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Consequences of intraspecific predation: A stage structured population model approach

by

Wilfried Gabriel[1] and Frank van den Bosch[2]

[1] Max Planck Institute for Limnology
Department of Physiological Ecology
P.O.Box 165, D - 2320 Plön, Fed. Rep. of Germany
and
[2] Institute of Theoretical Biology
P.O.Box 9516, NL - 2300 RA Leiden, The Netherlands

ZUSAMMENFASSUNG: DGLs mit zeitverzögerten Argumenten beschreiben ein Räuber-Beute-System, in dem nur die älteren Individuen räuberisch sind, aber neben der Beutepopulation auch Jungtiere der eigenen Art jagen. Mit zunehmendem innerartlichem Räuberdruck verringern sich zunächst die Amplituden der Räuber-Beute-Oszillationen, bevor mit weiterer Zunahme gedämpfte Schwingungen auftreten. Bei einer kannibalistischen Aktivität, die Labormessungen bei räuberischen Copepoden entspricht, werden die Oszillationen so stark gedämpft, daß sich schnell ein stabiles Gleichgewicht einstellt. Dadurch verringert sich das Aussterberisiko erheblich.

SUMMARY: By differential equations with time delayed arguments, a predator-prey system is described where only older animals are predacious but hunt, besides a prey population, also juveniles of their own species. Increasing intraspecific predation first reduces the amplitudes of predator-prey oscillations; a further increase then causes damping. With a cannibalistic activity as measured for copepods, the system turns very fast into a stable equilibrium. This reduces the risk of extinction drastically.

INTRODUCTION

Predator-prey-relationships are important biotic interactions in ecosystems. They are often modelled by various types of Lottka-Volterra-equations. With enormous effort mathematicians gave many valuable insights into principal mechanisms. The application to field populations, however, and also to laboratory experiments often failed. This augmented the prejudice against mathematical modelling among many biologists.

To improve the applicability of Lottka-Volterra-systems, it is indispensable to include more detailed information on the individuals into the mathematical description. Not only age structures are of great importance to population dynamics but also other traits and variabilities of the individuals within a population, e.g. behavior, physiological acclimation, genotypic variation, phenotypic plasticity, reaction norms. One of the attempts to include more of the individuals' characteristics into mathematical population models is done by the theory of structured populations (Nisbet et al. 1985, Metz and Diekmann 1986). In the following we apply this approach to the problem of intraspecific predation. We present a model for a species that becomes predacious during life time, feeding on smaller animals of other species as well as on its own juveniles.

Consequences of intraspecific predation on population dynamics will be discussed by calibration of the model to experimental data on a freshwater cyclopoid copepod.

INTRASPECIFIC PREDATION

Intraspecific predation is a widespread phenomenon especially when food becomes scarce. Well known examples are fish populations wherein adults become carnivorous and feed on their own young. It is interesting to study the population when adults have no other food sources than their own species. One may also

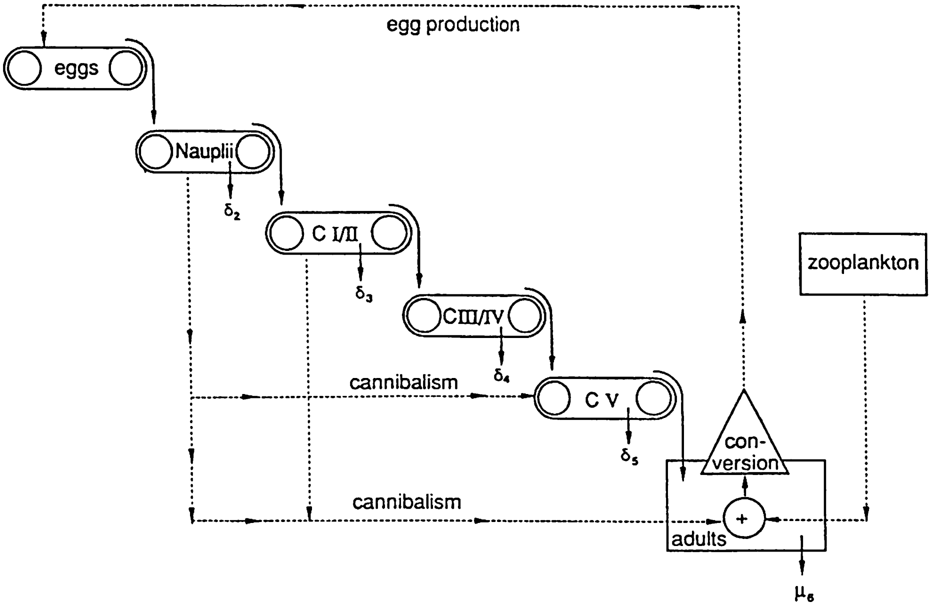


Fig. 1: Stage structured population model visualized by conveyor belts.

ask which amount of cannibalism is tolerable for a population if adults (and older juveniles) live partially on pre-adults which have access to other food sources. This problem has been analyzed for cyclopoid copepods by a detailed simulation model based on difference equations (Gabriel 1985a, Gabriel and Lampert 1985). It has been concluded that copepod populations can hardly survive cannibalism without sufficient alternative prey for the adults. For periods of food shortage in the alternative prey, cannibalism increases drastically the survival probability of a population (Gabriel 1985b). These models, however, did not allow to draw more general conclusions. Applying the methods of structured populations (van den Bosch et al. 1988), a general mathematical description for population survival under cannibalism has been obtained. With this analysis it was possible to estimtate the boundary conditions under which populations can survive in spite of heavy intraspecific predation.

A MODEL FOR PHYSIOLOGICALLY DISTINCT AGE CLASSES AND ITS APPLICATION TO CYCLOPOID COPEPODS

We use the method of stage structured populations and expand the previous approach (van den Bosch et. al. 1988) to a more specific model. The aim is to describe a species in which the individuals change their feeding behavior during lifetime. They start as herbivores and become carnivorous or omnivorous in later stages. The various stages differ in physiology, energy content and food selectivity. The model is applicable not only to the cyclopoid copepod species we had in mind during construction. In copepods, the various life stages can be identified because they are distinguishable in morphology. This makes it easier to measure the model parameters in experiments.

We differentiate five stages: the first three stages are herbivorous, stage four is partially predacious and stage 5 is obligatory carnivorous. The prey population (other zooplankter than the predator) is assumed to follow the usual logistic population growth in absence of the predator. Predation is modelled by a Holling type II functional response which determines an additional death rate (see equation 1). The dynamics of a stage

Table: Equations and parameters

(1) $$dn_1/dt = r\, n_1(t)\ [1 - n_1(t)/K] - n_1(t) \sum_{j=5}^{6} F_{j1}(t) n_j(t)$$

(2-5) $$dn_i/dt = R_i(t) - R_{i+1}(t) - \delta_i(t)\ n_i(t) \qquad \text{for } i=2,\ldots,5$$

(6) $$dn_6/dt = R_6(t) - \mu_6(t)\ n_6(t)$$

(7-10) $$dP_i/dt = P_i(t)\ [\delta_i(t-\tau_i) - \delta_i(t)] \qquad \text{for } i=2,\ldots,5$$

(11) $$R_2(t) = \epsilon\ n_6(t-\tau_E) \sum_{i=1}^{5} E_i\ F_{6i}(t-\tau_E)\ n_i(t-\tau_E)$$

(12-15) $$R_i(t) = R_{i-1}(t-\tau_{i-1})\ P_{i-1}(t) \qquad \text{for } i=3,\ldots,6$$

(16-19) $$\delta_i(t) = \sum_{j=5}^{6} F_{ji}(t) n_j(t) + \mu_i \qquad \text{for } i=2,\ldots,5$$

(20-29) $$F_{ji}(t) = C_{ji} \,/\, [1 + \sum_{i<j} C_{ji}\ H_{ji}\ n_i(t)] \qquad \text{for } i=1,\ldots,5 \text{ and } j=5,6$$

n_1	alternative prey (zooplankton)
n_2	predator stage 1 (nauplii)
n_3	predator stage 2 (copepodites CI and CII)
n_4	predator stage 3 (copepodites CIII and CIV)
n_5	predator stage 4 (copepodites CV)
n_6	adult predator (copepodes)
P_i	probability to survive through stage i
R_i	rate of recruitment into stage i
δ_i	per capita intrinsic death rate of stage i
F_{ji}	Holling type II functional response of stage j on i
r	intrinsic growth rate of alternative prey
K	carrying capacity of alternative prey (n_1)
μ_6	natural intrinsic mortality rate of adult predator
ϵ	conversion efficiency of uptaken energy into eggs
τ_E	development time of eggs
E_i	energy content of an individual prey n_i
τ_i	development time of stage i
C_{ji}	attack rate of stage j on stage i
H_{ji}	handling time of stage j on stage i

of the predator population is described by the difference between the rate of recruitment into a stage and its following stage and by an additional loss term due to natural and predator induced mortality in the stage (equations 2-6).

It is important to mention that this description of the stages by differential equations is not done in the usual way of compartment models in which the information of cohorts inside the compartments is lost. An appropriate picture of model is a system of conveyor belts (see Figure 1), each stage represented by its own belt: individuals falling onto the belt from a previous stage are traced during aging with modifications due to death until they reach the end of the belt and fall onto the next belt. The time spent on a belt - or equivalently the stage duration - enters, as time delay, into the equations. Thereby, necessary information is kept in time delayed variables. The input onto the belts are equivalent to the rates of recruitment into the stages. These rates are obtained by multiplying the recruitment rate of the previous stage with the probabilities to survive through the stage (equations 12-15). The survival probability of a stage is described by a differential equation using the death rate in the stage at actual time besides its value delayed by the stage duration (equations 7-10). Stage specific death rates are calculated by the summation over the natural death rates and the mortality due to cannibalism (equations 16-19). Cannibalism is described by a Holling type II functional response which depends on prey densities (alternative prey and cannibalized stages of the own species). To calculate the recruitment into the first stage, one has to sum over the food uptakes and to convert it into eggs. The production of newborns occurs with a time delay of the egg development period (equation 11).

With reference to previous work (Nisbet et al. 1985, van den Bosch et al. 1988) the justification of the whole equation system (see Table) is straight forward. The quite complex system of delayed differential equations can be implemented and integrated on personal computers by a special software (Maas et al. 1982). One has to specify the starting conditions of the variables as well as its time delayed values very carefully in a consistent manner. For our studies of the dynamical behavior of the system, it was appropriate to inoculate the system by a well defined pulse (we used a Gamma distribution) of nauplii and then let evolve the system. The model parameters have been partially taken from literature data and partially from experiments (van den Bosch and Santer, in prep.) which have been designed especially for this model.

RESULTS AND DISCUSSION

Intraspecific predation does not only stabilize the population dynamics for short periods of food shortage (Gabriel 1985b) but also in the long run. For cyclopoid copepodes, this striking effect has been demonstrated by van den Bosch and Gabriel (in press) applying the stage structured model approach presented in this paper.

Figure 2 shows a typical cycle of the predator prey interaction in case of zero intraspecific predation. The fact that the abundance of the CIII/CIV-stage (=n_4) is larger than the CI/CII-stage (=n_3) just reflects that the duration time for n_4 is longer than for n_3. In Figure 3, only the time courses of alternative prey (=n_1), nauplii (=n_2), and adult predators (=n_6) are shown. The various panels display the population dynamics for different degrees C of intraspecific predation. C=1 means intraspecific predation according to the attack rates measured in the laborato-

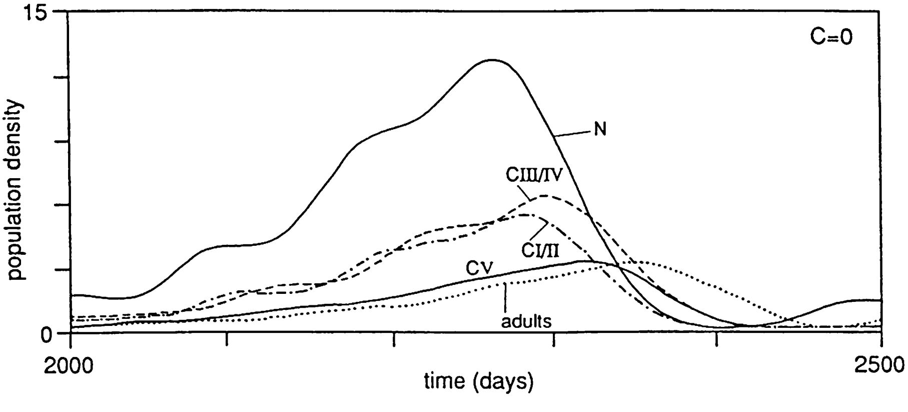
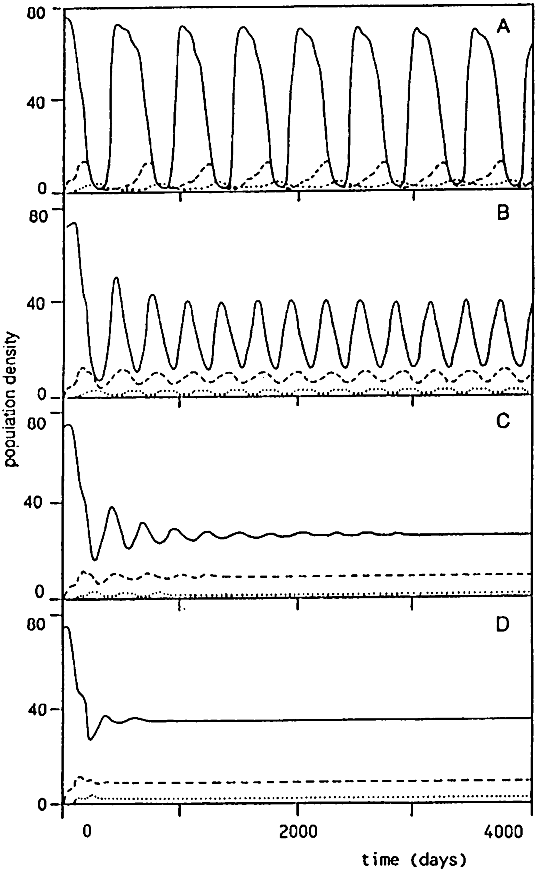


Fig. 2: Time course of various stages of the predator during one predator prey cycle without cannibalism (cannibalistic activity C=0). The stages are indicated in the figure (N = nauplii, CI...CV juvenile stages).



A) Without cannibalism. (C=0)

B) Attack rates of the predator on conspecifics are 40% of the values measured in the labatory. (C=0.4)

C) Attack rates are 60% of the measured values. (C=0.6)

D) Attack rates are equal to the measured values. (C=1)

Fig. 3: Time course of predator and prey population for various degrees of cannibalistic activity C of the predator. Continuous line: prey (zooplankton). Dashed line: predator nauplii. Dotted line: predator adults.

ry experiments, C=0 (upper panel) means no cannibalistic activity so that only the alternative prey is consumed. With increasing intraspecific predation, amplitudes of the predator-prey oscillations decrease but frequency increases (panel with C=0.4), then, for C > 0.5 we observe damped oscillations resulting in a stable equilibrium of the system. The transition time from the initial state to the stable equilibrium is very short for C=1. With this cannibalistic activivty, the predacious adults still live mainly on the alternative prey population: less the 10% of the uptaken energy is gained by cannibalism.

Large oscillations of the predator prey system endanger the species because of the high extinction risk by random fluctuations. Therefore, the observed stabilizing effect of intraspecific predation may be of great importance for species survival.

The model presented is valid only for the unrealistic case of stable environment. For example, the developmental times vary with temperature, but temperature is far from being constant during the growing season of the predator. In addition, growth rate and carrying capacity of the alternative prey population show high variability during season. To apply the model to field populations, one has to modify the model equations e.g. by making several parameters time dependent. The approach of structured populations can still be applied, but before doing so we have to perform experiments to determine additional parameter values.

Such complicated experiments are already planned. This may indicate that the approach of stage structured population is promising also for experimental biologists.

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