Behavior of a simple plankton model with food-level acclimation by herbivores

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Abstract

The acclimation of herbivores to variation in their phytoplankton food source was expressed mathematically and its effect on phytoplankton, herbivore and nutrient cycles explored with a plankton model. The grazing formulation is a modified version of the function experimentally determined by Mayzaud and Poulet. Their function differs from the traditional Ivlev expression for herbivore grazing in that there is no asymptotic limit to the grazing rate. The steady-state solutions of the phytoplankton-herbivore-nutrient model were similar with the two grazing formulations, but the time-dependent behavior of the two models differed markedly. The model with Ivlev grazing showed oscillations when the grazing pressure was high. The model with acclimated herbivore grazing showed only small, highly damped oscillations as it approached steady state. The latter is more similar to the evolution of plankton trophic levels observed in controlled ecosystem experiments.

Introduction

Modellers have been known to attempt to recreate the seasonal phytoplankton, herbivore and nutrient cycles in the sea by using equations that exhibit oscillatory behavior (e.g. Parker, 1975; Sjoberg, 1977; Evans and Parslow, 1985). We will show that a class of simple plankton models that contains a formulation of grazing where herbivores acclimate to the level of available food are not oscillatory, or exhibit oscillations which are quickly damped if used with realistic parameter values. This allows the modeller to simulate the spring bloom phenomenon as a response of the plankton to physical oceanographic factors, rather than as an oscillation induced by herbivore grazing.

Marine copepods show an increasing ingestion rate as food concentrations increase (Parsons et al., 1967; McAlister, 1970; Frost, 1972 and references therein). The functional form of this response has generally been of the Holling Type II shape (Holling, 1959), showing a saturation of the ingestion rate with high prey concentrations. Commonly, Ivlev's (1955) formulation is used to describe this functional response in curve-fitting and modelling (Mullin et al., 1975; Steele and Mullin, 1977; Vidal, 1980). The Ivlev formulation requires two parameters: the maximum ingestion rate $R_m$ (with units of time$^{-1}$), and $A$, the rate at which saturation is achieved with increasing food levels (with units of concentration$^{-1}$). The ingestion rate is then

$$I_1 = R_m (1 - e^{-AP}),$$

where $P$ is the phytoplankton concentration.

More recently, however, Mayzaud and Poulet (1978) demonstrated a near linear response of five neritic copepod species to changes in food levels. This lack of saturation was thought to be due to variations in gut enzyme levels in response to varying phytoplankton concentrations. Increased levels of enzymes such as amylase, maltase and cellulobise would allow a decreased gut clearance time, and thus a higher ingestion rate could be accommodated. The mathematical formulation of this grazing response offered by Mayzaud and Poulet (1978) was

$$I = K P (1 - e^{-AP}),$$

where $K$ is a constant. Following Dubois and Mayzaud (1975), we relate $K$ to $R_m$ and $A$ to give the modified form:

$$I_2 = R_m A P (1 - e^{-AP}).$$

This formulation is dependent upon the same two parameters as the Ivlev formulation. However, as $P$ gets large, the formulation tends to be linear with slope $R_m A$,
parameterization of many varied processes including physiological death, exudation of organic substances, etc. The zooplankton dynamics include growth due to assimilated ingested ration and a loss rate of $g$ (d$^{-1}$) due to whatever cause: predation, physiological death, etc. The unassimilated fraction of ingested phytoplankton, $\gamma$, goes immediately into dissolved nutrients, as do the dead zooplankton and phytoplankton. The total amount of nitrogen in the system, $N_t$, is constant.

The above equations are dependent upon seven dimensional parameters. By scaling the equations by $V_m$ and $N_t$, this dependency is reduced to six dimensionless parameters, and the values of $P$, $Z$ and $N$ are constrained to lie between 0 and 1. The scaled equations are:

$$\frac{dP}{d\tau} = \frac{N^\prime P^\prime}{\alpha + N^\prime} - \epsilon P^\prime - \lambda Z^\prime$$ (1)

$$\frac{dZ}{d\tau} = (1 - \gamma) L_1 Z^\prime - \omega Z^\prime$$ (2)

$$\frac{dN}{d\tau} = -\frac{N^\prime P^\prime}{\alpha + N^\prime} + \epsilon P^\prime + \omega Z^\prime + \gamma L_1 Z^\prime$$ (3)

and $N^\prime + P^\prime + Z^\prime = 1$ (4)

where $L_1 = \beta (1 - e^{-\lambda P^\prime})$ (Ivlev)
or $L_2 = \beta \lambda P^\prime (1 - e^{-\lambda P^\prime})$ (Mayzaud-Poulet).

The scaling factors and dimensionless parameters are given in Table 1. For simplicity, the primes denoting dimensionless state variables will henceforth be dropped. The six dimensionless parameters include $\alpha$, which is analogous to the half-saturation constant of nutrient up-take by phytoplankton, and $\gamma$ which is unchanged from before scaling. The parameters $\epsilon$ and $\omega$ describe the phytoplankton and zooplankton death rates, respectively. In the grazing function $\beta$ is the ratio $R_m/N_m$, the maximal grazing rate over the maximal phytoplankton growth rate. Parameter $\lambda$ plays the role of $A$ in describing the rate at which grazing saturation is reached in the Ivlev formulation. The dimensionless combination $\beta \lambda$ which appears in the modified Mayzaud and Poulet formulation is important in determining the ingestion rate at high phytoplankton concentrations.

### Parameter values

Here we discuss the choice of dimensional parameter values for the model. Not all parameters are well known. For example, the zooplankton and phytoplankton death rates are controversial in the literature. Values for the rate of zooplankton death used in other models range from 0.07 to 1.75 d$^{-1}$ (Steele, 1974b; Steele and Frost, 1977; Steele and Henderson, 1981). Checkley (1980) found that Paracalanus parvus with no food would starve to death in four to five days, while Dagg (1977) found that Centropages typicus could live only three to six days without food. A death rate of 0.2 d$^{-1}$ gives an e-folding timescale of five days for zooplankton death, and is used in this study.

Few data exist on the process of phytoplankton death, important in the aphotic zone (Lehman et al., 1975). A value of 0.07 d$^{-1}$ was suggested by Harris and Piccinin (1977). A value of 0.1 d$^{-1}$ was used in this study to give an e-folding timescale of ten days. The model is not very sensitive to the choice of this parameter.

The literature pertaining to assimilation efficiency is fairly extensive (see Raymont, 1980 for a review), with efficiencies ranging from 30 to 80%, depending on the food source and species of copepod, the majority being between 65 and 70%. An efficiency of 70% was chosen for the herbivores in this study, i.e. $\gamma = 0.3$.

A typical value for the half saturation constant of phytoplankton nutrient uptake, $k_e$, appears to be about 1 $\mu$g-at N L$^{-1}$ for neritic diatoms (Eppley et al., 1969; MacIsaac and Dugdale, 1969), and is used here.

A large range of values is reported in the literature for the Ivlev parameters for various copepods. $R_m$ is reported to vary between 0.16 and 1.5 d$^{-1}$, while $\lambda$ falls between 0.1 and 2 $\mu$g-at N L$^{-1}$ (McAllister, 1970; Frost, 1972; Checkley, 1980). Because of the wide range of possible values, the biological models' behavior and steady-state solutions were explored over this entire parameter space.

### Solution of the model with Ivlev grazing

The first method of analysis used is the determination of the model's steady-state analytical solutions. To do this, $dP/d\tau$, $dZ/d\tau$ and $dN/d\tau$ are set equal to zero, and the resulting
below describes the state variables \( (P, Z, N) \) in terms of their nitrogen content, the total nitrogen in the system being conserved. The simplicity of a model with few parameters and limited fluxes allows a more complete understanding of the influence of any particular parameter on the model outcome. This understanding of the basic biological equations in an implied constant physical regime (i.e. instantaneous mixing, constant light, etc.) is a necessary prelude to understanding the model’s dynamics in more complicated physical settings. For example, this model has been utilized in an investigation of plankton dynamics in a warm-core ring of the Gulf Stream (Franks, 1984).

One might criticize the model for ignoring certain recent discoveries about the size structure of marine systems. A major finding in biological oceanography during the last few years is the surprisingly large contribution of nano- and ultra-phytoplankton to the overall primary productivity of the water column. Net phytoplankton may not be the dominant primary producers in offshore waters (Malone, 1980). In addition, a new paradigm has emerged regarding the role of heterotrophic bacteria and microzooplankton in the recycling of nutrients (Pomeroy, 1974; Williams, 1981; Ducklow, 1983). Although they may represent a small fraction of the biomass in the water column, small-sized organisms have such a high metabolism that their presence in the plankton community is significant to ecosystem dynamics (Pace et al., 1984). In the interest of keeping the plankton dynamics as simple as possible to investigate the properties of the Mayzaud-Poulet grazing formulation, we aggregate all autotrophs into one dependent variable called \( P \), all heterotrophs into a variable called \( Z \) and all limiting nutrient species into a variable called \( N \).

**Methods**

The model framework is a common one (see for example Steele, 1974a; Parker, 1975; Wroblewski and O’Brien, 1976; Hallam, 1977) and will be explored using the two herbivore grazing formulations. The equations for the plankton model are:

\[
\frac{dP}{dt} = \frac{V_m NP}{k_s + N} - mP - I_1Z
\]
\[
\frac{dZ}{dt} = (1 - \gamma)I_1Z - gZ \quad \text{where } I_1 = I_1 \text{ or } I_2
\]
\[
\frac{dN}{dt} = - \frac{V_m NP}{k_s + N} + mP + gZ + \gamma I_1Z
\]

and

\[
P + Z + N = N_i.
\]

The phytoplankton grow according to Michaelis-Menten uptake of dissolved nutrient, with a maximum growth rate of \( V_m \) and a half-saturation constant of \( k_s \). The loss terms of phytoplankton include a linear death rate of \( m \) \((d^{-1})\) and losses due to grazing. Phytoplankton death is a gross
equations solved to obtain P, Z and N in terms of the equation parameters (see Appendix A).

The steady-state solutions of the Ivlev model may be seen in Fig. 3, plotted for a range of values of \( \beta \) and \( \lambda \). Note that solutions for \( Z \leq 0 \) are invalid, as the model is no longer a P–Z–N model, but a P–N model. The zooplankton steady-state biomass approaches zero when \( \beta \) or \( \lambda \) become small, i.e., when the maximum grazing rate is low, or the approach to saturation is very slow. For these low grazing rates, the zooplankton are unable to support themselves against their death rate. At high \( \beta \) and \( \lambda \), the phytoplankton and zooplankton biomasses are low, while the dissolved nutrient increases. In this case the phytoplankton are grazer limited, not nutrient limited. For mid-values of \( \beta \) and \( \lambda \), the biomasses of zooplankton and phytoplankton are relatively high, with little dissolved nutrient. Hence, the zooplankton graze fast enough to support themselves, yet not so fast as to decimate the phytoplankton crop.

The second analysis performed on the model is a parameter sensitivity analysis (see Appendix B). This analysis gives a quantitative measure of the sensitivity of the model's steady state to a change in a parameter. It is proposed that in some sense the sensitivity of the model to its parameters is a reflection of the sensitivity of the plankton ecosystem to those processes parameterized. The less sensitive the model, the larger the degree of inaccuracy which may be tolerated in the choice of parameters.

In Fig. 4, the Ivlev model's sensitivities are plotted for a range of values of \( \beta \). For high values of \( \beta \) the phytoplankton are the most sensitive to the choice of parameters, this sensitivity being less than 2% for any parameter (i.e., a 1% change in any parameter would lead to less than a 2% change in the steady-state solution). At low values of \( \beta \), where the zooplankton and nutrient values approach zero, the sensitivities of these components increase markedly. This is reflected in the slope of the steady-state surfaces of Fig. 3 at low \( \beta \). The model is most sensitive to the four zooplankton parameters, \( \beta, \gamma, \lambda, \omega \). In particular, the \( \beta \) and \( \lambda \) tend to be paired, as do \( \gamma \) and \( \omega \). The model responds in an opposite sense to changes in either \( \beta \) or \( \lambda \), relative to changes in \( \gamma \) or \( \omega \) (Fig. 4).

Solution of the model with Mayzaud-Poulet grazing

The steady-state solutions to the model with the modified Mayzaud and Poulet formulation of grazing are shown in Fig. 5. These solutions differ only slightly from those with the Ivlev formulation. The zooplankton are much more persistent for low values of \( \beta \) and \( \lambda \) than in the Ivlev model. As \( \beta \) and \( \lambda \) increase, the zooplankton fall off less quickly than with the Ivlev formulation. The shapes of the surfaces are similar to the corresponding surfaces of the Ivlev model, but translated to the left along the \( \beta \) axis.

The results of the sensitivity analysis may be seen in Fig. 6. The phytoplankton and nutrient are found to be generally less sensitive to the choice of parameters than in the Ivlev model. The zooplankton are also fairly insensi-

Fig. 3. Steady-state solution of the model with Ivlev grazing for a range of values of \( \beta \) and \( \lambda \).

tive, but slightly more sensitive to \( \beta \) and \( \omega \) than in the Ivlev model. The magnitude of these differences is less than 1%.

Results

Let us compare the two models. Looking only at the steady-state solutions and the sensitivity analysis, the Ivlev
Fig. 4. Sensitivities of the model incorporating Ivlev grazing. The values on the ordinate represent a percentage change of the state variable (P, Z or N) with a 1% change in the indicated parameter.

and Mayzaud and Poulet models show little difference. However, an examination of the time-dependent behavior of the two models demonstrates a fundamental difference in the properties of the two sets of equations. Figure 7 shows a time-dependent solution of the two models using a common suite of parameter values. Whereas the Mayzaud and Poulet model quickly reaches its steady state with only small initial oscillations, the Ivlev model continues to oscillate with extremely large fluctuations in the state variables. This can be seen clearly in the P–Z phase-plane plots of Fig. 8. While the Mayzaud and Poulet model quickly approaches the steady-state, the Ivlev model is only slightly damped and is effectively in a limit cycle. The onset of oscillations in the Ivlev model is strongly dependent on the values of β and λ. For low β and λ, no oscillations are seen, while for high β and λ, strong oscillations occur.

Fig. 5. Steady-state solution of the model with Mayzaud-Poulet grazing for a range of values of β and λ.

The magnitude of the damping of the oscillations in the neighborhood of the equilibrium (steady-state) point can be found using the stability analysis described by May (1973). The magnitude of the damping indicates how quickly the solutions approach steady state. The values of the damping constants for the two models can be seen in Fig. 9, calculated for a range of β. These values give the timescale of the exponential decay of the oscillations—the larger the value, the faster the decay, and the greater the damping. Also indicated in the figure are the regions in
which the equations are naturally oscillatory about the equilibrium point. For all values of $\beta$ which cause the solutions to oscillate, the Mayzaud and Poulet model is much more highly damped than the Ivlev model. Similar analyses using a range of values of $\lambda$ give identical results: the Mayzaud and Poulet model is highly damped and shows consistent behavior within the range of $\lambda$ used. The Ivlev model, however, becomes less damped with increasing $\lambda$, the resulting oscillations growing in magnitude and period.

Acclimation time lag

When examining time-dependent behavior, one must carefully consider the dynamics being described. Acclimation is a process which only takes place when the herbivores are food limited with respect to their maximal growth potential. As Mayzaud and Poulet (1978) pointed out, the acclimation of the herbivores would not be expected to occur instantaneously. Rather, a time lag, $\tau^a$, would exist between the stimulus of the phytoplankton food and the acclimation response of the zooplankton through gut
enzyme synthesis. If the phytoplankton fluctuate with a period less than $\tau^*$, the ingestion response should follow the Ivlev curve. With fluctuations of period greater than $\tau^*$, the ingestion response should be linear with slope $R_m A$ due to acclimation. In reality the ingestion rate will be at some intermediate between these two curves as the maximal ingestion rate, $R_m$, accommodates itself to fluctuating phytoplankton concentrations. The rate of change of the maximal ingestion rate is thus dependent upon the difference between the potential ingestion rate and the present ingestion rate, and also upon the time lag, $\tau^*$. The ingestion rate should approach the potential ingestion rate quickly if $\tau^*$ is small (short acclimation time) and more slowly if $\tau^*$ is large (long acclimation time). These dynamics can be described by the following equations:

$$ I = A (1 - e^{-AP}), $$

$$ \frac{\partial A}{\partial t} = \frac{R_m A P - A}{\tau^*}, $$

where $A$ is the actual (present) ingestion rate, $R_m A P$ is the potential grazing rate, and $\tau^*$ the time lag in the acclimation response.

The above equations were used to examine the effect of time lags in the acclimation response on the time-dependent behavior of the model. In general, time lags have a destabilizing effect on a system of equations of this sort (May, 1973). For lags between one and six days (Mayzaud and Poulet, 1978), however, only a slight de-

stabilizing effect was observed, as shown in Fig. 10. Thus, even with a time lag included in the Mayzaud and Poulet formulation, it is still much more stable than the Ivlev formulation.

It should be noted that using the steady-state values of $P$, $Z$ and $N$ and the requirements of a high damping coefficient as constraints, a parameter set could be found such that the Ivlev model showed identical behaviour to the Mayzaud-Poulet model and vice-versa. However, as discussed below, it is felt that these parameters would not agree well with those found in laboratory or controlled ecosystem experiments. In addition, functional forms could be chosen for the growth of phytoplankton or death of zooplankton that lead to oscillatory behavior similar to the Ivlev model, independent of the choice of the grazing function. An examination of these cases may be found in Steele and Henderson (1981).

Discussion and conclusions

The destabilizing effect of saturating functional responses in general has been noted previously (May, 1973). Many models have been designed with destabilizing grazing functions as a means of generating spatial patchiness and temporal variation in plankton concentrations (Steele, 1974a, b; Parker, 1975; Dubois and Closset, 1975; Dubois and Mayzaud, 1975; Sjöberg, 1977). When coupled with various forcing functions for light and temperature, these oscillations may show fluctuations similar in magnitude and period to spring and fall phytoplankton blooms (Sjöberg, 1977; Evans and Parslow, 1985). That such cycles may be produced with no reference to physical oceanographic conditions (Parker, 1975; Sjöberg, 1977) goes somewhat against dogma concerning the role of vertical mixing governing the spring bloom (Sverdrup, 1953). The fact that these oscillations are sensitive in magnitude and period to small changes in a given biological parameter has implications for either the stability of biological systems or the robustness of the model (Parker, 1975;
Hallam, 1977; Sjöberg, 1977; Steele and Henderson, 1981). In this sense the Mayzaud and Poulet formulation is more robust – the model behavior remains unchanged for large ranges of parameter values.

The pertinent question, though, is whether the robustness is realistic. One might compare the temporal behavior of these two models against the temporal evolution of experimental ecosystems such as CEPES, MERL, and Loch Ewe bag experiments (see Grice and Reeve, 1982 for reviews and discussions). It appears that in the majority of these enclosures, the sampled trophic levels did not oscillate during the timescales observed (two weeks to four months), but tended toward some equilibrium value. This is not to say that species’ successions were not seen within trophic levels, but that as a whole the biomass of a trophic level followed a generally non-oscillatory trend. For these systems at least, accepting the fact that neither the model nor the enclosure is an accurate representation of all the processes influencing plankton growth in the open water, the modified Mayzaud and Poulet formulation of grazing would appear to be a more accurate portrayal of the processes occurring.

It is significant that Mayzaud and Poulet’s (1978) study was performed on a community of non-migratory copepods. Similar experiments on single species of migratory copepods have failed to demonstrate the same increase in digestive enzymes with increased food levels (e.g. Hassett and Landry, 1983; Yen, 1983). Yen (1983) proposed that the lack of an acclimatory response may be a strategy evolved by vertical migrants which encounter discrete bands of prey. Hassett and Landry (1983) did find an increased ingestion rate in adult female Calanus pacificus, but only after acclimation to low food levels. This response is similar to that reported by Runge (1980) for starved copepods.

However, when considering groups of non-migratory copepods, as in many ecosystem models, the modified Mayzaud and Poulet formulation for herbivore grazing seems to be a more appropriate representation than the Ivlev formulation. The stabilizing lack of a saturation response in the Mayzaud and Poulet formulation allows a more predictable and robust model behavior, and perhaps a more realistic simulation of gross plankton dynamics.

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Literature cited


Appendix A

Steady-state analytical solutions

Here we present the algebra for the steady-state solution of the model with Ivlev grazing. From Eq. (2) at steady state, we immediately find

$$ P = -\frac{1}{\alpha} \ln \left\{ 1 - \frac{\omega}{\beta (1 - \gamma)} \right\}. $$

Thus the steady state phytoplankton abundance is determined solely by the zooplankton parameters $\beta, \gamma, \lambda$, and $\omega$ when $Z > 0$. Using equations (1), (2), and (4), a quadratic expression for $Z$ is obtained:

$$ Z^2 \left( \frac{\omega}{1 - \gamma} \right) + Z \left( \frac{\omega}{1 - \gamma} (\alpha + 1 - P) + P - eP \right) + P \left( e (\alpha + 1 - P) + P - 1 \right) = 0. $$

This is easily solved for $Z$ using the above expression for $P$. Knowing $P$ and $Z$, $N$ is easily found using Eq. (4).

The form of the Mayzaud-Poulet grazing function makes finding the steady-state solution of this model slightly more difficult, as the transcendental equation

$$ P (1 - e^{-\lambda P}) = \frac{\omega}{\beta (1 - \gamma)} $$

is obtained from Eq. (2) for $P$. This was solved using the Modified Regula-Falsi algorithm of Conte and de Boor (1972). Once $P$ is found, $Z$ and $N$ are found using the same equations as for the Ivlev model.

Appendix B

Sensitivity analysis

The first step in the sensitivity analysis of the Ivlev grazing model is the differentiation of the steady-state forms of Eq. (1), (2) and (3) (i.e. $\frac{dP}{d\tau} = 0$, $\frac{dZ}{d\tau} = 0$, $\frac{dN}{d\tau} = 0$)

With respect to each parameter. This yields a square matrix $A$ with

$$ A_{11} = \frac{\alpha N}{\alpha + N} - \frac{Z \beta \lambda \exp(-\lambda P)}{\alpha + N}, $$

$$ A_{12} = -\beta (1 - \exp(-\lambda P)), $$

$$ A_{13} = -\frac{NP}{(\alpha + N)^2}, $$

$$ A_{21} = (1 - \gamma) \beta \lambda \exp(-\lambda P), $$

$$ A_{22} = (1 - \gamma) \beta (1 - \exp(-\lambda P)) - \omega, $$

$$ A_{23} = 0, $$

$$ A_{31} = A_{32} = A_{33} = 1. $$

For example, for the parameter $\alpha$, we obtain the matrix equation

$$ \begin{bmatrix} A_{11} & A_{12} & A_{13} \\ A_{21} & A_{22} & A_{23} \\ A_{31} & A_{32} & A_{33} \end{bmatrix} \begin{bmatrix} \frac{\partial P}{\partial \alpha} \\ \frac{\partial Z}{\partial \alpha} \\ \frac{\partial N}{\partial \alpha} \end{bmatrix} = \begin{bmatrix} \frac{NP}{(\alpha + N)^2} \\ 0 \\ 0 \end{bmatrix}. $$

Using Gaussian elimination we may solve for $A^{-1}$ to find the magnitude of $\frac{\partial P}{\partial \alpha}, \frac{\partial Z}{\partial \alpha}, \frac{\partial N}{\partial \alpha}$, etc. These values are then normalized by $\frac{\alpha}{P}, \frac{\alpha}{Z}, \frac{\alpha}{N}$, etc., so that the final sensitivity is expressed as a percentage change of the state variable due to a 1% change in the parameter. The model's sensitivity will vary in the parameter space, so it is instructive to calculate the sensitivities for a range of parameter values.

The sensitivity analysis of the model with Mayzaud and Poulet grazing is performed in an identical manner as that above.