource allocation, in which case the allocation of resources can alter both the strength and shape of multiple functional relationships as in the work of Armstrong (1999). A major challenge lies in deriving trade-offs between processes linked to dissimilar gain and cost terms: how could a gain in light-harvesting ability be related to the cost of reduced nutrient-uptake capacity? This apples-and-oranges problem can be circumvented as long as trade-offs can be formulated in a single currency, e.g., energy as in Armstrong (1999), although this is not generally possible, particularly in cases where more than two different currencies are required (e.g., C, N, P, chlorophyll [Chl] in phytoplankton, Wirtz and Pahlow 2010).

Adaptation: A community perspective

Competition for resources determines ecological dynamics, and at longer timescales populations are also subject to mutations that determine long-term evolutionary dynamics. Evolutionary changes are driven by the appearance of new genetically distinct forms of organisms, the mutants, characterized by changes in their traits with respect to other organisms of the same species.

Table 1. Trade-offs considered for each class of processes reviewed.

Trade-offs	References
Adaptive dynamics of communities	
Max. growth rate vs. edibility	Wirtz and Eckhardt 1996
Growth (minus cost of defense) vs. defense against grazers	Fussmann et al. 2005
Max. growth rate vs. assimilation of nitrate	Follows et al. 2007
Half-sat. value for ammonium vs. ability to use nitrate	Follows et al. 2007
Half-sat. value for nutrient vs. resistance to grazing	Merico et al. 2009
Half-sat. value for ammonium vs. ability to use nitrate	Hickman et al. 2010
Half-sat. value for nutrients vs. optimal temp. for growth	Hickman et al. 2010
Regulation of autotrophic growth	
Energy requirements vs. inverse growth rate	Shuter 1979
Iron for light harvesting vs. iron for N assimilation	Armstrong 1999
Competitive ability for light vs. competitive ability for P	Klausmeier and Litchman 2001
Energy for nutrient uptake vs. energy for biosynthesis	Pahlow 2005
Energy for nutrient uptake vs. energy for biosynthesis	Pahlow and Oschlies 2009
N for biosynthesis vs. N for photosynthesis	Pahlow and Oschlies 2009
P for nucleus and membranes vs. P for N uptake, biosynth.	Pahlow and Oschlies 2009
Energy for nutrient uptake vs. energy for C acquisition	Wirtz and Pahlow 2010
Energy for light harvesting vs. energy for Calvin cycle	Wirtz and Pahlow 2010
N for light reactions vs. N for dark reactions	Armstrong 2006
Uptake and grazing	
Accumulating energy stores vs. avoiding predation	Fiksen and Carlotti 1998
Half-sat. value for substrate vs. max. growth rate	Wirtz 2002
Energetic cost of predation vs. energy gained from prey	Tschirhart 2004
Opportunity to capture prey vs. risk of being preyed upon	Tschirhart 2004
Affinity for nutrient vs. max. uptake rate	Smith and Yamanaka 2007
Affinity for nutrient vs. max. uptake rate	Smith et al. 2009
Energy used swimming vs. energy gained from prey	Pahlow and Prowe 2010

Ever since Darwin proposed the theory of evolution of species by mutation and natural selection (Darwin 1859), scientists have been trying to describe adaptation and evolutionary changes with mathematical models. However, Fisher (1930), Wright (1931), and Haldane (1932), founders of the field of population genetics, made the first real attempts to combine into a rigorous framework the detailed mechanisms of inheritance with environmental selection forces.

In population genetics, evolution is considered as a sort of improvement and progress, so that the long-term evolutionary dynamics of a trait x can be pictured as a hill-climbing process on a so-called fitness landscape $F(x, \varepsilon)$, which measures the advantage of bearing the trait value x in environment ε (Wright 1931, 1969). The evolutionary rate of change of a certain trait (x) is given by its fitness gradient

$$\frac{dx}{dt} = \delta_x \frac{\partial F(x, \varepsilon)}{\partial x}, \quad (2)$$

where the fitness function (F) describes the interaction of individuals with their environment (ε) and hence how such interactions select the most advantageous trait, and the proportionality factor δ_x represents functional diversity (Fisher 1930). The solution of Eq. 2 is obtained by finding the x that maximizes $F(x, \varepsilon)$, a standard problem of optimization theory.

A recent theory called Adaptive Dynamics, which combines the frequency principle of game theory with the

population genetics framework outlined above, describes the long-term evolutionary dynamics of quantitative traits as driven by mutation and selection (McGill and Brown 2007). Adaptive Dynamics is being applied to ecological and evolutionary problems (Litchman et al. 2009). The theory is based on two important assumptions: mutations are extremely rare with respect to ecological timescales, and mutations are small, implying that evolutionary trajectories can be described by means of ordinary differential equations. Since ecological and evolutionary timescales are kept separated, the resident population can be assumed to be in a dynamical equilibrium when new mutants appear. In practice, Adaptive Dynamics aims at investigating the outcome of competition between the resident and the invader (i.e., the mutant with a slightly different trait from that of the resident) by determining the ESS, which is the trait such that, when the vast majority of individuals have it, no rare mutant with a different trait can increase in numbers.

Several studies (Wirtz and Eckhardt 1996; Fussmann et al. 2005) have relaxed these assumptions by considering the appearance of mutants (an evolutionary process) and the interaction with the resident population (an ecological process) to occur on the same timescales, thus allowing the coexistence of multiple types (mutants and residents) and introducing other sources of trait variability (such as immigration). This new framework, defined by Abrams (2005) as “adaptive dynamics,” describes species succession in ecosystems and the adaptive response of a community to

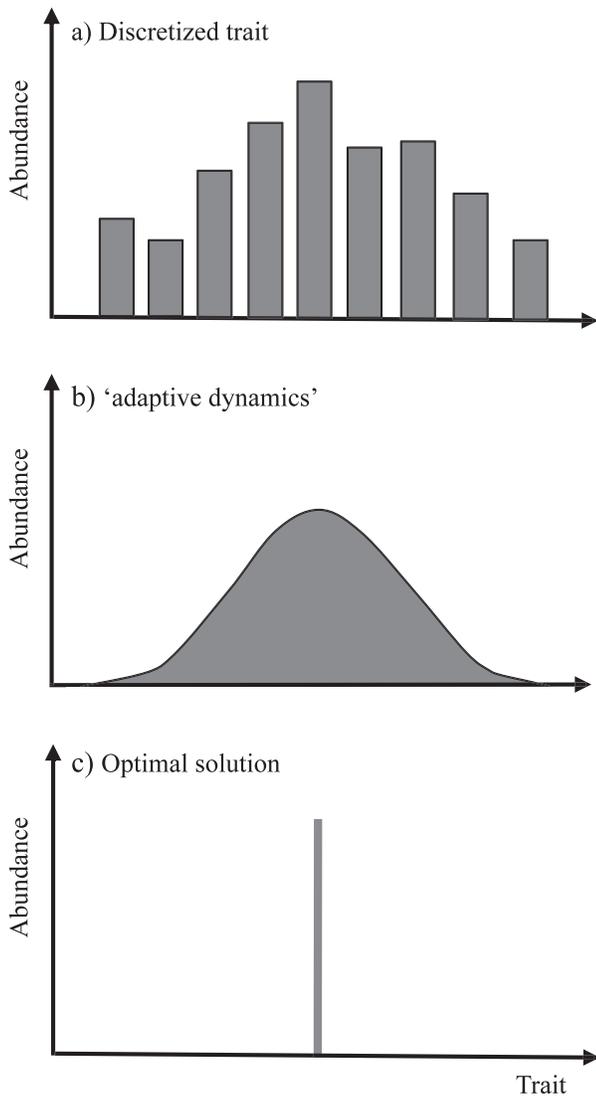


Fig. 3. Schematic of the three different approaches to solving optimality-based models: (a) discrete representation of the distribution of trait values, (b) “adaptive dynamics,” which calculates the rate of change of moments of trait distributions assuming Gaussian (normal) distributions, and (c) directly calculating only the optimal solution. Although approach (a), e.g., Follows et al. (2007), provides the most detailed and versatile representation of trait distributions, it is computationally very intensive. At the other extreme, approach (c), e.g., Smith and Yamanaka (2007), is computationally very efficient but makes the strong assumption that all organisms attain precisely the optimal trait value.

environmental variability on ecological timescales. It provides a computationally more efficient alternative to resolving discrete trait distributions (Fig. 3).

Other studies have similarly found ways around the considerable computational expense of explicitly modeling discretized trait distributions. For example, Moisan et al. (2002) derived an effective temperature function by matching a temperature-optimum function to the overall temperature dependence obtained from a simulated phytoplankton community. The resulting temperature function

thus reflects the trait variability within a certain spatio-temporal realm. This is computationally convenient for larger models compared with resolving explicitly the trait distribution, but their effective functional relationship mirrors a “frozen” image of trait variability and cannot respond to changes, e.g., in global temperature distribution or seasonality. Trait-based adaptive dynamics can also be simplified by dynamically simulating moments, e.g., mean and variance (Fig. 3), of a trait distribution (Wirtz and Eckhardt 1996; Fussmann et al. 2005; Pahlow et al. 2008). This approach retains the capacity of the trait distribution to adapt to changes not only in current ambient conditions but also in temporal and large-scale patterns. Direct simulation of trait distributions does have the important advantage of not requiring explicit formulations for the dynamics of their moments. For example, Follows et al. (2007) and Hickman et al. (2010) have simulated the adaptation of phytoplankton by letting natural selection operate on assemblages of species with relatively finely resolved trait distributions embedded within spatially explicit models of the marine environment.

These ideas have stimulated new developments in the modeling of plankton communities. The trait-based approach (Wirtz and Eckhardt 1996; Norberg 2004) appears particularly promising in this context. The key is a mechanistic definition of a trade-off governing interspecific differences; a realistic representation of community behavior is then obtained by letting natural selection operate on an assemblage of species with different trait values (Bruggeman and Kooijman 2007). Extending the method introduced by Norberg et al. (2001), Merico et al. (2009) provided an example of how to model a plankton community as a single adaptive entity such that the adaptive capacity results from the sorting of species. Such a modeling framework can be applied to any community of competing species for which relevant trade-offs can be defined.

Autotrophic growth

Physiological acclimation—Linkages between multiple resources: Probably the first optimization-based model of physiological acclimation in phytoplankton was that of Shuter (1979). Shuter described trade-offs in terms of intrinsic and extrinsic costs, which is a somewhat confusing terminology, with intrinsic costs defined as the energy requirements for maintenance and biosynthesis, and extrinsic cost as the inverse of growth rate. Armstrong (1999) described the interaction among Fe, NH_4^+ , NO_3^- , and light by optimal allocation of Fe between N- and C-acquisition machinery, such that one element (Fe) controlled assimilation of another (N). Ågren (2004) introduced the conceptually similar idea that N assimilation could be controlled by the capacity to combine amino acids into polypeptides during protein biosynthesis at the ribosomes. Since ribosomal ribonucleic acid constitutes a major cellular P pool (Stern and Elser 2002), this mechanism implies a strong dependence of N assimilation on P quota. The chain model of Pahlow and Oschlies

(2009) extends the optimal growth model of Pahlow (2005) on the basis of the same idea.

Nutrient uptake and light: Armstrong (1999) considered a trade-off defined through the allocation of Fe between nitrate reduction and light harvesting to address the long-vexing problem of how to consistently describe the interaction between NH_4^+ and NO_3^- , the two most important forms of nitrogen. He postulated that phytoplankton should have evolved to allocate scarce iron between these uses to maximize growth rate. Because nitrate reduction requires iron and more energy, ammonium is the preferred nitrogen source, and nitrate was predicted to be taken up only when ammonium uptake is insufficient to maximize growth rate. By allowing growth rate to be colimited by any combination of Fe, light, NO_3^- , and NH_4^+ , the model was able to consistently reproduce the different characteristic shapes of the relationship between nitrate uptake and ammonium concentration observed in different oceanic regions.

Phytoplankton can also acclimate to ambient light and nutrient environment by swimming or regulating their buoyancy. Klausmeier and Litchman (2001) constructed a model of poorly mixed water columns with nutrient supply only from the sediments, assuming that phytoplankton can be limited by either light or nutrient availability and that they can move vertically. They showed that, if mixing is not important and mortality is density independent (constant specific mortality rate), an ESS consists of forming a thin layer at the optimal depth as determined by the balance of competitive abilities for light and nutrients (*see below*).

Photoacclimation: Chl and nutrient content

Although Chl dynamics was part of Shuter's (1979) model, Chl:C variations in the photosynthetic apparatus were not formulated in terms of optimality arguments. Geider (1997) and MacIntyre et al. (2002) argued that maximizing growth rate could not explain photoacclimation because there could be no nitrogen trade-off between light and dark reactions since that would conflict with the observed invariance of maximum growth rate, and because Chl synthesis is down-regulated at relatively low light intensities. However, Armstrong (2006) pointed out that neither of these arguments contradicts optimality-based regulation of pigment synthesis and introduced a nitrogen trade-off between dark and light reactions with no effect on maximum photosynthetic rate, which correctly predicted the down-regulation of pigment synthesis as a function of light intensity. Optimal photoacclimation was based on a trade-off in carbon use instead in Pahlow (2005) and Pahlow and Oschlies (2009), which also avoids affecting maximum growth rate (because that depends only on nitrogen). Figure 4 contrasts the behavior of the formulations by Geider et al. (1998), Armstrong (2006), and Pahlow and Oschlies (2009) in terms of Chl:C and N:C. Only the two optimal-growth models can reproduce the relationship between N:C and Chl:C ratios for light-limited growth (upper right part of Fig. 4), where the model of Geider et al. (1998) predicts almost constant N:C. Even though the trade-offs in the optimality-based models are

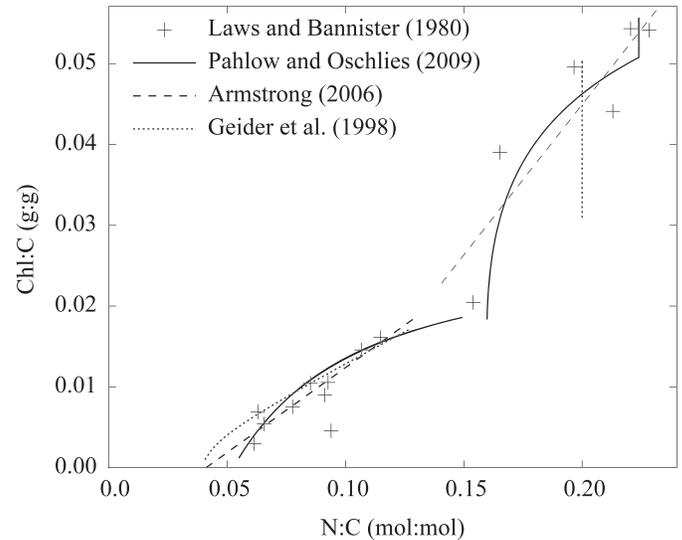


Fig. 4. Predicted relationship between Chl:C and N:C for the mechanistic model of Geider et al. (1998) and the optimality-based models of Armstrong (2006) and Pahlow and Oschlies (2009) compared with observations from Laws and Bannister (1980) for the diatom *Thalassiosira fluviatilis*.

qualitatively different, both explain the down-regulation of Chl:C at intermediate to high irradiance levels as a consequence of a negative relation between the light-harvesting and biosynthetic apparatuses.

Dynamic regulation of multiple resource uptake

Plankton require a variety of different resources, ranging from photosynthetically active radiation to organic substrates, macronutrients like nitrogen or phosphorous, to numerous trace elements. As a reflection of changing ratios in these resources, both in time and in space, the internal composition of planktonic organisms also varies. Because the cellular or organismic stoichiometry strongly affects physiological and ecological functions (Sterner et al. 1992; Hall 2009), a quantitative understanding of this variation is believed to be critical for advancing plankton modeling as a whole (Flynn 2003).

Klausmeier et al. (2004) suggested that phytoplankton cells manage internal pools (of energy, proteins) that can be freely diverted into individual uptake machineries. Variations in their stoichiometry then mirror the solution of an optimal partitioning problem: relative uptake rates of multiple resources are organized such that the steady-state growth rate becomes maximal. Optimal partitioning, not unlike analogous model approaches in microbiology (Vallino et al. 1996) or plant physiology (Givnish 1986; Wirtz 2003), at least qualitatively predicts physiological responses to varying environmental conditions (Klausmeier et al. 2004). More recently, Wirtz and Pahlow (2010) relaxed the steady-state assumption. Modeling the dynamics of multiple resource uptake regulation, however, requires solving the apples-and-oranges problem mentioned above. A partitioning coefficient, or more generally a trait x that regulates the nutrient uptake rate ($U[x]$) has

no *direct* relation to the actual nutrient quota (Q) itself. What, then, is the growth benefit of changing x ? This is equivalent to asking for the effect of varying x and, as a consequence, also $U(x)$, on the goal function (G), here taken as growth rate. Interestingly, one can produce all necessary terms for dynamic optimization using the steady-state balance equation ($U - QG = 0$) and implicit differentiation:

$$\frac{dG}{dx} = \frac{\partial G}{\partial x} + \frac{\partial G}{\partial Q} \frac{dQ}{dx}, \quad (3)$$

with

$$\frac{dQ}{dx} = - \frac{\partial G_B}{\partial x} \left(\frac{\partial G_B}{\partial Q} \right)^{-1}, \quad (4)$$

$$G_B = U(x) - QG(Q, x), \quad (5)$$

where G_B is the balance between uptake and growth, which is set equal to zero at steady state. This extension of the single-goal optimality approach allows quantitative reproduction of a wider spectrum of physiological responses observed in planktonic organisms (Wirtz and Pahlow 2010). It particularly helps by eliminating the need for some formerly required empirical assumptions and simplifications (e.g., Droop terms or lack of colimitation, Klausmeier et al. 2004). The extension also includes a consistent rationale (and refinement) for the trade-off between Chl synthesis and nitrogen uptake used by the photoacclimation model of Pahlow (2005).

Uptake and grazing

Optimal uptake (OU) kinetics—Considering the observations of Kudela and Dugdale (2000) that values of maximum uptake rate for nitrate (as fit to the Michaelis-Menten [MM] equation) increased hyperbolically with increasing nitrate concentration, Pahlow (2005) developed an equation for optimal nutrient uptake as part of his phytoplankton optimal growth model. This study extended the mechanistic uptake equation of Aksnes and Egge (1991) by separating the uptake sites into surface sites (nutrient transporters) and internal enzymes (for assimilating nutrients into biomass), and adding the optimality assumption that some portion of a cell's nitrogen subsistence quota is allocated instantaneously between these two proteinaceous components to maximize uptake rate, which would tend to maximize growth rate.

In contrast to the assumption of instantaneous acclimation, Smith et al. (2009) considered that in many cases the timescale for experimental determination of nutrient uptake kinetics is shorter than the time required for acclimation. Their short-term approximation predicts that the half-saturation constant for nutrient uptake should increase as the square root of the ambient nutrient concentration, which agrees with two independent compilations of data from oceanic field experiments (Smith et al. 2009).

Straightforward application of MM kinetics to growth on several nutrients can greatly overestimate uptake of

nonlimiting nutrients (Droop 1974; Gotham and Rhee 1981a,b). Various models have been formulated by adding parameters to inhibit uptake as a function of internal nutrient concentration (Gotham and Rhee 1981a,b; Flynn 2003). Taking a different approach, Smith and Yamanaka (2007) extended the equation of Pahlow (2005) to multiple nutrients without adding new parameters by assuming that the uptake hardware for all nutrients acclimates in the same proportion on the basis solely of the ambient concentration of whichever nutrient limits growth. The agreement with observations is comparable with that of the considerably more complex inhibition model of Gotham and Rhee (1981a,b) and that of Flynn (2003) (Fig. 5). Flynn's equation fits the data best, but requires choosing values for six parameters per nutrient to describe the feedbacks and the degree to which each nutrient is accumulated. The optimality-based simple phytoplankton optimal nutrient gathering equations (SPONGE) (Smith and Yamanaka 2007) has only two parameters per nutrient (the same as MM) and provides a very different interpretation for the observations. The key differences that allow this relative simplicity are the specification of the goal (namely, maximizing uptake rate of the growth-limiting nutrient) and the trade-off between maximum uptake rate and affinity.

The assumption of Smith and Yamanaka (2007) that uptake hardware for all nutrients is adjusted in the same proportion is not optimal in an immediate sense; i.e., an internutrient trade-off, allocating more resources to uptake of the limiting nutrient and less to the uptake of nonlimiting nutrients would allow faster growth. However, because that assumption agrees with observations from chemostats, Smith and Yamanaka (2007) hypothesized that phytoplankton may not adjust their uptake apparatus in response to changing ratios of ambient nutrient concentrations, but rather only in response to changes in the concentration of the growth-limiting nutrient. We caution that their argument depends on the existence of a unique optimal elemental composition. According to Klausmeier et al. (2007), colimitation indicates optimal composition, but colimitation is associated with a unique elemental composition only in threshold models, which do not adequately describe N-P interactions (Ågren 2004; Pahlow and Oschlies 2009). In general, colimitation can occur over a wide range of elemental compositions (Pahlow and Oschlies 2009) and, therefore, should not be relied upon to define optimal composition. Ideally, optimality criteria (goal functions) should not be based on specific assumptions implicit in (empirical) models that lack a mechanistic foundation, such as the threshold cell-quota formulation (Liebig's Law of the Minimum) considered by Smith and Yamanaka (2007).

Bacterial growth on multiple resources

Vallino et al. (1996) optimized bacterial growth rate in terms of a set of basic metabolic reactions, subject to constraints from energetics, electron balance, and the C:N of biomass. Their results agreed with observations of growth yield as a function of the degree of oxidation of

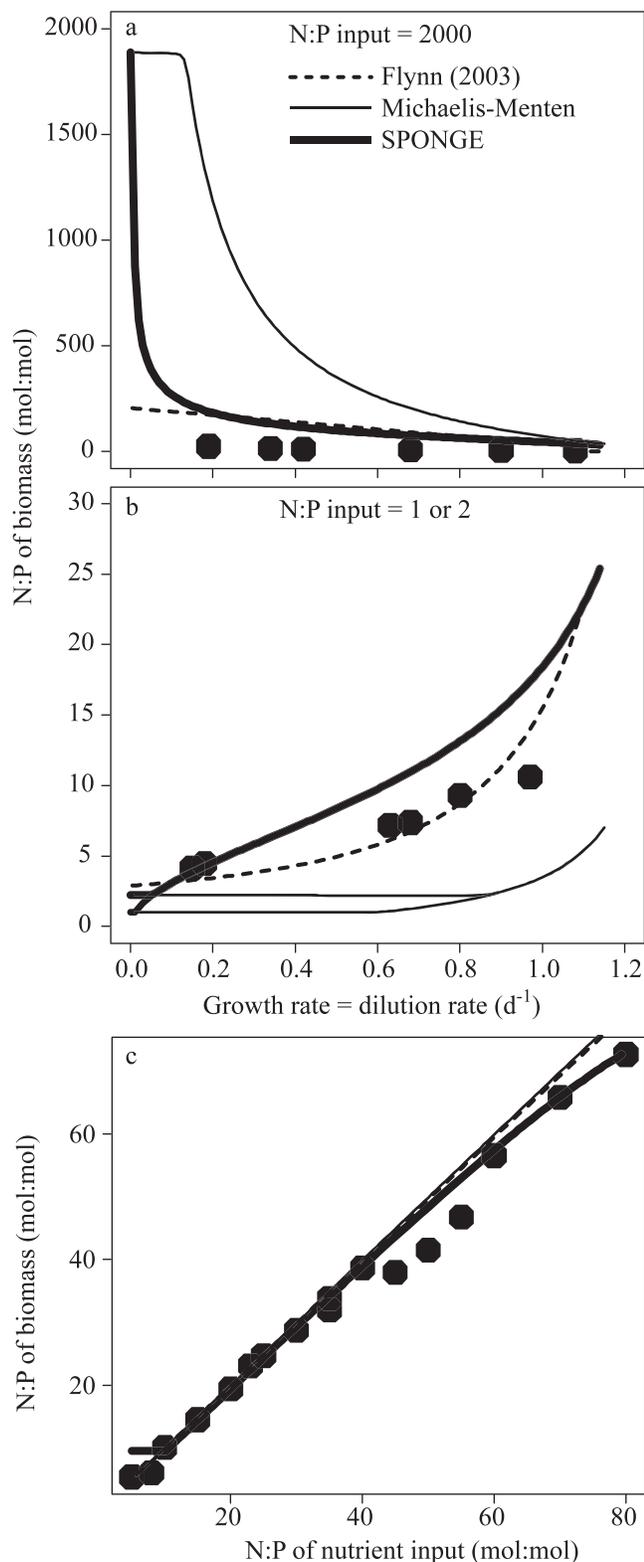


Fig. 5. Data (circles) for composition of phytoplankton biomass from the chemostat experiments of (a, b) Rhee (1974) and (c) Rhee (1978), and fits of models (lines). (Note that in [b] two simulations were run for each model, respectively, with input N:P = 1 or 2, as used in the experiments, which causes the models to diverge at low dilution rates.) Each model consists of the Droop

substrate. Vallino (2003) extended this approach to model bacterial consortia as distributed metabolic networks, which makes possible the interpretation of biogeochemistry as independent of the specific organisms responsible for mediating reactions. The idea is that some organism will evolve to exploit whatever chemical potential can yield energy for growth, and that therefore at least for biogeochemistry it is only necessary to represent the underlying chemical reactions.

Bacterial growth kinetics

Wirtz (2002) expressed as variables the “constants” in the Monod equation for growth rate, using optimization subject to a trade-off between maximum growth rate (μ_{\max}) and half-saturation concentration for growth on substrate (K_s). The model consistently reproduced observations from long-term chemostat experiments, whereas a Monod-type model with constant parameter values could not. This was achieved without increasing the number of parameters compared with the Monod model, but merely by specifying the optimization subject to a trade-off, which was based on the observed relationship between μ_{\max} and K_s (as fit to the Monod equation). The shape of this empirical trade-off is strikingly similar to the central trade-off in OU kinetics (Fig. 6).

This suggests a more concise equation for the essential result of Wirtz (2002), at least for steady state. Assuming constant growth yield, it is straightforward to derive an equation of the same form as the OU equation (Pahlow 2005; Smith et al. 2009), instead for growth rate (μ):

$$\mu = \frac{\mu_0 S}{\frac{\mu_0}{A_0} + 2\sqrt{\frac{\mu_0 S}{A_0}} + S}, \quad (6)$$

where μ_0 is the potential maximum growth rate, A_0 is the potential maximum affinity, and S is the substrate concentration. We term this the optimal growth (OG) equation. The data set of Senn et al. (1994) were collected with multiple replicates over a wide range of growth rates in chemostats, specifically to test different equations relating growth rate to substrate concentration. Compared with the Monod equation, Eq. 6 agrees better with the shape of this data set overall and yields more consistent estimates of parameter values when fitted to different subsets of the data (Fig. 7). For this bacterium, the Monod equation would be much more likely to give erroneous estimates of initial slope (affinity, which measures competitive ability) if data were only available over a limited range of growth rates.

←

quota model (Droop 1968) for growth combined, respectively, with a different equation for uptake rate: eq. 14 from Flynn (2003), the Michaelis-Menten equation (Dugdale 1967), and the optimality-based SPONGE (Smith and Yamanaka 2007).

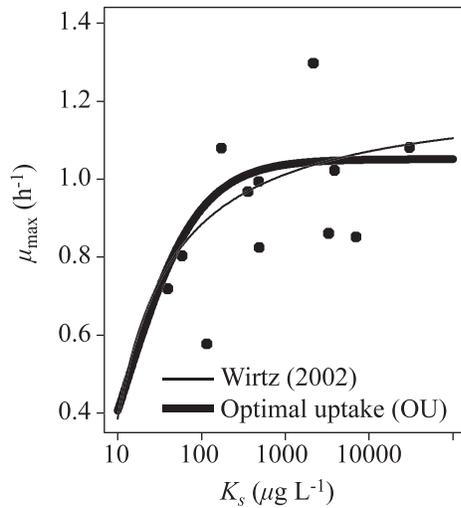


Fig. 6. Data (circles) for maximum growth rate vs. half-saturation constant for growth of the bacterium *Escherichia coli* on glucose, as compiled by Wirtz (2002) together with the empirical trade-off (thin line) and the theoretical OU trade-off (thick line). The empirical trade-off is: $\mu_{\max} = \mu^* \ln(K_s/K_s^*) / (1 + \ln[K_s/K_s^*]) - \rho$, where the last term is for respiration. Here the central trade-off in OU kinetics has been rewritten by combining the short-term equations for apparent maximum uptake rate V_{\max}^{app} and half-saturation constant K_s^{app} (Smith et al. 2009), and a constant yield has been assumed, making growth rate directly proportional to uptake rate: $\mu_{\max} = YV_{\max}^{\text{app}}$ for some constant Y . The OU trade-off for growth is then: $\mu_{\max} = YV_0K_s^{\text{app}} / (V_0/A_0 + K_s^{\text{app}}) - \rho$. Values of V_0 and A_0 in the latter equation were fit to match the empirical equation as reported by Wirtz (2002).

Regulation of foraging activity

In zooplankton optimal-foraging models, the goal function is usually (often implicitly) assumed to be instantaneous net growth rate. Other goals (e.g., longevity or a diverse gene pool) could also be considered, in particular on longer timescales, although these may be more closely related to life cycle rather than foraging strategies.

To maximize net growth, an optimal foraging strategy must balance the gain from ingestion of prey against several loss terms (L), namely respiratory requirement (R) of foraging, excretion (E) of undigested food, and mortality (M) due to predation (Visser et al. 2009), all of which may or may not be directly linked to foraging activity:

$$L = R + E + M, \tag{7}$$

The trade-offs can be derived from empirical or mechanistic links among the gain and loss processes. The exact nature of these links can have profound consequences for the predicted foraging behavior, which we will illustrate here with the example of the relationship between the formulation of the cost of foraging and the prediction of feeding thresholds. A feeding threshold can be understood in terms of optimality as the minimal food concentration that allows the predator to achieve a net energy gain from foraging, i.e., the predator gains more energy from ingestion than it has to spend for foraging (Pahlow and

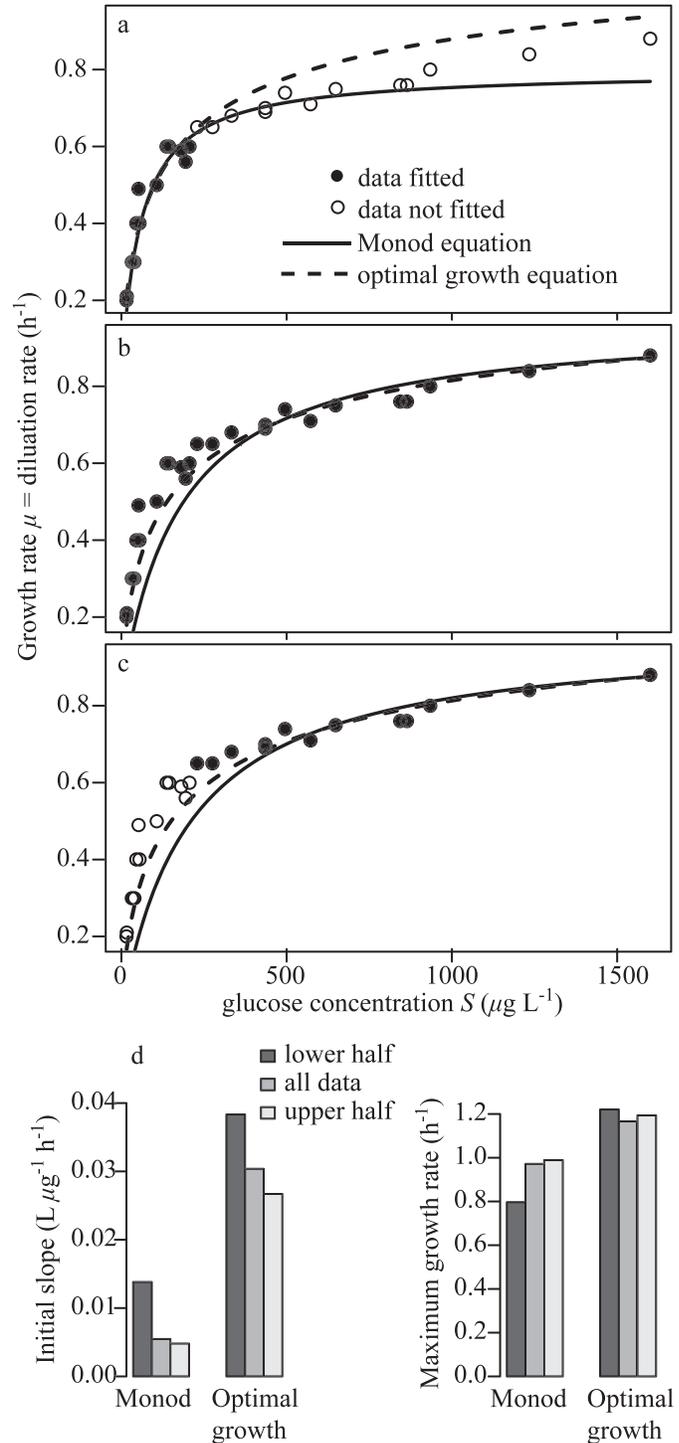


Fig. 7. Results of fitting the inverse of the Monod and OG equations, respectively, to observed glucose concentration (S) vs. growth rate for the: (a) lower half, (b) entire, and (c) upper half of a data set for glucose-limited growth of *Escherichia coli* in chemostats (Senn et al. 1994). Parameter values obtained by fitting to different subsets of the data (d) differed more for the Monod than for the OG equation. The initial slope is V_{\max}/K_s for the Monod equation, and A_0 for the OG equation.

Prowe 2010) or than is lost due to increased risk of predation (Mariani and Visser 2010). A feeding threshold differs from a growth threshold, which is the minimal food concentration allowing for positive net growth and thus additionally providing enough energy to cover maintenance and other energy requirements not directly related to foraging and assimilation.

In the absence of predators, e.g., in laboratory experiments, a linear relationship between R and L leads to a feeding threshold, whereas quadratic or higher-order relationships do not (Pahlow and Prowe 2010). R has been commonly taken to be a quadratic function of foraging activity for small planktonic predators because the drag force of a laminar flow is linearly related to velocity (Lehman 1976; Gerritsen and Strickler 1977; Visser et al. 2009). This view is based on the two implicit assumptions: viscous energy dissipation due to swimming or feeding-current generation is mainly responsible for the energy requirement of foraging, and foraging activity is directly proportional to swimming or feeding-current velocity. Both of these implicit assumptions are incorrect. Viscous energy dissipation contributes only a few percent to the total energetic cost of swimming (Buskey 1998), implying that the cost of foraging is dominated by processes inside the organism. Foraging activity appears to be regulated via the fraction of time spent foraging rather than swimming or feeding-current velocity, at least in current-feeding copepods (Price and Paffenhöfer 1986). Such a regulation of foraging activity also seems more practical since flow velocity directly affects not only encounter rate but also signal strength and, therefore, both mechano- and chemo-receptors used for prey detection can reasonably be assumed to operate most efficiently within a narrow range of flow velocities. Regulating the active time fraction implies a linear relation between foraging activity and cost of foraging (Pahlow and Prowe 2010) and consequently leads to the prediction of a feeding threshold.

Although feeding thresholds have often been demonstrated for copepods (Włodarczyk et al. 1992; Kiørboe and Saiz 1995), and recently for ciliates (Gismervik 2005), there is no evidence of feeding thresholds for other protist microzooplankton (Strom et al. 2000). Further research is warranted, because feeding thresholds are important for the stability of ecosystem models (Frost 1993) and have been implicated in the maintenance of minimum phytoplankton concentrations in oligotrophic and high-nutrient low-Chl areas (Strom et al. 2000).

Switching and foraging strategies

Switching is a change in feeding preference for one kind of prey in the presence of another. If feeding preferences respond to concentration in addition to prey kind, switching is active, otherwise passive. The kind of switching strongly influences model behavior, as only active (but not passive) switching has been found to impart stability to model ecosystems (Franks et al. 1986; Fasham et al. 1990). Evidence in laboratory observations for active switching has been presented for microzooplankton (Goldman and Dennett 1990; Strom 1991) and copepods (Paffenhöfer

1984; Saiz and Kiørboe 1995). Interestingly, active switching in copepods can be coupled to a change in foraging strategy depending on the kind of prey: immotile prey is gathered with a feeding current, whereas motile prey is obtained by ambush feeding (Saiz and Kiørboe 1995). Since feeding strategy is related to risk of foraging, such a coupling can provide additional constraints for developing optimal-foraging models (Mariani and Visser 2010). However, effects of foraging activity on predation mortality are more difficult to quantify than those on metabolic energy requirements. Computable general equilibrium models (Tschirhart 2004) could be a promising tool for this task and for defining optimal foraging strategies in the presence of multiple linked trophic levels.

Active switching as currently used in nutrient–phytoplankton–zooplankton–detritus-type models can lead to a reduction of ingestion with increasing food concentration, which is generally considered paradoxical (Gentleman et al. 2003), but Mariani and Visser (2010) showed that this approach is reasonable in an optimal-foraging context as along as the reduced ingestion is offset by an even stronger reduction in the risk of predation: Cruise feeding seems very effective even at low concentrations of nonmotile food, implying very low feeding thresholds (Pahlow and Prowe 2010), but swimming over relatively long distances will also increase the risk of predation by ambush feeders. Current feeding should be less effective in promoting prey encounter as the volume reached by the feeding current is much smaller than what could be covered by swimming, but the limited extent of the feeding current also reduces the risk of encountering ambush feeders. Ambush feeding only works for motile prey but has the least risk of predation (Visser et al. 2009) and should display no feeding threshold.

Recycling and export

Active switching of copepods between phytoplankton and microzooplankton food was the basis for the formulation of the implicit microbial loop by Steele (1998), which was the first attempt to rationalize differences in export ratios between oligotrophic and more eutrophic ocean regions in terms of the behavior of zooplankton communities. The implicit microbial loop assumed that food-chain length was a function of nutrient content and effectively increased assimilation efficiency at low phytoplankton concentrations. Since assimilation efficiency determines the ratio of export and recycling, this leads to lower export ratios in low-nutrient environments. An inverse relationship between food concentration and assimilation efficiency has also been demonstrated for copepods in the lab (Kiørboe et al. 1985), which may be due to reduced digestive enzyme activity or shorter gut passage times (or both) (Lehman 1976; Hassett and Landry 1983; Pahlow and Prowe 2010). A comparison between Steele's (1998) implicit microbial loop with an optimal-foraging model showed that the relationship between assimilation efficiency and food concentration predicted by the optimal-foraging model had a similar effect on export ratio as the varying food-chain length in the implicit microbial loop (Pahlow and Prowe 2010).

Diel and seasonal vertical migrations of zooplankton are also thought to affect export of carbon and nutrients from the surface ocean (Hays et al. 1997; Steinberg et al. 2000; Hannides et al. 2009), and they are usually explained as strategies to minimize predation loss. The optimal life-history model by Fiksen and Carlotti (1998) balances predation avoidance against the need for accumulating energy reserves required to survive the next winter. As their model was developed for copepods in highly seasonal environments, some modifications can be expected when moving to lower-latitude regions where overwintering is not necessary and zooplankton groups other than copepods are relatively more important. As an alternative modeling approach, balancing predation avoidance against (potential) ingestion could lead to a simpler and yet slightly more general description that is not as tightly linked to copepods and seasonality.

Challenges and future directions

Lack of observations of grazing—Advancement in modeling remains dependent on the availability of adequate observations suitable for hypothesis testing. For example, whether and how far the presence of predators can trigger feeding thresholds in microzooplankton is currently unknown, and this represents a gaping hole in the observational basis, preventing progress in the development of zooplankton feeding models. No experiments contrasting feeding as a function of prey concentration with and without predators present have, to our knowledge, been published. Given that observations are necessary for model validation, all current formulations of relationships between predation and feeding behavior are essentially guesswork.

Remaining challenges

Seeking optimality—Evidence of optimal behavior may be missed if one looks too narrowly at specific processes, rather than holistically at the trade-offs between different uses for a given resource. For example, the above-mentioned arguments by Geider (1997) and MacIntyre et al. (2002) against optimality were based on inappropriate, overly restrictive goal functions. Optimality may manifest itself as much in community compositions where each organism is highly optimized for a narrowly constrained and fixed set of conditions (Hickman et al. 2010) as in the ability for acclimation within a highly variable environment, such as the near-surface ocean with its persistent fluctuations in nutrient concentrations, light intensity, and temperature.

Interpreting data—As noted above, existing compilations of data, including parameter values fitted to empirical equations (Litchman et al. 2007), can be quite useful for defining and precisely quantifying trade-offs. However, as Fig. 7 shows, biases in such parameter values can result if the fixed shape of an empirical equation differs from that of the true response. Care is required to ensure that the parameter values were obtained from appropriate relation-

ships valid for the range of data and timescales considered (Wirtz 2002; Smith et al. 2009), and that all data were collected under comparable conditions. Preconditioning of samples can strongly affect the parameter values obtained from experiments (Smith et al. 2009; Wirtz and Pahlow 2010).

Defining trade-offs—The work of Wirtz and Eckhardt (1996), still one of the few applications of adaptive trait dynamics to in situ observations, formulated trade-offs in phytoplankton physiology and ecology using laboratory data and tested them through inverse modeling. However, empirically derived trade-offs, as applied by Wirtz and Eckhardt (1996), do not allow for reliable generalizations. This major weakness in early optimality-based studies should motivate us to seek and identify biophysical or biochemical laws or models that can explain the functional shape of relevant trade-offs. These models will have to go beyond the optimal allocation schemes described above, especially when extensive traits like body size or ecological interactions are considered. Furthermore, it remains challenging to define truly general trade-offs that apply across different species or functional types. It is often easier to obtain accurate models by making them more specific, e.g., as Wirtz and Pahlow (2010) did by applying different parameterizations for diatoms compared with other phytoplankton with respect to the regulation of light reactions vs. the Calvin cycle.

Computational efficiency vs. realism—Although solving directly for the steady-state optimal solution is computationally very efficient, this approach reveals nothing about the dynamics of trait values or their distribution (Fig. 3). The distribution is an important property related to the dynamics, because the rate of acclimation is proportional to the variance of traits (Eq. 2). Furthermore, this approach cannot account for the potentially important effects on the environment, and hence upon the fitness function, of organisms other than those represented by the single optimal solution. The adaptive dynamics approach, which solves for the moments of trait distributions, is a computationally efficient way to represent the distribution of trait values, but it assumes Gaussian distributions, which may not be realistic in all cases. Discrete resolution of trait values using models that represent many different species (or different mutants of each species) provides detailed information about the distributions of trait values, without assuming a fixed form of their distribution, but at great computational expense. For example, the model of Follows et al. (2007) requires supercomputers to resolve discrete trait distributions for phytoplankton only (not for zooplankton) within a three-dimensional ocean circulation field.

There is much interest in understanding how biodiversity affects the functioning and stability of ecosystems, and modeling biodiversity in planktonic ecosystems poses a major challenge (Duffy and Stachowicz 2006; Litchman et al. 2010). Will it be necessary to model explicitly many different species or functional types (LeQuere et al. 2005; Follows et al. 2007; Hickman et al. 2010)? Or will the much

more computationally efficient approaches of modeling the dynamics of the moments of trait distributions (Bruggeman and Kooijman 2007) or the adaptive dynamics of communities as in Merico et al. (2009) be adequate?

Constraints on model response—Trade-offs reflect inescapable physical or physiological constraints. These built-in trade-offs more narrowly constrain the response of optimality-based models compared with other mechanistic models, particularly in cases where the former include fewer adjustable parameters. This suggests a higher degree of predictive ability for optimality-based models compared with empirically based mechanistic models (Wirtz 2002; Smith et al. 2009; Hickman et al. 2010). These constraints on model response could alleviate some of the concerns raised by Flynn (2003) about oversimplified models generating unrealistic behavior in the “what if” scenarios of exploratory and predictive modeling.

Optimality-based models can also respond more sensitively to parameter values. For example, by assimilating an extensive data set from an oceanic iron-fertilization experiment, Smith et al. (2010) were able to constrain values of OU parameters more narrowly than the corresponding parameters for MM kinetics, with each, respectively, embedded in an otherwise identical ecosystem model. Still, the quantity and quality of observations can limit our ability to distinguish between even models that predict qualitatively different behaviors (e.g., it is difficult to decide which of the two optimal-growth models fits the data better in Fig. 4).

On the other hand, although it may not be intuitively obvious, trait optimization can produce wide variability in observed responses under relatively invariable environmental conditions. In case of a flat goal function, either multiple local optimal solutions may exist, or a single optimal state would only be weakly bound. Optimality-based regulation of clearance activity in grazers at very low prey concentration as in Frost (1975, fig. 1) and Pahlow and Prowe (2010, fig. 5), or of internal stoichiometry in algae at low growth rates (Wirtz and Pahlow 2010, fig. 2) produce highly sensitive results in models. Some data for both clearance (Frost 1972; Rothhaupt 1990; Gismervik 2005) and nitrogen stoichiometry (Elrifi and Turpin 1985; Healey 1985; Hillebrand and Sommer 1999), especially at low rates of ingestion (and hence also of growth), are in fact widely scattered. This evidence suggests that the quasi-stochastic behavior predicted by optimality-based models under those exceptional conditions may be realistic.

Timescales—In experimental design as in modeling, the timescale must be considered. The challenge remains of resolving short-term dynamics in a way consistent with long-term viability (ESS, as discussed above in the section on Goal functions). In this context, it is important to identify the timescales below which organisms should not acclimate or adapt to changing conditions. Both acclimation and adaptation require time and energy, which implies that there should be a minimum timescale for each. For example, yeast acclimate to slow changes in supply of glucose, but effectively filter out variations with frequencies

$\geq 1 \text{ h}^{-1}$ (Bennett et al. 2008). If the acclimation or adaptation process cannot keep up with the variability in certain fluctuating environments, it may be optimal to acclimate only to some extent or to temporally averaged conditions, such that it could be rare to be perfectly acclimated at any given time.

There is evidence for rapid evolution in laboratory predator–prey systems (Yoshida et al. 2003; Fussmann et al. 2005), where competitive ability and defense against grazing in the phytoplankton prey varied on a timescale of weeks. These results are interesting also in the respect that a stable steady state (assumed by ESS theory) did not develop but interaction between the predator and the adapting prey resulted in cyclic alternation between more competitive and more defensive populations. This kind of observation may be critical for the development of optimal-growth models also considering strategies for defending against predation.

Compared with mechanistic models not formulated in terms of optimality, several of the optimality-based models reviewed herein have more accurately reproduced the behavior of organisms over wide ranges of environmental conditions without increasing (Armstrong 1999; Wirtz 2002; Smith et al. 2009), and in some cases even reducing (Pahlow 2005; Smith and Yamanaka 2007; Pahlow and Oschlies 2009), the number of adjustable parameters. Even if organisms only tend toward optimality without ever truly attaining it, optimality can still define the goal and the expected limiting behavior of planktonic organisms. The studies reviewed here constitute more evidence from the past 2 decades supporting the argument made by Parker and Maynard Smith (1990) that optimality-based models can improve our understanding of acclimation and adaptation, even if organisms are not perfectly optimal.

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