

**Negative zooplankton do not exist—a response to
‘On the stability of some equilibrium points
in a plankton population model’**

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Simple models of the plankton ecosystem have been usefully analysed and understood using dynamical-systems techniques. These techniques have addressed important ecological questions and have provided insight into how models should be constructed. Edwards and Brindley [1996, *Oscillatory behaviour in a three-component plankton population model. *Dynamics and Stability of Systems*, 11, 347–370*] used such methods to investigate the dynamics of a model that represented the concentrations of nutrients, phytoplankton and zooplankton. Halanay [2003, *On the stability of some equilibrium points in a plankton population model. *Dynamical Systems*, 18, 227–229*] asserted that Edwards and Brindley incorrectly determined the stability of one of the model’s steady states. However, Halanay’s assertion requires the consideration of negative zooplankton concentrations, and so is not relevant to the biological meaning of the model.

The plankton ecosystem is often modelled using three or four coupled ordinary differential equations. Such sets of equations capture the essential features of the ecosystem without overwhelming the modeller with excessive biological detail. The best way of formulating these models continues to be an active area of research [1].

Edwards and Brindley [2] investigated the dynamics of a plankton population model that was based on the influential model of Steele and Henderson [3]. The model consists of three coupled ordinary differential equations that represent the variation in time of concentrations of nutrients (N), phytoplankton (P) and zooplankton (Z) within an oceanic mixed layer. Nutrients are taken up by the phytoplankton, which are in turn grazed upon by the zooplankton. Various recycling terms make the system more complicated than a simple food chain.

The purpose of Edwards and Brindley [2], hereafter abbreviated to EB96, was to perform a thorough investigation of the dynamical behaviour of the model in order to help improve the understanding of the dynamics of such models. EB96 was the first in a series that addressed various aspects of model formulation (e.g. [4]),

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and is one of the three most cited papers in the history of *Dynamics and Stability of Systems* and its successor *Dynamical Systems* (data from ISI Web of Science as of 14 July 2005, and excludes self-citations by authors).

EB96 commenced by looking for steady states of the model. The simplest steady state is the trivial dead-ocean state $(N, P, Z) = (N_0, 0, 0)$ for which phytoplankton and zooplankton are absent, and mixing between the surface water and deep water causes the nutrients to equilibrate to the deep-water concentration N_0 . The eigenvalues of the Jacobian matrix at this steady state are $-k$, Φ and 0, where $k > 0$ is the mixing rate between the surface and deep layers, and Φ (termed λ_2 by Halanay [5]) is a combination of parameters that gives the linearized phytoplankton growth rate at low phytoplankton concentration and maximal nutrient concentration N_0 . The zero eigenvalue corresponds to the manifold in the Z direction, and its zero value means that the eigenvalues alone do not give the full stability of the steady state.

Using the centre manifold analysis of Truscott [6], EB96 concluded that $(N_0, 0, 0)$ was stable for $\Phi < 0$ and unstable for $\Phi > 0$. Thus, given the dead-ocean state $(N_0, 0, 0)$, a small addition of phytoplankton would die out if $\Phi < 0$ (negative net growth rate), and would grow if $\Phi > 0$. Clearly, a small addition of zooplankton to the $(N_0, 0, 0)$ state could survive only if their food source, the phytoplankton, were also added and survive (this can be verified from the zooplankton equation given by EB96). Therefore, $\Phi > 0$ is the condition for perturbations of P (or of P and Z) to grow, and is thus the condition for the system to escape from the dead-ocean state. This conclusion also makes ecological sense.

However, Halanay [5] claimed that the steady state $(N_0, 0, 0)$ is, in fact, unstable when $\Phi < 0$. This would imply that even if the linearized phytoplankton growth rate Φ is negative, then a small perturbation from the dead-ocean state $(N_0, 0, 0)$ would grow, and the system would head away from the dead-ocean state. Such a claim is counter-intuitive, questions the validity of EB96's model, and is therefore worth investigating.

Halanay's analysis concludes by observing that his Lyapunov function, V , is not negative definite in any neighbourhood (small sphere) of $(N_0, 0, 0)$. Incorporating his previous analysis, he concludes that the dead-ocean state is therefore unstable for $\Phi < 0$.

The steady state is indeed unstable (for $\Phi < 0$) to a small perturbation, $Z = z < 0$, of 'negative zooplankton'. The dynamics of the perturbation become $dz/dt = -dz^2 < 0$, such that the perturbation becomes ever more negative and rapidly heads to $-\infty$. Only in this sense may the dead-ocean state be considered unstable for all parameter values, in line with Halanay [5], but this is an ecologically meaningless perturbation. By the same reasoning as above, Halanay's [5] conclusion regarding the general systems considered by Truscott and Brindley [7] is also not valid when restricting to the biologically realistic domain, and this resolves the contradiction.

A three-way transcritical bifurcation between the dead-ocean steady state and the more interesting 'living-ocean' steady states was numerically computed and shown graphically by Edwards and Bees [8]. When the quadratic Z mortality term used by EB96 is replaced by a linear term, the three-way bifurcation splits into two standard transcritical bifurcations. For this scenario, negative zooplankton steady-state values were indeed plotted by Edwards and Bees [8]. But the point

of considering such ecologically unrealistic steady states was to illustrate how the biologically realistic positive steady states arise as parameters are varied. McCann and Yodzis [9] also considered a similar negative steady state, noting that while it was ecologically meaningless it was valuable in performing their bifurcation analysis.

Dynamical-systems techniques have proven useful in understanding a variety of biological systems. However, care must be taken to ensure that the state variables remain biologically or physically meaningful to the system being modelled.

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