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# Acclimation, Adaptation, Traits and Trade-Offs in Plankton Functional Type Models: Reconciling Terminology for Biology and Modelling

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## HORIZONS

# Acclimation, adaptation, traits and trade-offs in plankton functional type models: reconciling terminology for biology and modelling

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We propose definitions in terminology to enhance ongoing collaborations between biologists and modellers on plankton ecology. Organism “functional type” should refer to commonality in ecology not biogeochemistry; the latter is largely an emergent property of the former, while alignment with ecology is also consistent with usage in terrestrial science. Adaptation should be confined, as in genetics, to consideration of species inter-generational change; most so-called “adaptive” plankton models are thus acclimative, modifying vital rates in response to stimuli. Trait trade-off approaches should ideally only be considered for describing intra-generational interactions; in applications between generations, and certainly between unrelated species, such concepts should be avoided. We suggest that systems biology approaches, through to complex adaptive/acclimative systems modelling, with explicit modelling of feedback processes (which we suggest should define “mechanistic” models), would provide realistic and flexible bases upon which to develop descriptions of functional type models.

**KEYWORDS:** model; trait trade-off; resource allocation model; functional type; functional trait; adaptation; acclimation; complex adaptive systems; systems biology

## INTRODUCTION

The stimulus for what follows arose during the conduct of a series of workshops exploring biological and ecological modelling. Efforts to resolve conflicts in nomenclature between, and sometimes within, groups of biologists and modellers often deflected the main focus of the workshops clearly indicating the lack of much needed consensus. A biological model is a mathematical representation of a biological system. The study of the model should generate knowledge about the underlying biology, but might be of interest in its own right as an intellectual discipline. Accordingly, there should be general agreement about biological terminology and nomenclature used to describe such models.

Some consideration should be given to the use of the term “model” itself, especially as this is used across various disciplines and methodological approaches. For example, “models” in mathematics range from simple statistics to massively complex dynamic computational descriptions. For biologists, usage of “model” also includes “model organisms”, species or strains presented as exemplars of groups of organisms. This is typically associated with the ease of growth, manipulation and analysis of the species in the laboratory in relation to the specific problem for which the model organism is well suited. For example, although the study of yeast has contributed substantially to the understanding of the effects of disruption of cell division in humans, extrapolation clearly has limitations. Biologists also generate conceptual models, which appear as flow diagrams or biochemistry pathway charts, or as complex food webs. Statistical models form another quite distinct group of applications in biology.

Here emphasis is placed on mathematical constructs that describe biological or ecological system dynamics (and thus upon models containing a temporal dimension) and that adhere to the law of conservation of mass. This is in reflection of the significant effort expended in the development and application of these types of models to enhance our understanding and predictive skills within the realm of plankton ecology and biogeochemistry. The importance of the biology-modelling interface in this context is witnessed by various papers on the subject that have appeared in this journal (Anderson, 2005; Flynn, 2005; Franks, 2009; Allen and Polimene, 2011). As a guide to the reader, in Table I we offer some definitions for the terms we discuss, and in Figs 1 and 2 some schematics indicating how some of these approaches overlap.

## FUNCTIONAL TYPE VS FUNCTIONAL TRAIT AND ECOLOGY

Models of biology, for example those in plankton research, take as their base either the individual or the

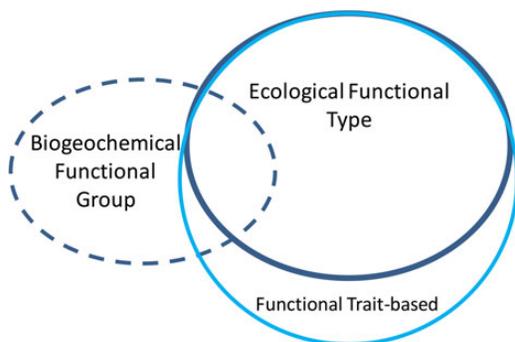
community biomass. In individual-based models (IBMs), the dynamics of individual organisms (e.g. growth, death, feeding, movement) are described over time in relation to abiotic and biotic conditions. In a variant of the IBM, groups of identical individuals are considered as a unit, as so-called “agents” or (perhaps confusingly for biologists) “super-individuals”. For plankton models, however, most frequently the base is biomass (e.g. g zooplankton-C m<sup>-3</sup>), and groups of species (and even phyla) are often merged (e.g. “zooplankton”) to define “functional group” or “functional type” descriptions.

The term “functional type” has a history in terrestrial ecology (Smith *et al.*, 1993) as defining sets of species showing similar responses to the environment and hence similar effects on ecosystem functioning. Such sets, or groups, share certain functional traits, features or properties (e.g. the ability to use nitrate, to feed in a particular fashion), which influence essential functional processes such as growth, reproduction and nutrient acquisition (Gitay and Noble, 1997; Weithoff, 2003). More recently, in oceanographic modelling, the term functional type has been assigned to biogeochemical functionality (Le Quéré *et al.*, 2005). However, biogeochemistry is a product of interactions between species and their environment and is thus largely an emergent property of biology and ecology. Further, many biogeochemical processes are supported or driven by organisms that have very different traits and ecological (trophic) functions. For example, planktonic calcification processes are driven by coccolithophorids, foraminiferans and many other taxonomically diverse plankton groups; one biogeochemical function is performed by very different functional types from an ecological perspective. In consequence, while there may be overlap between biogeochemically based and ecologically based functional descriptions (Fig. 1), there are also distinct differences (Flynn, 2006).

In some instances models are referred to as being functional-trait based (Follows and Dutkiewicz, 2011), rather than functional-type based. Traits are distinctive characteristics; for example, patterning of colour or surface texture (that taxonomists may use to differentiate between species), ability to fix nitrogen, differences in feeding strategies (e.g. raptorial vs suspension feeding). Some of these traits (e.g. differences in colouration, texture) may be non-significant for model development, and models will inevitably emphasize differences in trait expression between groups of species that affect ecological functionality. The high number of traits perceived to have ecological importance (e.g. for zooplankton; Litchman *et al.*, 2013) also demands some level of rationalization prior to modelling (or perhaps the use of modelling to help discern importance). Ecologically based plankton functional type approaches, as employed within models, are thus *de facto* analogous if not identical, to

Table I: Definitions and proposed applications within dynamic models of plankton

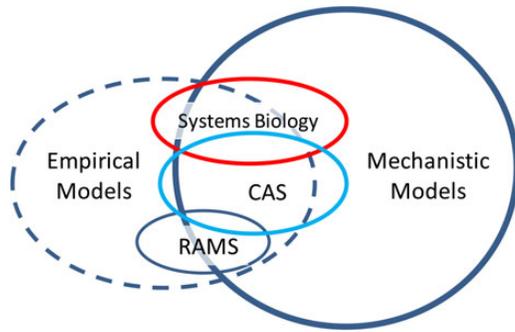
Term	Meaning	Application to dynamic models
Acclimation	Reversible intra-generational change through changes in expression of inherited traits (Cf. adaptation, epigenetic)	Changes to behaviour associated with some form of feedback (e.g. photoacclimation), and thence with mechanistic (q.v.) descriptions
Adaptation	Inter-generational change (evolution) to inherited traits involving changes to the DNA sequence (Cf. acclimation, epigenetic)	Changes in parameters usually considered as model constants, initiated through a process akin to mutation
Complex Adaptive System	Highly diverse system, comprising autonomous components, that modulates its behaviour depending on multiple feedback processes (Cf. Systems Biology)	A model-based concept, but one in which feedback through "acclimation", rather than "adaptation", often dominates. May be closely allied to Systems Biology (q.v.)
Empirical	Stemming from observations, with no explicit feedback link to underlying mechanisms (Cf. Mechanistic)	Responses to inputs described through simple equations, with no explicit feedbacks (e.g. Arrhenius equation, Holling type II)
Epigenetic	Changes to gene expression, not involving changes to the DNA sequence, which persist in organisms and may be transferred to the next and possibly later generations (Cf. acclimation, adaptation)	None known for explicit application to plankton models, though few models explicitly simulate generational changes so <i>de facto</i> likely handled through acclimation with mechanistic (q.v.) models
Fitness	Ability to survive and reproduce reflected in the relative contribution of a genotype or phenotype to the next or future generations; fitness depends not only the traits of the organism(s) in question, but upon all else in the ecosystem	An emergent property from simulations, and/or arising from an explicit trait description
Functional Type/ Group	Sets of species showing similar responses to the environment and similar effects on ecosystem functioning	Involves trait-based grouping of organisms, with those traits either providing functionality through emergent behaviour (as in reality) or typically functionality is defined by allocation of trait (q.v.) descriptions
IBM	Individual Based Model	Typically refers to collections of assumed identical individuals, as "agents"
Mechanistic	Stemming from reference to explicit, deterministic, interactions, which in biology invariably involves feedback events (Cf. empirical)	Inclusion of explicit feedback terms for control of key components (e.g. acclimation). May be closely allied to Systems Biology (q.v.)
Resource Allocation Model (RAM)	Approach (originally financial) through which resources are allocated to various components of a system, often linked to some form of value judgement of the benefits	A model-based concept that requires the use of a common currency for resource allocation and (usually) subsequent value judgement. For biology, the resource may be energy or an element (C, N, P). May be mechanistic through virtue of inclusion of feedback processes
Systems Biology	Modelling approach to describe the functioning of complex biological or ecological processes (Cf. Complex Adaptive Models)	Models with many mechanistic components (each of which seeks to replicate identifiable biological features), and cascades of feedback acclimations at the organism level
Trait	Defining characteristic	Defining characteristic of consequence (functional) to the system being modelled
Trait trade-off	Association (which may be explicit or assumed due to mutual exclusion of contrasting traits) of benefits in expression of one trait to detrimental expression of another trait	Trade-offs usually ascribed (e.g. "small organisms grow faster"), rather than developing through acclimation or adaptation. May be enacted via Resource Allocation Models (q.v.)



**Fig. 1.** Suggested relationships between descriptive terms for the basis for plankton models. Ecological functionality relates to expression of traits, but trait-based models need not necessarily involve grouping organisms according to ecological or biogeochemical functionality. Biogeochemistry is largely an emergent function of ecology and of trait expression set within a given environmental domain. Most models describe few traits, and these are selected to ascribe clear ecological, or biogeochemical, functionality.

Plankton (Functional) Trait-based approaches. The extension of "functional trait based" beyond "ecological functional type", in Fig. 1, is simply to acknowledge that models of plankton may seek to replicate single species, and hence the collective grouping of organisms that is synonymous with "type" descriptions is inappropriate.

From the above, defining plankton components within models according to functional types (i.e. PFT) in alignment with their ecology also gives an alignment for comparing traits. This preserves consistency with modelling philosophies employed in terrestrial science. A desire to compartmentalize planktonic groups according to inputs into biogeochemistry would thus be better not referring to functional type descriptors, but should use alternative terminology, ideally using the term "biogeochemistry" for clarity.



**Fig. 2.** Suggested relationships between descriptive terms for different model types. Empirical models do not contain explicit feedback functions. Mechanistic-based models do contain explicit feedbacks. Mechanistic-based models also contain empirical components, though in systems biology and Complex Adaptive Systems (CAS) models the preponderance is expected to be more mechanistic. Resource Allocation Models (RAMS) may include mechanistic components (with explicit feedback functionality). As systems biology approaches are closely allied to biochemistry and molecular biology, it is unlikely that they will (or need to) invoke resource allocation as a driver for feedback functionality.

## EMPIRICAL VS MECHANISTIC MODELS

Many models are described as being empirical or mechanistic, without a clear definition of what these terms actually mean. Empirical models may be considered as approaches that describe the relationships between variables without seeking an explanation beyond this description (e.g. statistical approaches). Mechanistic models, in contrast, are sold as invoking aspects of reality in their structure. Assuming they are well founded, mechanistic models may thus be argued to have potential to provide more robust descriptors of system behaviour outside of historic understanding. In contrast, empirical models could be considered akin to regression statistics, which should not be used for extrapolating beyond the conditions used in their construction. Much, however, depends on the exact formulation of the functions; an empirical model may contain many features of clear and direct consequence to the real characteristic in question, while other formulations may be little more than a curvilinear fit between features that a biologist may not necessarily see any cause for direct linkage.

A problem arises in that almost any dynamic model of biology contains components that could be argued as being mechanistic in their structure. For example, are not Holling type II and Droop quota formulations implicitly mechanistic? One could argue not. In most applications of Holling type II reference is made to prey availability, not to prey encounter, while the saturation constant relates to prey availability and not to satiation of the predator as it should do in reality. Michael Droop expressly declared his

quota formulation to be empirical (Flynn, 2008a). What we lack, then, is a useful defining feature that differentiates between empirical and mechanistic.

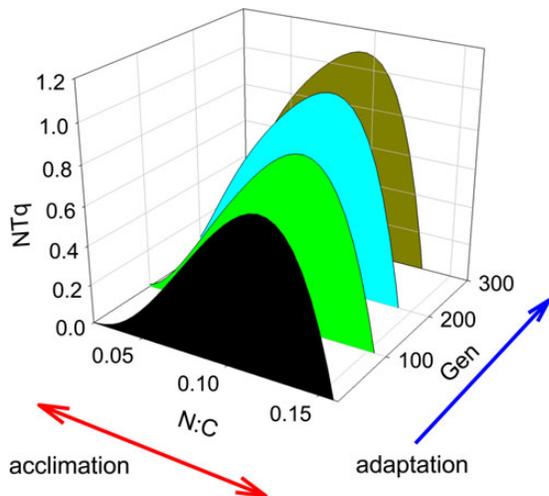
A critical feature of the way that real organisms function is the role of feedback processes that are responsible for regulation through (de)repression of vital rates. Feedbacks are particularly important in the modulation of physiology (including behaviour) in response to multiple stimuli or stressors (e.g. feedback from gut satiation and/or poor quality feed halts ingestion). Indeed, they are among the defining controllers of emergent properties, coupled with acclimation and adaptation (Table I) that ultimately extend all the way to global ecology. This provides us with a clear feature with which to characterize “mechanistic models” of organisms; they must contain explicit feedback functions within the model describing responses to processes that are internal or external to the organism (Table I and Fig. 2).

It must be emphasized that designating a model as empirical or mechanistic does not in itself necessarily indicate whether it gives a better or worse description of reality. Pragmatically, to restrict computational load, there are also good reasons to deploy simple empirical descriptions where appropriate. Plankton models claimed as being mechanistic are invariably more complex, containing numerous state variables with variable stoichiometry (e.g. C:N:P:Chl) or other indicators of physiological status (e.g. gut satiation), the values of which are used to modulate rate processes such as nutrient acquisition. In reality then, few if any models of plankton could fully justify the term “mechanistic model”; most will contain various empirical terms, with mechanistic components for key controls.

## ADAPTATION VS ACCLIMATION

Adaptation (and allies) is another term that in recent years has found increasing usage in ecological modelling. Indeed, there is a complete area of research, termed complex adaptive systems (CAS; Table I; Levin, 1998) that is focused on understanding and predicting the emergent features of natural systems as functions of adaptation, evolution and competition. Less frequently, there are models that vary trait expression that claim to be “acclimative”, rather than adaptive.

Adaptation in biology has a clear meaning; it is evolutionary, inter-generational change involving modification of the genetic material (Orr, 2005; Table I). It may be in part reversible, but is extremely unlikely to be fully reversible to the same start point. Acclimation also has a clear meaning, as intra-generational change that typically occurs rapidly and in itself is totally reversible (Horowitz,



**Fig. 3.** Plot showing hypothetical expression of traits through acclimation and adaptation, with changes in the potential for ammonium transport (NTq) into a phytoplankton cell and changes in the cell's N-status (as indicated by cellular N:C; Flynn *et al.*, 1999). Occurring within a generation such changes are acclimative, while changes in the extent of expression over many generations represent adaptations. Note that initially with increasing N-stress (decreasing N:C) more nitrogenous resources are expended on attempted acquisition of ammonium; conversely when N is in excess (or C lacking) and N:C rises then the number of transporters decreases. Expenditure on transport proteins for nutrient acquisition does thus not simply track demand for the nutrient.

2001; Table I). The form of an acclimation process is subject to adaptation; this is illustrated in Fig. 3.

In line with the biological definitions (Table I) it can be seen that the vast bulk of so-called “adaptive” biological models are actually not of (genetic) adaptation but of (physiological or behavioural) acclimation. Acclimation is the route to modify vital physiological rates of the modelled organisms in response to external and internal stimuli. Thus, acclimation plays an important role in determining short-term system responses which in turn impact upon future selection and the evolution of adaptations. To this, we need to acknowledge the added complication of epigenetics (Table I). However, this inter-generational transmission of what amounts (in simple terms) to a long-term acclimation can likely be simulated in most instances as acclimation because plankton models most frequently do not explicitly simulate organism generations, as they are not true IBMs.

The increasing importance of the correct usage of acclimation versus adaptation develops additionally because there is increasing interest in modelling adaptation (i.e. evolution) as a result of climate change (Schaum *et al.*, 2012; Reusch and Boyd, 2013). It is also important to ensure that model functionality is appropriate in these capacities prior to exploring concepts such as the linkage between ecological and evolutionary dynamics (Pelletier *et al.*, 2009).

An example of an adaptive plankton model is Sauterey *et al.* (Sauterey *et al.*, 2015), where the success of mutated plankton functional types is simulated. In fully developed versions of such models one may expect to see that parameters traditionally held as constant (e.g. maximum growth rate, or the parameters such as those describing the acclimation event shown in Fig. 3) change (adapt) over generations, while within generations acclimatization controls rates within the limits imposed by adaptation. The challenge is then extended to how to control acclimations and adaptations in models. An established approach (though typically not explicitly invoking biological acclimation vs adaptation) is through the concept of trait trade-offs.

### TRAIT TRADE-OFFS AND RESOURCE ALLOCATION MODELS

Both possession and expression of traits are important for the competitive advantage of real organisms. Trait expressions thus help to define fitness (Table I; e.g. Litchman *et al.*, 2013), but ultimately fitness depends on the environmental setting and for the individual is hence an emergent property of the functioning of the whole system (e.g. Sauterey *et al.*, 2015). Controlling the mathematical expression of acclimation within, and adaptation of, traits are thus useful in functional type descriptors in models.

The notion of trade-offs (Table I) is common in life sciences and in modelling, with a particularly rich vein in theoretical studies, though certainly not without its critics (e.g. White *et al.*, 2007). Trade-offs can be considered at the level of acclimation or at adaptation. Examples in acclimation include for zooplankton behaviour between hiding versus feeding (Gliwicz, 2003), or in phytoplankton for the allocation of Fe between photosynthesis, respiration and  $\text{NO}_3^-$  assimilation (e.g. Armstrong, 1999). Classic examples in adaptation include size and growth rate (e.g. for plankton; Sauterey *et al.*, 2015) and the question of allocation of resources for growth or for defence. That there is great scatter for data inversely relating size to growth rate for phytoplankton (Finkel *et al.*, 2010) indicates the lack of generality for this particular trade-off when considered across different groups. There is also evidence that actually phytoplankton growth rate is a function of the rate of environmental change (Schaum and Collins, 2014) and that fast growth potential is lost in systems that cannot support expression of such a rate (Flynn, 2009). For the trade-off between growth and defence in marine protists, it is typically assumed that toxins are costly to make (actually toxins are produced as secondary metabolites during nutrient imbalanced growth; Granéli and Flynn, 2006), and indeed that toxins

that kill grazers are even of benefit to the producer (Cf., Flynn, 2008b). And herein lies a problem; how can we assign values to traits when assessing the costs and benefits of trade-offs?

For modellers, as well as for biologists, assessment of trade-offs is challenging particularly given the involvement in modelling of more recent knowledge of molecular biology (genomics, proteomics, metabolomics, etc.; collectively, the “omics”). To be of consequence for selection, species must have the potential to express a trait; i.e. it must not only be encoded in the DNA but also must be transcribable, or be epigenetic (though in the latter case the possibility of long-term inheritance is unclear, apart from the genetic assimilation of environmentally caused changes). The trait must be realized, with regulatory controls enabling expression (noting that the breadth and magnitude and rates of that expression are themselves important traits; Fig. 3; Kingsolver *et al.*, 2004). Finally, the trait must be operable, with conditions met for its functionality (e.g. substrates must be present). There is thus plenty of scope for confusion in the modelling of traits, often challenging conceptual understanding by biologists as well as non-biologists; a few examples follow.

Diazotrophs have the genetic ability to fix  $N_2$ ; it may thus be tempting to automatically assume that they always fix  $N_2$ , and to model the process accordingly. However, the expression of nitrogenase, the enzyme enabling  $N_2$  fixation, occurs only when the diazotrophs cannot attain sufficient N from fixed inorganic N sources (e.g.  $NH_4^+$ ) in order to satisfy cellular demand (modelled as an acclimative event by Stephens *et al.*, 2003). Another trait often incorporated within plankton models are constants to describe maximum prey ingestion or nutrient transport rates. However, these processes are impacted by feedback from processes such as satiation and repression and therefore the expressed maximum rates at any instant in time vary as a function of the nutritional history of the organism (Flynn *et al.*, 1999; Mitra and Flynn, 2007). A common issue in models, and indeed in the interpretation of experimental results, is an underestimation of the importance of acclimative processes that control the expression of traits, on the degree of acclimation expressed by organisms set against their physiological history, and thence in drivers for adaptation of acclimative traits.

While mathematically tractable to implement, trait trade-offs in biology present serious challenges in their parameterisation for models. Most obviously, implementation requires that we can appropriately rank the significance of all of the traits that contribute to the evolutionary persistence of an organism. One approach is to build a resource allocation model (RAM; Table I); such structures may be empirical or mechanistic (involving explicit feedback functionality; Table I and Fig. 2). The first step in

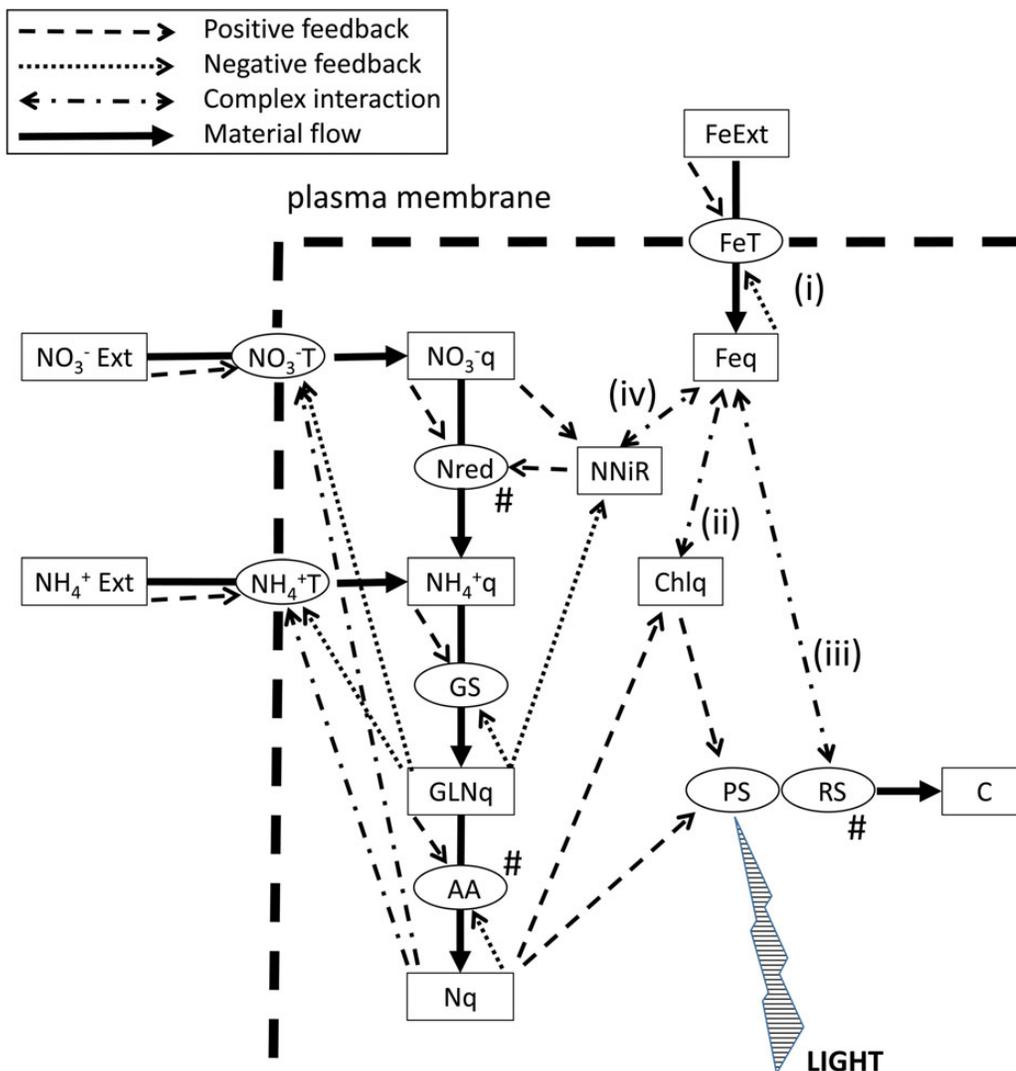
making a RAM is selecting the currency for ranking and/or describing the trade-off, using conversion factors if there are multiple currencies (e.g. energy, C, N, P). We also need to understand the dynamics of their inter-conversion during acclimation. Consider the trade-off in resource allocation between C-fixation and N-source acquisition; the energy required and C,N,P elemental allocation to C-fixation is great, while that for N and P acquisition is minor (Falkowski and Raven, 2007; Raven, 2013; Raven *et al.*, 2013). However, if one considers the interaction in terms of Fe, then the relative allocation to nitrate assimilation can be highly significant (Flynn and Hipkin, 1999). Critically, configuring a RAM for plankton requires an ability to measure resource allocation with sufficient accuracy set against the noise (error) in analytical techniques (Flynn *et al.*, 2010).

Finally, there is also a more profound problem with the concept of trait trade-off in adaptation. The concept implicitly assumes that organisms have access to a back catalogue of all traits upon which selection acts, and they do not. Adaptive traits seen today in different species never co-existed in their current form to trade-off.

## SYSTEMS BIOLOGY AND COMPLEX ADAPTIVE SYSTEMS

Traits expressed by individuals reflect events at the molecular and biochemical level, and thus lend themselves to modelling through “systems biology” (Table I and Fig. 2). There is no strict simple definition of systems biology (Kitano, 2002; Kremling, 2014), but in crude terms, the philosophy behind systems biology modelling converts a biochemical pathway chart into a dynamic model of physiology. Thus in its grandest vision, systems biology attempts to provide a holistic unifying thread from genome to whole organism functioning, linking omics and/or biochemistry to physiology, production, and growth. The implementation can be as detailed as desired, but the explicit description of feedback processes to control interactions is a common feature in dynamic applications of systems biology. Earlier we suggested feedback as a defining feature of “mechanistic” models. Dynamic system biology approaches are thus heavily mechanistic in their formulation, as one may expect given that their origins.

The application of systems biology approaches in plankton modelling is not new, and examples cover the full range of nutrient interactions in phytoplankton and fundamental features of consumer dynamics. Thus, the description of ammonium-nitrate interactions together with Fe and light (Flynn and Hipkin, 1999) included descriptions of enzyme synthesis, controlled by (de)repression, flows of metabolic intermediates, all linked



**Fig. 4.** Schematic of a dynamic systems biology model describing interactions between ammonium, nitrate, Fe and light through a series of feedbacks (from Flynn and Hipkin, 1999). Line types indicate the nature of feedback or other interactions. Interactions (i)–(iv) indicate control of Fe-transport (i), partitioning of Fe into photosystems (ii), into respiration (iii), and into enzymes of nitrate reduction (iv). AA, amino acid and nucleic acid synthesis; FeExt, external Fe; Feq, cellular Fe:C mass ratio; FeT, Fe transport; GLNq, glutamine N as a cellular N:C mass ratio; GS, glutamine synthesis; NH<sub>4</sub><sup>+</sup>q, internal pool of ammonium N as a cellular N:C mass ratio; NH<sub>4</sub><sup>+</sup>Ext, external ammonium; NNiR, nitrate and nitrite reductases; NO<sub>3</sub><sup>-</sup>Ext, external nitrate; NO<sub>3</sub><sup>-</sup>q, internal pool of nitrate N as a cellular N:C mass ratio; NO<sub>3</sub><sup>-</sup>T, nitrate transport; Nq, structural cellular N:C mass ratio; Nred, nitrate and nitrite reduction; PS, photosynthesis; RS, oxidative respiration; #, Nred, AA and RS generated drain on C.

through positive and negative feedbacks (Fig. 4). The model has been used in an ecological context (Fasham *et al.*, 2006). Similarly, systems biology approaches have been used to study interactions between food quality and quantity, ingestion, assimilation, and avoidance in consumers (Mitra and Flynn, 2007).

A major advantage of a systems biology approach over the use of trait trade-off concepts is that the former has a clear basis in biochemistry and physiology. Optimizations of processes occur as they do in reality, through interactive feedbacks, which are generated without the need

to specify the relative values of traits. Through using normalized response feedback curves (Flynn, 2003; Mitra and Flynn, 2007), computational load and system sensitivities are readily controlled. In addition, the rate of acclimation, itself another important trait and one that affects whether a model tracks reality, can also be readily described (Flynn *et al.*, 2001).

Explicit inclusion of feedbacks is a shared feature between dynamic systems biology and CAS modelling, with the two concepts representing extremes of scale in mechanistic modelling. The CAS approach (Levin, 1998)

represents a macroscopic attempt to explore large complex systems. It thus contains various levels of feedback, plasticity of responses and competition between potentially thousands of processes. This macroscopic approach can be employed on different scales; e.g. simplifying biochemical processes to the species or functional type level, simplifying functional type interactions to the level of global ecology. As with all models, behaviour in CAS depends on the conceptual basis of the structure. One could argue that for CAS at the level of organismal biology (= systems biology) we have a reasonably firm understanding of the underlying interactions through biochemistry and molecular biology. However, CAS applications to ecology will be more subjective in their constructions. Machine learning techniques including the utilization of so-called genetic evolutionary algorithms and artificial neural networks used in the modelling of CAS provide tools to escape the constraints of deterministic and empirical modelling approaches enabling us to better understand system evolution.

## CONCLUSIONS

Clarity in nomenclature enables groups of researchers to converse with an emphasis on science. Within a given realm of discussion, where “everyone knows what we mean” non-critical usage is all too often forgiven or ignored. Thus, non-critical usage of the term “adaptation” to describe what in reality is acclimation is all too common between biologists. However, this leads to confusion especially when modelling biological processes. Within the realm of biological modelling, a strict adherence to the biological meaning of adaptation vs acclimation would pay dividends. Likewise, historic precedence and the dominant role of ecological processes in biogeochemistry demands that “plankton functional type” (PFT) refers to ecological, and not biogeochemical, functionality.

As a means to aid the integration of molecular biology, biochemistry/physiology, ecology and modelling, we propose that systems biology approaches offer various advantages. Through such methods, a fundamental feature of biology, feedback regulation, is replicated explicitly; we suggest that this key feature should be at the heart of any model claiming to be mechanistic in its portrayal of physiology. While systems biology approaches are non-trivial to parameterize, at least the conceptual basis in biochemistry, physiology and/or behaviour is often well studied. This aids nonparametric validation; does it do what an expert would expect it to do under all forcings? Certainly there appears to be as much if not more to commend systems biology approaches than the usage of trait trade-offs and RAMs; not least this is because there are no teleological judgement calls to be

made on the relative values of traits, or problems in parameterising trade-offs.

There is significant overlap between dynamic systems biology and complex adaptive systems (CAS) approaches. For both the differentiation between acclimative and adaptation is of critical importance for system dynamics. An argument could perhaps be made for CAS to be re-described as “CAAS” to explicitly stress the importance of both Acclimative and Adaptive processes for the temporal scale of events.

As we move towards an increasingly integrated multidisciplinary view of biology, ecology and indeed planetary science, increasing effort should be expended on enforcing clarity of nomenclature. We hope that this discussion will act as a stimulus for such developments.

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## REFERENCES

- Allen, J. I. and Polimene, L. (2011) Linking physiology to ecology: towards a new generation of plankton models. *J. Plankton Res.*, **33**, 989–997.
- Anderson, T. R. (2005) Plankton functional type modelling: running before we can walk? *J. Plankton Res.*, **27**, 1073–1081.
- Armstrong, R. A. (1999) An optimization-based model of iron–light–ammonium colimitation of nitrate uptake and phytoplankton growth. *Limnol. Oceanogr.*, **44**, 1436–1446.
- Falkowski, P. G. and Raven, J. A. (2007) *Aquatic Photosynthesis*, 2nd edn. Princeton University Press, Princeton, NJ, USA.
- Fasham, M. J. R., Flynn, K. J., Pondaven, P., Anderson, T. R. and Boyd, P. W. (2006) Development of a robust ecosystem model to predict the role of iron on biogeochemical cycles: a comparison of results for iron-replete and iron-limited areas, and the SOIREE iron-enrichment experiment. *Deep Sea Res. I*, **53**, 333–366.
- Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V. and Raven, J. A. (2010) Phytoplankton in a changing world: cell size and elemental stoichiometry. *J. Plankton Res.*, **32**, 119–137.
- Flynn, K. J. (2003) Modelling multi-nutrient interactions in phytoplankton; balancing simplicity and realism. *Prog. Oceanogr.*, **56**, 249–279.
- Flynn, K. J. (2005) Castles built on sand; dysfunctional plankton models and the failure of the biology-modelling interface. *J. Plankton Res.*, **27**, 1205–1210.
- Flynn, K. J. (2006) Reply to Horizons Article ‘Plankton functional type modelling: running before we can walk’ Anderson (2005): II. Putting trophic functionality into plankton functional types. *J. Plankton Res.*, **28**, 873–876.

- Flynn, K. J. (2008a) Use, abuse, misconceptions and insights from quota models: the Droop cell-quota model 40 years on. *Oceanogr. Mar. Biol. Ann. Rev.*, **46**, 1–23.
- Flynn, K. J. (2008b) Attack is not the best form of defense; lessons from harmful algal bloom dynamics. *Harmful Algae*, **8**, 129–139.
- Flynn, K. J. (2009) Going for the slow burn: why should possession of a low maximum growth rate be advantageous for microalgae? *Plant Ecol. Divers.*, **2**, 179–189.
- Flynn, K. J. and Hipkin, C. R. (1999) Interactions between iron, light, ammonium and nitrate: insights from the construction of a dynamic model of algal physiology. *J. Phycol.*, **35**, 1171–1190.
- Flynn, K. J., Marshall, H. and Geider, R. J. (2001) A comparison of two N-irradiance models of phytoplankton growth. *Limnol. Oceanogr.*, **46**, 1794–1802.
- Flynn, K. J., Page, S., Wood, G. et al. (1999) Variations in the maximum transport rates for ammonium and nitrate in the prymnesiophyte *Emiliania huxleyi* and the raphidophyte *Heterosigma carterae*. *J. Plankton Res.*, **21**, 355–371.
- Flynn, K. J., Raven, J. A., Rees, T. A. V., Finkel, Z., Quigg, A. and Beardall, J. (2010) Is the growth rate hypothesis applicable to microalgae? *J. Phycol.*, **46**, 1–12.
- Follows, M. J. and Dutkiewicz, S. (2011) Modeling diverse communities of marine microbes. *Ann. Rev. Mar. Sci.*, **3**, 427–451.
- Franks, P. J. S. (2009) Planktonic ecosystem models: perplexing parameterizations and a failure to fail. *J. Plankton Res.*, **31**, 1299–1306.
- Gitay, H. and Noble, I. R. (1997) What are functional types and how should we seek them? In Smith, T. M., Shugart, H. H. and Woodward, F. I. (eds), *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge, UK, pp. 3–19.
- Gliwicz, Z. M. (2003) *Between Hazards of Starvation and Risk of Predation: the Ecology of Offshore Animals*. International Ecology Institute, Nordbunte, Germany.
- Granéli, E. and Flynn, K. J. (2006) Chemical and physical factors influencing toxin production. In Granéli, E. and Turner, J. T. (eds), *Ecology of Harmful Algae. Ecological Studies*, Vol. 189. Springer-Verlag, Berlin, pp. 229–241.
- Horowitz, M. (2001) Heat acclimation: phenotypic plasticity and cues to the underlying molecular mechanisms. *J. Therm. Biol.*, **26**, 357–363.
- Kingsolver, J. G., Ragland, G. J. and Shlichta, J. G. (2004) Quantitative genetics of continuous reaction norms: thermal sensitivity of caterpillar growth rates. *Evolution*, **58**, 1521–1529.
- Kitano, H. (2002) Systems biology: a brief overview. *Science*, **295**, 1662–1664.
- Kremling, A. (2014) *Systems Biology: Mathematical Modeling and Model Analysis*. CRC Press, Boca Raton, USA.
- Le Quéré, C., Harrison, S. P., Prentice, I. C. et al. (2005) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Glob. Change Biol.*, **11**, 2016–2040.
- Levin, I. C. (1998) Ecosystems and the biosphere as complex adaptive systems. *Ecosystems*, **1**, 431–436.
- Litchman, E., Ohman, M. D. and Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. *J. Plankton Res.*, **35**, 473–484.
- Mitra, A. and Flynn, K. J. (2007) Importance of interactions between food quality, quantity, and gut transit time on consumer feeding, growth, and trophic dynamics. *Am. Nat.*, **169**, 632–646.
- Orr, H. A. (2005) The genetic theory of adaptation: a brief history. *Nat. Rev. Genet.*, **6**, 119–127.
- Pelletier, E., Garant, D. and Hendry, A. P. (2009) Eco-evolutionary dynamics. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, **364**, 1483–1489.
- Raven, J. A. (2013) The evolution of autotrophy in relation to phosphorus requirement. *J. Exp. Bot.*, **64**, 4023–4046.
- Raven, J. A., Beardall, J., Larkum, A. W. D. and Sanchez-Baracaldo, P. (2013) Interactions of photosynthesis with genome size and function. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, **368**, 2012064.
- Reusch, T. B. H. and Boyd, P. W. (2013) Experimental evolution meets marine phytoplankton. *Evolution*, **67**, 1849–1859.
- Sauterey, B., Ward, B. A., Follows, M. J., Bowler, C. and Claessen, D. (2015) When everything is not everywhere but species evolve: an alternative method to model adaptive properties of marine ecosystems. *J. Plankton Res.*, **37**, 28–47.
- Schaum, C. E. and Collins, S. (2014) Plasticity predict evolution in a marine alga. *Proc. R. Soc. B*, **281**, 20141486.
- Schaum, E., Rost, B., Millar, A. J. and Collins, S. (2012) Variation in plastic responses of a globally distributed picoplankton species to ocean acidification. *Nat. Clim. Chang.*, **3**, 298–302.
- Smith, T. M., Shugart, H. H., Woodward, F. I. et al. (1993) Plant functional types. In Solomon, A. M. and Shugart, H. H. (eds), *Vegetation Dynamics and Global Change*. Chapman & Hall, New York, pp. 272–292.
- Stephens, N., Flynn, K. J. and Gallon, J. R. (2003) Interrelationships between the pathways of inorganic nitrogen assimilation in the cyanobacterium *Gloeothece* can be described using a mechanistic mathematical model. *New Phytol.*, **160**, 545–555.
- Weithoff, G. (2003) The concepts of ‘plant functional types’ and ‘functional diversity’ in lake phytoplankton—a new understanding of phytoplankton ecology? *Freshw. Biol.*, **48**, 1669–1675.
- White, C. R., Cassey, P. and Blackburn, T. M. (2007) Allometric exponents do not support a universal metabolic allometry. *Ecology*, **88**, 315–323.