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Food limitation and the structure of zooplankton communities

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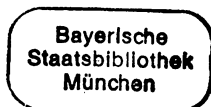
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Overcoming food limitation by cannibalism: A model study on cyclopoids

By WILFRIED GABRIEL, Plön

With 5 figures in the text

Abstract

Many cyclopoid copepods change their feeding habits during development. Young stages are herbivorous, whereas adults are carnivores or omnivores. A demographic model based on physiological parameters is developed to study the effect of cannibalism on the population dynamics of cyclopoids and their prey. If alternative prey are available and their potential growth rate is higher than the potential growth rate of the cyclopoids, the survival of predator and prey populations without cannibalism is guaranteed only if the prey population is above a critical density. Cannibalism allows the survival below this critical density independent of the actual age distribution and even prevents extinction at densities much below the critical point. Therefore, cannibalism is considered to be a stabilizing factor in predator-prey interactions during and after periods of food limitation.

Introduction

Intraspecific predation is a widespread process (Fox 1975; Polis 1981). It influences the population dynamics of numerous species and may significantly affect the structure of many communities.

Size and species composition of zooplankton are considered to be correlated with the predators present (Lane 1978; Kerfoot 1980; Brandl & Fernando 1981). Therefore, a change in a predaceous behaviour, such as cannibalism triggered by food limitation, may be an important factor in structuring zooplankton communities. Cyclopoid copepods are of special interest in this respect because of the switch in their feeding habit: nauplii are herbivorous, late copepodites and adults are carnivores. Cannibalism is observed in the field and in experiments (Fryer 1957; McQueen 1969; Gras et al. 1971; Gophen 1977; Brandl & Fernando 1979; Landry 1981). It has been shown to be advantageous in cyclopoids in a constant environment (Gabriel & Lampert 1985), but its benefit may be much greater in a variable environment with fluctuating food conditions which can cause a sudden, dramatic shift in the relative abundances of predator and prey. For example, a depletion of algal food may cause a decrease in abundance of the prey population below a level, where the growth of the prey cannot compensate the predation pressure, even after reestablishment of good food conditions. Without cannibalism, the predaceous *Cyclops* would eliminate its own prey, but also cannibalism implies the risk of self-extinction. The model presented is designed to study the impact of cannibalism around such critical situations.

Model description

Population dynamics of the cyclopoid copepods

Calculation of the population dynamics of the cyclopoids is based on physiological data, field and laboratory observations taken from the literature (Brandl & Fernando 1975; Elgmork 1959; Gophen 1976, 1980; Jamieson 1980 a, b; Peacock & Smyly 1983; Schober 1980; Smyly 1970, 1973; Vijverberg 1977, 1980; Williamson 1980).

To construct a representative cyclopoid copepod averaging across different species, temperatures, food conditions etc., all time scales are normalized by the age at maturity and all weights are expressed relative to the weight of adult females. Differences between males and females are considered only by a correction factor in the birth rate calculation. For given feeding rates, metabolic parameters and efficiencies, the time course of growth can be calculated. The carnivorous portion of the diet is assumed to be zero until the cyclopoids have grown to a certain weight (i. e. 15 % of the final weight) and then to increase linearly with weight so that the adults are obligate carnivores.

As the onset of cannibalism can cause rapid and dramatic changes in the age-structure of the population, the compartments have to be small enough to keep track of the dynamics. Using the instars as compartments is inadequate. I have verified that 40 age classes from birth until first reproduction are sufficient to describe the dynamics of the age structure without systematic errors for the applications presented.

It can be unrealistic to describe a discontinuous process like predation by differential equations. Therefore, the changes in the abundances of the different age classes are modelled by difference equations, but the time step is variable and adjusted during calculation. Starvation is implemented by prolonging development in an age class, if the net production is positive, and by an additional mortality, if the food intake is lower than the metabolic requirement.

Cannibals are known to prefer smaller prey. The data available, however, are not sufficient to determine the exact preference function. Fortunately, I have been able to prove that the general results of this study are independent of the preference structure used. For the data presented, the relative preference of prey is calculated from the length difference between the predaceous cyclopoid and the one eaten by assuming a Gaussian distribution around an optimal length difference. Thereby the age specific mortality under cannibalism and the birth rate are highly dependent on the actual population structure and on the food availability. The detailed mathematical description of these problems is given elsewhere (Gabriel in prep.).

Interaction with alternative prey populations

The special aim of this model is to establish the requirements necessary for the predator-prey-system to recover from critical situations where the probability of extinction is high. For this purpose the dynamics are studied only on a short time scale. Therefore, the interaction between cyclopoids and their alternative prey populations can be treated in a simple way by neglecting second order effects such as carrying capacities, time lags, internal structure of the alternative prey populations, and long term stability.

Let A represent the density of alternative prey populations in units of body weight of an adult of the cyclopid population C . If r_A describes the potential growth rate of A without the mortality caused by C , then the interaction between A and C can be regarded (in differential form) by

$$(1) \quad \frac{dA}{dt} = r_A A - g C,$$

where the complex dynamics of C are calculated by the model described verbally above, and where g is the specific consumption rate of alternative prey by cycloids:

$$(2) \quad g = \sum_{i=1}^n N_i f_i \epsilon_i (1 - \kappa_i)$$

- i = index of cyclopid age classes,
- n = number of age classes,
- f_i = relative food demand,
- ϵ_i = carnivorous part of food demand,
- N_i = relative frequency of an age class ($\sum_{i=1}^n N_i = 1$),
- κ_i = intensity of cannibalism.

The intensity of cannibalism is zero for a population without cannibalism; otherwise κ_i is determined by A , C , and the internal structure of C . For the model it is assumed that the predator is not able to discriminate cycloids from the alternative prey:

$$(3 a) \quad \kappa_i = \alpha_i C / (A + \alpha_i C),$$

where α_i gives the proportion of C available for interspecific predation:

$$(3 b) \quad \alpha_i = \sum_{j=1}^i N_j w_j$$

- w_j = relative body weight of an animal of age class j compared to the weight of an adult.

Approximate conditions for coexistence without cannibalism

Without any food limitation cannibalism becomes negligible and the cycloids approach a stable age distribution. The corresponding intrinsic growth rate may be called the potential growth rate r_C of the cycloids. It is fully determined by the parameters chosen for the representative copepod. By integration of (1) under the assumptions of approximate time independence of r_A , r_C , and g , which implies exponential growth of C so that in (1) C can be substituted by $C = C_0 * \exp(r_C t)$, one gets

$$(1') \quad A(t) = \exp \{ r_A \} [gC(t_0) (\exp \{ -(r_A - r_C)t \} - 1) / (r_A - r_C) + A(t_0)].$$

By asking for $A(t) > 0$, two necessary conditions for the coexistence of A and C can be derived. The first is trivial:

$$(4) \quad r_A > r_C;$$

the second is a relation between A and C at the starting point t_0 :

$$(5) \quad A(t_0) > C(t_0)g/(r_A - r_C).$$

Therefore, coexistence of the predacious cyclops and its prey can be expected in the absence of cannibalism only if the potential growth rate of the alternative prey population is higher than that of the cyclopoid copepods, and only if the relative abundance of the alternative prey population is above the value given by (5). The influence of cannibalism around this critical point will be discussed now by a local analysis.

Results and discussion

In unstable natural environments the potential intrinsic growth rates are time dependent. For that reason the approximate conditions (4) and (5) for coexistence are strictly valid only in idealized situations. To demonstrate the essential impact of cannibalism, however, it is useful to look at some isolated dynamic aspects locally. Therefore, r_A is chosen as constant and is slightly greater than r_C ($r_A = 1.25 r_C$) allowing coexistence in principal. The constants r_C and r_A represent the potential growth rates under the local environmental conditions. The actual growth rates of A and C are time dependent even during a period of an unchanging environment; the actual growth rate of the cyclopoids can be smaller or greater than r_C depending on the actual age structure and the magnitude of A.

With this assumption, the alternative of allowing intraspecific predation or of avoiding cannibalism is studied under different starting conditions.

Fig. 1 a and 1 b show the time courses of the *Cyclops* and its prey population. Broken lines are drawn for the case of cannibalism; solid lines give the corresponding population development when the predator does not cannibalize. The starting value of the prey population is 10 % above the critical value. The stable age distribution resulting from the potential growth rate is used as the starting age distribution of the cyclopoids, so that there is an exponential decrease in the abundance with age. As expected, the *Cyclops* population increases faster without cannibalism, and the prey population is less hindered by cannibalizing *Cyclops*. Predator and prey populations can grow in both cases. Of course, they do not grow exponentially to infinity, but for this local analysis it is sufficient to know whether the populations reach the exponential growth.

In Fig. 2 a and 2 b the starting prey density is changed to 10 % below the critical value. In the beginning the non-cannibals do better, but then they consume all the prey and starve without any further reproduction. In contrast, the cannibals do not annihilate the alternative prey. In this instance, cannibalism secures the survival of predator and prey. When the prey density is in the critical region, the actual age distribution may have a dramatic influence. In Fig. 3 and 4 the starting exponential age distribution ($\sim \exp \{ -ba \}$) with $a = \text{age}$) is varied lowering the exponent in

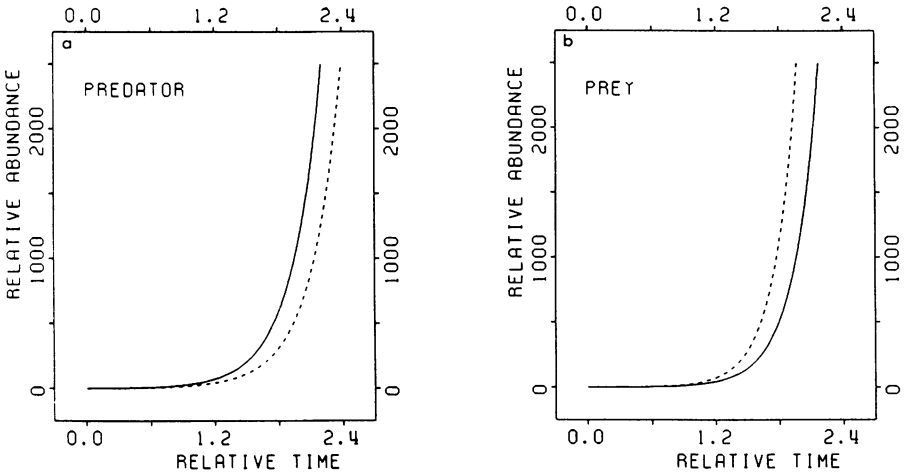


Fig. 1 a, b. Comparisons of the time courses of the relative abundances of predator (a) and prey (b) for cannibalism allowed (broken lines) and with cannibalism not allowed (solid lines). The starting prey population is 10 % above the critical value. One relative time unit corresponds to the development time until maturity.

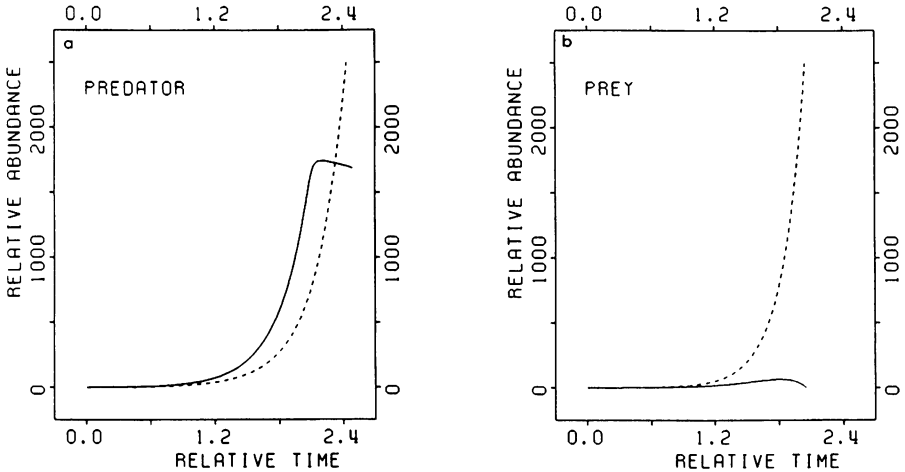


Fig. 2 a, b. Same as Fig. 1 but with a starting prey population density 10 % below the critical value.

steps of 10 % starting with a value for $b = b_5$ that corresponds to the stable age distribution with the potential growth rate. The starting prey population is set 30 % below the critical value. As b decreases (or equivalently the more older animals exist at the beginning), the first increase in the non-cannibals becomes steeper (Fig. 3 a) but the survival time of the prey becomes shorter (Fig. 3 b). As the critical starting prey population is derived for a growing predator population with more

young than old animals, it can easily be shown that, if the age structure of the *Cyclops* is shifted to older animals, the populations are destroyed even at starting prey densities above the critical value.

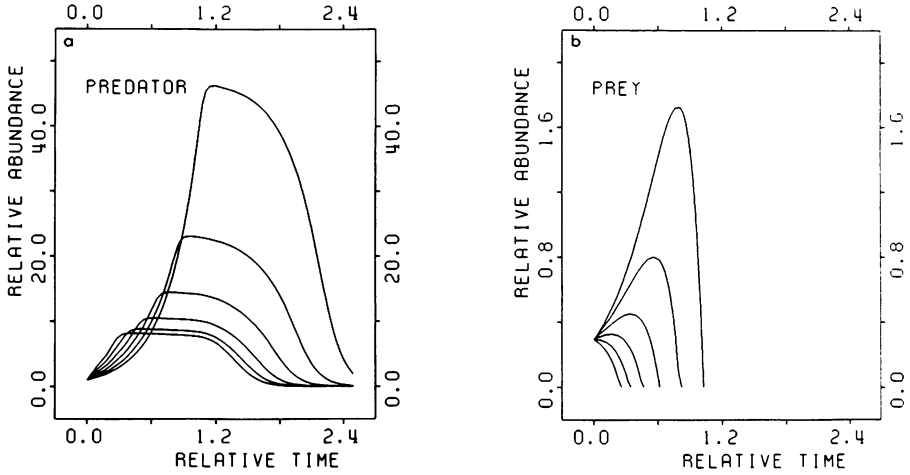


Fig. 3 a, b. Effect of different starting age distributions of the predator in case of avoiding cannibalism. The exponent b of the starting age distribution is lowered in steps of 10 % from $b = b_S$ to $b = 0.5 b_S$. The lines with the higher maximum abundances for both predator and prey belong to the higher b values (which is equivalent to more pronounced young animals in the age structure).

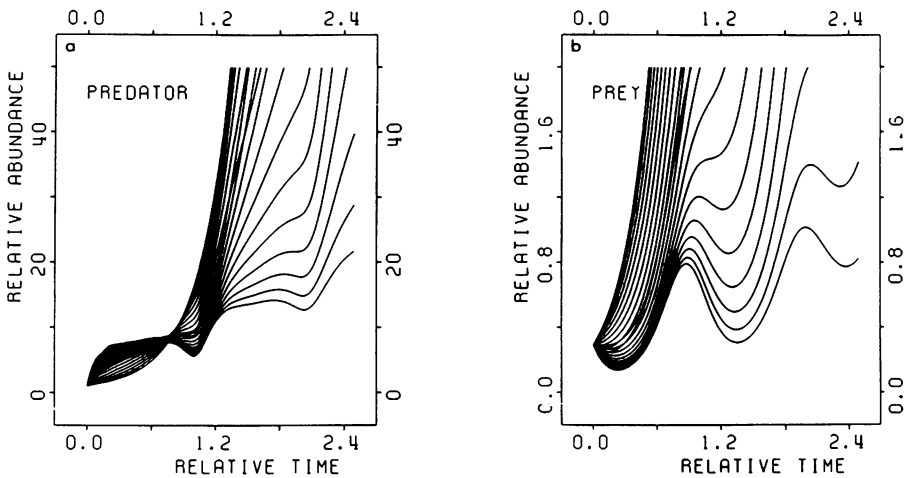


Fig. 4 a, b. Effect of different starting age distributions of the predator in case of cannibalism. The exponent b of the starting age distribution is lowered in steps of 10 % from $b = b_S$ to $b = -b_S$. The lines with the faster increase belong to the higher b values.

In the case of cannibalism the growth of predator (Fig. 4 a) and prey (Fig. 4 b) is retarded, but their coexistence is not imperilled when the starting age distribution is shifted. This is even true for populations with more old than young animals as demonstrated in Fig. 4 where b ranges from $b = b_S$ to $b = -b_S$.

This shows that cannibalism leads to a high robustness in relation to perturbations in the age structure of the predator, whereas the survival of the non-cannibals is highly dependent of the actual age structure.

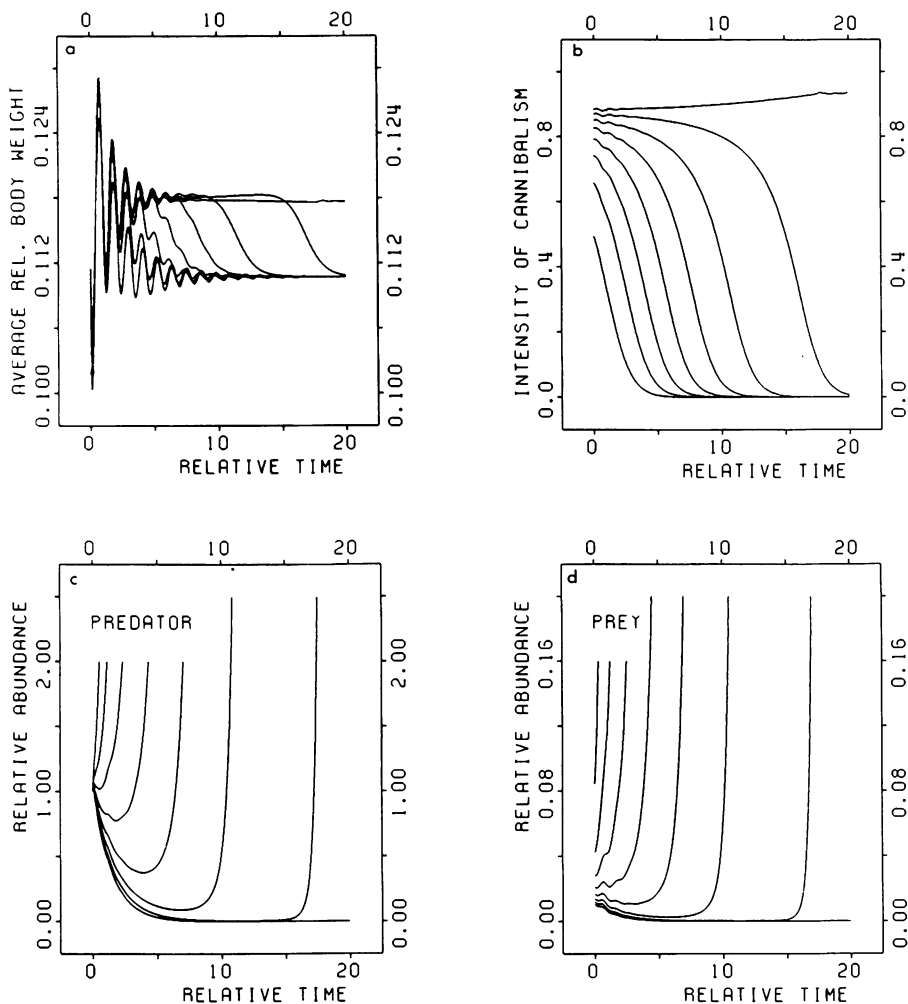


Fig. 5 a, b, c, d. Tolerance to lowering the starting prey density under cannibalism. Effects on the average relative body weight (a), the average intensity of cannibalism (= part of carnivorous food gained by cannibalism) (b), and the population size of predator (c) and prey (d). The starting prey population is 5, 10, 15, 20, 25, 30, 35, and 40 times lower than the critical value. The lower the starting prey density, the later the population approaches to the common limit value (a, b) or increases (c, d).

Another quantity of interest is the minimum prey density necessary for the preservation of the predator-prey system. In Fig. 5 the starting prey population is below the critical value by factors of 5, 10, 15, 20, 25, 30, 35, and 40. Not until the starting prey population is more than 35 times lower than the critical value does cannibalism become unable to compensate for the predation pressure. To demonstrate the dynamics, the time course of the average body weight of the predators (Fig. 5 a), the part of carnivorous food gained by cannibalism (= average intensity of cannibalism) (Fig. 5 b), and the predator (Fig. 5 c) and prey populations (Fig. 5 d) are illustrated. The average body weight (Fig. 5 a) initially oscillates around a value above the equilibrium value corresponding to the stable age distribution. The equilibrium is reached later for lower starting prey populations. The average intensity of cannibalism also converges to zero more slowly for smaller starting prey populations. Only for the prey density starting 40 times below the critical value is the growth of the prey insufficient to reduce the intensity of cannibalism. The time courses of predator (Fig. 5 c) and prey (Fig. 5 d) show how after more or less pronounced and extended reductions in population sizes the whole system grows exponentially, which means for this local analysis that the system recovers from the dangerous situation.

The benefit of cannibalism is demonstrated by the higher resilience of the predator around the critical prey density and, in particular, by the maintenance of coexistence at prey densities much below the critical value. The small disadvantage of cannibalism under good food conditions is likely to be more than compensated for by the advantage during periods of food limitation, so that cannibalism can be expected to be an evolutionarily stable strategy in fluctuating environments. With its self-regulatory and stabilizing capabilities, cannibalism has to be considered a powerful strategy for predators to overcome periods of food limitation. It may be an especially important factor in structuring zooplankton communities.

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