Dysfunctionality in ecosystem models: An underrated pitfall?

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Abstract:

Including causal mechanisms in model formulations is the key to predictive success. Yet it would appear that much of our latest (specifically ecophysiological) understanding accruing from phenomological evidence and experimental work is often not being included within model structures. Dysfunctional equations (which fail to capture mechanistic understanding, and which lead to incorrect model behaviour) are often used instead, the use of fixed Monod formulations to simulate multiple-nutrient interactions in phytoplankton, or Holling type II descriptions of resource-limited predatory activity, being typical examples. In some instances, dysfunctional equations may be adopted through sheer ignorance, a worrying prospect given our incomplete knowledge of many processes occurring in marine ecosystems. One wonders, for example, to what extent the parameterisations used in the current generation of complex ecosystem models being developed for climate studies, and the predictions thereof, can be relied upon. Here, we investigate the underlying problems leading to the use of dysfunctional models within marine food web systems, our perusal of the subject suggesting that ignorance is by no means the only factor, other reasons being indifference, inertia, and subservience to simplicity.

1. Introduction

Understanding the operation of the natural world lies at the heart of science, forming the basis from which predictions can be made. If one knows that vitamin C deficiency causes scurvy, or that chlorine compounds cause depletion of atmospheric ozone, then preventative measures can be taken. With the advent of the modern computer, ever more complicated simulation models are being developed for studying marine ecosystems. The use of mechanistic understanding, i.e., equations that explain the underlying functional processes, in such models is surely the gold standard, to be preferred over purely empirical constructs that can only be applied in predictive mode with care.

Nowhere is the argument for the inclusion of mechanism made more forcefully than by Flynn (2003; 2008; this volume) who articulates the case for using normalised-quota or mechanistic models when modelling multinutrient interactions in plankton communities. In particular, he bemoans the ongoing use of Monod formulations employing fixed Redfield ratios for this purpose, leading to incorrect predictions for the fate of non-limiting nutrients with consequences for biogeochemical cycling and the ecosystem as a whole. Equally, concern is expressed at the application of Monod-type (Holling II) descriptions of resource-limited grazing in models, paying scant recognition to the role of stoichiometric issues in the ingestion and processing of food by consumers. New models are arriving that address the impact of, for example, the interactions between food quantity and quality on zooplankton growth and trophic dynamics (Anderson et al., 2005; Mitra and Flynn, 2007). The importance of multi-nutrient stoichiometry in determining the cycling and fate of carbon in aquatic ecosystems is acknowledged (e.g., Hessen et al., 2004; Mitra et al., 2007; Flynn, 2008; Hessen and Anderson, 2008), further emphasising the need for realistic and accurate parameterisations of trophic interactions in ecosystem models.

Why, Flynn then asks, should modellers persist with using dysfunctional equations when readily available alternatives, incorporating our latest knowledge of the underlying processes, are at hand? Here, we address this question, and discuss this apparent failing in context of the need for ever more realistic models for simulating, for example, the response of marine ecosystems to changing climate.

2. Dysfunctionality in focus

Just what is dysfunctionality? In general parlance, dysfunction means to be functioning incorrectly, or abnormality in process. Examples are most prevalent in the field of medicine, sexual dysfunction being an obvious instance. In similar fashion, dysfunctional DNA is that leading to errors in processes such as replication and transcription (Arthanari and Bolton, 2001). Flynn (this volume) defines a model as being definitely dysfunctional if the output "runs contrary to that expected from empirical evidence". But just what are our expectations? The answer is relatively straightforward where we have mechanistic understanding about processes, underpinned by empirical evidence – our expectations are this understanding. The examples given by Flynn (this volume) – nutrient uptake by phytoplankton, grazing by zooplankton on multiple prey – illustrate where this understanding is well formulated. Equations that give behaviour that is contrary to this understanding are dysfunctional.

It is curious that quite erroneous views can often become established as scientific knowledge and not be eliminated despite evidence to the contrary (Ziman, 1978). Why, for example, should dysfunctional equations continue to be used in ecosystem modelling studies when we have sufficient understanding of the processes in question to do otherwise? There are a number of non-mutually exclusive possibilities:

1) Ignorance – lack of up-to-date knowledge
2) Indifference – insufficient care
3) Inertia – resistance to change
4) Oversimplification – use of insufficient detail
5) Instrumentalism – eschewing mechanism

The very thought that ignorance and/or indifference may be prevalent in contemporary ecosystem modelling is worrying. Lack of interaction between experimental biologists and modellers is likely partly to blame here. As Flynn (2005) laments, mathematicians often do not understand, or cannot/do not want to reproduce the subtleties of biological interactions. Matters are compounded by the fact that biologists usually do not agree with the biological simplicity used within model structures. The trend towards increasing specialisation undoubtedly contributes to these difficulties. Given the pressure to publish and the need to keep up with the ever burgeoning literature, each individual scientist tends to focus on a restricted range of problems. Specialisation thus compels even the most scholarly researchers to become increasingly myopic, as it becomes harder to follow wider ecological developments in lieu of the specific, often esoteric, advances made in their own areas of study (Graham and Dayton, 2002). Creativity is stifled, as is the cross fertilisation of ideas across disciplines, and indeed between experts of different specialities of the same discipline (Burton, 1975). Furthermore, the pressures exerted by the expectations borne by scientists in modern life, such as the "publish or perish" syndrome, increase the zeal of individuals to get through work quickly at the expense of thoroughness in their analyses. Indifference to the opinions of others is a likely outcome. A notorious example was provided by Martin Fleischmann and Stanley Pons when they rushed to publish their "discovery" of cold fusion, despite scepticism from many in the scientific community, before properly checking their experiments and theoretical calculations (Huizenga, 1992).

Inertia may also inhibit scientists from embracing new formulations and parameterisations as they become known. The trend nowadays is towards ever increasing structural complexity in models (e.g., Blackford et al., 2004, Le Quéré et al., 2005), with parameters being counted by the hundred. The models themselves constitute whole research programmes, and the scientists involved become wedded to their beloved equations. Scientists pursuing this form of "Big Science" are in danger of becoming elitist and of losing their dedication to truth while pursuing the ever constant need for research funds (Weinberg, 1967). As time goes by, these models tend to become progressively tuned – tweaked and nudged to minimise those irritating mismatches with data. It may be that, at least in some instances, the work involved in replacing an old dysfunctional submodel entails revisiting the model as a whole, a mighty task if wholesale changes are required. From a cynical point of view one could argue that it is much easier to go with the flow than defy a well established system even if it is erroneous.

Simplicity has long been held to be a virtue in science with Karl Popper, for example, exalting the merits of simple theories which are both widely applicable and easily falsifiable (Popper, 1959). The great theories of Newton and Einstein, lauded as "laws of

nature", are both remarkably simple and universally applicable. Simple theories are in a sense beautiful, many scientists being convinced that their aesthetic appeal can lead to the truth (McAllister, 1996). Biological systems are, however, remarkably complex (e.g., Verity et al., 2007) requiring sophistication in the formulation of biogeochemical processes in order to generate realistic behaviour (Raick et al., 2006). The concept of optimum model complexity is well known in this context (Constanza and Sklar, 1985), the challenge being to define an optimum setup that minimises complexity, but which facilitates valid and robust predictions (Fulton et al., 2003). While Flynn acknowledges the requirement for optimum complexity, for example suggesting that there may be little advantage in progressing beyond Monod for single-nutrient ecosystem models (Flynn, 2003), he does however also point out that omission (oversimplification) should not be a function of ignorance but by virtue of demonstration of an aspect being unnecessary (Flynn, 2005). Finding the optimum is by no means easy, there being a danger of becoming mathematically ensconced in a comfort zone of simple yet potentially erroneous equations.

Finally, there is the old argument that models are only approximations of reality and, therefore, it is not a question of equations being right or wrong, only shades of grey. Indeed, it has been argued that there are no laws in biology akin to the close knit theories of physics (Smart, 1963), leading to the instrumentalist claim that theories do not explain things, but have status only as instruments or calculating devices for prediction (theories cannot then be true or false, only empirically adequate). Most scientists would however contend that the concept of causal (mechanistic) understanding is entirely valid and that theories can therefore be tested as to whether they are true or false. In order to infer cause, they often use what is known as inference to the best explanation in which the available evidence is implicated such that, if true, it would provide the best explanation (Lipton, 1991). Thus, watching someone pull their hand away from a stove, one infers that they are in pain, this acting as an explanation of their excited behaviour. Using this kind of logic, Flynn (this volume) argues that normalised-quota and mechanistic models capture the necessary underlying processes, based on the available experimental evidence, when simulating multi-nutrient interactions in plankton. In contrast Redfield ratios and Monod models are mechanistically incorrect. Of course, inference to the best explanation is not infallible, but nevertheless acts as a powerful means of developing reliable models providing sufficient experimental work has been undertaken to provide the necessary insight into processes of interest.

3. Concluding remarks

We conclude that dysfunctionality is indeed often underrated as a pitfall by modellers. Nevertheless, the potential problems associated with dysfunctional equations must be put into perspective given the various sources of error in models: the model structure and equations, assignment of parameter values and initial conditions. In particular, the aggregation problem, in which many species with differing physiologies, life histories and interactions with the rest of the ecosystem are lumped into state variables such as bulk phytoplankton or zooplankton, poses significant problems for marine ecosystem modellers (Anderson, 2005). Many problems may also arise from what might be called lack of functionality, i.e., the omission of essential processes, rather than dysfunctionality per se. The current drive towards ever more complex ecosystem models is an attempt to remedy these problems. While modellers could argue that this leads to further difficulties

given our ignorant state regarding the ecology, life history and physiology of many organisms, biologists could point out the absence of well known phenomological and/or eco-physiological aspects such as changes in stoichiometry with nutrient stress (Droop, 1973; Elrifi and Turpin, 1985; Flynn this volume) and their implications for grazing (Mitra and Flynn, 2005, 2006) within extant ecosystem models.

Having decided on model structure and equations, many modelling studies go to considerable lengths to tune parameter values to ensure a close fit with data. Yet problems with functionality, be it a lack of or dysfunction, may account for much if not most of the uncertainty in the current generation of complex marine ecosystem models. Only rarely is significant effort put into structural sensitivity analysis – varying equations or the model structure itself – although this kind of analysis can be most informative (Battaglia and Sands, 1998; Cox et al., 2006). Parameter fitting can mask underlying problems with the model structure and equations (e.g., Mitra et al., 2007) – the danger is that models are turned into "mathematical exercises" by incorporating erroneous complexity that does not improve performance (Arhonditsis and Brett, 2004).

Models of complex systems tend to be sensitive to the equations used to describe the interactions between components, as was demonstrated from early work with cellular automata models (Lewin, 1992). Anderson (2005) suggested that the current generation of complex plankton functional type models may also be prone to such sensitivity. Every effort must therefore be made to avoid errors not only in the parameter values used, but more importantly in the model construction and functional forms employed in the chosen equations. Where there is a clear case of right and wrong, i.e., mechanistic understanding is at hand, modellers must grasp the nettle and implement the correct parameterisations in their models.

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