

## Size specific mortality rates in zooplankton populations

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With 3 figures in the text

### Introduction

As a result of the application of experimental field techniques to lake plankton communities, the theory of zooplankton community structure has been developing at a rapid pace (KERFOOT 1980). Yet the existing theory is still based on several unevaluated assumptions, the most important of which involves the size-specificity of mortality experienced by zooplankton living in environments containing different predators. The literature is replete with explicit and implicit statements that zooplankton inhabiting lakes which contain vertebrate predators should experience increasing mortality as they get larger, whereas in the absence of vertebrates mortality is expected to decline monotonically with increasing size (ALLAN 1974; DODSON 1974; KERFOOT 1975; ZARET 1975, 1978; HALL et al. 1976; LYNCH 1977, 1979, 1980). These conclusions are drawn from numerous, consistent observations that vertebrate planktivores selectively prey on large-bodied prey (WERNER & HALL 1975; O'BRIEN et al. 1976), while invertebrates (which are the dominant predators in the absence of vertebrates) prefer small ones (FEDORENKO 1975; KERFOOT 1975), and from the apparent additional assumption that invertebrate predators which do coexist with vertebrates are of negligible importance compared to the latter.

However, knowing the size-specificity of any one, or even all, mortality sources does not provide any information on the pattern of size-specific mortality experienced by a zooplankton unless the relative importance of all mortality sources is known. Since this has never been established, and since zooplankton are not amenable to standard mark-and-recapture techniques, patterns of size-specific mortality have actually never been measured for natural zooplankton populations.

It now appears that the careful application of a sequential sampling technique can provide this information (LYNCH in prep.). Here we present the patterns of size-specific mortality which we have determined to be falling on a community of three coexisting cladocerans (*Bosmina longirostris*, *Ceriodaphnia lacustris*, and *Diaphanosoma leuchtenbergianum*). These preliminary results strongly suggest that our preconceived notions concerning the mechanistic bases for zooplankton community structure warrant a close reexamination.

### Methods

The sequential sampling technique is described in detail in LYNCH (in prep.). Its application requires an accurate description of the size-abundance distribution of the population on two closely spaced dates (generally about an instar's duration) and of the size-specific growth and reproductive rates. This information allows the estimation of flux rates of individuals into and out of different size classes and, thus, the expected size distribution of the population on the second sampling date had no mortality occurred over the experimental period. A comparison of these predicted numbers with the actual size-abundance distribution is the basis for determining the size-specific mortality rates.

Our study site, Dynamite Lake, Illinois, provides an ideal setting for examining the relative importance of vertebrate and invertebrate predators as mortality sources. This shallow (2 m mean depth), quarry lake contains dense schools of planktivorous bluegill sunfish (*Lepomis macrochirus*) as well as predatory copepods (*Mesocyclops edax*) and

rotifers (*Asplanchna priodonta*). On four occasions (25–27 June, 9–11 July, 23–25 July, 6–9 August 1979) we attempted to partition the impact of fish predation from other mortality sources by excluding fish from triplicate 1 m<sup>2</sup> polyethylene enclosures. These cylinders were open at the surface and the weighted bottoms, which were covered with 0.5 cm mesh, were firmly embedded in the sediments. Unfortunately, as the bags were extended to the bottom of the lake most of the predaceous copepods were able to avoid being captured; the *Asplanchna* were not. Our technique improved with time, however, so that the proportion of the adult *Mesocyclops* excluded from the enclosures in the four experiments was 1.00, 0.95, 0.60 and 0.43, respectively. The effect of the enclosures, then, was to remove all vertebrate predation and a substantial proportion of the invertebrate predation.

The size-abundance distributions were determined by measuring to the nearest 0.01 mm a minimum of 200 individuals from 15 pooled vertical haul samples. Growth rates of *Ceriodaphnia* and *Diaphanosoma* were determined for each experiment in the laboratory by isolating fifty individuals of a range of sizes in lake water at the appropriate temperature and measuring their increment in growth over the experimental period. Such a procedure was not possible for *Bosmina* which generally became caught in the surface tension; instead its size-frequency distributions were analysed in detail to determine average instar-specific body sizes, the duration of instars being calculated from the equation of KERFOOT & PETERSON (1979). Second order polynomial regressions for size on day *t* vs. size on day 0 were used to describe the growth functions.

Size-specific clutch sizes were generally means of 30–50 measures for each size class. Egg development times for *Ceriodaphnia* were calculated from KWIK & CARTER (1975), while those for *Diaphanosoma* were estimated by the averages for *Bosmina* and *Ceriodaphnia*. Recruits including newborns, for all size classes were corrected for the mortality which they were expected to incur before entering the size class for which mortality rates were being estimated.

Since errors in the estimates of total population density on either sampling date can lead to general underestimates or inflated mortality rates during an experiment, we have standardized the mortality estimates for each date by converting them to minimal expected values. For each experiment, a constant was added to (or subtracted from) all of the mean enclosure mortality estimates so that the minimum rate for that date equaled zero. Then since mortality in the lake should equal or exceed that in the bags, the lake mortality functions for each date were standardized by adding (or subtracting) a constant to (from) all of the direct estimates of lake mortality so that they were all just equal to or greater than the standardized enclosure values for that date. Note that the shapes of the mortality functions, with which we are most concerned, are not altered by this procedure.

## Results

Since the results for all four experiments were quite similar, we simply present the average mortality rates fitted with polynomial regressions in Fig. 1. The size-specific mortality functions for the lake *Bosmina* were U-shaped on all four occasions with minimal mortality occurring in either the 0.25–0.30 or the 0.30–0.35 mm size class. Excluding fish had very little impact on the mortality rates of the large *Bosmina*, but mortality was substantially reduced in the smallest size class in the enclosures on all dates.

Except for the first experiment when mortality decreased monotonically with size, the size-specific patterns of mortality for the lake *Ceriodaphnia* were also U-shaped with highest survivorship in the 0.3–0.4 mm size class. The enclosed *Ceriodaphnia* exhibited an increase in mortality with size in the largest size classes on all four dates, but mean survival in the smallest size class was substantially improved relative to that in the lake.

*Diaphanosoma* exhibited a U-shaped mortality pattern in the lake on 3 of 4 dates, but the average size of minimum mortality (0.5–0.6 mm) was higher and the

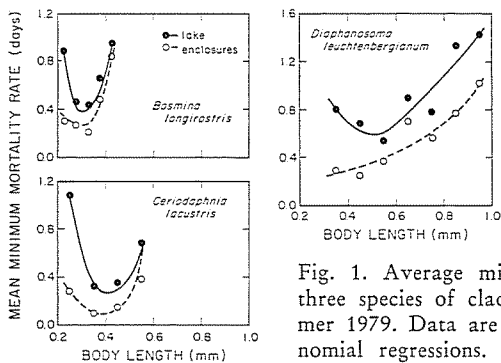


Fig. 1. Average minimum instantaneous mortality rates for three species of cladocerans in Dynamite Lake, Illinois, summer 1979. Data are fitted with second and third order polynomial regressions. Solid points and lines are for the lake; open points and dashed lines are for enclosures which excluded all fish and most cyclopoid copepods.

relative importance of early instar mortality lower than in the smaller species. The reduction in mortality for the enclosed *Diaphanosoma* was greatest in the extreme size classes, but as with the smaller species, mortality increased with size in the larger instars despite the absence of fish.

These results do not appear to be artifacts of the experimental technique. The two problems which would be most likely to yield inaccurate mortality estimates can be ruled out. First, errors in the mortality estimates could result from incorrect determinations of the flux rates of individuals between size classes. We tested for this by comparing the size-specific patterns of mortality for *Ceriodaphnia* estimated using the laboratory growth rate functions with those determined by an analysis of instar sizes as for *Bosmina*; in all four cases the two predicted patterns were nearly identical. Second, differential movement of size classes into or out of our sampling area could lead to either underestimates or overestimates of mortality in certain size classes. The consistent shape of the estimated mortality functions between dates argues against this as a general problem, since it would require a consistent movement of specific size classes with respect to our sampling site on all dates, which seems highly unlikely for a shallow well-mixed lake.

## Discussion

Contemporary zooplankton theory would have us expect to find patterns of size-specific mortality in Dynamite Lake which increase monotonically with size. Yet we find that mortality in the smallest size classes of *Bosmina* and *Ceriodaphnia* generally equals or exceeds that in their largest instars. An examination of the relation between *Mesocyclops* density and the death rates of the smallest size class of the three species in both the lake and enclosures during the four experiments suggests that early instar mortality is largely a consequence of copepod predation. Excluding one data point for *Ceriodaphnia* (a very high value of  $m$  which fell on a day when *Asplanchna* was exceptionally abundant), this relationship is highly significant for both *Bosmina* and *Ceriodaphnia* ( $P < 0.005$ ), accounting for 93% and 82% of the variation in mortality. For *Diaphanosoma* which exhibits only a slight tendency for mortality to increase in the smallest size classes, the regression is not significant ( $r^2 = 0.02$ ).

If we ignore the one or two smallest size classes for these species we do find a general increase in mortality with size in the presence of fish as expected. Yet the mechanism appears to be inconsistent with the theory since similar increases occurred even in the absence of fish. Although the bluegill sunfish in this lake prey intensively and size-selectively on all three cladocerans (Fig. 2), we are left with the impression that their predation is of minor importance relative to other mortality sources.

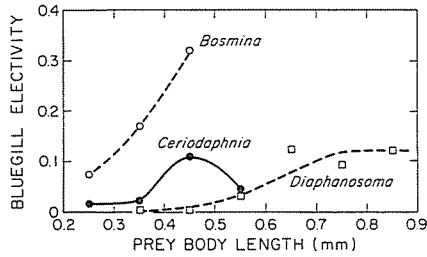


Fig. 2. Size-specific patterns of preference for bluegill sunfish feeding on the three species of cladocerans in Dynamite Lake, averaged for 25 July and 9 Aug. 1979 (after CHESON 1978). The entire stomach contents of three fish were analysed on each date. All three species are standardized with respect to each other, i. e. *Bosmina* is highly preferred over similar size classes of the other species.

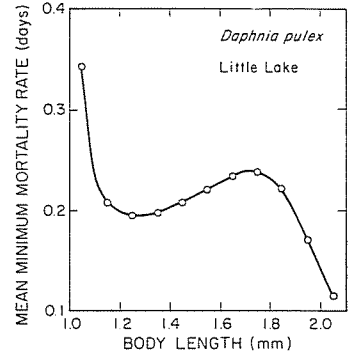


Fig. 3. Average minimum instantaneous mortality rates for *Daphnia pulex* in Little Lake, 1978 and 1979. This lake contains planktivorous fish. Curve fitted by eye.

Clearly, one could argue that size-selective predation by vertebrates is only perceived as an important mortality source by zooplankton which are not already adapted to living in the presence of fish as the Dynamite Lake community must be. Perhaps the pattern of increasing mortality with size expected to result from fish predation is only of major importance when much larger zooplankton are exposed to fish. Direct size-selective predation would then still be supported as the mechanism causing the shift of zooplankton communities to small species so often observed when fish are introduced to previously fishless lakes (BROOKS & DODSON 1965; GALBRAITH 1967; NILSSON & PEJLER 1973; LYNCH 1979).

Yet the results obtained in another lake containing fish (bluegill sunfish and smallmouth bass) and a large cladoceran species (*Daphnia pulex*) suggest that this may not even be the general case. The cladoceran community in this lake shifts to a smaller species (*Ceriodaphnia reticulata*) in mid-summer each year giving the impression that it is a consequence of size-selective predation by fish. However, of seven size-specific mortality functions measured for this *Daphnia* population over a period of two years, only one exhibited a general increase in mortality with size. Although the average pattern of mortality is complex, it clearly does not increase monotonically with size, and actually decreases in the largest size classes (Fig. 3).

In toto these results are in striking contrast to the widely accepted paradigm that direct size-selective predation by fish is the primary factor influencing lake zooplankton community structure. An alternative hypothesis is that secondary effects of planktivorous fish are of equal or greater significance in structuring zooplankton communities. For instance, by modifying the grazing community, the consumptive activity of fish generally results in a dramatic shift in the phytoplankton community relative to that found in the absence of fish, frequently in an increased dominance of blue-green algae (HRBÁČEK 1962; LOSOS & HETEŠA 1973; LYNCH & SHAPIRO 1981). Such changes may affect the survival of some zooplankton much more significantly than others (NEILL 1975; GLIWICZ 1977; LYNCH 1978). The presence of fish also generally results in a shift in the invertebrate predators from large species to much higher densities of smaller species (POPE & CARTER 1975; LYNCH 1979). Although the smaller invertebrates have lower individual predation rates and are incapable of handling prey as large as the larger invertebrate predators can (BRANDL & FERNANDO 1975; KERFOOT 1977; LI & LI 1979), we do not know how the total impact of such different populations compares. Until these secondary consequences of fish predation have been examined in more detail, the mechanistic relation between fish and zooplankton community structure will remain unresolved.

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