Comment on “The paradox of the “paradox of the plankton”” by Record et al.

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\textbf{ABSTRACT}

The biodiversity of plankton ecosystems is no longer a paradox. The mathematical mechanisms that determine coexistence of competitors in a general class of models, that includes almost all theoretical and applied mass conserving ecosystem models in present use, are clear. Knowledge of these mechanisms simplifies the identification and construction of models with the structural property that all species coexist for all time, irrespective of environmental forcings, spatial interactions, and further model complexities. Here, we discuss the ‘paradox of the “paradox of the plankton”’ proposed by Record et al. (ICES JMS doi:10.1093/icesjms/fst049) and explain the mechanisms that underpin the solution.

\textbf{KEYWORDS:} Paradox of the Plankton
Competitive exclusion
Coexistence
Linear mortality
Introduction

Record et al. (2013) define the ‘paradox of the “Paradox of the Plankton”’ (Paradox II) as the dilemma facing ecosystem modellers resulting from the availability of an ‘abundance of viable solutions to the Paradox’ but the lack of a single mechanism [that] allows for coexistence across global, multi-trophic ocean ecosystems and across a range of spatial and temporal scales.”

Record et al. (2013) propose a solution to Paradox II in the form of a simple method to build coexistence into simple NPZ models. This approach is based on two criteria: simple form with few parameters, and the ability to reproduce observed patterns at the community level. The approach they adopted was to parameterise a generic mortality coefficient $\mu \bar{Z}$, where $\bar{Z} = \sum Z_i$, which was intended to articulate a dependence of the per capita mortality on all populations. Record et al. (2013) implemented this term in a simple zooplankton equation to demonstrate its efficacy:

$$\frac{dZ_i}{dt} = \gamma_i Z_i - \mu_i \bar{Z}^{1-\phi} Z_i^{1+\phi}. \quad (1)$$

They then use computer simulations to show (Record et al., 2013, Figure 1) that multiple Z populations coexist for long times when $0 < \phi < 1$, and suggest that the approach produces similar results when applied to phytoplankton equations and to grazing. The key argument they propose for this approach is that it allows competition to have a structuring effect on the community without excluding all but one species, and they suggest that $\phi$ provides an ability to “dial up or down the degree to which competition structures the community”.

The approach Record et al. (2013) have used certainly works to ensure the coexistence of $Z_i$ in their model. Here we wish to examine why it works and why this places caveats on their claim that $\phi$ provides a mechanism to control the structure of the community. We also show that although $\phi$ is presented as encapsulating the effect of competition, this is not the mechanism that delivers coexistence in models.
The mechanisms of coexistence

The equations that describe homogeneous well-mixed populations in ecosystem models are, with few (generally unrealistic) exceptions (Huang and Zhu, 2005), of the form:

\[
\frac{dx_i}{dt} = x_i f_i(x_i, x_2, \cdots, x_n)
\]  

(2)

This is commonly referred to as Kolmogorov form after the early paper on systems of this type (Kolmogorov, 1936). Here, the life function \( f_i(x_i, x_2, \cdots, x_n) \) describes how the \( x_i \) population grows, and how other populations (competitors, predators, etc.) affect its growth. Models that explicitly represent the dependence of autotroph growth on the availability of a limiting inorganic nutrient may be written in Kolmogorov form if the mass of limiting nutrient is conserved. We note that the initial model of Record et al. (2013, equations (1)-(3)) conserves the mass of the limiting nutrient \( \bar{N} \) and hence may be written in Kolmogorov form.

Cropp and Norbury (2012b) described the mathematical mechanism that ensures coexistence in ecosystem models of Kolmogorov form. Extinction of a population \( x_j \) in models of Kolmogorov form occurs when one or more boundary critical points \( \{x_1^*, x_2^*, \cdots, x_n^*\} \), defined by \( x_i^* f_i(x_1^*, x_2^*, \cdots, x_n^*) = 0 \) for all \( i \) and at which \( x_j^* = 0 \) (for some \( j \), and this is then the \( j \)th boundary), is locally stable (Kot, 2001). The local (Lyapunov) stability of a critical point is determined by the eigenvalues \( \{\lambda_i, i=1,2,\cdots,n\} \) of the Jacobian matrix of the system, obtained by linearising the system equations in the vicinity of the critical point. Local stability requires the real parts of all the eigenvalues of the Jacobian (an \( n \) equation Kolmogorov system has \( n \) eigenvalues) to be negative. One positive real part of an eigenvalue is sufficient to make a critical point unstable (Kot, 2001).

Each population \( x_j^* \) that is zero at a (boundary) critical point has an eigenvalue \( \lambda_j \in \{\lambda_1, \lambda_2, \cdots, \lambda_n\} \) associated with it for which an analytic expression is easily
obtained as it is just the \( f_j \) of the population evaluated at the critical point (i.e. 
\( \lambda_j = f_j(x_1^*, x_2^*, \ldots, x_n^*) \) (Cropp and Norbury, 2012a, Cropp and Norbury, 2012b). It 
is this property that reveals the mechanism that controls extinction, and 
consequently coexistence, in ecosystem models of Kolmogorov form.

Coexistence of competitors is ensured if each competitor \( x_j \) has the property 
that its \( \dot{x}_j = f_j(x_1^*, x_2^*, \ldots, x_n^*) > 0 \) at every critical point where its population \( x_j^* \) is 
zero. This may be achieved in two ways: a parameter set may be found that 
ensures this property (parameterised coexistence); or the ecosystem may be 
composed of equations that always have the desired property over any feasible 
range of parameters (structural coexistence, Cropp and Norbury, 2012b).

The original postulation of the Paradox of the Plankton and its continuing source 
of interest for more than fifty years is testament to the difficulty of finding, in any 
given model without structural coexistence, parameter sets that deliver 
parameterised coexistence. Such parameter sets may not exist for some models.

The classic phytoplankton competition models that embody the Paradox of the 
Plankton, such as those considered by Tilman (2007), have the property that 
coexistence is only possible on coincident zero isosurfaces that correspond to 
parameter sets for which all populations are functionally identical, the essential 
assumption of neutral theory (Hubbell, 2006). The probability of finding such 
parameter sets by randomly sampling the space of all potential parameter sets 
for any model is vanishingly small.

In contrast, structural coexistence is quite easy to achieve by minor modification 
of parameterised models. Further, it may be done using functions commonly 
used to model interacting populations and (material) mass-conserving ecologies. 
Cropp and Norbury (2012b) classified commonly used functional forms into two 
types: those forms that vanish (i.e. go to zero) from a population’s \( f_i \) as the 
population \( x_i \) goes to zero; and those that do not. All commonly used population 
growth terms (including Holling Types I and II) are non-vanishing and contribute
positive terms to their $f_i$. When combined with vanishing loss terms, such as Holling Type III grazing and nonlinear mortality, the population’s $f_i$ will be positive at every boundary critical point. Any population described by an equation of Kolmogorov form that has at least one non-vanishing growth term and all vanishing loss terms will never go extinct in computer simulations (Cropp and Norbury, 2012b). The simplest way to do this in cases such as Record et al. (2013) consider is via nonlinear (say quadratic) mortality as a replacement for the very commonly used linear mortality.

The solution to the Paradox of the Plankton described by Cropp and Norbury (2012b) applies to models with any number of competing species or trophic levels, to food-webs of any complexity, and it ensures coexistence of competing species across all spatial and temporal scales. Further, the solution to the paradox is surprisingly simple and easy for modellers to implement in theoretical and computer models, and is the general case of the solution for the particular application that Record et al. (2013) demonstrate.

**Coexistence in the Record et al. (2013) prototype**

The isolated model of Record et al. (2013) is of Kolmogorov form as equation (7) may be written in the form:

$$\frac{dZ_j}{dt} = Z_j f_i = Z_j \left( \gamma_i - \mu_i \bar{Z}^{1-\phi} \right).$$

The mechanism that prevents $Z_j$ from becoming extinct is the $Z_j^\phi$, which causes the mortality (in this case, model closure) term to vanish as $Z_i \to 0$ for any value of $\phi > 0$. This ensures that $\lambda_j > 0$ at every critical point where its population $x_j^*$ is zero. Irrespective of the veracity of any ecological arguments for $\bar{Z}^{1-\phi}$ (or even of its smooth modifications), it does not affect the property of long-time coexistence attributes of the population. It may be removed from the mortality term without affecting the properties that ensure coexistence, although it does modify the coexisting relative amounts of individual species. In fact, the addition of the $Z^\phi$ terms for $\bar{Z} = \sum_j Z_j, \quad j = 1, 2, \cdots, n, j \neq i$ to the $Z_i$ equation in the
absence of structural coexistence (i.e. no $Z_i^\phi$ term) would make parameterised coexistence more difficult to achieve.

Record et al.’s (2013) observation that the approach they have used for mortality applies equally as well to grazing should be qualified. Assuming that the prey population has a vanishing mortality term, it is the raising above one of the exponent of the prey in the numerator of the function describing the dependence of predator grazing on prey availability that is the key property that ensures coexistence of the prey. This is independent of whether the function describes interaction or inter-dependence of the predator or prey on other populations explicitly or implicitly represented in the model.

The role of $\phi$ in structuring the community

Record et al. (2013) observe that their computer simulations suggest that $\phi$ can stabilise systems, and structure the community. When we analyse the mechanisms that underlie the observed numerical behaviour, we see that manipulating $\phi$ might provide a useful “rule of thumb” for determining some community-level properties, but will not necessarily produce these properties in all models.

Increasing $\phi$ can affect population sizes in a Kolmogorov system because each population ($x_i$) for which coexistence is guaranteed (i.e. $\lambda_i > 0$ whenever $x_i^* = 0$) has at each boundary critical point at least one unstable eigenvector, orthogonal to the boundary, along which the population grows. The rate at which the population grows is determined by the magnitude of the $f_i^*$ in the case of equation (3), $f_i^* = \gamma_i - \mu_i^{1-\phi}Z_i^\phi$. This becomes $f_i^* = \gamma_i > 0$, a maximum at the boundary critical point where the mortality is zero, but reduces as the system travels along the eigenvector because the growing population (in this case $Z_i$) causes its loss to mortality to increase. The mortality increases more slowly for larger values of $\phi$ and hence the population moves more rapidly away from its extinction point and maintains relatively rapid growth for longer. While the
value of $\phi$ clearly affects the community structure, it is the value of $\phi$ in $Z_i^{\phi}$ that
produces this effect. The $Z_i^{\phi}$, which reflects the competition between the $Z_i$, does not produce the effect but does modify it (as does the value of $\mu_i$).

However, we note that the $Z_i^{\phi}$ reflects competition only because Record et al. (2013) have removed the explicit competition for limited resources of phytoplankton ($P$) between the $Z_i$ in their starting model (equations (1)-(3) in their paper) and re-introduced it as implicit competition ($Z_i^{\phi}$) in equations (4)-(8).

Lyapunov stability is based on a linear approximation to a nonlinear system and hence the role of $\phi$ should be considered only a rule of thumb. The linear approximation is only valid ‘close to’ critical points; as we move away from a critical point the eigenvalues and eigenvectors derived from the linear approximation lose veracity as descriptors of the system behaviour. If the system has a globally stable interior coexistence point (as Record et al.’s (2013) model appears to) then the rule of thumb is useful; however, for systems that do not have interior coexistence points, or have unstable ones, then $\phi$ only controls the minimum size to which populations fall in their “bloom-bust” cycles. While this may also be a useful property, it could not be considered to structure the community in the way it does in the Record et al. (2013) model (see the section on pinball dynamics in Cropp and Norbury (2012b) for an extreme example of this).

We note, however, the apparent ubiquity of equilibrium solutions to models that have structural coexistence. The model simulations shown by Record et al. (2013) all have equilibrium solutions, as do the simulations shown for models with structural coexistence in Cropp and Norbury (2012b). In fact, in Cropp and Norbury (2012b) we randomly generated 4,517,053 parameter sets for $NPPP$, $NPPZ$, $NPPZZ$ and $NPZZZ$ models with structural coexistence. Computer simulations suggest that every parameterisation of every model had an equilibrium solution. We are currently not aware of a mathematical explanation
for this behaviour, but it implies that the properties of the boundary critical
points may be an important determinant of system dynamics in models with
structural coexistence.

An alternate view on Paradox II

Record et al. (2013) propose Paradox II as the dilemma that faces NPZ modellers
because of an overabundance of solutions to the paradox of the plankton. They
correctly identify that, in competition models with only growth and mortality
terms, the paradox of the plankton is only evident in models with exactly linear
mortality terms. Competitive exclusion does not technically occur in these
models for even slightly nonlinear mortality, that is, in this case, for any $\phi$ that is
even infinitesimally greater than zero.

As Record et al. (2013) note, there are many forms of mortality at work in
populations. To our knowledge, no theoretical arguments exist that suggest that
these forms are without exception exactly linear. Further, experimental
measurements of per capita mortality ($\frac{1}{x_i} \frac{dx_i}{dt}$) would have to produce results
that were precisely independent of the size of the population $x_i$ to justify
linearity. Any spread in the data would preclude an assumption of linearity as
many regressions with non-zero slopes that were statistically indistinguishable
from the zero slope case could be fitted to the data.

This apparent obsession of ecological modellers with linear mortality appears to
us the real paradox of the paradox of the plankton. Linear mortality is often
justified as the simplest or least biased assumption in the absence of compelling
data or theory that suggests otherwise. However, exact linearity is a very precise
and restrictive assumption – there is only one functional form in which mortality
can be exactly linear but a potentially infinite number of forms in which it can be
nonlinear. Linear mortality was originally chosen for its simplicity as it typically
enables explicit analytical evaluation of interior critical points.
It could be argued that the unfortunate effect of the assumption of linear
mortality has been to distract ecological theory for the past fifty or so years.
Hardin (1960) quotes reports of the 21 March 1944 meeting of the British
Ecological Society devoted to the ecology of closely allied species that "Capt.
Diver made a vigorous attack on Gause's concept [of competitive exclusion
(Gause, 1934)], on the grounds that the mathematical and experimental
approaches had been dangerously over simplified." Perhaps if Capt. Diver's view
had prevailed the paradox of the plankton would never have eventuated.

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