

Optimality-based modeling of planktonic organisms

S. Lan Smith,^{a,*} Markus Pahlow,^b Agostino Merico,^c and Kai W. Wirtz^d

^a Environmental Biogeochemical Cycles Research Program, Japan Agency for Marine-Earth
Science and Technology, Yokohama, Japan

^b Leibniz Institute of Marine Sciences at Kiel University (IFM-GEOMAR), Kiel, Germany

^c Leibniz Center for Tropical Marine Ecology (ZMT), Bremen, Germany

^d Helmholtz Center for Materials and Coastal Research, Geesthacht, Germany

* Corresponding author: lanimal@jamstec.go.jp

Acknowledgments

The work of SLS herein was supported by the grant "Marine Environmental Simulation for Future Projection of Marine Ecosystems", Core Research for Evolutional Science and Technology (CREST) to Y. Yamanaka from the Japan Science and Technology Agency (JST), and by a Grant-in-aid for Scientific Research on Priority Areas to SLS (21014011) from the Ministry of Education, Culture, Sports, Science and Technology (MEXT) of Japan.

1 **Abstract**

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

20 **Introduction**

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

32 Deterministic modeling is the primary means of expressing and examining quantitatively our
33 understanding of ecological and biogeochemical systems. In an approach that is complementary
34 to trait-based ecology (McGill et al. 2006; Bruggeman and Kooijman 2007; Litchman and
35 Klausmeier 2008), several recent studies have developed improved models of phytoplankton,
36 bacteria and zooplankton based on some form of the assumption that organisms dynamically
37 re-arrange their physiology or alter their behavior in order to make the most efficient use of their
38 resources (Merico et al. 2009). The basis for the optimality assumption is that through natural
39 selection only organisms with the most efficient strategies could survive and reproduce in the
40 continual competition for resources. Optimality-based approaches are of course not restricted to
41 plankton but have also been very successful in the analysis of terrestrial systems (Verdolin 2006).

42 We review recent studies which have applied the concept of optimality to physiological
43 acclimation or behavioral regulation of planktonic organisms or to the dynamics of communities,
44 by formulating models to represent the adaptive capacity of life in terms of trade-offs, balancing
45 the benefits vs. costs of competing resource requirements. Rather than organizing our review
46 around the entity (organism or species) considered in each study, we proceed by considering

47 major ecophysiological processes (e.g., uptake, photosynthesis, grazing, Fig. 1) as they affect the
48 fitness of organisms, populations, species and communities, similar to the process-based view of
49 Wilkinson (2003) for ecosystems and life in general. However, in order to be as concrete as
50 possible we consider only processes about which extensive studies have yielded detailed
51 information specifically for plankton, which we classify as follows: 1) Community dynamics, 2)
52 Autotrophic growth (including regulation of multiple physiological processes), and 3) Uptake and
53 grazing (considered as a continuum of processes, all of which include both internalization and
54 processing of resources). We frame the review in the context of these classes of processes in order
55 to transcend the specifics of each organism and process. Thus we aim to give a coherent overview
56 of the concept of optimality as applied to modeling planktonic organisms.

57 **Optimization, acclimation, and adaptation**

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

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

72 **Goal functions**

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

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

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

79 Any goal function geared towards maximizing short-term fitness must also enable the species
80 to survive in the long-term in order for the strategy to be viable on evolutionary time scales; i.e., it
81 must be an Evolutionarily Stable Strategy (ESS) (Maynard Smith and Price 1973; Maynard Smith
82 1982; Mylius and Diekmann 1995). At least in principle, ESS theory can therefore provide
83 constraints on the choice of goal function. For example, a central condition for an ESS is that it
84 must exclude the possibility of invasion by a competing species, which would require the
85 invader's net growth rate to exceed that of the resident species. Thus, maximizing net growth rate
86 (G) in Eq. 1 is an obvious choice for the fitness term for an ESS.

87 However, in order to resolve short-term dynamics, e.g., phytoplankton blooms and response
88 of grazers, it is necessary to consider the timescales relevant to individual organisms, as opposed
89 to the much longer timescales (or the assumption of steady state) often considered for
90 ESS-centered models in theoretical ecology. In the latter, it is common to solve for the ESS
91 having zero net growth rate, such that any other strategy has negative net growth rate. This
92 ensures that the ESS cannot be invaded. However, it is often not practical to formulate detailed
93 models of short-term processes at the level of organisms in ways that include external loss terms
94 such as grazing by other organisms. Hence many studies at the organism level have taken specific
95 growth rate (excluding external losses) as a goal function to be maximized, to a non-zero value

96 (Fig. 2). Goal functions can also be specified for cellular sub-systems relevant to particular
97 processes. For example, the recently developed optimal uptake kinetics considers the goal of
98 maximizing nutrient uptake as an isolated process (Pahlow 2005; Smith and Yamanaka 2007).

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

103 Furthermore, ESS theory rests on the assumption of asexual reproduction, and most models
104 of plankton assume asexual reproduction and constant cell size, in which case growth rate is
105 equivalent to rate of reproduction. However, in order to model short-term dynamics of sexually
106 reproducing organisms, including zooplankton and some phytoplankton, it may be necessary to
107 consider goal functions that explicitly account for the distinction between rates of reproduction
108 vs. growth.

109 **Trade-offs**

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

119 The large amount of data compiled for variations in the values of parameters fitted to
120 empirical relationships has been valuable for identifying and quantifying trade-offs for
121 phytoplankton (Litchman et al. 2007) and bacteria (Vallino et al. 1996). Although not defining a

122 trade-off per se, the trait of stoichiometric body composition, together with mass balance, can
123 provide constraints relating resource supply, species composition and nutrient recycling (Hall
124 2009). This can play an important role in quantifying trade-offs (Vallino et al. 1996; Bruggeman
125 and Kooijman 2007).

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

137 **Adaptation: A community perspective**

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

143 Ever since Darwin proposed the theory of evolution of species by mutation and natural
144 selection (Darwin 1859), scientists have been trying to describe adaptation and evolutionary
145 changes with mathematical models. However, Fisher (1930), Wright (1931), and Haldane (1932),
146 founders of the field of *Population Genetics*, made the first real attempts to combine into a

147 rigorous framework the detailed mechanisms of inheritance with environmental selection forces.

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

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

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

157 A recent theory called *Adaptive Dynamics*, which combines the frequency principle of Game
158 Theory with the Population Genetics framework outlined above, describes the long-term
159 evolutionary dynamics of quantitative traits as driven by mutation and selection (McGill and
160 Brown 2007). Adaptive Dynamics is being applied to ecological and evolutionary problems
161 (Litchman et al. 2009). The theory is based on two important assumptions: mutations are
162 extremely rare with respect to ecological timescales, and mutations are small, implying that
163 evolutionary trajectories can be described by means of ordinary differential equations. Since
164 ecological and evolutionary timescales are kept separated, the resident population can be assumed
165 to be in a dynamical equilibrium when new mutants appear. In practice, Adaptive Dynamics aims
166 at investigating the outcome of competition between the resident and the invader (i.e., the mutant
167 with a slightly different trait than the resident) by determining the Evolutionarily Stable Strategy
168 (ESS), which is the trait such that, when the vast majority of individuals have it, no rare mutant
169 with a different trait can increase in numbers.

170 Several studies (Wirtz and Eckhardt 1996; Fussmann et al. 2005) have relaxed these
171 assumptions by considering the appearance of mutants (an evolutionary process) and the
172 interaction with the resident population (an ecological process) to occur on the same timescales,

173 thus allowing the coexistence of multiple types (mutants and residents) and introducing other
174 sources of trait variability (such as immigration). This new framework, defined by Abrams (2005)
175 as 'adaptive dynamics' (in lower case), describes species succession in ecosystems and the
176 adaptive response of a community to environmental variability on ecological timescales. It
177 provides a computationally more efficient alternative to resolving discrete trait distributions
178 (Fig. 3).

179 Other studies have similarly found ways around the considerable computational expense of
180 explicitly modeling discretized trait distributions. For example, Moisan et al. (2002) derived an
181 effective temperature function by matching a temperature-optimum function to the overall
182 temperature dependence obtained from a simulated phytoplankton community. The resulting
183 temperature function thus reflects the trait variability within a certain spatio-temporal realm. This
184 is computationally convenient for larger models compared to resolving explicitly the trait
185 distribution, but their effective functional relationship mirrors a 'frozen' image of trait variability
186 and cannot respond to changes, e.g., in global temperature distribution or seasonality. Trait-based
187 adaptive dynamics can also be simplified by dynamically simulating moments, e.g., mean and
188 variance, (Fig. 3) of a trait distribution (Wirtz and Eckhardt 1996; Fussmann et al. 2005; Pahlow
189 et al. 2008). This approach retains the capacity of the trait distribution to adapt to changes not
190 only in current ambient conditions but also in temporal and large-scale patterns. Direct simulation
191 of trait distributions does have the important advantage of not requiring explicit formulations for
192 the dynamics of their moments. For example, Follows et al. (2007) and Hickman et al. (2010)
193 have simulated the adaptation of phytoplankton by letting natural selection operate on
194 assemblages of species with relatively finely-resolved trait distributions, embedded within
195 spatially explicit models of the marine environment.

196 These ideas have stimulated new developments in the modeling of plankton communities.
197 The trait-based approach (Wirtz and Eckhardt 1996; Norberg 2004) appears particularly
198 promising in this context. The key is a mechanistic definition of a trade-off governing interspecific
199 differences; a realistic representation of community behavior is then obtained by letting natural

200 selection operate on an assemblage of species with different trait values (Bruggeman and
201 Kooijman 2007). Extending the method introduced by Norberg et al. (2001), Merico et al. (2009)
202 provided an example of how to model a plankton community as a single adaptive entity, such that
203 the adaptive capacity results from the sorting of species. Such a modeling framework can be
204 applied to any community of competing species for which relevant trade-offs can be defined.

205 **Autotrophic growth**

206 **Physiological acclimation**

207 **Linkages between multiple resources**

208 Probably the first optimization-based model of physiological acclimation in phytoplankton
209 was that of Shuter (1979). Shuter described trade-offs in terms of intrinsic and extrinsic costs,
210 which is a somewhat confusing terminology, with intrinsic costs defined as the energy
211 requirements for maintenance and biosynthesis, and extrinsic cost as the inverse of growth rate.
212 Armstrong (1999) described the interaction among Fe, NH_4^+ , NO_3^- , and light by optimal allocation
213 of Fe between N and C acquisition machinery, such that one element (Fe) controlled assimilation
214 of another (N). Ågren (2004) introduced the conceptually similar idea that N assimilation could
215 be controlled by the capacity to combine amino acids (AA) into polypeptides during protein
216 biosynthesis at the ribosomes. Since ribosomal ribonucleic acid (RNA) constitutes a major
217 cellular P pool (Sterner and Elser 2002), this mechanism implies a strong dependence of N
218 assimilation on P quota. The chain model of Pahlow and Oeschle (2009) extends the optimal
219 growth model of Pahlow (2005) based on the same idea.

220 **Nutrient uptake and light**

221 Armstrong (1999) considered a trade-off defined through the allocation of Fe between nitrate
222 reduction and light harvesting to address the long-vexing problem of how to consistently describe

223 the interaction between NH_4^+ and NO_3^- , the two most important forms of nitrogen. He postulated
224 that phytoplankton should have evolved to allocate scarce iron between these uses in order to
225 maximize growth rate. Because nitrate reduction requires iron and more energy, ammonium is the
226 preferred nitrogen source, and nitrate was predicted to be taken up only when ammonium uptake
227 is insufficient to maximize growth rate. By allowing growth rate to be co-limited by any
228 combination of Fe, light, NO_3^- and NH_4^+ , the model was able to consistently reproduce the
229 different characteristic shapes of the relationship between nitrate uptake and ammonium
230 concentration observed in different oceanic regions.

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

238 **Photoacclimation: Chl and nutrient content**

239 Although chlorophyll dynamics was part of Shuter's (1979) model, Chl:C variations in the
240 photosynthetic apparatus were not formulated in terms of optimality arguments. Geider (1997)
241 and MacIntyre et al. (2002) argued that maximizing growth rate could not explain
242 photoacclimation because there could be no nitrogen trade-off between light and dark reactions
243 since that would conflict with the observed invariance of maximum growth rate, and because
244 chlorophyll synthesis is down-regulated at relatively low light intensities. However, Armstrong
245 (2006) pointed out that neither of these arguments contradict optimality-based regulation of
246 pigment synthesis and introduced a nitrogen trade-off between dark and light reactions with no
247 effect on maximum photosynthetic rate, which correctly predicted the down-regulation of
248 pigment synthesis as a function of light intensity. Optimal photoacclimation was based on a

249 trade-off in carbon use instead in Pahlow (2005) and Pahlow and Oschlies (2009), which also
250 avoids affecting maximum growth rate (because that depends only on nitrogen). Fig. 4 contrasts
251 the behavior of the formulations by Geider et al. (1998), Armstrong (2006), and Pahlow and
252 Oschlies (2009) in terms of Chl:C and N:C. Only the two optimal-growth models can reproduce
253 the relationship between N:C and Chl:C ratios for light-limited growth (upper right part of Fig. 4),
254 where the model of Geider et al. (1998) predicts almost constant N:C. Even though the trade-offs
255 in the optimality-based models are qualitatively different, both explain the down-regulation of
256 Chl:C at intermediate to high irradiance levels as a consequence of a negative relation between
257 the light-harvesting and biosynthetic apparatuses.

258 **Dynamic regulation of multiple resource uptake**

259 Plankton require a variety of different resources, ranging from photosynthetically active
260 radiation to organic substrates, macro-nutrients like nitrogen or phosphorous, to numerous trace
261 elements. As a reflection of changing ratios in these resources, both in time and in space, the
262 internal composition of planktonic organisms also varies. Because the cellular or organismic
263 stoichiometry strongly affects physiological and ecological functions (Sterner et al. 1992; Hall
264 2009), a quantitative understanding of this variation is believed to be critical for advancing
265 plankton modeling as a whole (Flynn 2003).

266 Klausmeier et al. (2004) suggested that phytoplankton cells manage internal pools (of energy,
267 proteins) which can be freely diverted into individual uptake machineries. Variations in their
268 stoichiometry then mirror the solution of an optimal partitioning problem: Relative uptake rates
269 of multiple resources are organized such that the steady-state growth rate becomes maximal.
270 Optimal partitioning, not unlike analogous model approaches in microbiology (Vallino et al.
271 1996) or plant physiology (Givnish 1986; Wirtz 2003), at least qualitatively predicts physiological
272 responses to varying environmental conditions (Klausmeier et al. 2004). More recently, Wirtz and
273 Pahlow (2010) relaxed the steady state assumption. Modeling the dynamics of multiple resource
274 uptake regulation, however, requires solving the apples-and-oranges problem mentioned above. A

275 partitioning coefficient, or more generally a trait x that regulates the nutrient uptake rate ($U(x)$)
 276 has no *direct* relation to the actual nutrient quota (Q) itself. What, then, is the growth benefit of
 277 changing x ? This is equivalent to asking for the effect of varying x and, as a consequence, also
 278 $U(x)$, on the goal function (G), here taken as growth rate. Interestingly, one can produce all
 279 necessary terms for dynamic optimization using the steady state balance equation ($U - QG = 0$)
 280 and implicit differentiation:

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

281 with

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

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

282 where G_B is the balance between uptake vs. growth, which is set equal to zero at steady state.
 283 This extension of the single-goal optimality approach allows quantitative reproduction of a wider
 284 spectrum of physiological responses observed in planktonic organisms (Wirtz and Pahlow 2010).
 285 It particularly helps by eliminating the need for some formerly required empirical assumptions
 286 and simplifications (e.g., Droop terms or lack of co-limitation, Klausmeier et al. 2004). The
 287 extension also includes a consistent rationale (and refinement) for the trade-off between
 288 chlorophyll synthesis and nitrogen uptake employed by the photoacclimation model of Pahlow
 289 (2005).

290 **Uptake and grazing**

291 **Optimal uptake (OU) kinetics**

292 Considering the observations of Kudela and Dugdale (2000) that values of maximum uptake
 293 rate for nitrate (as fit to the Michaelis-Menten (MM) equation) increased hyperbolically with
 294 increasing nitrate concentration, Pahlow (2005) developed an equation for optimal nutrient

295 uptake, as part of his phytoplankton optimal growth model. This study extended the mechanistic
296 uptake equation of Aksnes and Egge (1991) by separating the uptake sites into surface sites
297 (nutrient transporters) and internal enzymes (for assimilating nutrients into biomass), and adding
298 the optimality assumption that some portion of a cell's nitrogen subsistence quota is allocated
299 instantaneously between these two proteinaceous components in order to maximize uptake rate,
300 which would tend to maximize growth rate.

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

307 Straightforward application of MM kinetics to growth on several nutrients can greatly
308 over-estimate uptake of non-limiting nutrients (Droop 1974; Gotham and Rhee 1981*a,b*). Various
309 models have been formulated by adding parameters to inhibit uptake as a function of internal
310 nutrient concentration (Gotham and Rhee 1981*a,b*; Flynn 2003). Taking a different approach,
311 Smith and Yamanaka (2007) extended the equation of Pahlow (2005) to multiple nutrients
312 without adding new parameters by assuming that the uptake hardware for all nutrients acclimates
313 in the same proportion, based solely on the ambient concentration of whichever nutrient limits
314 growth. The agreement with observations is comparable to that of the considerably more complex
315 inhibition model of Gotham and Rhee (1981*a,b*) and that of Flynn (2003) (Fig. 5). Flynn's
316 equation fits the data best, but requires choosing values for six parameters per nutrient, in order to
317 describe the feedbacks and the degree to which each nutrient is accumulated. The
318 optimality-based Simple Phytoplankton Optimal Nutrient Gathering Equations (SPONGE)
319 (Smith and Yamanaka 2007) has only two parameters per nutrient (the same as MM) and provides
320 a very different interpretation for the observations. The key differences that allow this relative
321 simplicity are the specification of the goal (namely, maximizing uptake rate of the

322 growth-limiting nutrient), and the trade-off between maximum uptake rate and affinity.

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

339 **Bacterial growth on multiple resources**

340 Vallino et al. (1996) optimized bacterial growth rate in terms of a set of basic metabolic
341 reactions, subject to constraints from energetics, electron balance and the C:N of biomass. Their
342 results agreed with observations of growth yield as a function of the degree of oxidation of
343 substrate. Vallino (2003) extended this approach to model bacterial consortia as distributed
344 metabolic networks, which makes possible the interpretation of biogeochemistry as independent
345 of the specific organisms responsible for mediating reactions. The idea is that some organism will
346 evolve to exploit whatever chemical potential can yield energy for growth, and that therefore at
347 least for biogeochemistry it is only necessary to represent the underlying chemical reactions.

348 **Bacterial growth kinetics**

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

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

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

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

369 **Regulation of foraging activity**

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

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

$$L = R + E + M, \quad (7)$$

378 The trade-offs can be derived from empirical or mechanistic links among the gain and loss
379 processes. The exact nature of these links can have profound consequences for the predicted
380 foraging behavior, which we will illustrate here with the example of the relationship between the
381 formulation of the cost of foraging and the prediction of feeding thresholds. A feeding threshold
382 can be understood in terms of optimality as the minimal food concentration that allows the
383 predator to achieve a net energy gain from foraging, i.e., the predator gains more energy from
384 ingestion than it has to spend for foraging (Pahlow and Prowe 2010) or than is lost due to
385 increased risk of predation (Mariani and Visser 2010). A feeding threshold differs from a growth
386 threshold, which is the minimal food concentration allowing for positive net growth and thus
387 additionally providing enough energy to cover maintenance and other energy requirements not
388 directly related to foraging and assimilation.

389 In the absence of predators, e.g., in laboratory experiments, a linear relationship between R
390 and L leads to a feeding threshold, whereas quadratic or higher-order relationships do not
391 (Pahlow and Prowe 2010). R has been commonly taken to be a quadratic function of foraging
392 activity for small planktonic predators because the drag force of a laminar flow is linearly related

393 to velocity (Lehman 1976; Gerritsen and Strickler 1977; Visser et al. 2009). This view is based on
394 the two implicit assumptions: viscous energy dissipation due to swimming or feeding-current
395 generation is mainly responsible for the energy requirement of foraging, and foraging activity is
396 directly proportional to swimming or feeding-current velocity. Both of these implicit assumptions
397 are incorrect. Viscous energy dissipation contributes only a few percent to the total energetic cost
398 of swimming (Buskey 1998), implying that the cost of foraging is dominated by processes inside
399 the organism. Foraging activity appears to be regulated via the fraction of time spent foraging
400 rather than swimming or feeding-current velocity, at least in current-feeding copepods (Price and
401 Paffenhöfer 1986). Such a regulation of foraging activity also seems more practical since flow
402 velocity directly affects not only encounter rate but also signal strength and, therefore, both
403 mechano- and chemo-receptors employed for prey detection can reasonably be assumed to
404 operate most efficiently within a narrow range of flow velocities. Regulating the active time
405 fraction implies a linear relation between foraging activity and cost of foraging (Pahlow and
406 Prowe 2010) and consequently leads to the prediction of a feeding threshold.

407 Although feeding thresholds have often been demonstrated for copepods (Włodarczyk et al.
408 1992; Kiørboe and Saiz 1995), and recently for ciliates (Gismervik 2005), there is no evidence of
409 feeding thresholds for other protist microzooplankton (Strom et al. 2000). Further research is
410 warranted, because feeding thresholds are important for the stability of ecosystem models (Frost
411 1993) and have been implicated in the maintenance of minimum phytoplankton concentrations in
412 oligotrophic and High-Nutrient Low-Chlorophyll (HNLC) areas (Strom et al. 2000).

413 **Switching and foraging strategies**

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

419 for microzooplankton (Goldman and Dennett 1990; Strom 1991) and copepods (Paffenhöfer
420 1984; Saiz and Kiørboe 1995). Interestingly, active switching in copepods can be coupled to a
421 change in foraging strategy depending on the kind of prey: immotile prey is gathered with a
422 feeding current whereas motile prey is obtained by ambush feeding (Saiz and Kiørboe 1995).
423 Since feeding strategy is related to risk of foraging such a coupling can provide additional
424 constraints for developing optimal-foraging models (Mariani and Visser 2010). However, effects
425 of foraging activity on predation mortality are more difficult to quantify than those on metabolic
426 energy requirements. Computable general equilibrium models (Tschirhart 2004) could be a
427 promising tool for this task and for defining optimal foraging strategies in the presence of
428 multiple linked trophic levels.

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

441 **Recycling and export**

442 Active switching of copepods between phytoplankton and microzooplankton food was the
443 basis for the formulation of the implicit microbial loop by Steele (1998), which was the first
444 attempt to rationalize differences in export ratios between oligotrophic and more eutrophic ocean

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

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

466 **Challenges and future directions**

467 **Lack of observations of grazing**

468 Advancement in modeling remains dependent on the availability of adequate observations
469 suitable for hypothesis testing. For example, whether and how far the presence of predators can

470 trigger feeding thresholds in microzooplankton is currently unknown, and this represents a gaping
471 hole in the observational basis, preventing progress in the development of zooplankton feeding
472 models. No experiments contrasting feeding as a function of prey concentration with and without
473 predators present have, to our knowledge, been published. Given that observations are necessary
474 for model validation, all current formulations of relationships between predation and feeding
475 behavior are essentially guesswork.

476 **Remaining Challenges**

477 **Seeking optimality**

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

486 **Interpreting data**

487 As noted above, existing compilations of data, including parameter values fitted to empirical
488 equations (Litchman et al. 2007), can be quite useful for defining and precisely quantifying
489 trade-offs. However, as Fig. 7 shows, biases in such parameter values can result if the fixed shape
490 of an empirical equation differs from that of the true response. Care is required to ensure that the
491 parameter values were obtained from appropriate relationships valid for the range of data and
492 timescales considered (Wirtz 2002; Smith et al. 2009), and that all data were collected under
493 comparable conditions. Pre-conditioning of samples can strongly affect the parameter values

494 obtained from experiments (Smith et al. 2009; Wirtz and Pahlow 2010).

495 **Defining trade-offs**

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

509 **Computational efficiency vs. realism**

510 Although solving directly for the steady state optimal solution is computationally very
511 efficient, this approach reveals nothing about the dynamics of trait values nor their distribution
512 (Fig. 3). The distribution is an important property related to the dynamics, because the rate of
513 acclimation is proportional to the variance of traits (Eq. 2). Furthermore, this approach cannot
514 account for the potentially important effects on the environment, and hence upon the fitness
515 function, of organisms other than those represented by the single optimal solution. The adaptive
516 dynamics approach, which solves for the moments of trait distributions, is a computationally
517 efficient way to represent the distribution of trait values, but it assumes Gaussian distributions,
518 which may not be realistic in all cases. Discrete resolution of trait values using models that

519 represent many different species (or different mutants of each species) provides detailed
520 information about the distributions of trait values, without assuming a fixed form of their
521 distribution, but at great computational expense. For example, the model of Follows et al. (2007)
522 requires supercomputers in order to resolve discrete trait distributions for phytoplankton only (not
523 for zooplankton) within a three-dimensional ocean circulation field.

524 There is much interest in understanding how biodiversity affects the functioning and stability
525 of ecosystems, and modeling biodiversity in planktonic ecosystems poses a major challenge
526 (Duffy and Stachowicz 2006; Litchman et al. 2010). Will it be necessary to model explicitly
527 many different species or functional types (LeQuere et al. 2005; Follows et al. 2007; Hickman
528 et al. 2010)? Or will the much more computationally efficient approaches of modeling the
529 dynamics of the moments of trait distributions (Bruggeman and Kooijman 2007) or the adaptive
530 dynamics of communities as in Merico et al. (2009) be adequate?

531 **Constraints on model response**

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

540 Optimality-based models can also respond more sensitively to parameter values. For
541 example, by assimilating an extensive data set from an oceanic iron-fertilization experiment,
542 Smith et al. (2010) were able to constrain values of OU parameters more narrowly than the
543 corresponding parameters for MM kinetics, with each, respectively, embedded in an otherwise
544 identical ecosystem model. Still, the quantity and quality of observations can limit our ability to

545 distinguish between even models that predict qualitatively different behaviors (e.g., it is difficult
546 to decide which of the two optimal-growth models fits the data better in Fig. 4).

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

558 **Timescales**

559 In experimental design as in modeling, the timescale must be considered. The challenge
560 remains of resolving short-term dynamics in a way consistent with long-term viability (ESS, as
561 discussed above in the section on Goal functions). In this context, it is important to identify the
562 timescales below which organisms should not acclimate or adapt to changing conditions. Both
563 acclimation and adaptation require time and energy, which implies that there should be a
564 minimum timescale for each. For example, yeast acclimate to slow changes in supply of glucose,
565 but effectively filter out variations with frequencies $\gtrsim 1 \text{ h}^{-1}$ (Bennett et al. 2008). If the
566 acclimation or adaptation process cannot keep up with the variability in certain fluctuating
567 environments, it may be optimal to acclimate only to some extent or to temporally averaged
568 conditions, such that it could be rare to be perfectly acclimated at any given time.

569 There is evidence for rapid evolution in laboratory predator-prey systems (Yoshida et al.
570 2003; Fussmann et al. 2005), where competitive ability and defense against grazing in the

571 phytoplankton prey varied on a time scale of weeks. These results are interesting also in the
572 respect that a stable steady state (assumed by ESS theory) did not develop but interaction between
573 the predator and the adapting prey resulted in cyclic alternation between more competitive and
574 more defensive populations. This kind of observation may be critical for the development of
575 optimal-growth models also considering strategies for defending against predation.

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

References

- Abrams, P. A. 2005. 'Adaptive Dynamics' vs. 'adaptive dynamics'. *J. Evol. Biol.* **18**: 1162–1165.
- Ågren, G. I. 2004. The C:N:P stoichiometry of autotrophs – theory and observations. *Ecol. Lett.* **7**: 185–191.
- Aksnes, D. L., and J. K. Egge. 1991. A theoretical model for nutrient uptake in phytoplankton. *Mar. Ecol. Prog. Ser.* **70**: 65–72.
- Armstrong, R. A. 1999. An optimization-based model of iron-light-ammonium colimitation of nitrate uptake. *Limnol. Oceanogr.* **44**: 1436–1446.
- Armstrong, R. A. 2006. Optimality-based modeling of nitrogen allocation and photoacclimation in photosynthesis. *Deep Sea Res. II* **53**: 513–531.
- Battistuzzi, F. U., A. Feijao, and S. B. Hedges. 2004. A genomic timescale of prokaryote evolution: insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BMC Evol. Biol.* **4**: 44, doi:10.1186/1471-2148-4-44
- Bennett, M. R., W. L. Fang, N. A. Ostroff, B. L. Baumgartner, S. Nayak, L. S. Tsimring, and J. Hasty. 2008. Metabolic gene regulation in a dynamically changing environment. *Nature* **454**: 1119–1122.
- Bloom, A. J., F. S. C. III, and H. A. Mooney. 1985. Resource limitation in plants –an economic analogy. *Ann. Rev. Ecol. Syst.* **16**: 363–392.
- Bruggeman, J., and S.A.L.M. Kooijman. 2007. A biodiversity-inspired approach to aquatic ecosystem modeling. *Limnol. Oceanogr.* **52**: 1533–1544.
- Buskey, E. J. 1998. Energetic costs of swarming behavior for the copepod *Dioithona oculata*. *Mar. Biol.* **130**: 425–431.

Cermeño, P., C. de Vargas, F. Abrantes, and P. G. Falkowski. 2010. Phytoplankton biogeography and community stability in the ocean. PLoS ONE **5**: e10037, doi: 10.1371/journal.pone.0010037

Darwin, C. 1859. On the origin of species. John Murray.

Droop, M. R. 1968. Vitamin B12 and marine ecology. 4. the kinetics of uptake, growth and inhibition of *Monochrysis lutheri*. J. Mar. Biol. Ass. U. K. **48**: 689–733.

Droop, M. R. 1974. The nutrient status of algal cells in continuous culture. J. Mar. Biol. Ass. U. K. **54**: 825–855.

Duffy, J. E., and J. J. Stachowicz. 2006. Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. Mar. Ecol. Prog. Ser. **311**: 179–189.

Dugdale, R. C. 1967. Nutrient limitation in the sea: dynamics, identification, and significance. Limnol. Oceanogr. **12**: 685–695.

Elrifi, I. R., and D. H. Turpin. 1985. Steady-state luxury consumption and the concept of optimum nutrient ratios: A study with phosphate and nitrate limited *Selenastrum minutum* (Chlorophyta). J. Phycol. **21**: 592–602.

Fasham, M. J. R., H. W. Ducklow, and S. M. McKelvie. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. J. Mar. Res. **48**: 591–639.

Fiksen, Ø., and F. Carlotti. 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. Sarsia **83**: 129–147.

Fisher, R. A. 1930. Genetical theory of natural selection. Claredon Press.

Flynn, K. J. 2003. Modeling multi-nutrient interactions in phytoplankton: balancing simplicity and realism. Progr. Oceanogr. **56**: 249–279.

- Follows, M. J., S. Dutkiewicz, S. Grant, and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. *Science* **315**: 1843–1846.
- Franks, P. J. S., J. S. Wroblewski, and G. R. Flierl. 1986. Behavior of a simple plankton model with food-level acclimation by herbivores. *Mar. Biol.* **91**: 121–129.
- Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* **17**: 805–815.
- Frost, B. W. 1975. A threshold feeding behavior in *Calanus pacificus*. *Limnol. Oceanogr.* **20**: 263–266.
- Frost, B. W. 1993. A modelling study of processes regulating plankton standing stock and production in the open subarctic Pacific Ocean. *Prog. Oceanogr.* **32**: 17–56.
- Fussmann, G. F., S. P. Ellner, J. Nelson G. Hairston, L. E. Jones, K. W. Shertzer, and T. Yoshida. 2005. Ecological and evolutionary dynamics of experimental plankton communities. *Adv. Ecol. Res.* **37**: 221–243.
- Geider, R. J. 1997. Photosynthesis or planktonic respiration? *Nature* **388**: 132.
- Geider, R. J., H. L. MacIntyre, and T. M. Kana. 1998. A dynamic regulatory model of phytoplanktonic acclimation to light, nutrients, and temperature. *Limnol. Oceanogr.* **43**: 679–694.
- Gentleman, W., A. Leising, B. Frost, S. Strom, and J. Murray. 2003. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep Sea Res. II* **50**: 2847–2875.
- Gerritsen, J., and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. *J. Fish. Res. Board Can.* **34**: 73–82.
- Gismervik, I. 2005. Numerical and functional responses of choreo- and oligotrich planktonic ciliates. *Aquat. Microb. Ecol.* **40**: 163–173.

- Givnish, T. J. 1986. Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration, p. 171–213. *In* T. J. Givnish [ed.], *On the economy of plant form and function*. Cambridge University Press.
- Goldman, J. C., and M. R. Dennett. 1990. Dynamics of prey selection by an omnivorous flagellate. *Mar. Ecol. Prog. Ser.* **59**: 183–194.
- Gotham, I. J., and G.-Y. Rhee. 1981*a*. Comparative kinetic studies of nitrate-limited growth and nitrate uptake in phytoplankton in continuous culture. *J. Phycol.* **17**: 309–314.
- Gotham, I. J., and G.-Y. Rhee. 1981*b*. Comparative kinetic studies of phosphate-limited growth and phosphate uptake in phytoplankton in continuous culture. *J. Phycol.* **17**: 257–265.
- Haldane, J. 1932. *The causes of evolution*. Longmans, Green & Co.
- Hall, S. R. 2009. Stoichiometrically explicit food webs: Feedbacks between resource supply, elemental constraints, and species diversity. *Ann. Rev. Ecol. Evol. Syst.* **40**: 503–528.
- Hannides, C. C., M. R. Landry, C. R. Benitez-Nelson, R. M. Styles, J. P. Montoya, and D. M. Karl. 2009. Export stoichiometry and migrant-mediated flux of phosphorus in the North Pacific Subtropical Gyre. *Deep-sea Res. I* **56**: 73–88.
- Hassett, R. P., and M. R. Landry. 1983. Effects of food-level acclimation on digestive enzyme activities and feeding behavior of *Calanus pacificus*. *Mar. Biol.* **75**: 47–55.
- Hays, G. C., R. P. Harris, and R. N. Head. 1997. The vertical nitrogen flux caused by zooplankton diel vertical migration. *Mar. Ecol. Prog. Ser.* **160**: 57–62.
- Healey, F. P. 1985. Interacting effects of light and nutrient limitation on the growth rate of *Synechococcus linearis* (Cyanophyceae). *J. Phycol.* **21**: 134–146.
- Hedges, S. B., H. Chen, S. Kumar, D. Wang, A. Thompson, and H. Watanabe. 2001. A genomic timescale for the origin of eukaryotes. *BMC Evol. Biol.* **1**: 4, <http://www.biomedcentral.com/1471-2148/1/4>.

- Hickman, A. E., S. Dutkiewicz, R. G. Williams, and M. J. Follows. 2010. Modelling the effects of chromatic adaptation on phytoplankton community structure in the oligotrophic ocean. *Mar. Ecol. Prog. Ser.* **406**: 1–17.
- Hillebrand, H., and U. Sommer. 1999. The nutrient stoichiometry of benthic microalgal growth: Redfield proportions are optimal. *Limnology and Oceanography* **44**: 440–446.
- Kjørboe, T., F. Møhlenberg, and K. Hamburger. 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.* **26**: 85–97.
- Kjørboe, T., and E. Saiz. 1995. Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Mar. Ecol. Prog. Ser.* **122**: 135–145.
- Klausmeier, C. A., and E. Litchman. 2001. Algal games: The vertical distribution of phytoplankton in poorly mixed water columns. *Limnol. Oceanogr.* **46**: 1998–2007.
- Klausmeier, C. A., E. Litchman, and S. A. Levin. 2004. Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnol. Oceanogr.* **49**: 1463–1470.
- Klausmeier, C. A., E. Litchman, and S. A. Levin. 2007. A model of flexible uptake of two essential resources. *J. Theor. Biol.* **246**: 278–289.
- Kudela, R. M., and R. C. Dugdale. 2000. Nutrient regulation of phytoplankton productivity in Monterey Bay, California. *Deep Sea Res. II* **47**: 1023–1053.
- Laws, E. A., and T. T. Bannister. 1980. Nutrient and light limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. *Limnol. Oceanogr.* **25**: 457–473.
- Lehman, J. T. 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol. Oceanogr.* **21**: 501–516.

- LeQuere, C., S. P. Harrison, I. C. Prentice, E. T. Buitenhuis, O. Aumont, L. Bopp, H. Claustre, L. C. da Cunha, R. Geider, X. Giraud, C. Klaas, K. E. Kohfeld, L. Legendre, M. Manizza, T. Platt, R. B. Rivkin, S. Sathyendranath, J. Uitz, A. J. Watson, and D. Wolf-Gladrow. 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology* **11**: 2016–2040.
- Litchman, E., P. de Tezanos Pento, C. A. Klausmeier, M. K. Thomas, and K. Yoshiyama. 2010. Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia* **653**: 15–28.
- Litchman, E., and C. A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Ann. Rev. Ecol. Evol. Syst.* **39**: 615–639.
- Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecology Letters* **10**: 1170–1181, doi: 10.1111/j.1461-0248.2007.01117.x
- Litchman, E., C. A. Klausmeier, and K. Yoshiyama. 2009. Contrasting size evolution in marine and freshwater diatoms. *Proc. Natl. Acad. Sci.* **106**: 2665–2670.
- MacIntyre, H. L., T. M. Kana, T. Anning, and R. J. Geider. 2002. Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria. *J. Phycol.* **38**: 17–38.
- Mariani, P., and A. W. Visser. 2010. Optimization and emergence in marine ecosystem models. *Prog. Oceanogr.* **84**: 89–92.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press.
- Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. *Nature* **246**: 15–18.
- McGill, B., B. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**: 178–185.

- McGill, B. J., and J. S. Brown. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Ann. Rev. Ecol. Evol. Syst.* **38**: 403–435.
- Merico, A., J. Bruggeman, and K. Wirtz. 2009. A trait-based approach for downscaling complexity in plankton ecosystem models. *Ecol. Model.* **220**: 3001–3010.
- Moisan, J. R., T. A. Moisan, and M. R. Abbott. 2002. Modelling the effect of temperature on the maximum growth rates of phytoplankton populations. *Ecol. Model.* **153**: 197–215.
- Mylius, S. D., and O. Diekmann. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**: 218–224.
- Norberg, J. 2004. Biodiversity and ecosystem functioning: A complex adaptive system approach. *Limnol. Oceanogr.* **49**: 1269–1277.
- Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proc. Natl. Acad. Sci.* **98**: 11376–11381.
- Paffenhöfer, G.-A. 1984. Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. *Mar. Biol.* **80**: 323–333.
- Pahlow, M. 2005. Linking chlorophyll-nutrient dynamic to the Redfield N:C ratio with a model of optimal phytoplankton growth. *Mar. Ecol. Prog. Ser.* **287**: 33–43.
- Pahlow, M., and A. Oschlies. 2009. Chain model of phytoplankton P, N and light colimitation. *Mar. Ecol. Prog. Ser.* **376**: 69–83.
- Pahlow, M., and A. E. F. Prowe. 2010. Model of optimal current feeding in zooplankton. *Mar. Ecol. Prog. Ser.* **403**: 129–144.
- Pahlow, M., A. F. Vézina, B. Casault, H. Maass, L. Malloch, D. G. Wright, and Y. Lu. 2008. Adaptive model of plankton dynamics for the North Atlantic. *Prog. Oceanogr.* **76**: 151–191.

- Parker, G. A., and J. Maynard Smith. 1990. Optimality theory in evolutionary biology. *Nature* **348**: 27–33.
- Price, H. J., and G.-A. Paffenhöfer. 1986. Effects of concentration on the feeding of a marine copepod in algal monocultures and mixtures. *J. Plankton Res.* **8**: 119–128.
- Rhee, G.-Y. 1974. Phosphate uptake under nitrate limitation by *Scenedesmus* sp. and its ecological implications. *J. Phycol.* **10**: 470–475.
- Rhee, G.-Y. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol. Oceanogr.* **23**: 10–25.
- Rothhaupt, K. O. 1990. Changes of the functional responses of the rotifers *Brachionus rubens* and *Brachionus calyciflorus* with particle sizes. *Limnol. Oceanogr.* **35**: 24–42.
- Saiz, E., and T. Kiørboe. 1995. Predatory and suspension-feeding of the copepod *Acartia tonsa* in turbulent environments. *Mar. Ecol. Prog. Ser.* **122**: 147–158.
- Senn, H., U. Lendenmann, M. Snozzi, G. Hamer, and T. Egli. 1994. The growth of *escherichia coli* in glucose-limited chemostat cultures: a re-examination of the kinetics. *Biochim. Biophys. Acta* **1201**: 424–436.
- Shuter, B. 1979. A model of physiological adaptation in unicellular algae. *J. Theor. Biol.* **78**: 519–552.
- Smith, S. L., and Y. Yamanaka. 2007. Optimization-based model of multinutrient uptake kinetics. *Limnol. Oceanogr.* **52**: 1545–1558.
- Smith, S. L., Y. Yamanaka, M. Pahlow, and A. Oschlies. 2009. Optimal Uptake kinetics: physiological acclimation explains the pattern of nitrate uptake by phytoplankton in the ocean. *Mar. Ecol. Prog. Ser.* **384**: 1–12, doi: 10.3354/meps08022

- Smith, S. L., N. Yoshie, and Y. Yamanaka. 2010. Physiological acclimation by phytoplankton explains observed changes in Si and N uptake rates during the SERIES iron-enrichment experiment. *Deep Sea Res. I* **57**: 394–408, doi:10.1016/j.dsr.2009.09.009
- Steele, J. H. 1998. Incorporating the microbial loop in a simple plankton model. *Proc. R. Soc. Lond. B* **265**: 1771–1777.
- Steinberg, D. K., C. A. Carlson, N. R. Bates, S. A. Goldwait, L. P. Madin, and A. F. Michaels. 2000. Zooplankton vertical migration and the advective transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea Res. I* **47**: 137–158.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton Univ. Press.
- Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry* **17**: 49–67.
- Strom, S. L. 1991. Growth and grazing rates of the herbivorous dinoflagellate *Gymnodinium* sp. from the open subarctic Pacific Ocean. *Mar. Ecol. Prog. Ser.* **78**: 103–113.
- Strom, S. L., C. B. Miller, and B. W. Frost. 2000. What sets the lower limit to phytoplankton stocks in high-nitrate, low-chlorophyll regions of the open ocean? *Mar. Ecol. Prog. Ser.* **193**: 19–31.
- Tschirhart, J. 2004. A new adaptive system approach to predator-prey modeling. *Ecol. Model.* **176**: 255–276.
- Vallino, J. J. 2003. Modeling microbial consortiums as distributed metabolic networks. *Biol. Bull.* **204**: 174–179.
- Vallino, J. J., C. S. Hopkinson, and J. E. Hobbie. 1996. Modeling bacterial utilization of dissolved organic matter: Optimization replaces Monod growth kinetics. *Limnol. Oceanogr.* **41**: 1591–1609.

- Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav. Ecol. Sociobiol.* **60**: 457–464.
- Visser, A. W., P. Mariani, and S. Pigolotti. 2009. Swimming in turbulence: zooplankton fitness in terms of foraging efficiency and predation risk. *J. Plankton Res.* **31**: 121–133.
- Wilkinson, D. M. 2003. The fundamental processes in ecology: a thought experiment on extraterrestrial biospheres. *Biol. Rev.* **78**: 171–179.
- Wirtz, K. W. 2002. A generic model for changes in microbial kinetic coefficients. *J. Biotechnol.* **97**: 147–162.
- Wirtz, K. W. 2003. Adaptive significance of c partitioning and regulation of specific leaf area in *betula pendula*. *Tree Physiol.* **23**: 181–190.
- Wirtz, K. W., and B. Eckhardt. 1996. Effective variables in ecosystem models with an application to phytoplankton succession. *Ecol. Model.* **92**: 33–54.
- Wirtz, K. W., and M. Pahlow. 2010. Dynamic chlorophyll and nitrogen:carbon regulation in algae optimizes instantaneous growth rate. *Mar. Ecol. Prog. Ser.* **402**: 81–96.
- Włodarczyk, E., A. G. Durbin, and E. G. Durbin. 1992. Effect of temperature on lower feeding thresholds, gut evacuation rate, and diel feeding behavior in the copepod *Acartia hudsonica*. *Mar. Ecol. Prog. Ser.* **85**: 93–106.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* **12**: 97–159.
- Wright, S. 1969. Evolution and the genetics of populations. The University of Chicago Press.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* **424**: 303–306.

Figure Captions

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 defense. 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.

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.

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.

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 to observations from Laws and Bannister (1980) for the diatom *Thalassiosira fluviatilis*.

Figure Captions (continued)

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 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 re-written 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:

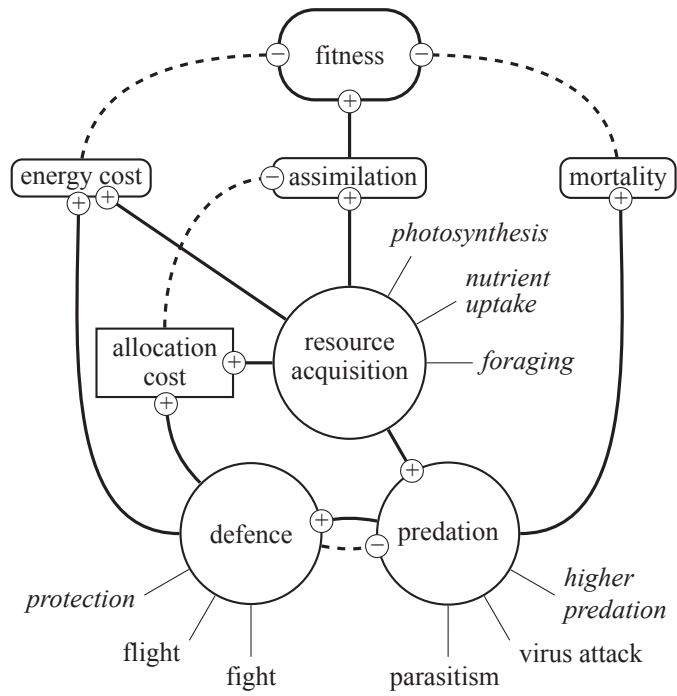
$\mu_{\max} = Y V_{\max}^{\text{app}}$ for some constant Y . The OU trade-off for growth is then:

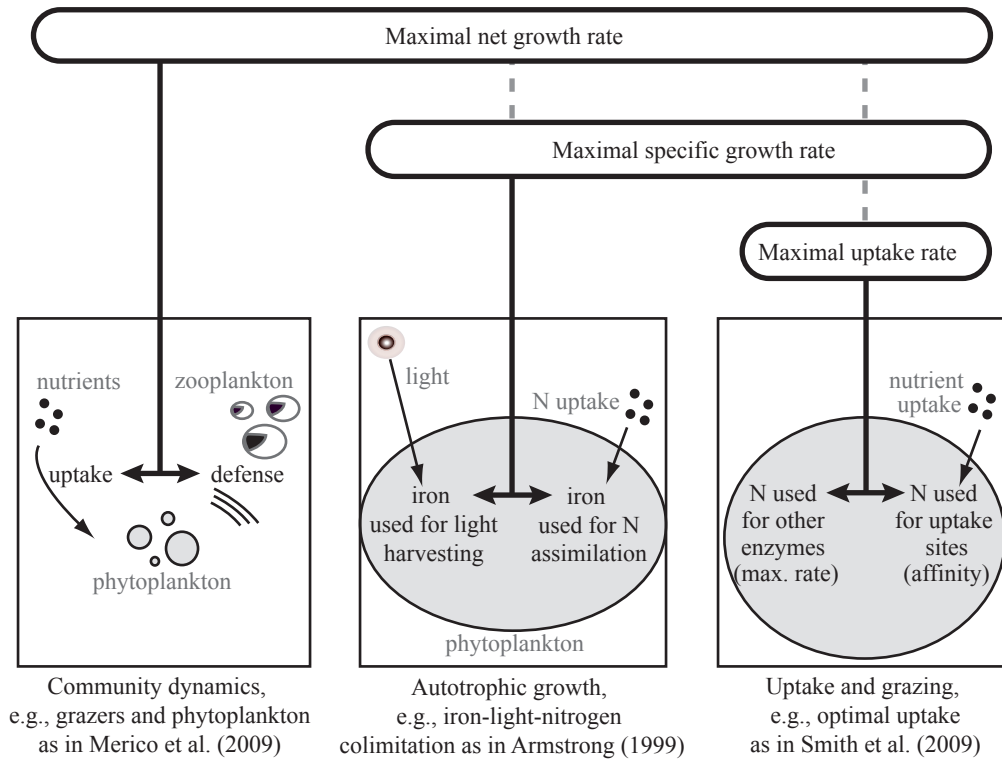
$\mu_{\max} = Y V_0 K_s^{\text{app}} / (V_0/A_0 + K_s^{\text{app}}) - \rho$. Values of V_0 and A_0 in the latter equation were fit to match the empirical equation as reported by Wirtz (2002).

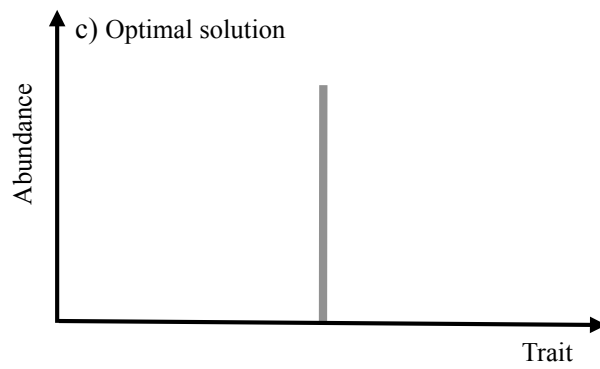
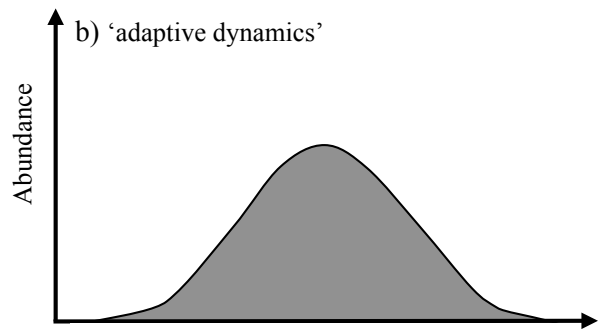
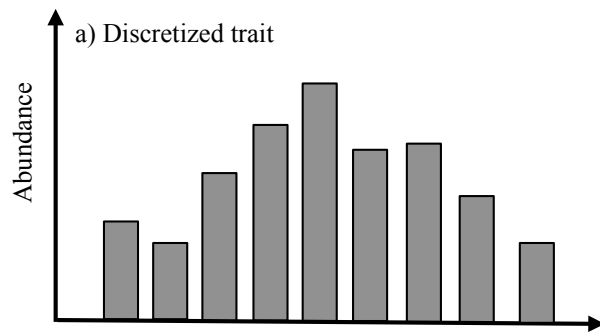
Fig. 7. Results of fitting the inverse of the Monod and Optimal Growth (OG) equations, respectively, to observed glucose concentration (S) vs. growth rate for the: (a) lower half, (b) entire, and (c) upper half of a data set for glucose-limited growth of *Escherichia coli* in chemostats (Senn et al. 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.

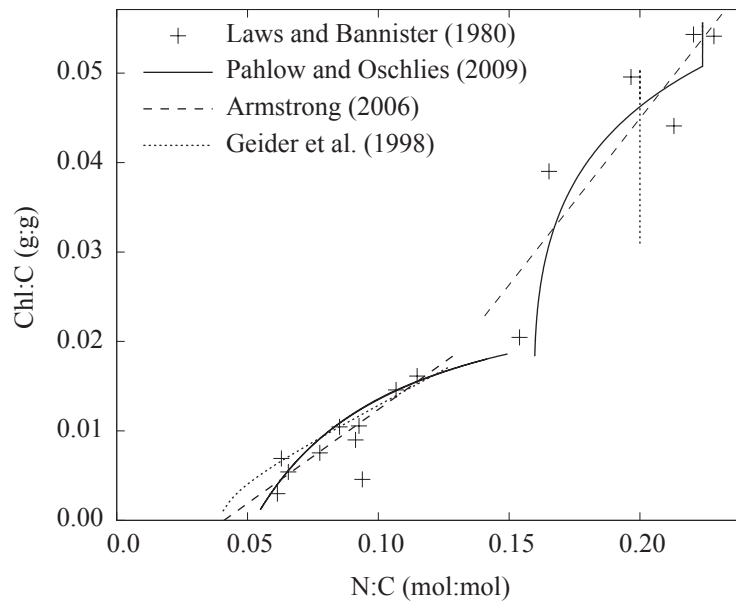
Table 1: Trade-offs considered for each class of processes reviewed.

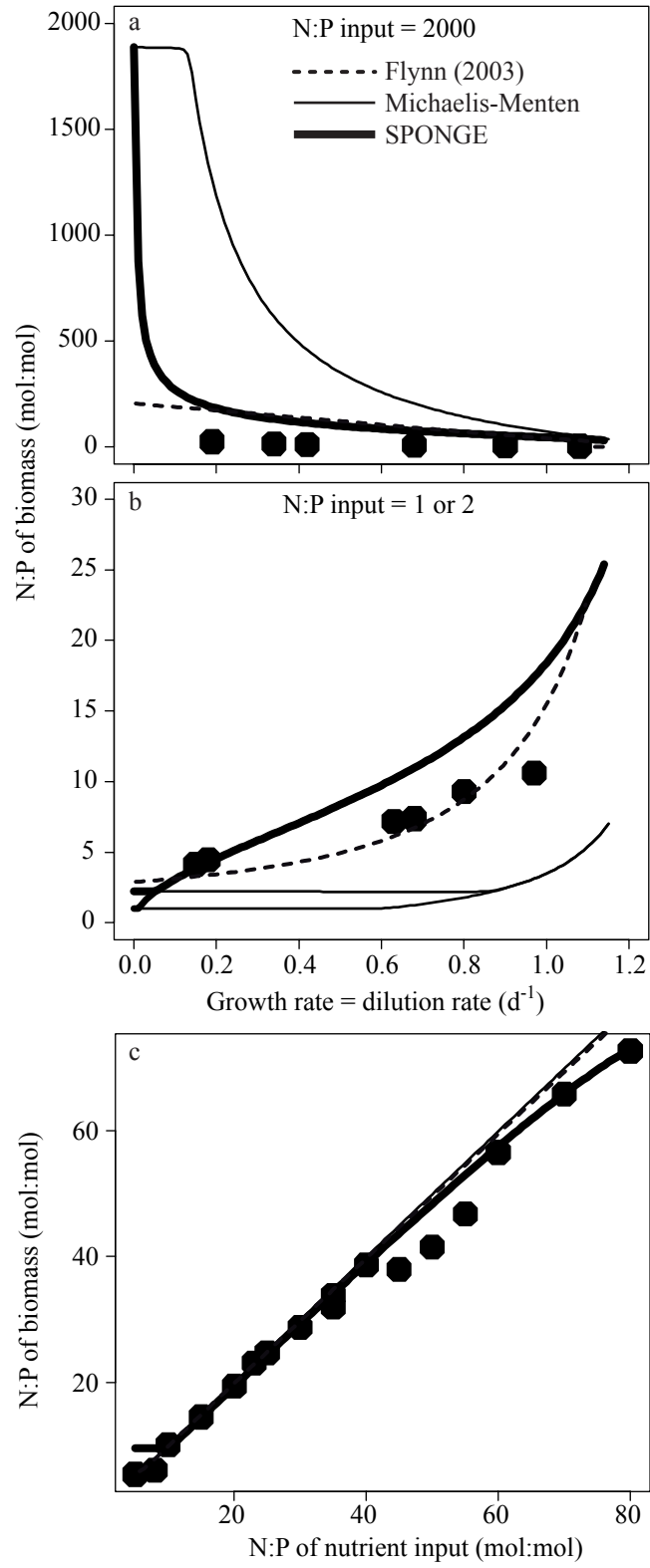
Trade-offs		References	
adaptive dynamics of communities			
max. growth rate	vs.	edibility	Wirtz and Eckhardt 1996
growth (minus cost of defense)	vs.	defense against grazers	Fussmann et al. 2005
max. growth rate	vs.	assimilation of nitrate	Follows et al. 2007
half sat. value for ammonium	vs.	ability 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











Smith et al. Fig. 5

