Reply to Horizons Article ‘Plankton functional type modelling: running before we can walk’ Anderson (2005):
II. Putting trophic functionality into plankton functional types

KEVIN J. FLYNN*
INSTITUTE OF ENVIRONMENTAL SUSTAINABILITY, UNIVERSITY OF WALES SWANSEA, SINGLETON PARK, SWANSEA SA2 8PP, UK
*CORRESPONDING AUTHOR: k.j.flynn@swansea.ac.uk

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While Anderson (Anderson, 2005) considers the pros and cons of plankton functional type models, I question whether we are missing something far more basic—trophic functionality, the ways in which organisms interact with each other. What is a functional type? Does the grouping accord with physiology (e.g. ‘Si-requiring’; mainly diatoms) or with respect to ecological function (‘dominant primary producer in an immature ecosystem’; diatoms need not always fulfil that role)? There is some level of acknowledgement (e.g. ERSEM; Blackford et al., 2004) that plankton functional types (PFTs) describe ‘ecological functionality’, but their description is still based on simple physiology. Even on a physiological basis, PFT design is fraught with problems; summer diatoms will not have the same physiology as their winter, spring or autumnal counterparts. That is not to say that physiology is unimportant; it is indeed vital because without it we cannot appreciate how the performance of an individual organism or group may be affected by the presence or absence of others. But is such gross physiological detail sufficient?

Surely, competitive advantage for phytoplankton must be a function of more than just maximum growth rates, the value of alpha (slope of the Chl-specific photosynthesis–irradiance curve) or substrate affinity constants? Even if it were described in these terms, the simple sad fact is that not for a single clone of a plankton species can we construct a model describing its activity under a realistic range of environmental conditions. This is before we consider the impact of genetic diversity. I suspect that the vast majority of PFT models used in ecological simulations would fail to describe adequately a culture flask experiment in a manner representative of the organisms they purport to describe, even if one could find such a data set for verification.

We need data, and lots of them. But we do not need them just for the growth of individual organisms; vitally we also need data for combinations of organisms. What is becoming increasingly clear is that there are a whole host of interactions between members of the plankton that the vast majority of models do not even hint at. Although it may appear that PFT approaches are developing such that ‘complexity in nature is mirrored by complexity in models’ (Anderson, 2005), I fear that the description will have to become more complex yet before we make real progress, even if it is to appreciate better how we must then simplify models back down again.

Most models of planktonic systems take a collection of very crude models, at best purporting to have a physiological basis, parameterized using rather few, and sometimes unreliable, values taken from the literature or by tuning between parameter values from the same literature. Complexity is more than using an increasing number of arrayed boxes describing different groups; we must recognize not only that interactions between groups exist (Anderson, 2005) but also how these change during population growth and trophic dynamics. Currently, for example, even in the more comprehensive models, predator–prey interactions are usually described using a fixed set of rules based on
presence (e.g. Table 5 in Blackford et al., 2004), often using rather suspect prey selectivity terms (Gentleman et al., 2003), with no consideration of changes in selectivity with changes in prey palatability. Thus, although at first sight the description of PFTs accords with what food web analysts term ‘trophic species’ (organisms having similar prey and/or predators), in reality, we are missing a great deal of information about how these organisms interact with each other. There are important lessons in food web science that we need to heed.

Inclusion of increased numbers of trophic species leads to decreased stability in simple food web models (May, 1975) unless changes in behaviour are acknowledged (Link et al., 2005). It is thus not surprising that problems are encountered in assembling PFT models to describe particular bloom types (Anderson, 2005). At present, PFT models may best aid science by showing us what we do not understand. Although this is indeed helpful, we must be very careful using them for any other purpose. Unfortunately, that is what can sometimes happen; the models take on a life of their own and then proceed to take over the ecology, politics (scientific and otherwise) and so on, in the style of Frankenstein’s monster. Models can be horribly persuasive tools, especially when demonstrated to those who do not understand their workings.

There are many examples in the literature of models that are unproven and, more worryingly, contain components that appear dysfunctional (Flynn, 2005), which are claimed to give insight into the workings of the world. Plugging values for maximum growth rates, assimilation efficiencies and so on, gleaned from experimental results, into models of questionable construction is not good enough and neither is testing models in steady state. Unless the model is actually satisfactorily run against a time series of data, it is not proven to be fit for use in any dynamic simulations. This does not mean that one should be happy if the total ecosystem model can be made to reproduce the general gist of what is going on, either; it requires, to my mind, that the performance of the submodels for each functional group is proven to be up to the task. The more detailed the model structure, the more trophic levels that are described, the more scope there is for getting it wrong, perhaps with a propagation of errors that cancel each other out.

There are a range of interactions that stabilize multitrophic species models, including omnivory (which requires prey selectivity switches with greater fidelity than are typically used) and the development of defence mechanisms. Clearly, we cannot consider modelling every interaction. However, there are certain interactions that seem to have a common theme (notably those associated with nutrient status). At the least, we need to explore these.

The production of allelopathic chemicals, for example, which control the growth of competitor phytoplankton, is related to nutrient status (Legrand et al., 2003), while their effectiveness must also be a density-dependent interaction. What about vitamins and other growth factors? These seem to have been rediscovered recently (Croft et al., 2005); rather ironic given that the much-used Droop quota model was originally based on growth limitation by B12 (Droop, 1968). Anyone growing algal cultures knows that summer species are very difficult to grow in artificial seawater; they need ‘aged seawater’ containing chemicals released by previous biological activity. What about the induction of resting stages linked with nutrient exhaustion, and emergence when conditions are good? The switch to mixotrophy is also triggered by nutritional stress. Turning to other trophic interactions, although it has long been known that the nutritional status of the diet impacts significantly on zooplankton growth and development, the context into which that knowledge is now placed is very different (Jones and Flynn, 2005). Food quality is not just concerned with inclusion of one species versus another in the diet but with the nutritional status of those species, and importantly beyond the simple stoichiometric implications of that status (Mitra and Flynn, 2005). As grazing resistance in phytoplankton may be associated with production of noxious chemicals during nutrient-stressed growth it would appear to be more realistic to relate grazing and prey switching to algal nutrient status. One may expect significant changes not only to phytoplankton populations but also to zooplankton dynamics when deterrents are active; the implications may be expected to be just as great as when keystone species are removed by ecosystems. Who would have predicted a decade ago that the role of diatoms in the support of copepod production would have been called into doubt because of the formation of poly-unsaturated aldehydes that may damage copepod reproduction (Paffenhofer et al., 2005 Frost, 2005)? For sure, if we look, we will find other examples.

It is difficult to believe that the structure of plankton communities is not strongly affected by behaviour modulated by chemicals produced by one organism that then act on others, whether they are competitors or predators. Only a deeper understanding and appreciation of these processes can enhance our modelling of plankton ecology and conceivably could change it significantly. Although the identification and biochemistry of the chemical agents will aid understanding and may indeed ultimately overturn the way in which to detail the action in models, we should certainly not await that stage; identification and elucidation are certainly not a prerequisite for the inclusion of these mediations in dynamic models (Mitra and Flynn,
2006) any more than it is a block on our study of the ecological impacts. We do not need to know the name of the organism or the structure of the toxin responsible for Black Death for us to understand the fundamental dynamics of that plague. In any case, we must look for generic patterns because it would be impossible to simulate the details of them all.

In conclusion, the lack of numeric data describing physiology is only one of the problems for the next generation of plankton models. Inadequacies and dysfunctionality in models are not compensated for by the collection and use of data describing only part of the story. The devil is indeed in the details; nutrient–phytoplankton–zooplankton (NPZ) models get away with an awful lot by not exploring the details. If we are going to open Pandora’s box to explore the details, then we had better be ready to handle the demons that escape from it.

REFERENCES