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Relating behavior to population dynamics: a predator–prey metaphysiological model emphasizing zooplankton diel vertical migration as an inducible response

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Abstract

We present a continuous-time deterministic model, for the population dynamics of a predator-prey system. The model which includes a function of refuge-use by the prey is developed in order to account for the interaction between lake zooplankton and fish populations, assuming the 'predator avoidance hypothesis' as the ultimate explanation for the behavior of zooplankton diel vertical migration. Nevertheless, this model is flexible enough as to be utilized in other qualitatively similar scenarios. The model is based on the metaphysiological approach to population modeling proposed by Getz [Getz, W.M., 1994. A metaphysiological approach to modeling ecological populations and communities. In: Levin, S.A. (Ed.), Frontiers in Mathematical Biology. Lecture Notes in Biomathematics 100. Springer-Verlag, New York, pp. 411–442]. Thermal stratification of the environment is explicitly incorporated in the model and, consequently, a temperature-dependence function for physiological processes. A Holling type II sub-model is used as the extraction function of prey-biomass by predators, and an abruptness function is used for the induction of the zooplankton vertical migration by fish density. The model is reparametrized, resulting in a ten-parameter equivalent system, where we analytically identify the presence of three equilibrium points. By means of computer simulation, some dynamic properties of the system are studied, evidencing the occurrence of limit-cycles, and trivial and non-trivial locally stable equilibrium points, depending on the parameter values. Stability of dynamic properties of the model are studied on selected bidimensional parameter-spaces, and the ecological significance of results is discussed. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The behavior of diel vertical migration (DVM) in zooplankton has been extensively documented for freshwater and marine environments for

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decades (Hutchinson, 1967). DVM is most pronounced in thermally-stratified lakes (Hutchinson, 1967; Lampert, 1989). The typical pattern appears as a difference between the night and day vertical distributions of zooplankton abundance, that is interpreted as an ascending movement of the organisms at evening, followed by a descending movement at dawn. The specific pattern varies largely from system to system (Hutchinson, 1967), in terms of amplitude of the population displacement, and the frequency-distribution of zooplankters during day and night.

The vertical spatial structure of temperate aquatic systems, especially freshwater ones, normally involves steep gradients of light and temperature, defining two sub-environments whose physical conditions differ strongly, namely a superficial, less-dense water layer that is well-illuminated during daytime and presents a higher and near-homogeneous temperature, and a deep, more-dense, dark and cool water layer, where the accumulation of detritus and oxidative processes take place.

Historically, there have been two lines of investigation to explain DVM. Initially, research focused on the physiological processes that make possible the performance of the DVM behavior, the so-called ‘proximate’ causes. In this respect, there is general agreement that the relative changes in light intensity drive the swimming direction and speed of the migrating animals (Ringelberg, 1964, 1991; Loose, 1993; De Meester et al., 1999). However, more recently, research has focused on a search for the evolutionary mechanisms that make possible the acquisition of this behavioral trait. In other words, the search for the so-called ‘ultimate’ cause or the adaptive significance of DVM. A widely accepted explanation for the ultimate cause of DVM is the ‘predator-avoidance’ hypothesis (Zaret and Suffern, 1976; Stich and Lampert, 1981, 1984, but see also Lampert et al., 1988; Lampert, 1989; Guisande et al., 1991; Gabriel, 1993; De Meester et al., 1999). The main statements of this hypothesis can be summarized as follows: (1) visually-oriented predators like pelagic fish need visible light to feed; (2) visible light is present, in pelagic environments, only in surface waters and during daytime; (3) zooplankton can enhance their survival rate if they locate in darkness; (4) ‘non risk’ environments are present in the entire water-column during night, but only occur in deep waters during daytime; and (5) it is advantageous for zooplankters to stay near the surface when predation risk is low, in order to take advantage of food and a higher temperature. Using this logic, the optimal pattern is a cyclic vertical movement of the organisms when the predation risk is high, ascending during nightfall to take advantage of temperature and food and descending at dawn towards the safety of the dark. Optimization studies by dynamic programming have confirmed this (Mangel and Clark, 1988; Fiksen and Giske, 1995; Fiksen, 1997). The deep waters are, in this context, defined as a refuge zone, in which some zooplankters are protected during daytime, against the activity of visually-oriented predators. Moreover, the steep vertical gradients of temperature and dissolved oxygen concentration actually restricts the vertical distribution of many freshwater fish that are not able to tolerate neither hypoxic environments nor large temperature changes on a short time-scale (Wright and Shapiro, 1990). On the other hand, if survival, fecundity or developmental rates of zooplankters are reduced in superficial waters and during daytime by factors other that fish predation, for example some toxicant pulses, the expectable optimal behavior is qualitatively the same.

In addition to the above mentioned importance of predation as an ultimate cause of DVM, it has recently proposed that DVM behavior is an inducible response, mediated by organic substances released by predators (Ringelberg, 1991; Frost and Bollens, 1992; Loose and Dawidowicz, 1994; Von Elert and Loose, 1996; De Meester et al., 1999). In this case predators do not act only as the most likely selective driving-force in the acquisition and maintenance of DVM, but also they act as switch that initiates the DVM behavior. Nevertheless, DVM could be triggered by many other stimuli other than predator-specific chemicals, provided that the stimulus is highly correlated in time with the density changes of predators.

Regarding the wide spectrum of specific modes of DVM over many different taxa, populations and environments, it has been suggested that several physical, chemical and biological conditions of the water may modify the general behavioral response (Calaban and Makarewicz, 1982; Geller, 1986; Lampert et al., 1988; De Meester et al., 1999; Tollrian and Dodson, 1999). Likewise, internal status of the zooplankters (De Meester et al., 1999; Tollrian and Dodson, 1999), genetic differences of the populations (Boersma et al. 1998; De Meester et al., 1999) and predation types (Mangel and Clark, 1988; Frost and Bollens, 1992) are also important determinants of the specificity of DVM and other predator-mediated plastic traits.

Despite the large amount of information concerning the occurrence and modes of zooplankton DVM, there are relatively few intents to formulate mathematical models that incorporate the minimal but necessary complexity implied in zooplankton behavior, in order to predict the population consequences of DVM at one or more trophic levels (Gabriel, 1993).

In this work, a deterministic continuous-time model is presented for the population dynamics of a predator-prey system. The model accounts for the interaction between freshwater zooplankton and fish predators, and is flexible enough to accommodate other predator-prey interactions. For simplicity, the model assumes that zooplankton's resource density is homogeneously distributed over depth and time, water temperature at any depth is constant over time and fish do not migrate into deep waters. Populations' age or size-structure and cannibalism in top consumers are not explicitly considered.

1.1. Conceptual departure

The introduction of biological complexity in population models derived from theoretical, experimental or field observations requires, as a starting point, a plausible scheme for the general processes governing the changes of population size through time and/or space. This general scheme should be represented by a suitable relation of selected parameters, provided that both parameters and their relationships are clear enough to allow a straightforward interpretation of the essential biological pieces of the system. The metaphysiological approach of Getz (1991, 1993, 1994) satisfies the above requirements and we adopted some of his proposals as a template in order to elaborate other theoretical suggestions based on empirical observations. This approach to modeling population dynamics treat the population as a single meta-organism whose rate of change is governed by processes of resource extraction and conversion to biomass, as well as by the rate of biomass loss derived from the extraction carried out by consumers (Getz, 1993). The main advantage in using this way of modeling population dynamics rests in that most of parameters values can be estimated from field or laboratory data (Bustamante et al., 1994) and therefore the introduction of variable's dependence on environmental conditions is straightforward.

Let x_i represent the size of a species' population at trophic level 'i' in the instant 't'. The dimension of x_i or currency could be, among others, number of individuals per unit space, biomass, energy or any proportional unit, but we shall consider biomass density as the currency-unit of our system. Consistently, the term 'per capita' will be used in the sense of 'per unit-currency'. The rate of change in time of x_i is represented by the per capita rate of net production (reproductive + somatic growth) 'f_i' times population size, minus the rate at which the population is predated by organisms at a higher trophic level, that is to say, x_{i+1} g_{i+1}. Thus, the general form of the population rate of change will be:

$$\frac{dx_i}{dt} = x_i f_i - x_{i+1} g_{i+1} \tag{1}$$

with $g_{i+1} = 0$ in the equation of top consumers. The per capita production rate f_i is defined according to Getz (1994) as an hyperbolic function of the food extraction rate g_i from level $i-1$:

$$f_i(g_i) = \rho_i\left(1 - \frac{\kappa_i}{g_i}\right) \tag{2}$$

where ρ_i denotes the upper limit of the conversion rate from food extracted to per capita growth, and κ_i the level of resource uptake that allows population maintenance when predation does not take place (Fig. 1). The extraction process is modeled here as a generalized Holling type II functional response (DeAngelis et al., 1975, see also Getz, 1991, 1994):

$$g_i(x_i, x_{i-1}) = \frac{\delta_i x_{i-1}}{\beta_i + \gamma_i x_i + x_{i-1}} \tag{3}$$

where δ_i is the maximal amount of currency that a predator-unit can extract from preys per unit-time, β_i is the half-saturation constant of predators and γ_i is a self-interference term, which account for the reduction in per capita consumption rate with increasing consumers density (Fig. 2). As quoted by Getz (1991), using Eqs. (2) and (3) into Eq. (1) and assuming $g_{i+1} = 0$, results in an analogous and more general form of the logistic growth model, if the self-interference term γ_i is greater than 0, otherwise the growth is exponential.

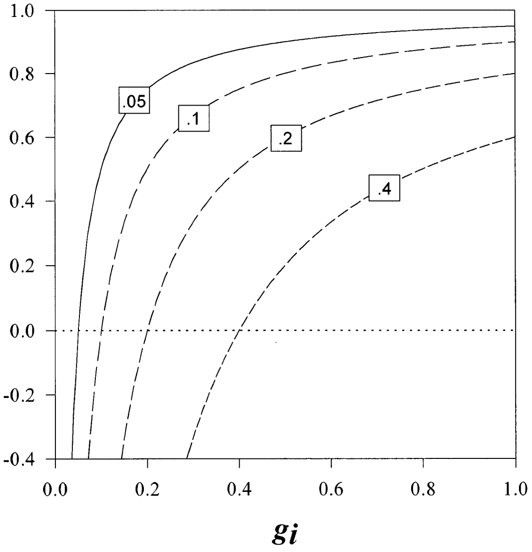

Fig. 1. Graphical representation of Eq. (2), showing the per capita production rate f_i as a function of the per capita food extraction rate g_i. Each curve was obtained using different values of parameter κ_i (in the boxes) which represents the level of resource uptake for zero production. The upper limit of the function is done by ρ_i and it was set as 1.

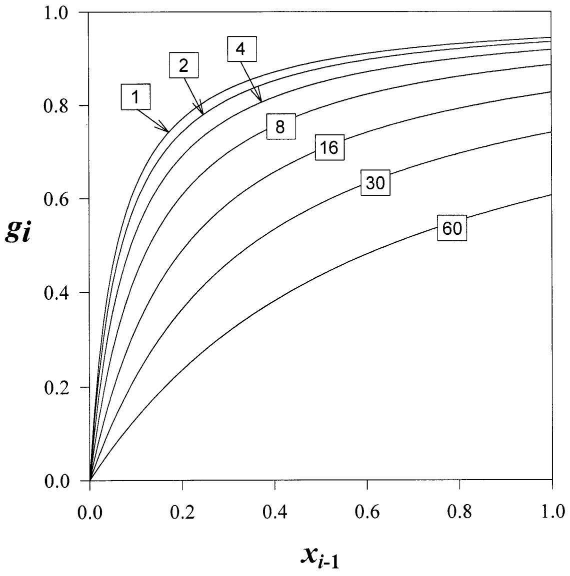

Fig. 2. Graphical representation of Eq. (3), a generalized Holling Type II functional response of resource extraction rate (g_i) to resource density (x_{i-1}). δ_i is the maximal amount of currency that a predator-unit can extract from preys per unit-time, β_i is the half-saturation constant of predators and γ_i is a self-interference term, which account for the reduction in per capita consumption rate with increasing consumers density. x_i = values shown in the boxes; $\delta_i = 1$; $\beta_i = 0.05$; and $\gamma_i = 0.01$.

2. The model

2.1. Basic terms

We denote as x_1, x_2 and x_3 the population sizes of zooplankton's resource (mainly picoplankton, nanoplankton and detritus), zooplankton itself and zooplankton's consumers (fishes), respectively. Then, it will be useful to split the zooplankton population (with size x_2) into three discrete fractions, disregarding the fact that at different time, the same fraction is not necessarily conformed by the same group of individual organisms. Thus, we define: $a = a(x_3)$ = proportion of x_2 located outside the refuge zone during the risky time (daytime). b = proportion of x_2 that remains inside the refuge during the non-risky time (night). $c(x_3) = 1 - a - b$ = proportion of x_2 that moves periodically inside and outside the refuge zone (Table 1). Here it is assumed that b is a

Table 1
Partitioning of the zooplankton population into the different fractions used in the model (see a complete explanation in the text), on the base of the vertical migration behavior

		Time	
		Day (risky time)	Night (non-risky time)
Space	Surface-waters (outside the refuge zone)	a	$a+c=1-b$
	Deep-waters (inside the refuge zone)	$b+c=1-a$	b

constant, so the transfer of individuals is only possible between a and c, in both directions. At the same time, we define two parameters related with the timing of the vertical migration behavior: $1/m =$ fraction of the time-unit (day) that c spends outside the refuge. $1/n =$ fraction of the time-unit (day) in which a is effectively exposed to predators. Although these two later terms are not related by definition, in practice they do because n depends on duration of daytime and penetration of the light into the water, while m is determined by the swimming speed and direction of the zooplankters, factors which are controlled by changes in intensity of light perceived by the organisms (Ringelberg, 1964, 1991). A list of the parameters and variables with their dimensions is provided in Table 2.

2.2. Inducible response

Most recent theoretical and empirical evidences strongly suggests that the strategy of vertical migration has mainly evolved as a predator-avoidance mechanism and this response is switched-on by the presence of chemical cues released by predators, in a concentration above some critical level (Loose and Dawidowicz, 1994; De Meester et al., 1999). This kind of inducible response would be advantageous if there are metabolic or demographic costs associated to the behavioral pattern of DVM. If so, those costs are paid only when the benefits obtained by increasing survival probability of organism currently exist. On the other hand, the chemical cues are released from predators and degraded by bacteria very quickly, so it is not necessary to consider any time-lag in the behavioral response of preys respect to predators' density. What we need, on these basis, is an equation with the following basic properties: (1) the migrating fraction of the population is zero when predators are scarce, in this point fraction a

Table 2
Parameters and variables used in the model

Symbol	Short definition	Dimension
t	Time	d
x_i	Population size, in biomass per unit-space	g m^{-3}
f_i	Per capita rate of net production	d^{-1}
g_i	Extraction rate	d^{-1}
ρ_i	Maximal conversion rate of food to production	d^{-1}
κ_i	Extraction level for zero production	d^{-1}
δ_i	Maximal extraction rate	d^{-1}
β_i	Half-saturation constant of predators	g m^{-3}
γ_i	Self-interference coefficient	Dimensionless
a	Fraction of x_2 in surface during daytime	Dimensionless
b	Fraction of x_2 in deepness during night	Dimensionless
$c=1-a-b$	Migrating fraction of x_2	Dimensionless
z	Abruptness of the zooplankton response to x_3	Dimensionless
x_c	Threshold of x_3 for the induction of DVM	g m^{-3}
$a_{\min}$	Minimal value of a	Dimensionless
Q_{10}	Magnitude of temperature-dependence	Dimensionless
$1/n$	Day-fraction where a is exposed to predation	Dimensionless
$1/m$	Day-fraction that c spend outside the refuge	Dimensionless
θ	Average body temperature	°C

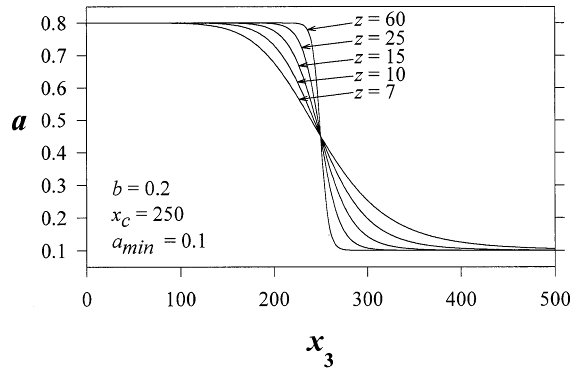

Fig. 3. Graphical representation of Eq. (4), showing fraction a of preys as a function of predator density (x_3). Parameter values are shown in the graph (see the text for explanation).

is maximal; and (2) the migrating fraction is maximal when predators' density is above a threshold level, and a is minimal. Based on these arguments the following equation is presented, which is similar to one used by Getz (1996) for distinct purposes.

$$a(x_3) = \frac{1 - b - a_{\min}}{1 + \left(\dfrac{x_3}{x_c}\right)^z} + a_{\min} \tag{4}$$

where $a_{\min}$ is proportion of x_2 that still remains outside the refuge under maximal vertical migration activity (with a large predators' density); x_c is the midpoint in the critical region of x_3, in which the response of x_2 is induced; and z is the abruptness of the response to the change in predators' density into the critical region. Note that upper and lower limits of the function are done by $1 - b$ and $a_{\min}$, respectively. This function accounts for the steep decreasing in the prey population fraction exposed to predators, once the response of DVM is switched-on (see Fig. 3). Once the density of predators cross down the critical region, the movement ceases.

This sub-model of predators'-mediated inducible response of refuge utilization could, with some minor modifications, be used to describe the time-budget of other taxa, such as animals with facultative nocturnal habits.

2.3. Effect of DVM on average body temperature

Temperature is undoubtedly a key factor in the demographic output of aquatic ectotherms. Furthermore, it has been proposed that the most costly consequence of DVM is the reduction in developmental rates as a result of the exposition of the organisms to lower environmental temperatures (Dawidowicz, 1994). It is then extremely important to consider the trade-off between survival and activity rates involved in the strategy of vertical migration of zooplankton. The first step in this direction will be to define a function for average body temperature against the average behavioral state of the organisms.

If we consider the zooplankton population as partially moving among two thermal patches, we obtain a fraction a of the population exposed constantly to θ_0 degrees in warmer surface-waters, a fraction b exposed to θ_1 degrees in cool deep waters, and the rest $1 - b - a$ alternating between θ_0 and θ_1 degrees, spending $1/m$ of the time at θ_0 and $1 - (1/m)$ of the time at θ_1. In this way, we can define the average body temperature (θ) of the organisms as:

$$\theta = a\theta_0 + b\theta_1 + (1 - b - a)\frac{[\theta_0 + \theta_1(m - 1)]}{m}. \tag{5}$$

After simple algebraic operations and defining $h = [\theta_0(1 - b) + \theta_1(b - 1 + m)]m^{-1}$, we obtain:

$$\theta = h + a\frac{\theta_0(m - 1) + \theta_1(1 - m)}{m} \tag{6}$$

that is, a linear increase in θ with a.

For simplicity, it is assumed here that the temporal changes in environmental temperature are negligible, which is approximately true for θ_1 but not for θ_0. Nevertheless, we are concentrated here with the environmental changes as a result of the spatial heterogeneity, and one can realize that the spatial differences in temperature experimented by the migrating organisms in a hourly time-scale are equivalent in magnitude to the temporal differences only over a seasonal time-scale. Moreover, as a result of the alternation by migrating organisms between θ_0 and θ_1, the effect of change in θ_0 will only affect them during $1/m$ of the time and the corresponding alteration of θ over the seasons will be to a much lesser extent. Additionally, we assume that fish population does not move from superficial waters, so if $\partial\theta_0/\partial t = 0$, then $\partial\theta_{\mathrm{fish}}/\partial t = 0$.

2.4. Effect of DVM on physiological rates

We consider here that all physiologically-controlled rates are temperature-dependent, and other sources of variation are negligible. Also, we assume a linear relationship between every physiological rate and metabolic rate, for the naturally-occurring temperature range. One can choose among a wide range of functions that account for the dependence of metabolic rate respect to temperature (see McLaren, 1963; Lampert, 1984 referring to zooplankton data), and many of those functions present an acceptable goodness of fit against one or another data set. If we don't have a particular reason to prefer one function over others, the simplest one should be selected. On the other hand, only if we attempt to fit a model to a specific field or laboratory situation, then the use of some specific and more complex function could be justified.

Although the use of Q_{10} equation is controversial, its simplicity and its long tradition over a wide spectra of taxa, together with the fact that it can give approximate predictions if the temperature range is not too large, make its careful use advisable. We consider as temperature-dependent, the physiological parameters ρ_i, κ_i and δ_i, under the form:

$$\rho_i = \rho_i^1 Q_{10} \exp\left(\frac{\theta - \theta_1}{10}\right) \tag{7}$$

$$\kappa_i = \kappa_i^1 Q_{10} \exp\left(\frac{\theta - \theta_1}{10}\right) \tag{8}$$

$$\delta_i = \delta_i^1 Q_{10} \exp\left(\frac{\theta - \theta_1}{10}\right) \tag{9}$$

where ρ_i^1 is the value of ρ_i when $\theta = \theta_1$ (minimal environmental temperature respect to the space), and the same notation for κ_i and δ_i equations. The value of Q_{10} must be estimated according with the natural temperature range. In our case, only the population with trophic level $i = 2$ is concerned with the above equations.

2.5. Predator's functional response to prey density

Because the preys available to predators are defined as the fraction a while it is exposed to them, and the available preys are exposed only $1/n$ of the total time,

$$\text{'average available preys'} = ax_i/n \tag{10}$$

then, the general Holling type-II extraction function g_{i+1} (with $i = 2$ for our case) is rewritten as:

$$g_{i+1}(x_i, x_{i+1}) = \frac{\delta_{i+1} a x_i}{n\beta_{i+1} + n\gamma_{i+1}x_{i+1} + ax_i} \tag{11}$$

that which account for the reduction in predator's capture-effectiveness in proportion to the avoidance behavior of the preys and the extent of the risky-time.

2.6. The rate of population change

From the above definitions, by including the sub-models 4–11 into Eqs. (2), (3) and (1) and rearranging the terms, now we can derive the final non-linear differential equations system for the population dynamics of zooplankton and fish:

$$\frac{\mathrm{d}x_2}{\mathrm{d}t} = \rho_2^1 Q_{10}^{\Phi} x_2 \left[1 - \frac{\kappa_2^1(\beta_2 + x_1 + x_2\gamma_2)}{\delta_2^1 x_1}\right] + \frac{\delta_3 x_2 x_3 \left[b - 1 - a_{\min}\left(\frac{x_3}{x_c}\right)^z\right]}{\left(\frac{x_3}{x_c}\right)^z [\beta_3 n + a_{\min} x_2 + n x_3 \gamma_3] + \beta_3 n + x_2 - b x_2 + n x_3 \gamma_3} \tag{12a}$$

$$\frac{\mathrm{d}x_3}{\mathrm{d}t} = \rho_3 x_3 \left[1 + \frac{\kappa_3\left\{-\beta_3 n - x_2 + b x_2 - \beta_3 n\left(\frac{x_3}{x_c}\right)^z - a_{\min} x_2\left(\frac{x_3}{x_c}\right)^z - n x_3 \gamma_3 - n x_3\left(\frac{x_3}{x_c}\right)^z \gamma_3\right\}}{\delta_3 x_2\left\{1 - b + a_{\min}\left(\frac{x_3}{x_c}\right)^z\right\}}\right] \tag{12b}$$

being

$$\Phi = \left[(\theta - \theta_1)\right.$$

$$\left\{m - bm + \left(\frac{x_3}{x_c}\right)^z - a_{\min}\left(\frac{x_3}{x_c}\right)^z - b\left(\frac{x_3}{x_c}\right)^z\right.$$

$$+a_{\min}m\left(\frac{x_3}{x_c}\right)^z\Bigg\}10^{-1}\Bigg\{m+m\left(\frac{x_3}{x_c}\right)^z\Bigg\}^{-1}\Bigg]. \tag{12c}$$

2.7. Reparametrization

By using the standard procedures for dynamic systems, system (12) is expressed as a ten-parameter equivalent form (see details in Appendix A):

$$\frac{du}{d\tau}=Cu\left[PQ_{10}\exp\left(\frac{D(M+v^z)}{1+v^z}\right)(1-u)\right.$$
$$\left.-\frac{v(B+v^z)}{E(N+v)(1+v^z)+u(B+v^z)}\right] \tag{13a}$$

$$\frac{dv}{d\tau}=v\left[S-\frac{(N+v)(1+v^z)}{u(B+v^z)}\right] \tag{13b}$$

where all parameters are assumed to have non-negative values.

The relation between original and redefined state-variables is given by:

$$u=Kx_2 \tag{14}$$

and

$$v=\frac{x_3}{x_c} \tag{15}$$

and the new parameters are defined (see Appendix A) as

$$B=\frac{1-b}{a_{\min}} \tag{16}$$

$$M=\frac{mB}{B+m-1} \tag{17}$$

$$D=\frac{\theta_0-\theta_1}{10m}a_{\min}(B+m-1) \tag{18}$$

$$K=\frac{x_1\delta_2^1-\kappa_2^1\beta_2-\kappa_2^1x_1}{\kappa_2^1\gamma_2} \tag{19}$$

$$P=\frac{\rho_2^1K(x_1\delta_2^1-\kappa_2^1\beta_2-\kappa_2^1x_1)}{x_1\delta_2^1x_c\delta_3} \tag{20}$$

$$E=\frac{n\gamma_3x_c}{a_{\min}K} \tag{21}$$

$$N=\frac{\beta_3}{\gamma_3x_c} \tag{22}$$

$$S=\frac{\delta_3-\kappa_3}{\kappa_3E} \tag{23}$$

$$C=\frac{x_c(\delta_3)^2}{\rho_3\kappa_3KE}. \tag{24}$$

3. Results and discussion

Three equilibrium points were identified: $P_0=(0, 0)$; $P_1=(1, 0)$ and $P_e=(u_e, v_e)$, where

$$u_e=\frac{(N+v_e)(1+v_e^z)}{S(B+v_e^z)} \tag{25}$$

and v_e satisfies the equality:

$$P(SE+1)Q_{10}\exp\left(\frac{D(M+v^z)}{1+v^z}\right)$$
$$[S(B+v^z)(N+v)(1+v^z)-(N+v)^2(1+v^z)^2]$$
$$-S^2v(B+v^z)^2=0. \tag{26}$$

Stability domains of the model (Eqs. (13a) and (13b)) were analyzed using computer simulations, in terms of the parameter spaces formed by B against N (Fig. 4, $D=1$), and B against D (Fig. 5, $N=2$). Other values were set as follow: For simplicity, it was assumed $C=P=M=E=S=1$, the canonical $Q_{10}=2$ and a moderately steep response to predators with $z=30$ (see Fig. 3). Parameters B, N and D were chosen to analyze stability properties of the system, because they represent relevant features of prey's behavior (B), prey's physiology (N) and environment (D).

Which fraction of the population effectively migrates once the response is switched-on, is reflected by the values of b and $a_{\min}$. When all individuals performs DVM, $b=a_{\min}=0$, and so B tends to infinity. Inversely, if only a small fraction of the population migrates, then $a_{\min}$ approaches $1-b$, and B tends to unity (see equality 16). Thus, parameter B could be interpreted as a measure of the responsiveness of the population, a magnitude indicative of the extent of DVM.

The ability of preys to react, switching-on the behavior of DVM under the presence of some critical density of predators-derived stimulus, is an important trait because organisms too sensitive (i.e. migrants under very low predators densities) probably pay a physiological cost larger than the benefit obtained from increasing survival, while organisms with too low sensibility (those requiring very high predators density to react) won't be able to prevent high population losses. The density of predators inducing zooplankton DVM (x_c) is related inversely to parameter N, which can be interpreted as a measure of the readiness in achieving the behavioral response of DVM (refuge use), assuming some constant positive values for β_3 and γ_3 (see equality 22). No migration occurs when x_c tends to infinite, and so N tends to zero.

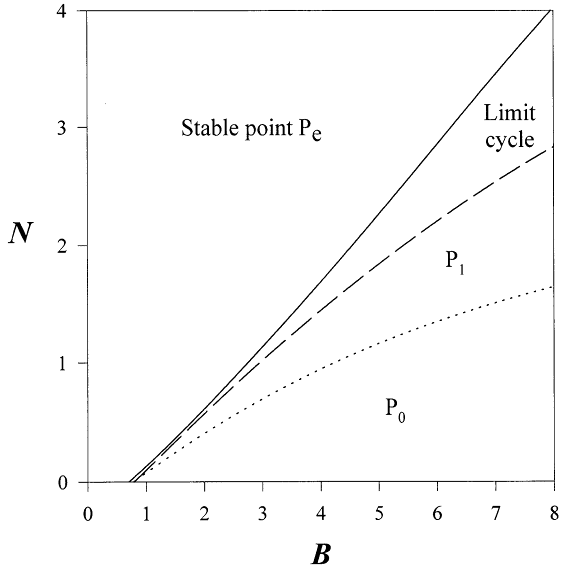

Fig. 4. Stability domains of the model, in the parameter space formed by B and N. Other parameter values were set as $D = 1$, $Q_{10} = 2$, $z = 30$, $C = P = M = E = S = 1$.

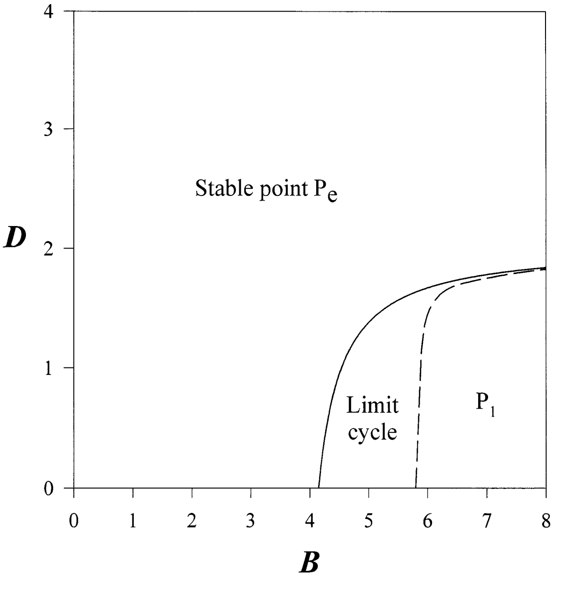

Fig. 5. Stability domains of the model, in the parameter space formed by B and D. Other parameter values were set as $N = 2$, $Q_{10} = 2$, $z = 30$, $C = P = M = E = S = 1$.

In freshwater ecosystems, the thermal spatial structure of the environment is thought to be a major determinant of the cost in avoiding fish predators by means of refuge exploitation. This cost represents a fitness reduction as a result of the effect of temperature on metabolic and developmental rates, and its magnitude is related to the thermal difference between surface and deep waters. This condition is reflected by parameter D, whose value increases with the difference in water temperature between inside and outside the refuge zone (see equality 18). If thermal stratification does not take place, then $D = 0$.

Focusing on the dynamic patterns of the system studied, it exhibits either a limit cycle or it tends to a stable equilibrium point, depending on the specific combination of parameter values. For low values of B and high values of N (Fig. 4) the system tends to a (locally) stable equilibrium point (P_e) where u_e and v_e are both different from zero. If B has a high value, the system exhibits limit cycles if N is large; or it tends to the equilibrium point $P_1 = (1, 0)$, that means extinction of predators and equilibrium density of preys, if N has a medium value; or extinction of both populations occurs [point $P_0 = (0, 0)$] with low values of N. Examples of trajectories in the phase plane illustrating the different outcomes of the model are shown in Fig. 6.

Fig. 5 shows that if B is low or D is high, the system tends to the non-trivial equilibrium point (P_e). If B has a larger value while D is low, the system exhibits a limit cycle, and it tends to the point $(1, 0)$ if B is indeed large and D low.

If only few or none zooplankters migrate while predators' density is above the critical level (low values of B), the predator-prey system tends to reach a stable point in the phase portrait, with equilibrium densities greater than zero.

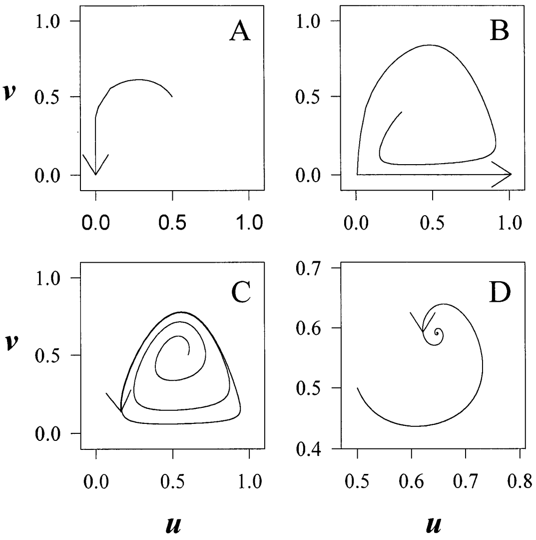

Fig. 6. Examples of the obtained trajectories, shown in the phase plane of v and u, the two redefined state-variables of the model. (A) Trivial equilibrium point $P_0 = (0, 0)$ acting as local attractor; (B) trivial equilibrium point $P_1 = (1, 0)$ acting as local attractor; (C) limit cycle; and (D) non-trivial equilibrium point $P_e = (u_e, v_e)$ acting as local attractor.

If DVM is performed by a large fraction of the zooplankton population (large B), then the system exhibits a limit cycle if zooplankters readily start to migrate as a function of predators' density (large N), otherwise fish population tends to zero while zooplankton reach either its equilibrium density (if N is not too low) or extinction (if its reactivity N is rather low).

Under a strongly thermally-stratified environment (large D) the system is more likely to reach a stable equilibrium point, the same as in poorly stratified waters (low D) if B (responsiveness) is low. This result is consistent with Geller (1986), who found a positive correlation between seasonal population stability and the relative temperature range experienced my migrating *Daphnia* in lake Constance.

Biotic interactions undoubtedly play a major role determining form and function of communities over a wide range of natural systems, and particularly in freshwater (Lampert, 1987). By far, predation is the empirically best-founded interaction that strongly influences zooplankton dynamics (Zaret, 1980; Gliwicz and Pijanowska, 1989), with profound implications for biogeochemical cycling. Predation pressure induces the development and achievement of preys' evolutionary strategies, either morphological (Hanazato, 1990; Tollrian, 1995; Tollrian and Dodson, 1999) as well as behavioral ones such as zooplankton DVM (De Meester et al., 1999). Accepting that fitness of the organisms is determined by a compromise between survival probability, developmental rates and fecundity, the evolutionary acquisition of DVM precludes a positive balance among costs and benefits coupled with an unavoidable trade-off in the fitness components when the strategy is adopted by zooplankters. In our study-case, the benefits of increasing survival depends, among other factors, on the inhabitability of the refuge zone for the organisms, condition which is often constrained by resource availability in oligotrophic environments and by physicochemical features such as oxygen concentration in eutrophic waters. On the other hand, the magnitude of costs in developmental rates are mainly determined by the environmental temperature in deep waters. In this scenario, the outcome of a particular strategy each population will adopt should depend on the specific combination of susceptibility to predators, energy demands and reaction norms to physicochemical conditions.

This model does not include many important elements such as seasonal changes in phytoplankton biomass, epilimnetic temperature, and time expended by zooplankters in refuge. Including these and other relevant variables will obtain this kind of modeling approach more realistic, but necessarily more complex. On the other hand, a future task is to use field information and laboratory research in order to validate the model and test hypotheses emerging from it. In this context, some question to be solved are: which is the best empirical model to describe the inducement of DVM as a function of predator density? Can we find qualitative differences, as predicted by the model, in the population dynamics of migrant zooplankton and fish as an effect of different degrees of thermal stratification? Can we find a trend, over different ecosystems, of widening the spectrum of predator-prey dynamics with increasing responsiveness of the zooplankton DVM?

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Appendix A

By making the substitution $v = x_3/(x_c)$, function $a(x_3)$ becomes:

$$a(v) = \frac{1-b-a_{\min}}{1+v^z} + a_{\min} = \frac{a_{\min}(B+v^z)}{1+v^z}$$

where

$$B = \frac{1-b}{a_{\min}}.$$

Considering now the temperature-related expression $\theta - \theta_1/(10)$, we have:

$$\frac{\theta-\theta_1}{10} = \frac{\theta_0-\theta_1}{10m}\,[1-b+a(v)(m-1)]$$
$$= \frac{\theta_0-\theta_1}{10m}\,a_{\min}\left[\frac{mB+(B+m-1)v^z}{1-v^z}\right]$$
$$= D\left(\frac{M+v^z}{1+v^z}\right)$$

where

$$D = \frac{\theta_0-\theta_1}{10m}\,a_{\min}(B+m-1) \quad \text{and}$$

$$M = \frac{mB}{B+m-1}.$$

On the other hand, metabolically-dependent parameters can be expressed as:

$$\rho_2 = \rho_2^1 Q_{10}\exp\left(\frac{D(M+v^z)}{1+v^z}\right)$$

and the same for κ_2 and δ_2.

Writing $Q(v^z) = Q_{10}\exp(D(M+v^z)/(1+v^z))$, we obtain:

$$g_2 = \frac{x_1\delta_2^1 Q(v^z)}{\beta_2+x_1+\gamma_2 x_2},$$

and

$$f_2 = \rho_2\left(1-\frac{\kappa_2}{g_2}\right) = JQ(v^z)\left[1-\frac{x_2}{K}\right]$$

where

$$J = \frac{\rho_2^1(x_1\delta_2^1-\kappa_2^1\beta_2-\kappa_2^1 x_1)}{x_1\delta_2^1} \quad \text{and}$$

$$K = \frac{x_1\delta_2^1-\kappa_2^1\beta_2-\kappa_2^1 x_1}{\kappa_2^1\gamma_2}.$$

As $g_3 = \delta_3 x_2 a(x_3)/(n\beta_3+n\gamma_3 x_3+x_2 a(x_3))$, we obtain:

$$g_3 = \frac{\delta_3 x_2 a_{\min}(B+v^z)}{(n\beta_3+n\gamma_3 x_c v)(1+v^z)+a_{\min}x_2(B+v^z)}.$$

Then, for $x_2' = x_2 f_2 - x_3 g_3$ we obtained:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = \frac{x_c\delta_3}{K}u\left[JQ(v^z)[1-u] - \frac{v(B+v^z)}{(W+Ev)(1+v^z)+u(B+v^z)}\right]$$

being

$$P = \frac{JK}{x_c\delta_3}, \quad W = \frac{n\beta_3}{a_{\min}K} \quad \text{and} \quad E = \frac{n\gamma_3 x_c}{a_{\min}K}.$$

As $f_3 = \rho_3(1-(\kappa_3)/g_3)$,

$$f_3 = \rho_3\left(1-\frac{\kappa_3}{\delta_3}-\frac{\kappa_3}{\delta_3}\left[\frac{(W+Ev)(1+v^z)}{u(B+v^z)}\right]\right)$$
$$= T\left[S-\frac{(N+v)(1+v^z)}{u(B+v^z)}\right]$$

where

$$N = \frac{W}{E} = \frac{\beta_3}{\gamma_3 x_c}, \quad S = \frac{\delta_3-\kappa_3}{\kappa_3 E} \quad \text{and} \quad T = \frac{\rho_3\kappa_3 E}{\delta_3}.$$

Thus, $\mathrm{d}x_3/(\mathrm{d}t) = x_3 f_3$ implies that

$$\frac{\mathrm{d}v}{\mathrm{d}t} = Tv\left[S-\frac{(N+v)(1+v^z)}{u(B+v^z)}\right].$$

Finally, we obtain the following non-linear differential equation system:

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = \dfrac{x_c \delta_3}{K} u \left[PQ(v^z)(1-u) \right. \\ \qquad \left. - \dfrac{v(B+v^z)}{E\left(\dfrac{W}{E}+v\right)(1+v^z)+u(B+v^z)} \right] \dfrac{\mathrm{d}v}{\mathrm{d}t} \\ \dfrac{\mathrm{d}u}{\mathrm{d}t} = Tv\left[S - \dfrac{(N+v)(1+v^z)}{u(B+v^z)} \right] \end{cases}$$

that is qualitatively equivalent to system:

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}\tau} = Cu\left[PQ_{10}\exp\left(\dfrac{D(M+v^z)}{1+v^z}\right)(1-u) \right. \\ \qquad \left. - \dfrac{v(B+v^z)}{E(N+v)(1+v^z)+u(B+v^z)} \right] \dfrac{\mathrm{d}v}{\mathrm{d}\tau} \\ \dfrac{\mathrm{d}u}{\mathrm{d}t} = v\left[S - \dfrac{(N+v)(1+v^z)}{u(B+v^z)} \right] \end{cases}$$

by rescaling the time as $\tau = Tt$. This equivalent system has only ten parameters, where

$$C = \frac{x_c \delta_3}{KT} = \frac{x_c (\delta_3)^2}{\rho_3 \kappa_3 KE} \quad \text{and} \quad P = \frac{P_1}{E}.$$

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