
LETTER TO THE EDITOR

Does exploitative or interference competition from *Daphnia* limit the abundance of *Keratella* in Loch Leven? A reassessment of May and Jones (1989)

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Introduction

May and Jones (1989) presented an interesting, 5 year data set from Loch Leven, Scotland clearly showing that the rotifer *Keratella cochlearis* was abundant only during times when *Daphnia hyalina* var. *lacustris* was rare or absent. Such an inverse relationship between rotifer and *Daphnia* abundances can be found in many descriptive and experimental studies of natural plankton communities, and suggests that the rotifers are being suppressed by the *Daphnia* through exploitative competition, mechanical interference competition (damage or ingestion), or both (see review, Gilbert, 1988a). May and Jones assessed the importance of these two types of competition from the population dynamics of the *Keratella* and *Daphnia*, the availability of phytoplankton (chlorophyll *a*) and predictions of the ability of *Daphnia* to kill *Keratella* using Burns and Gilbert's (1986a) laboratory-derived relationships. However, we believe that their analysis and interpretation of the data must be re-evaluated and that the evidence available contradicts their main conclusion: that the *Keratella* were being suppressed only by exploitative and not interference competition from *Daphnia*. Instead, our analyses of their data provide little or no evidence for *Daphnia* limiting *Keratella* abundance through exploitative competition but some evidence for it through interference. Our arguments are organized into discussions of interference competition and then exploitative competition. While we focus on the paper by May and Jones, many of the problems we describe, particularly those involving rate data, are common in the ecological literature.

Interference competition

May and Jones evaluated the importance of *Daphnia* interference by visually comparing temporal patterns of natural death rates of *Keratella* (d_n) with predicted death rates of *Keratella* attributable to *Daphnia* interference (d_D), estimated from Burns and Gilbert (1986a). The primary argument of May and

Jones against the importance of interference was based on the clear discrepancy between natural- and *Daphnia*-induced death rates. A number of factors appear to contribute to this discrepancy, leading us to question their analysis. First, we found that the *Keratella* d_n values presented in the upper panel of Figure 3a–d in May and Jones (1989) were incorrect for the years 1978–81.

Second, the calculation of d_n ($d_n = b - r$) relies on population density estimates necessary for the determination of population growth rates (r) (see Edmondson, 1977). Many of May and Jones' calculated values for r and d_n are based upon increases or decreases in small populations of *K.cochlearis* (their Figure 5). Since these calculations are sensitive to minor, absolute changes in the sizes of small but not large populations, the d_n values should be limited to periods when *Keratella* was relatively abundant. For example, a decline in population size from 5000 to 500 ind.l⁻¹ results in the same death rate as a decline from 50 to 5 ind.l⁻¹ over the same time interval, assuming a constant birth rate. Therefore, we feel it is advisable to disregard d_n values for months when *Keratella* population estimates were low (generally from December to March) and perhaps strongly affected by within-sample (date) variation. May and Jones provided no details on sampling replication or variability.

Third, comparisons of d_n and d_D values for *Keratella* should also be restricted to periods when *Daphnia* was abundant. *Keratella* population dynamics and natural death rates can be affected by many factors (e.g. predators, parasites and food quality) in the absence of *Daphnia*. Since these factors could impose substantial death rates on *Keratella* while *Daphnia*-induced death rates would be low or zero, the two death rates could bear little resemblance to one another during periods when *Daphnia* was rare. May and Jones stated that there was no correlation between the d_n and d_D values for *Keratella*, but they did not mention the times of year when such comparisons were made or provide statistical analyses.

Fourth, the correlation between d_n and d_D values is necessarily weakened by the manner in which each is estimated. The former value represents a daily death rate integrated over a sampling interval (usually 1 week), while the latter is a *Daphnia*-based discrete value that overlaps with d_n for only the first day of the sampling interval. The correspondence between the two death rates should improve as the interval over which d_n is estimated is reduced, because the possibility of the d_n of *Keratella* being confounded by other biotic or abiotic factors would likewise be reduced.

We chose not to correlate the d_n values we calculated from their data (not shown) with predicted *Daphnia*-induced death rates for two reasons. First, the time periods when predicted *Daphnia*-induced death rates are high correspond with periods when *Keratella* densities are low (Figure 1) and hence when estimates of *Keratella* natural death rates are problematical (see above). Second, many natural death rate values (both ours and those of May and Jones) are negative [e.g. see Figure 3, May and Jones (1989)]. Negative death rates are physically impossible; they represent limitations of the egg-ratio method (Edmondson, 1977) and imprecision in estimating population densities. They may occur if either the birth rate is underestimated or the population growth rate

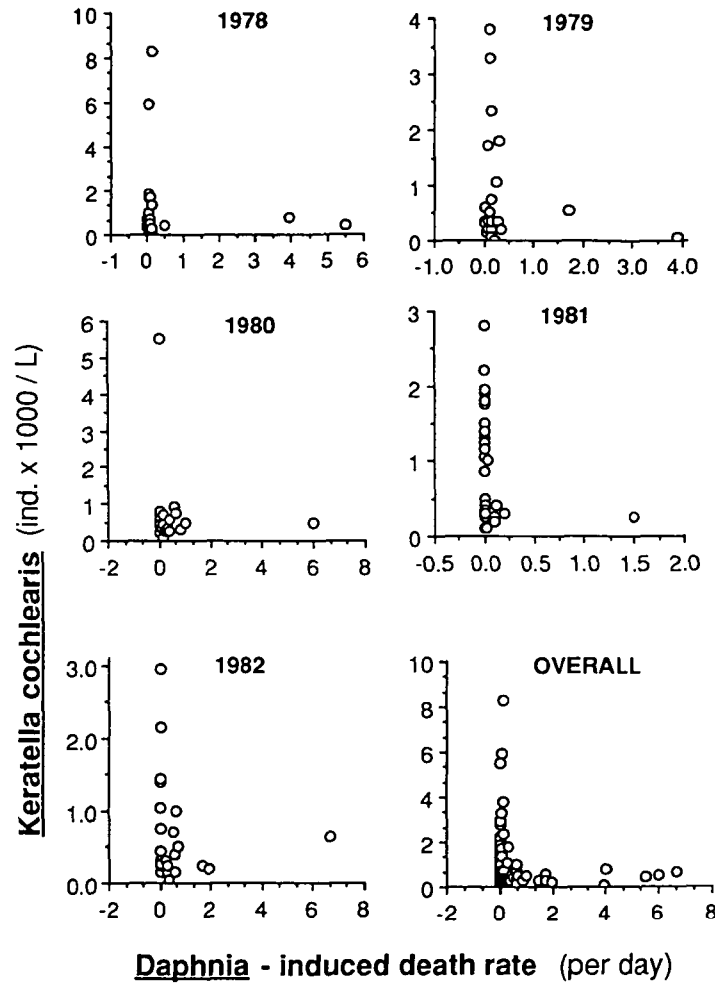


Fig. 1. Total *K. cochlearis* density in relation to *Daphnia*-induced *Keratella* death rate (d_D) for 5 years in Loch Leven, Scotland. Data were estimated from magnified figures in May and Jones (1989; Figure 5 for total *Keratella* densities—not Figure 1, in which densities of the *typica* form appear to be mislabelled as those of total *Keratella*). Only data with estimated *Keratella* densities ≥ 100 ind.l⁻¹ were used. See May and Jones (1989) for sampling and death-rate calculation procedures.

is overestimated. The prevalence of negative d_n calculations (30.2% of non-zero 1978–82 values) illustrates that this problem is common.

Because of the aforementioned concerns regarding d_n values, we compared *Keratella* abundance with *Keratella* d_D values for each of the 5 years (Figure 1). *Keratella* abundance was always low when predicted mortality from *Daphnia* interference was high and high only when the predicted mortality was low. We believe that these relationships are consistent with the hypothesis that *Daphnia* interference is important in suppressing *Keratella*. *Keratella* abundance need not

be high when predicted *Daphnia* interference is low (e.g. 1976 and 1981; Figure 1), because it may be affected by various abiotic and biotic (predation, parasitism) factors. For example, *Keratella* density in Loch Leven appears to be sensitive to water temperature (May, 1983).

May and Jones discounted the significance of *Daphnia* interference in Loch Leven without providing an explanation for why it might not be expected to occur. There is no question that *K.cochlearis* can be swept into *Daphnia*'s branchial chamber and that such encounters can lead to damage or ingestion and high mortality rates (Gilbert and Stemberger, 1985; Burns and Gilbert, 1986a,b; Stemberger and Gilbert, 1987; Gilbert, 1988b). While it is difficult to partition the importance of interference and exploitative competition from *Daphnia* using circumstantial field evidence, there is some direct evidence that the addition of *Daphnia* to a natural community suppresses *K.cochlearis* through interference (Gilbert, 1989). In addition, laboratory studies have permitted us to partition the effects of exploitative and interference competition in the suppression of *K.cochlearis* by *Daphnia*; interference competition was the predominant suppressive mechanism when *Daphnia* was of a body size (1.6–2.0 mm) and density (5–20 ind.l⁻¹) found in Loch Leven (MacIsaac, 1990).

Exploitative competition

May and Jones concluded that the inverse relationship between *Keratella* and *Daphnia* was due primarily to exploitative competition from *Daphnia*. To support this conclusion, they stated that *Keratella* birth rates (*b*) and chlorophyll *a* concentrations were low when *Daphnia* filtration rates were high. We believe that their data do not support these statements. First, the evidence for an inverse relationship between *Keratella* *b* values and *Daphnia* filtration rates is lacking. May and Jones provided no statistical analysis of the data, and visual inspection of the (discontinuous) data points (rather than the continuous points as plotted) in their Figure 4 reveals no obvious pattern. More importantly, if *Daphnia* feeding reduced chlorophyll *a* concentrations and *Keratella* *b* values in consequence, then there should be a positive correlation between chlorophyll *a* concentrations and *Keratella* birth rates. Although May and Jones did not look for such a correlation, we used their data to test for one (Figure 2). In only 1 of the 5 years (1980) was there evidence of a significant correlation ($r = 0.471$, $P = 0.032$) between chlorophyll *a* concentrations and *Keratella* *b* values. At any rate, uncorrected chlorophyll *a* concentrations may not reflect the food available to *Keratella*, since the pigment could be present in dead or living algal matter and in non-ingestible phytoplankton taxa. *Keratella* birth rates may be correlated with the abundance of specific algal groups, but data on the abundance of specific phytoplankton taxa were not provided.

Summary

While *Daphnia* can suppress *Keratella* and other rotifers through exploitative competition (Neill, 1984; Gilbert, 1985, 1988a,b; MacIsaac and Gilbert, 1989), we do not think that May and Jones have demonstrated this in Loch Leven. We

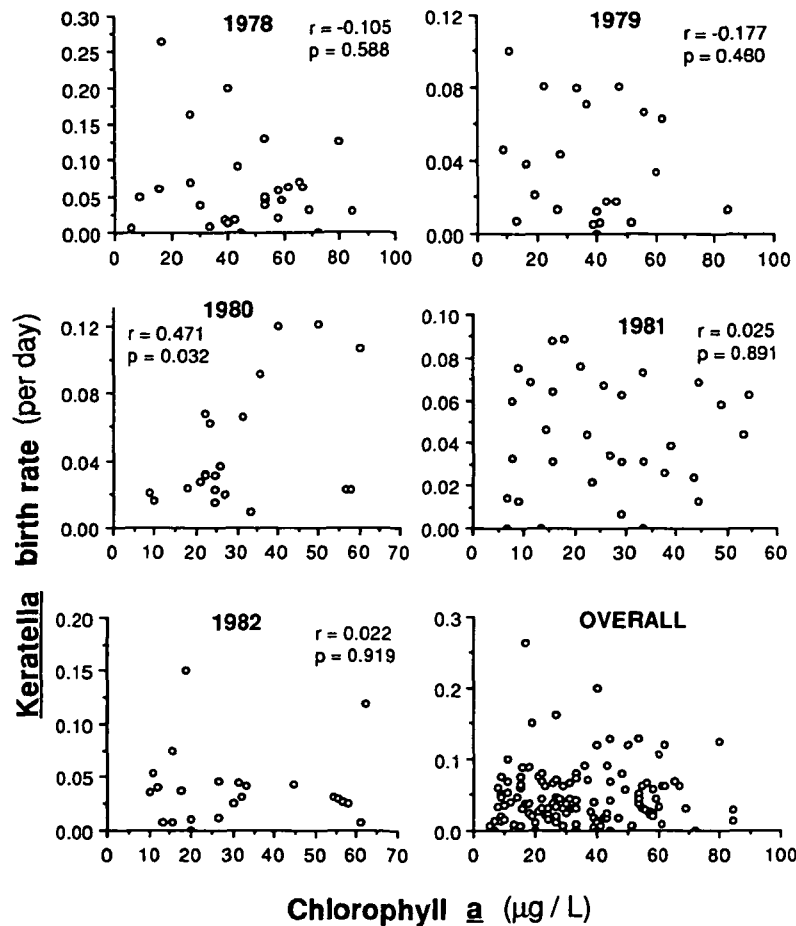


Fig. 2. Product-moment correlation coefficients relating *Keratella* birth rates to chlorophyll *a* concentrations for 5 years in Loch Leven. Data were estimated from magnified figures (4 and 5) in May and Jones (1989). Analyses were restricted to times when *Keratella* densities were $>100 \text{ ind. l}^{-1}$. Two outlying data pairs (birth rate, chlorophyll *a*: 1.1, 42.2; 0.2, 350) were excluded from the statistical analysis for 1979; inclusion of these data points did not affect the statistical outcome.

believe that *Daphnia* suppresses many rotifers through both exploitative and interference competition (Gilbert, 1988a) and have determined the relative importance of these mechanisms in laboratory experiments with several cladocerans and *K. cochlearis* (MacIsaac, 1990). The relative importance of indirect and direct competition from *Daphnia* in natural rotifer communities should vary with a number of factors: (i) the vulnerability of the rotifer species to interference (Gilbert, 1988a,b, 1989); (ii) the availability of food and the numerical response of the rotifer species (Gilbert, 1988a,b); (iii) the density and size distribution of the *Daphnia* (Burns and Gilbert, 1986a; Gilbert and MacIsaac, 1989); (iv) the temperature; and (v) the amount of spatial overlap between the taxa in the water column (Gilbert, 1988a). Vertical migrations by

Daphnia could decrease this overlap and, hence, the severity of both interference and exploitative competition (MacIsaac, 1990). The degree of spatial overlap between rotifers and *Daphnia* in Loch Leven is unknown because the collections were integrated vertical tows (*Daphnia*) or tube samples (*Keratella*).

Finally, it is worth noting that the ability of *Daphnia* to interfere with *Keratella* can increase when food is limited (Burns and Gilbert, 1986b). Thus, there may be an interaction between exploitative and interference competition, in which the former potentiates the latter.

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