



Zooplankton Competition and Plankton Community Structure

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The equivalent form of Eq. 3 is

$$\frac{d[\log_e N(a)]}{d\left\{\log_e \left[\frac{s_\infty - s(a)}{s_\infty}\right]\right\}} = \frac{m}{k}. \quad (7)$$

Equation 6 gives the correct expression for m/k when $N^*(s)$ represents relative numbers in equal length intervals, while Eq. 7 or 3 could be used if the frequency distribution were based on equal age classes. Of course, if a distribution with equal age classes is available, then Eq. 1 can be used to compute m , and growth information is unnecessary.

Allen (1967) has also distinguished between samples from size distributions and those from age distributions, and he derived expressions equivalent to Eq. 6 and 7. In addition, Allen presented estimation formulae for m when growth in length or weight is exponential. Equation 4 can be used to obtain estimates for m with any size measure, s , and growth curve, $g(s)$, and the assumption of stationarity.

The magnitude of the estimation error for m due to the use of Eq. 3 or 7 rather than 6 depends on the corresponding estimate for k . Smith used an altered form of

Eq. 3 to compute m for 15 populations of calcareous marine organisms. Of these estimates, eight are too low by a factor of at least two when compared with values obtained from Eq. 6.

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Zooplankton competition and plankton community structure

Recent attempts to resolve the significance of zooplankton competition have led to the conclusion that competition for food is trivial in plankton communities (Dodson 1974; Dodson et al. 1976). However, consideration of several assumptions underlying these field studies suggests that they are actually not rigorous tests of such competition.

The size-efficiency hypothesis (Brooks and Dodson 1965) implies that the density of food necessary for existence of small zooplankton species is greater than for larger ones. To test this hypothesis, Dodson et al. (1976) proposed that small species should be found where food is more abundant than where larger species exist. Examining a

series of ponds, they showed that ponds dominated by small species of zooplankton contain food resources similar in quantity and quality to those dominated by larger species. They concluded that competition for food is unimportant in zooplankton communities.

Several assumptions inherent in their approach may bias the interpretation of the results. First, their test of the size-efficiency hypothesis requires that food in ponds with large species be somewhere near the threshold for their existence. If it is not, then a lower food supply in ponds with small species does not vitiate the hypothesis. Second, as MacArthur (1972) pointed out, strong competition may be a rare phenomenon,

operating infrequently but severely enough to influence species composition in the interim. Pooling data as Dodson et al. have done may hide such instances. Indeed, in different years Sprules (1972) and Dodson (1974) obtained opposite results in the same pond when they enclosed a small daphnid with a larger congener.

Absolute abundance (standing crop) of resources is not sufficient to describe the available food supply. MacArthur (1972), Schoener (1974), and May (1975) emphasized the importance of weighting-terms, $K(j)w(j)/r(j)$, for resource items. For resource j , $K(j)$ expresses its carrying capacity, $w(j)$ its value to the consumer, and $r(j)$ its intrinsic rate of increase. While the precise formulation of these terms is debatable, the magnitudes of the components reflect the relative importance of different food items in competitive interactions. Weighting-terms are critical to field studies of competition, but they are generally ignored because the data are difficult to obtain. This predicament imposes the assumption that weighting-terms are equivalent for all food items—an assumption clearly untenable for phytoplankton species that have highly variable growth kinetics and antipredatory adaptations. However, the possibility of considering these terms is now perhaps most feasible in plankton communities, especially with the refinement of track autoradiographic techniques by Knoechel and Kalff (1976).

Sprules (1972) and Dodson (1974) tested for competition by enclosing paired species in containers with suitable mesh to allow passage of food particles. These experiments have additional problems. Where other herbivores are present in the enclosed water, the food supply entering and maintained in the enclosures may be a function of more than the paired species. Indeed, Neill (1974) pointed out that competition between two species can be modified by the presence of a third. In addition, the densities at which competition is expressed in such cases would depend on the flow rate of the food.

There is no doubt that predation plays a dominant role in maintaining plankton community structure (Hrbáček 1962; Brooks and Dodson 1965). The consequences of zooplankton competition are less clear. The mechanism of resource-based competition is an alteration in the quality or quantity of food supply (or both). In general, the outcome is reduced abundance of competitors. Recent research indicates that there is a threshold density for *Daphnia* below which blue-green algae may form colonies large enough to escape predation (Lynch unpublished). In this sense, competition between zooplankton species may have important consequences for phytoplankton community structure.

Although recent work (Dodson 1974; Neill 1975) casts doubt on the universality of the size-efficiency hypothesis, it does not mean that competition is unimportant in maintaining zooplankton communities. Measuring competition is difficult and has plagued ecologists for years. Insight may be gained by studying resource partitioning by consumers and the nature of the food supply. However, the relevance of resource depression is in its effects on population processes and community dynamics. Thus, a knowledge of the relation of resource-based competition to population phenomena is central to the problem, and the intervening mechanisms must be defined. Neill (1975) used this approach for laboratory microcosms, but it must be expanded to the field.

Several questions must be answered before the significance of zooplankton competition can be generalized. When and how often do food levels decline to the extent that competition becomes important? To what extent do age-specific characteristics dictate competitive interactions? How does competition among consumers affect the community structure of primary producers?

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Predicting the future with lakes and rivers: A note on the *Awda Negast*

The *Awda Negast* is an Ethiopian book of fortune telling. The Italian scholar, Conti Rossini (1941), published a description of two manuscript versions of it, together with a portion of one of them (in Ethiopic, or Ge'ez) and a partial Italian translation in 1941. From internal evidence he concluded that it was probably written in the 15th century. More recently an Ethiopian scholar, the late Zemenfes-Kedus Abraha, published an Amharic version along with a variety of other magical and religious material (Abraha 1958). Otherwise the book probably exists only in manuscript and seems to be little known outside Ethiopia.

The words "Awda Negast" mean "Circle of the Kings." According to Conti Rossini the book is also referred to in Eritrea as *Metsehaf Bahr* which means roughly "Book of the Seas." The word "Bahr" can be applied to any fair-sized body of fresh or salt water, or even to a river.

The main part of the book is a series of 16 circular diagrams. Figure 1 is a rendering

of the first of these, partly translated, based on Abraha's version; Conti Rossini's is very similar. The figure consists of five concentric circles, with 16 equally spaced lines running from the rim of the next-to-innermost circle to the rim of the outermost. The lines are red and black in the original; the two colors are badly out of register in my copy of the book.

In the outermost 16 of the sections thus formed are written, clockwise from the top, the first 16 characters of the Ethiopian syllabary (seven vocalizations of "H," seven of "L," and two of a second form of "H"). These are printed in red in the original. In the next ring of 16 sections are the figures representing 1 to 16, also running clockwise from the top, printed in black in the original except for the figure "1," which is in red.

In the following chart (not shown), the outer positions are occupied by the 17th to 32nd characters, and so on. Since however there are only 202 characters the last positions are occupied by numbers (1-20;