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Can cannibalism be advantageous in cyclopoids? A mathematical model

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With 3 figures in the text

Introduction

Intrazooplankton predation by copepods is considered to greatly influence the species and size composition of a plankton community (CONFER 1971; LANE 1978; BRANDL & FERNANDO 1981). Cyclopoid copepods often change their feeding habits during development. Nauplii and small copepodites are usually herbivorous, but become omnivorous or carnivorous as late copepodites and adults (GRAS 1971; GOPHEN 1977; LANDRY 1981). Cannibalism is frequently observed (FRYER 1957; MCQUEEN 1969; BRANDL & FERNANDO 1979) and may play an important role when cyclopoids are the dominant species or even appear as nearly a monoculture (BURGIS & WALKER 1972; JOHNSON & WALKER 1973). In the absence of alternative prey, carnivorous cyclopoids could utilize nanoplanktonic primary production by consuming their own herbivorous offspring. Thus, when combined with a shift from herbivory to carnivory during copepod development, cannibalism may be advantageous. We used a mathematical model to: (1) study the effect of cannibalism on population dynamics; and (2) assess the level of cannibalism tolerable without population extinction.

The model

In order to be as general as possible, we constructed a representative animal from literature data (BRANDL & FERNANDO 1975; ELGMORK 1959; GOPHEN 1976, 1980; JAMIESON 1980a, b; PEACOCK & SMYLY 1983; SCHOBER 1980; SMYLY 1970, 1973; VIJVERBERG 1977, 1980; WILLIAMSON 1980). To eliminate differences in species and environmental conditions, we used relative units created by: (1) normalizing the weights of the developmental stages with the weight of the adults; and (2) choosing the development time till maturity as a time scale. By use of metabolic parameters and efficiencies, and feeding rates, it was possible to describe the time course of growth for a single animal and to calculate its weight-dependent food intake. We assumed that the carnivorous portion of the total food intake of the copepods increased linearily from 0 (when the cyclopoids had 15% of their final weight) to 1 (in adults). Looking for general properties, we modelled the interaction of the copepods and the effect of external predators not by following individuals but by dividing the whole population arbitrarily into age classes. Thereupon the population dynamics could be described by a set of coupled differential equations. This was done by calculating the relative abundance in each class, using the inflow from the lower age class, the outflow to the higher age class, and the mortality rates caused by natural death, predation, and cannibalism. As cannibalistic copepods prefer smaller prey, we assumed that the prey preference is proportional to the difference in length between predator and prey. The effect of cannibalism on each age class was calculated by a rather complex procedure which accounted for the actual population structure and all relative preferences. A detailed description will be given elsewhere (GABRIEL in prep.).

By dividing the whole population into single age classes, information about the age distribution within each class may be lost, if the population has not established a stable age distribution. Therefore, the number of age classes had to be large enough to insure that the true age structure of the whole population is well-represented. We found that our results were independent of the number of age classes if more than 40 age classes were considered.

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Results and discussion

The aim of this model is to study the effects of cannibalism on the population dynamics of cyclopoid copepods. The qualitative results are independent of the magnitude of the parameters, even if the numerical results are more or less dependent on the choice of the "representative" copepod. Thus, the model allows a qualitative description of the population and leads to the following general statements:

(1) An increase of the strength of cannibalism (defined as the amount of animal food which is gained by cannibalism) dramatically prolongs the time for reaching a stable age distribution (which is equivalent to a constant intrinsic growth rate r). This is demonstrated in Figs. 1 and 2, where the time course of r shows larger amplitudes if the cannibalism is stronger. In further comparisons, we are referring to the terminate value of r (which is nearly identical to the average of one cycle).

(2) If we consider a case without predation pressure by other species and if we increase the strength of cannibalism, then the average growth rate becomes negative at a certain limit. Although the whole population is decreasing, it can survive with animals in all age classes for a longer period. A relatively small further increase in the strength of cannibalism, however, causes the population to go extinct, because the bigger animals consume all smaller ones and the latest survivors are starving adults consuming

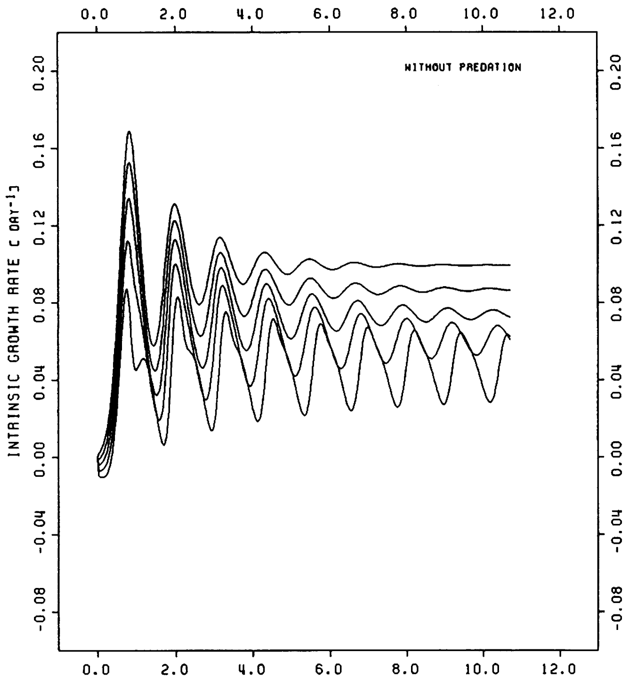

Fig. 1. Time course of the intrinsic growth rate r: Approximation to a constant value (where a stable age distribution is reached) for different intensities of cannibalism. From top to bottom: 0.0; 0.075; 0.15; 0.225; 0.3. One relative time unit is equivalent to the age at maturity.

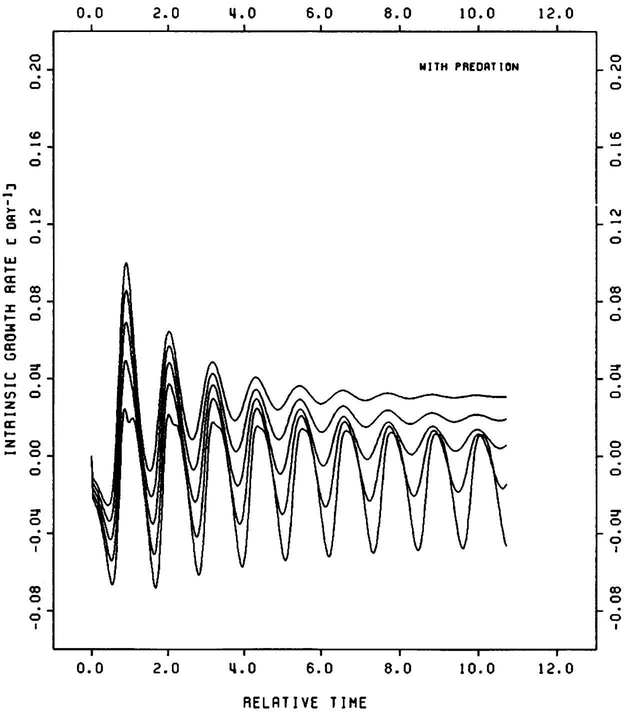

Fig. 2. Same as Fig. 1 with an additional (interspecific) predation pressure on the cyclopoids.

all newborns. The point where the population suddenly vanishes is determined not only by the strength of cannibalism, but also by the initial age distribution which may be important in determining whether extinction occurs at higher or lower levels of cannibalism.

Especially if the population consists of many old animals it may become extinct within a time period relatively short compared to the generation time. If alternative food becomes scarce and cannibalism is an important factor, diapause may be a necessary strategy for survival (Nilssen 1980).

(3) If the cyclopoids themselves are exposed to predation, but the predators are not size-selective, then the qualitative behaviour of the model is not changed with exception of a shift to lower and even negative growth rates.

(4) If the interspecific predators select bigger animals, as in many cases of fish predation, they reduce the number of copepods with the most pronounced cannibalistic behaviour. Intense size-selective predation can prevent a population from destroying itself. The stronger the size-selective predation, the greater the strength of cannibalism which can be tolerated (see crosses in Fig. 3). The predation pressure is assumed to decrease by the square of the animal's length (e. g. if PRE is the mortality rate for the adults, the corresponding rate for the nauplii in the first age class is 0.01 PRE). Therefore, interspecific size-selective predation may enhance survival of the prey.

(5) The potential importance of size-selective predation becomes obvious, if we compare the alternatives: Either the copepods are cannibalistic or the copepods avoid can-

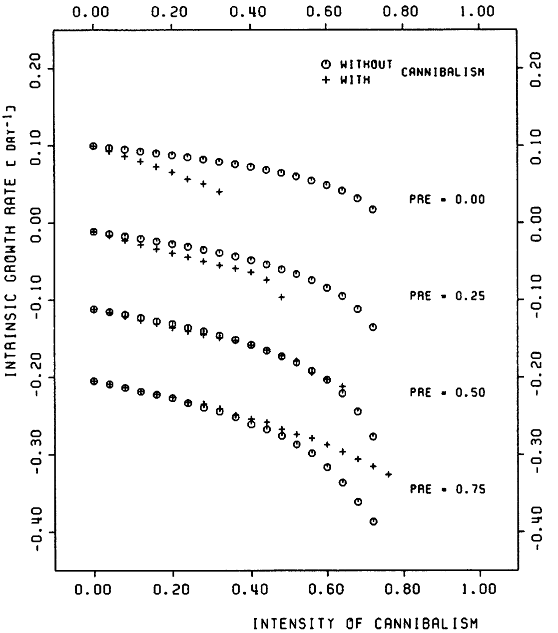

Fig. 3. Comparison of the intrinsic growth rates *r* (after reaching stable age distribution) as it varies with size selective predation (PRE) and intensity of cannibalism (crosses). The open circles give the *r* values in the absence of cannibalism, thereby decreasing the total food intake.

nibalism and hence have a proportionally lower food intake thus prolonging the development time. Fig. 3 demonstrates clearly that the advantage of non-cannibalistic behaviour is reduced if size selective predation increases. At high levels of predation pressure the population density decreases faster without cannibalism.

These results show that cannibalism need not be a disadvantage to a population of cyclopoids. As long as sufficient alternative prey is present the effect of cannibalism is rather small. In this case the costs of selective avoidance of conspecific prey might be greater than the negative effect of cannibalism. Under poor food conditions accompanied by intense size-selective predation, the population may gain some benefit from eating young of its own species.

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