BODY SIZE, FOOD AVAILABILITY AND SEASONAL ROTIFER COMMUNITY STRUCTURE IN DEER LAKE, BRITISH COLUMBIA

by

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ABSTRACT

The differential effects of body size on species' demographic parameters has long been hypothesized to be a powerful structuring force in zooplankton communities. The size-efficiency hypothesis predicts that large species, due to metabolic efficiency and greater effectiveness of food collection, should displace small species when food is limiting, in the absence of predation. According to the threshold-food concentration hypothesis, small-bodied rotifers achieve $r=0$ at a lower food concentration than large rotifers; however, large rotifers have higher maximal reproductive rates. I attempted (1) to assess the importance of food concentration in structuring the species and size composition of a natural rotifer community in Deer Lake, Burnaby B.C., and (2) describe seasonal changes in rotifer community structure with reference to temperature, competition and predation.

The threshold food hypothesis relates specifically to rotifers, and its significance has been tested in published laboratory studies. Therefore, I predicted that the y-intercepts of regression equations relating food concentration (measured as size-fractioned chlorophyll a) and reproductive output would be higher for small species than for large ones, and that the slopes of these lines would be higher for large species than for small ones. I found no patterns with respect to body size in either of these two parameters; however, I found some evidence for size-efficiency within a single species, *Keratella cochlearis*. The large form of *K. cochlearis* reproduced at a significantly lower food concentration than either of the two smaller forms. Average rotifer body size of the whole community showed no change with chlorophyll concentration. Recent research which suggests that threshold food levels change along several environmental gradients may explain the lack of support my data provided for the threshold-food hypothesis. Additionally, selective grazing may change the food requirements needed for reproduction of various species.

Temperature was important in determining seasonal species abundance, likely because of physiological responses of development rate to temperature. I did not find that species with high loadings on those principal components axes that were significantly correlated with *Daphnia* or cyclopoid copepod abundance had attributes which conferred resistance to interference competition or predation. However, spined, small *Keratella cochlearis* co-occured seasonally with predatory cyclopoid copepods. Although competition and predation may not have been measured adequately, or at a scale relevant to rotifer survival and reproduction, it appears that temperature is the most important factor I measured in organizing rotifer species into communities in Deer Lake.

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CHAPTER 1: GENERAL INTRODUCTION

Importance of Rotifera

Traditionally, studies of the planktonic communities of lakes have focused
heavily on the Crustacea; rotifers are an often overlooked component of
freshwater zooplankton communities. In some situations this group of small
metazoans may contribute over 75% of the total zooplankton biomass (Pace and
Orcutt 1981), and perform major roles in nutrient cycling and energy transfer
(Makarewicz and Likens 1979). The grazing rate of rotifers often contributes a
substantial amount to the overall community grazing; although small
crustaceans usually have higher clearance rates than rotifers, rotifers can exert
greater grazing pressure on phytoplankton than some small cladocerans
(Bogdan and Gilbert 1984). Expanding our concept of planktonic systems to
include rotifers may allow us to better understand the factors determining
community structure of freshwater zooplankton.

Life-history

All zooplankters are faced with the problem of allocating resources among
the conflicting demands of predator avoidance, competitive ability, and
maximizing the potential for rapid increase. Relative to most other groups,
rotifers are classic "r selected", opportunistic species with high intrinsic rates of
increase, compensating for small clutch sizes through short development time

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(Allan 1976). Among the dominant taxonomic groups of metazoan zooplankton, rotifers have the shortest life span, with a high intrinsic rate of population increase. As a result of this high reproductive potential, rotifers can become extremely abundant, particularly under eutrophic conditions, and can reach densities upwards of 5,000 individuals per liter (Wallace and Snell 1991).

Reproduction in the Monogonota, to which most planktonic rotifers belong, is primarily asexual. The reproductive strategy of these rotifers allows for rapid population growth through many generations of female parthenogensis. These diploid amictic females produce diploid eggs, which hatch into amictic females. Rotifers develop from egg to reproductive adult over the course of several days, and their population dynamics should therefore rapidly respond to increases and decreases in phytoplankton concentration.

Spatial and seasonal distribution in natural communities

Most lakes contain a large diversity of rotifer species over the course of a year. Changes in the seasonal distribution of planktonic rotifer populations are complex and difficult to generalize (Wetzel 1983). This complex arrangement of zooplankton species over time is often offered as an example of the "n-dimensional hypervolume" niche concept (Hutchinson 1957), where spatial and temporal variation in habitat allows specialized species to persist without being competitively excluded by other members of the zooplankton community. Both

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physical and biological factors may provide the niche dimensions that allow coexistence of many species.

The freshwater rotifer fauna is a useful example of the puzzling co-occurrence of closely related species. Taxonomic differentiation of rotifers is done largely by means of identification of subtle variations in the trophi, or jaws, which are composed of several hard parts and their associated musculature in very specific arrangements (Wallace and Snell 1991). Although diverse families of rotifers have dissimilar types of trophi (Wallace and Snell 1991), which may lead to differences in feeding, coexistence of congeneric species with very similar mouthparts is a common phenomenon. These observations suggest that numerous biological and physical processes work simultaneously to create the multi-dimensional niche space of a rotifer species. Therefore, factors besides food availability may need to be invoked in any full explanation of a successional sequence.

Herzig (1987), who analyzed the rotifer communities of 16 temperate waters, with varying morphometric, trophic, and climatic conditions, recognized that five factors appear to influence species' abundances and cause species succession: (1) physical and chemical limitations, (2) food and exploitative competition, (3) mechanical interference competition and (4) parasitism. These diverse and often opposing constraints are likely to allow for the coexistence of a large diversity of planktonic organisms, the "paradox of the plankton" (Hutchinson 1957).

This study is divided into two parts. In Chapter 1, I discuss the relationship between food availability and the reproductive response of Deer Lake rotifers; I am mainly interested in how body size affected reproduction at various food concentrations. In Chapter 2, I explore the structure of the rotifer community in Deer Lake using multivariate methods. I evaluate the importance of other constraints on rotifer survival and reproduction, such as temperature, competitors and predators.

GENERAL METHODS

Study site

Deer Lake is a eutrophic lake located within the municipality of Burnaby, southwestern British Columbia. The lake is small (surface area 35 ha) and relatively shallow (mean depth 3.5m, maximum depth 6m), with 71% of its area at depth of 3m or less (Chapman et al. 1985), (Figure 1). The watershed consists of open, rolling, terrain that has seen extensive agricultural and urban development over the last century. High nutrient inputs result from run-off and the large waterfowl population residing on the lake. Humans exacerbate the eutrophication problem by feeding these birds. The mixing regime is polymictic due to the open, wind-exposed terrain. Spatial patchiness in the lake is minimal due to frequent wind-mixing and shallow depth (Chapman et al. 1985 and personal observations). Zooplankton samples taken at replicate depths and stations show the same variation in abundances as ones taken at a single station (coefficient of variation was 10 to 15% between replicates).

Field sampling and laboratory analysis

I collected zooplankton and chlorophyll samples at a station 200m from the east shore, where the depth was 3.5m. Zooplankton were collected with a 27L Schindler-Patalas plankton trap, with a 34μm mesh netting on the outlet. Three replicate trap samples were taken near the surface at a depth of 0.5m every 4th day between January 4, 1999 and August 9, 1999. I chose this sampling

interval because the generation time of rotifers is short, and therefore does not lend itself to the weekly sampling schedule traditional in limnology. In order to reduce the loss of attached eggs, zooplankton were narcotized with carbonated water before preservation in sugared 5% formalin.

Due to the small body size of the rotifer component of the zooplankton, I counted the samples at a magnification of 150x using an inverted compound microscope with a gridded ocular. The zooplankton was first concentrated by settling, and then split using a Folsom plankton splitter. The size of the split (subsample) counted varied, depending on the density of the sample; however, I continued to count splits until I reached a total count of 2000 for each replicate. The coefficients of variation of abundance counts between replicate samples on a date were between 10 and 15%.

Rotifers, as well as crustacean zooplankton, were enumerated in the samples. At each sampling date, those rotifer species which carry eggs attached to the lorica were examined for the presence and number of eggs, allowing me to calculate an egg-ratio (eggs/female) for each of these species. Egg-ratios for *Asplanchna*, a transparent rotifer, were calculated by determining the presence of an egg within the body cavity. *Synchaeta pectinata* is a broadcast spawner, and the eggs of this species were consequently not sampled. Using an ocular micrometer, I also measured the first 10 individuals of each species encountered in my sample on each sampling date.
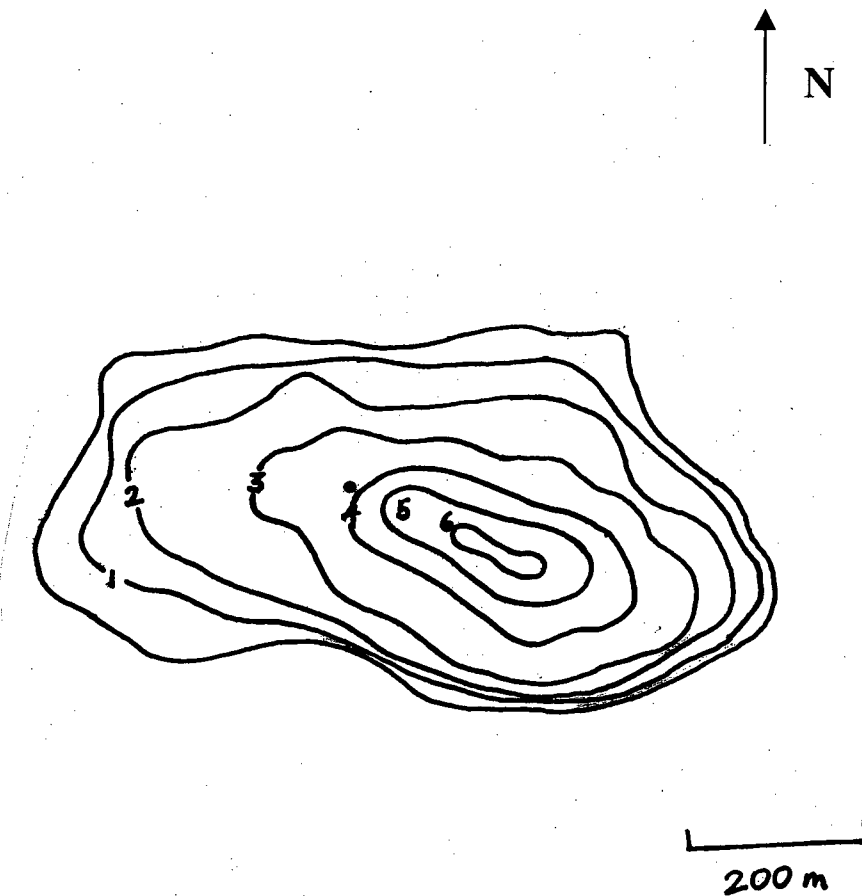
Figure 1. Morphometry of Deer Lake, with depth contours in meters. The sampling station is indicated by a bullet. Map is adapted from Northcote et al. 1992).

Although there are several short-comings to measurement of food availability as chlorophyll a, including the lack of detailed information on species composition and rates of supply, time and labor constraints made it necessary to use this index of phytoplankton concentration. I collected water for chlorophyll analysis using a 2L Van Dorn water bottle at 0.5m. The water was transported back to the laboratory on ice in a darkened bottle. I examined three size fractions of phytoplankton: chlorophyll from cells less than 8μm in length, chlorophyll from cells less than 25μm in length, and total chlorophyll a. Depending on the concentration, I filtered either 50 or 100mL of lake water, first through membrane filters (8μm and 22-25μm ashless Millipore) to accomplish the size fractionation, and then onto glass-fiber filters (Whatman, glass microfiber GF/F) using ~100mm Hg of vaccuum pressure. I stored these filters in a −20°C freezer for up to 7 days before extracting the chlorophyll in acetone for 18h in the refrigerator at 5°C. Readings were taken using a Model 10 Turner Designs analog fluorometer, and chlorophyll a concentration was calculated.

Temperature was measured using a WTW Multiline P4 meter at 1 m intervals from the surface to 3m depth, on each sampling date.

Calculation of population characteristics

I analyzed the population dynamics of rotifer populations using Edmonson's (1960) method, as modified by Caswell (1972) and Paloheimo (1974).

I used published regression equations for embryonic development time, available in the form

$$D = a/(t-b)^c,$$

where D is the number of days to hatching, t is temperature (°C) and a, b, and c are fitted constants. Table 1 summarizes the regression equations derived from a table in Herzig (1983), and the sources of the data from which these equations were calculated.

Species	a	b	c	source
Keratella quadrata	196	-5.88	1.51	Herzig 1983
Keratella cochlearis	45	0.84	1.144	Edmonson 1960
Polyarthra dolichoptera	899	-4.78	2.248	Herzig 1983
Kellicottia longispina	899	-4.78	2.248	Herzig 1983

Table 1. Constants in the regression equation ($D=a/(t-b)^c$), used to compute embryonic development time in days from temperature in degrees Celcius.

The instantaneous per capita birthrate is calculated from

$$b' = \ln[(E_t/N_t) + 1]/D,$$

where E_t is the number of eggs in the population at time t, N_t is the population size at the same time and D is the embryonic developmental time (after Paloheimo 1974). Therefore, E_t/N_t is equivalent to the egg ratio. In order to increase the number of individuals used to calculate egg ratio, and obtain a more accurate estimate of E_t/N_t, I pooled all three replicates collected on each date for this calculation. This was done because egg ratios tended to be low, (below 0.2 eggs/female). As a result, I was not able to calculate a variance associated with this measure of reproduction.

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The instantaneous rate of population increase, r, is calculated from

$$N_t = N_o e^{rt},$$

where N_o, N_t, are population densities at times 0 and t,

The instantaneous death rate, d', is calculated from

$$d' = b' - r.$$

The finite death rate D_t is calculated from

$$D_t = 1 - e^{-d'}.$$

Only *Keratella cochlearis* and *Polyarthra dolichoptera* were found to change in body size over the sampling period; therefore, I took weekly measurements of 20 individuals of each species. I calculated the average body volume for all species using the method of Ruttner-Kolisko (1977), (see Appendix 1). I used measurements of twenty individuals for each species for these calculations, taking the first four measurements of 5 randomly selected sampling dates.

Data analysis

I used a combination of statistical methods to investigate rotifer community structure and the relationship of size-fractioned food availability and temperature with rotifer body size and species composition. For each species, I performed simple linear regressions on egg ratio and birthrate data in relation to the log-transformed concentrations of various size fractions of chlorophyll a. I

used confidence intervals, and analysis of covariance to determine whether there were any inter-species differences in the slopes and y-intercepts. I used analysis of covariance to test for an interaction between species and chlorophyll, and then did pairwise comparisons (t-tests) to look for differences in intercept among those species which did not differ in elevation (slopes). To gain further insight into the relationship between food concentration and body size, I used one-way analysis of variance to detect differences in the food concentration at which three different forms of the species *Keratella cochlearis* reproduce with an egg ratio > 0.1. As a further descriptor of seasonal changes in the rotifer community, I calculated Simpson's diversity index, D, (Begon 1990) for each sampling date. Simpson's index is the simplest measure of the character of a community that takes into account both abundance patterns and species richness. P_i is the proportion that a species contributes to the total number of rotifers in a sample:

$$D = \frac{1}{\sum P_i^2}$$

I used multivariate ordinations of my abundance data to summarize the variation that could not necessarily be explained by univariate factors alone. I used weighted averages to compute a body-size score for each sampling date. The weight assigned each species was a constant: the average body volume for that species, calculated as described above. The score Sj for each sample j was calculated as:

$$S_j = \frac{\sum A_{ij} W_i}{\sum A_{ij}}$$

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where the summations are over all species i, A_{ij} is the abundance of species i in sample j, and W_i is the weight for species i.

I used Principal Components Analysis (PCA) in order to summarize total variation in the zooplankton abundance data set. The correlation matrix produced by this technique requires all variables to be transformed $[\log_{10}(x+1)]$ in order to standardize the data and conform with assumptions of multivariate normality (Gauch 1982). To be strictly applicable, a data set must meet several assumptions of the PCA model, primarily that the components have normal distribution and be uncorrelated. Although field data sets rarely, if ever, meet the requirements precisely, for merely descriptive purposes, larger departures from ideal data structure are tolerable (Gauch 1982). The use of a non-parametric ordination method, multi-dimensional scaling, resulted in similar groupings of rotifer species; this reinforces my confidence in the PCA method. Correlations of the first two factors derived from the PCA with various biotic and abiotic conditions measured at each sampling date allowed me to provide a biological interpretation for the ordination results. Additionally, I performed PCA on rotifer r values and egg ratios, in order to investigate processes that may be important in abundance patterns. In order to evaluate the significance of correlations between species, I used Bonferonni's correction for multiple comparisons: 0.05/k, where k is the number of comparisons, and 0.05 the original probability of a Type 1 error.

CHAPTER 2: FOOD AVAILABILITY AND REPRODUCTION IN DEER

LAKE ROTIFERS

Introduction

In laboratory experiments, body size in rotifers appears to influence strongly the food concentration necessary for reproductive rates to balance death rates (per capita rate of population growth, $r=0$). This level of required food availability was termed the "threshold food concentration" by Stemberger and Gilbert in 1985. Rotifer threshold food concentrations vary considerably (by up to a factor of 17) among species (Stemberger and Gilbert 1985). In general, the threshold food concentration becomes smaller as body size of the species decreases (Stemberger and Gilbert 1985). At the same time, large species have considerably higher maximum rates of population growth (r_m) than smaller species at high food concentration. In theory, the threshold food requirement imposes competitive limitations on the occurrence of species; larger species should be excluded from food-poor environments in which small-bodied rotifers are able to maintain positive rates of population growth. The proposed mechanism behind this phenomenon is that relative swimming speeds decrease allometrically with increasing body size, such that small-bodied rotifers have higher length-specific encounter rates with food particles than larger species. As a result, larger species, while moving through the water at similar overall speeds

to small rotifers, move slower per unit body length (Stemberger and Gilbert 1987).

Some general patterns from natural communities lend support to the threshold food level hypothesis. For example, deep-water, oligotrophic environments of the Laurentian Great Lakes commonly contain small species such as *Keratella cochlearis* (150-200μm), *Synchaeta oblonga* (300-400μm), *Polyarthra remata* (150-200μm), and *Polyarthra earlinae* (150-200μm) (Nauwerck 1978). Eutrophic, food-rich environments such as embayments and river outfalls of the Great Lakes are commonly inhabited by large species such as *Brachionus calyciflorus* (500-600μm), *Asphlanchna brightwelli* (500-1200μm), and *Euchlanis dilatata* (~500-600μm), where the capacity for high r is more important than the capacity for positive population growth rate at low food-concentration (Bricker et al. 1976). On a seasonal basis too, it appears that the composition of the rotifer community is linked to food concentration and the associated population growth rate. Bricker et al. (1976) and Stemberger et al. (1979) report that field collections from the Great Lakes show a dominance of *Synchaeta* only in early spring, when cryptomonad populations are moderately high.

In contrast, the size-efficiency hypothesis, first proposed by Brooks and Dodson in 1965, predicts that larger zooplankton have greater reproductive success than their smaller competitors on a given quantity of food. They propose that large crustacean zooplankton are dominant over small-bodied zooplankton in the absence of predation because energetic (metabolic) costs have a lower rate

of increase with body size than do energetic inputs (ingestion). The size-efficiency hypothesis therefore makes the opposite prediction to the threshold food-level hypothesis: that optimal size should increase with decreasing food concentration.

Although the size-efficiency hypothesis was developed primarily from observations of crustacean zooplankton, its basic principles should apply to rotifers as well. As a general principle, the metabolic economy per unit body size decreases with an increase in body size (Odum 1971), and there is no reason why this principle should not apply to rotifers. Also, in related species of zooplankters, the food-collecting surfaces are proportional to the square of some characteristic linear dimension such as body length (Brooks and Dodson 1965). It is easy to imagine that this is also the case for rotifers that concentrate algal particles into a ciliated buccal field as they swim.

Further complicating the relationship between these herbivorous rotifers and their phytoplankton food is the discovery that suspension-feeding rotifers may differ greatly from one another in the types of cells they select or are able to ingest (Gilbert and Bogdan 1984b). As well, rotifers differ in their food-niche breadth, with the functional morphology of the coronae of the "generalist" rotifers differing markedly from that of the more "specialist" rotifers. Although rotifers are highly selective feeders, they all utilize small phytoplankters in the size range 0-25um in length. There exists some evidence that congeneric rotifer species partition their food environment in accordance with their body size; for

example, the smaller species, Brachionus rubens, feeds most efficiently on particles of about 5um diameter, whereas the larger species, Brachionus calyciflorus does best on particles around 10 um diameter (Rothhaupt 1990). However, in general, groupings of rotifers with similar food preferences do not follow either taxonomic or body-length groupings (Bogdan and Gilbert 1984). Various rotifer species make fine-grained choices between species within the same phytoplankton genus, or between different genera of closely related phytoplankters (Gilbert and Bogdan 1984). Selectivity itself is a complex process, because preference for a certain prey species may depend on its nutritional quality, its concentration, overall particle concentration, and temperature (Starkweather 1980, DeMott 1986).

Objectives

I examined the relationship between rotifer body size and reproductive rates at different food concentrations. I predicted that laboratory studies on this issue, which provided strong evidence for the success of small-bodied rotifers at low food concentration (Stemberger and Gilbert 1985), could explain the size structure of natural rotifer communities. Temperate lakes exhibit large seasonal fluctuations in phytoplankton concentration, so I hypothesized that seasonal differences in the occurrence of various body sizes are a consequence of changes in food availability to rotifers. In fact, Stemberger and Gilbert (1985) suggested

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that resource abundance is a primary determinant of body size patterns between eutrophic and oligotrophic environments.

I adjusted Stemberger and Gilbert's predictions about population growth rates to fit the reproductive data I was able to gather in my field study (Figure 2). I predicted that at low food concentration, small rotifer species would exhibit higher reproduction (measured as egg ratio or birthrate) than large species, but that at high food concentration, large species would achieve a higher reproduction.

I evaluated these predictions by looking in detail at two features of the food-reproduction relationship for each taxon. The y-intercept of the regression equation between food and egg ratio describes the reproductive output at zero or near-zero food concentration. According to Stemberger and Gilbert (1985) this value should increase as the body size of rotifer species decreases. The slope of this regression line describes the magnitude of change in egg production for unit changes in food concentration. I predicted that this slope would be larger for larger-bodied rotifer species than for smaller-bodied ones. This prediction follows directly from the idea that r_{max} in large rotifers is higher than in small ones. If y-intercepts of small rotifers are higher than those of large rotifers but large rotifers achieve a higher r_{max}, then the slope of the line relating egg ratio to food concentration must be higher for large rotifers.

RESULTS

Chlorophyll

Total chlorophyll a concentrations ranged over three orders of magnitude and were low in both midwinter and summer. A spring phytoplankton bloom occurred between mid-March and mid-April, during which time total chlorophyll-a levels reached 10 000 μg/L, most of which was in particles >25μm (greatest linear dimension). As well, during this time, both smaller size-fractions, all cells <8μm, and all cells <25μm, exhibited a period of approximately 100 and 200-fold increase in concentration, respectively (Figure 3).

The phytoplankton during January and February was dominated by *Cryptomonas*, a flagellate, and *Melosira*, a colonial diatom that forms long chains. In the spring, large, ungrazable forms tended to dominate the phytoplankton community. During March and April, *Melosira* continued to feature prominently in the composition of the phytoplankton, and it was joined by other large (>100 μm) diatoms, the pennate *Synedra* and *Asterionella*, as well as filamentous green algae.

Between mid-May and the beginning of June, there was a second bloom of *Cryptomonas*, associated with a general decrease in diatom abundance, though *Fragilaria*, a colonial large diatom first appeared then. Colonial cyanobacteria first appeared in mid-May, increased rapidly to high abundance in early June, and then persisted at intermediate density for the remainder of the sampling period. The onset of the blue-green bloom was associated with an increase in the

abundance of ciliates that possibly were grazing on these cyanobacteria. During June and July, *Asterionella* and *Fragilaria*, as well as the colonial, generally ungrazable *Dinobryon* became prominent.

Variation and change in rotifer body size

The calculated body volume of rotifers in Deer Lake ranged between 47 and 19197 thousands of μm^3, depending on species (Table 2). *Keratella cochlearis* and *Kellicottia longispina* were the smallest-bodied taxa observed, whereas *Polyarthra dolichoptera*, *Keratella quadrata*, and *Tricocerca sp.* were medium-bodied. The two soft-bodied rotifers, *Synchaeta pectinata* and *Asplanchna sp.* had the largest mean body volume.

Taxon	Volume (thousands of μm^3)	SE of mean
Polyarthra dolichoptera	499.89	35.43
Keratella cochlearis (small, spined)	70.42	3.92
Keratella cochlearis (large, spined)	134.75	5.59
Kellicottia longispina	47.23	2.39
Keratella quadrata	368.04	14.41
Synchaeta pectinata	1948.06	376.25
Asplanchna sp.	19197.46	1932.12
Trichocerca sp.	496.09	118.52

Table 2. Mean body sizes and standard errors of Deer Lake rotifer species.

The average body size of the rotifer community, weighted by species abundance, increased over the winter and early spring, reached a maximum in March, and then declined again, returning to its winter average by May (Figure

4a). There appears to be no relationship, however, between the concentration of <25μm chlorophyll a, and this measure of mean rotifer body size (Figure 4b).

I detected three forms of the species *Keratella cochlearis* in Deer Lake which were variable in their size and the presence of a posterior spine: a spined, small variety, an unspined small form, and a spined, large form. Whereas the small, spined form was present throughout the sampling period, the small, unspined form occurred in winter, and the large spined form only in the summer. These varieties differ not only in size, but also morphologically. The dorsal surface of the small forms contain 7 plates; the same surface in the large form is composed of 11 connected plates. The three *K. cochlearis* forms are depicted in Figure 5.

Two species, *Polyarthra vulgaris* and *Keratella cochlearis*, changed in body length over the sampling period. The total length of the small, spined form of *K. cochlearis* increased by 27%, from 127μm in January, to 161μm in mid-June (Figure 6a).   This increase was due to a lengthening in the spine, as body length (which excludes the spine), remained constant. Over the period that the large variety of *K. cochlearis* was present in Deer Lake, there was no change in either the spine length, or overall body length (Figure 6b). *Polyarthra vulgaris* lacks spines, but it too increased in size over the course of the sampling period by 41%, from 114μm to 161μm (Figure 6c). Other Deer Lake rotifer species showed no measurable variation in body size.

Utility of egg ratios as a measure of reproduction

Egg ratios were found to be a useful surrogate measure of birthrate. I selected the 3 species present in Deer Lake for which published regression equations relating temperature to development rate exist , and haphazardly selected three other such equations from the literature (*Epiphanes brachionus, Brachionus calyciflorus* and *Brachionus angularis*). I tested whether the variation between groups (where birthrates are the values, and egg ratios are the groups) was larger than the variation within groups (birthrates of different species at a given egg ratio). An analysis of variance showed that there is no significant effect of developmental rate on birthrate at 10°C for six different egg ratios, ranging from 0.1 to 0.6 (df=35, F=2.00, P=0.107). However, analysis of variance demonstrated a highly significant effect of egg ratio on birthrate, even at six different developmental rates (df=35, F=14.17, P<0.001). Therefore, egg ratio was found to be a useful surrogate for birthrate when developmental rates of all species are not known.

Y-intercepts of regressions relating food and egg ratio

The y-intercepts in the regression equations relating egg ratio to food concentration indicate the reproductive output at zero or near-zero food concentration. The y-intercepts in this study are, with one exception, below zero (Table 3); however, their values still provide information about relative reproductive levels when food resources are very low. The y-intercepts given in

Taxon	slope	lower 95% confidence interval	upper 95% confidence interval	y-intercept	lower 95% confidence interval	upper 95% confidence interval
Keratella quadrata	0.329	0.047	0.612	-0.551	-1.4	0.301
Keratella cochlearis (unspined)	0.165	-0.02	0.349	-0.183	-0.721	0.357
Keratella cochlearis (small, spined)	0.293	0.216	0.37	-0.56	-0.766	-0.354
Kellicottia	0.09	0.009	0.171	-0.135	-0.364	0.093
Asplanchna	0.223	-0.259	0.706	-0.307	-1.411	0.795
Keratella cochlearis (large)	0.037	-0.333	0.409	0.017	-0.844	0.879
Polyarthra dolichoptera	0.076	0.05	0.102	-0.146	-0.216	-0.078

Table 3. Slopes, y-intercepts and confidence intervals of regression equations relating chlorophyll a concentration of cells less than 25μm in length on the x-axes and egg ratios on the y-axes for 7 species of rotifers.

Table 3 do not follow any clear patterns with respect to body size. The small, spined rotifer *Keratella cochlearis* has a y-intercept near that of *Keratella quadrata*, a medium-bodied rotifer. Furthermore, *Asplanchna sp.*, the largest rotifer I encountered in my study, had an intermediate y-intercept. Confidence intervals for y-intercepts of all species overlap; there are no significant differences between species in the value of the y-intercept. After using analysis of covariance to look for differences in slopes (see next section), I used pairwise comparisons to test differences in elevation of lines for that subset of species for which no difference in slopes could be detected. This revealed that *Asplanchna* had a different y-intercept in the relationship between <25μm chlorophyll and egg ratio than large *K.cochlearis, Kellicottia longispina,* or *Polyarthra dolichoptera* (p=0.005, p=<0.001, p<0.001, respectively). The large morph of *K.cochlearis* and *Polyarthra* also differed significantly in their y-intercepts (p=0.013).

Slopes of regressions relating food and egg ratio

The egg ratios of all six rotifer taxa which carry their eggs, and the one taxon for which internal eggs can be observed, increased with rising food concentration (Figures 7-10). Food concentration, measured as the concentration of chlorophyll a in 3 size fractions of cells, varied over two orders of magnitude, and was associated with egg ratios between 0 and 0.8. Although higher food availability was positively related to the egg ratio observed on that sampling date, the intra-species variation in the average number of eggs per female for a given food concentration was considerable.

Three taxa, *Keratella quadrata*, *Keratella cochlearis* (small, spined form), and *Asplanchna sp.* exhibited a change in egg ratio > 0.2 for a unit change in log (<25μm chlorophyll a concentration) (Table 3). This group includes both the largest and the smallest rotifer taxa measured in Deer Lake (Table 2). Large *Keratella cochlearis* had the lowest slope in its relationship between food concentration and egg ratio (Table 3). However, confidence intervals for the slopes of all regression lines overlap widely. Table 4 summarizes the regression results for the 7 taxa. The egg ratios of *Asplanchna* and large *Keratella cochlearis* were not significantly related to the concentration of chlorophyll a in cells <25μm, and those of unspined *Keratella cochlearis* were only marginally significantly correlated with food concentration.

An analysis of covariance showed that there was a significant interaction between species and the concentration of <25μm chlorophyll a (df=6, F=3.35,

p=0.004). However, pairwise comparisons showed that the slopes of the linear relationships between chlorophyll and egg ratio differed only in some cases. Small, unspined *K. cochlearis* had a higher slope than either *Kellicottia* or *Polyarthra* (p=0.011, p<0.001). As well, *K. quadrata* had a higher slope than either *Kellicottia* or *Polyarthra* (p<0.001 in both cases). Small spined *K.cochlearis* also exhibited a higher slope than either *Kellicottia* or *Polyarthra* (p=0.034, p<0.001).

Species	df	F	p	R^2
Polyarthra dolichoptera	45	35.300	<0.001	0.445
Kellicottia longispina	18	5.579	0.030	0.247
Keratella quadrata	16	6.176	0.025	0.292
Keratella cochlearis, unspined	23	3.414	0.078	0.134
Keratella cochlearis, spined small	45	58.840	<0.001	0.570
Keratella cochlearis, large	11	0.051	0.825	0.005
Asplanchna sp.	13	1.019	0.332	0.078

Table 4. Degrees of freedom, variance, significance levels, and coefficients of determination for the regression equations presented in Table 3.

The rotifer taxa which had the lowest y-intercepts in these regressions were also those with the highest slopes. Figure 11 shows the highly significant (R^2=0.94, df=6, F=77.56, p<0.001) negative relationship between the values of the slope and y-intercept of the regression lines described in Table 3. It appears that the larger the change in egg ratio for a unit change in food concentration, the lower the egg ratio at near zero chlorophyll concentration. Alternatively, those taxa least able to reproduce at low food concentration responded most vigorously to an increase in food.

Rates of change in egg ratio

For each rotifer species, I examined the relationship between the change in the concentration of chlorophyll (<25μm size fraction) from one sampling date to the next, and the corresponding change in egg ratio. This analysis gives some insight into the influence of non-equilibrium food conditions on reproduction. However, variation in the change in egg ratio for a given change in food concentration was high, and no pattern between these two factors could be deduced for any of the Deer Lake rotifer species.

Birthrates

Table 5 summarizes the regression equations derived from the relationship between <25μm chlorophyll concentration and birthrate (Figure 12), for the four species for which temperature dependent development rate functions are available in the literature.

Taxon	slope	lower 95% confidence interval	upper 95% confidence interval	y-intercept	lower 95% confidence interval	upper 95% confidence interval
Polyarthra dolichoptera	0.008	-0.01	0.026	0.005	-0.043	0.054
Keratella cochlearis	0.031	0.01	0.051	-0.03	-0.085	0.025
Keratella quadrata	0.075	0.029	0.121	-0.141	-0.282	-0.001
Kellicottia longispina	0.011	-0.012	0.034	0	-0.067	0.067

Table 5. Slopes, y-intercepts and confidence intervals of regression equations relating chlorophyll a concentration (of cells less than 25μm in length) on the x-axes and birthrates on the y-axes, for four species of rotifers.

As well, for each species food concentrations were lagged by one sampling date for those dates on which development time exceeded the sampling interval. Both species in the genus *Keratella* have a higher increase in birthrate for a unit increase in log [chl a] than either of the other two species. By comparing y-intercepts of the four species in Table 5, it is clear that *Polyarthra dolichoptera* has the highest birthrate at zero or near zero food concentration. However, confidence intervals for x-variables and y-intercepts overlap widely, and it is unclear whether there exist any real species differences in these measures of reproductive response to food conditions (Table 5). Table 6 shows that the birthrates of *Kellicottia* and *Polyarthra* were not significantly correlated with the availability of phytoplankton food less than 25μm in size.

Species	df	F	p	R^2
Kellicottia longispina	13	1.162	0.302	0.088
Polyarthra dolichoptera	44	0.832	0.367	0.019
Keratella cochlearis	41	9.075	0.004	0.185
Keratella quadrata	15	12.266	0.004	0.467

Table 6. Degrees of freedom, variance, significance levels, and coefficients of determination for the regression equations presented in Table 5.

Response of *Keratella cochlearis*

An analysis of variance demonstrated that there are significant taxa effects in the food concentration at which three different subspecies of *Keratella cochlearis* produce more than 0.1 eggs/female (df=54, F=4.81, p=0.012). This value is

indicative of low reproduction; the modal egg ratio was between 0.2 and 0.3. The spined *K. cochlearis* exhibited this level of reproduction at a food (<25μm chl a) concentration of 1020.5μg/L (SD=807.8), the unspined form at 1271.4μg/L (SD=803.1), and the large, spined form at only 203.2 μg/L (SD=44.1). Based on non-overlap of 95% confidence intervals, the large variant reproduced at significantly lower chlorophyll levels than either the spined or the unspined small form (Figure 13). An analysis of variance on the concentration of (8-25μm) chlorophyll a associated with an egg ratio of 0.1 or higher also significantly varied with the subspecies (df=54, F=4.25, P=0.020). However, the remaining size fractions, <8μm (df=54, F=2.26, P=0.114) and >25μm (df=54, F=0.93, P=0.400), did not give this result.
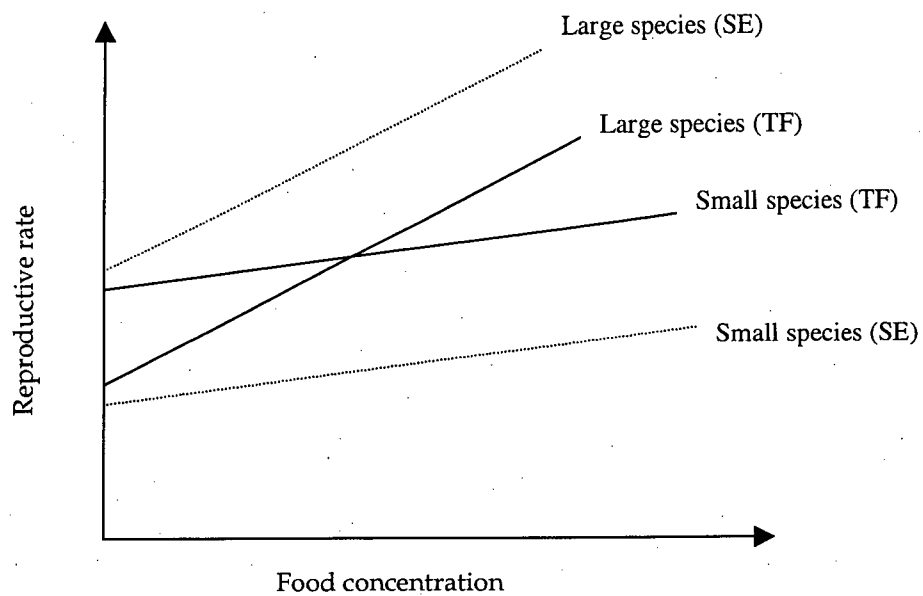
Figure 2. Theoretical relationship between food concentration and reproductive rate for small and large rotifer species, according to the threshold-food concentration hypothesis (TF), shown in solid lines, and the size-efficiency hypothesis (SE), shown in dotted lines.
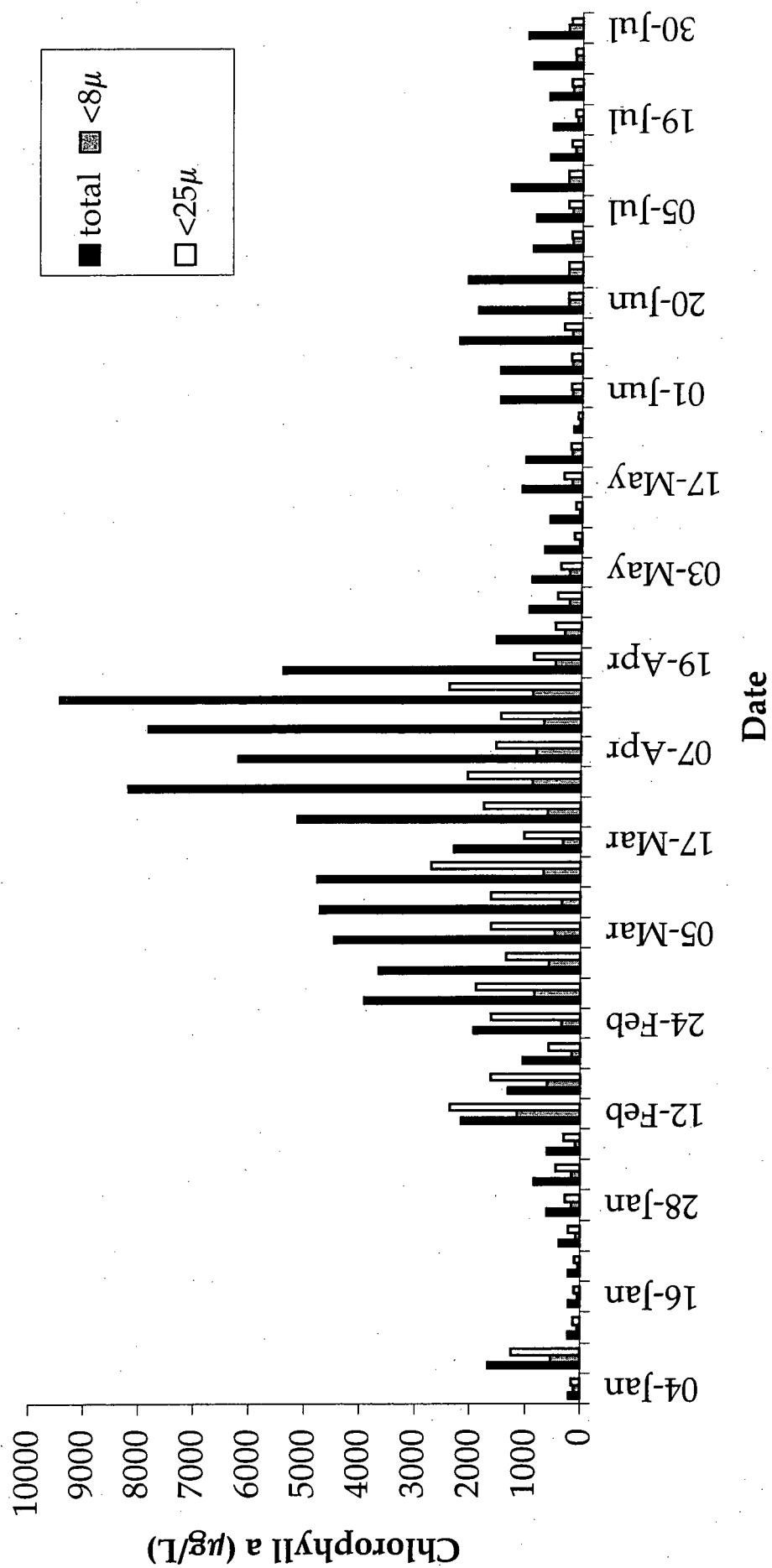
Figure 3. Concentrations of three size fractions of phytoplankton cells, (measured as chlorophyll a) at 0.5m depth in Deer Lake, between early January and early August, 1999.
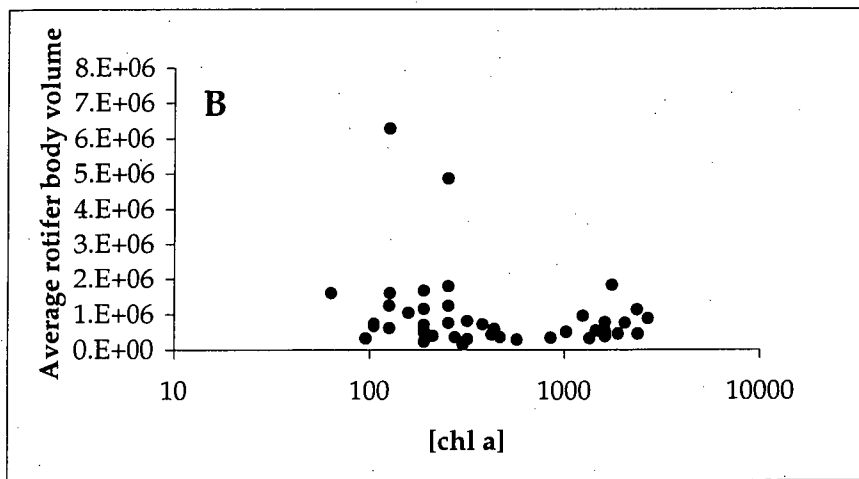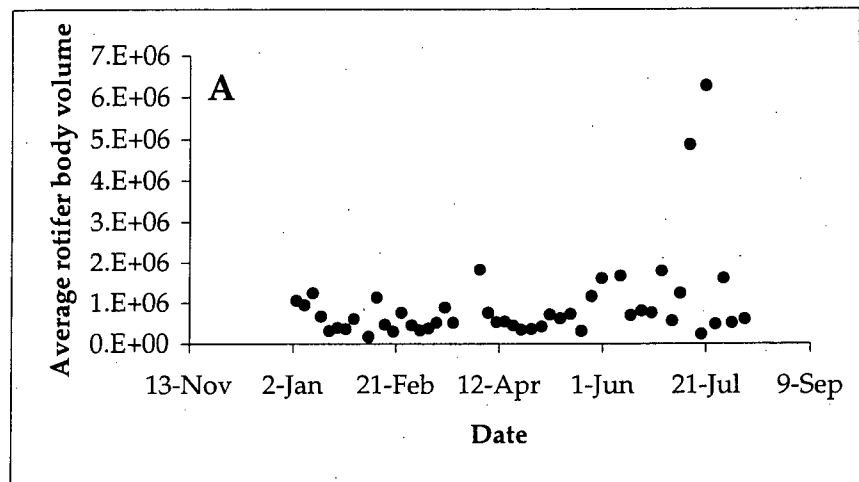
Figure 4. The relationship between the weighted average of rotifer body volume (measured in μ^3) and (a) sampling date (b) chlorophyll a concentration (μg/L) of cells < 25μm in length.
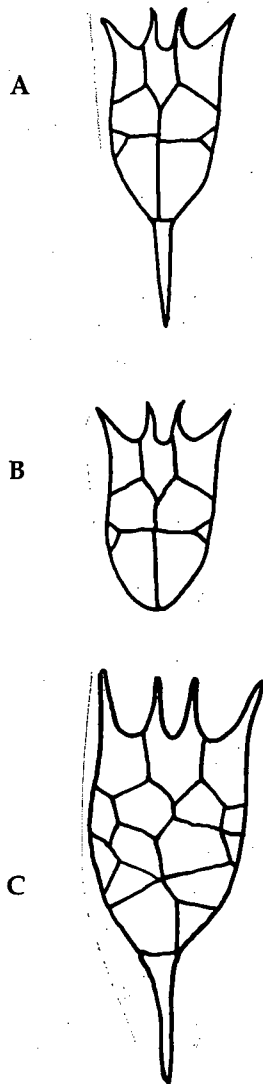
Figure 5. Three forms of *Keratella cochlearis* (a) the small, spined form, (b) the small, unspined form, and (c) the large spined form. Drawn from photographs taken under an inverted light microscope at a magnification of 400x.
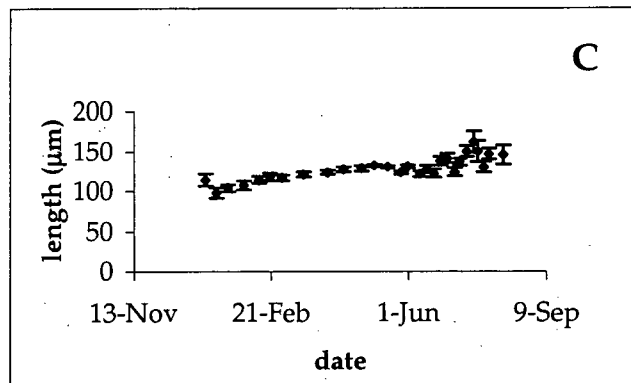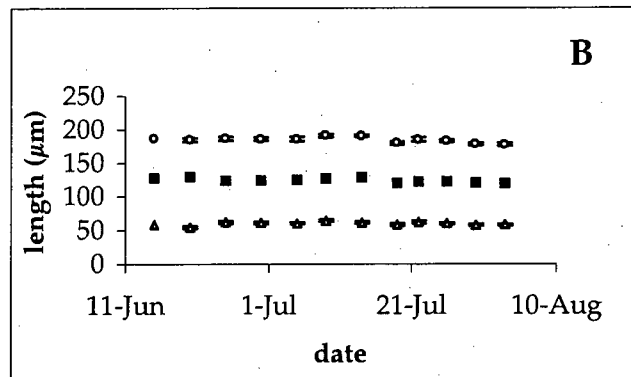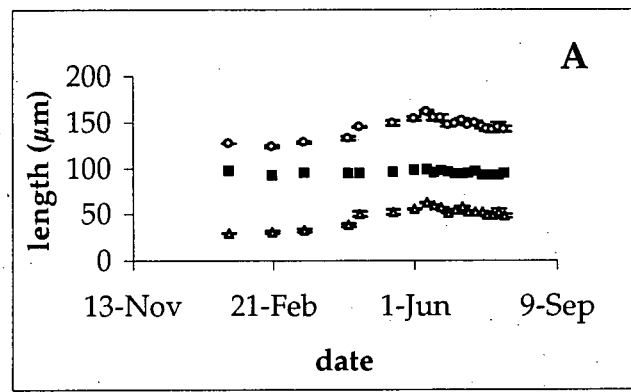
Figure 6. A) Body size for small *Keratella cochlearis*. B) Same as in (A) for large *Keratella cochlearis*. C) Changes in total body length for *Polyarthra dolichoptera*. Open circles indicate total length, open triangles indicate length of the dorsal spine, closed squares indicate total length minus the dorsal spine, and closed diamonds denote total body length in *Polyarthra*. Error bars are standard errors of the means.
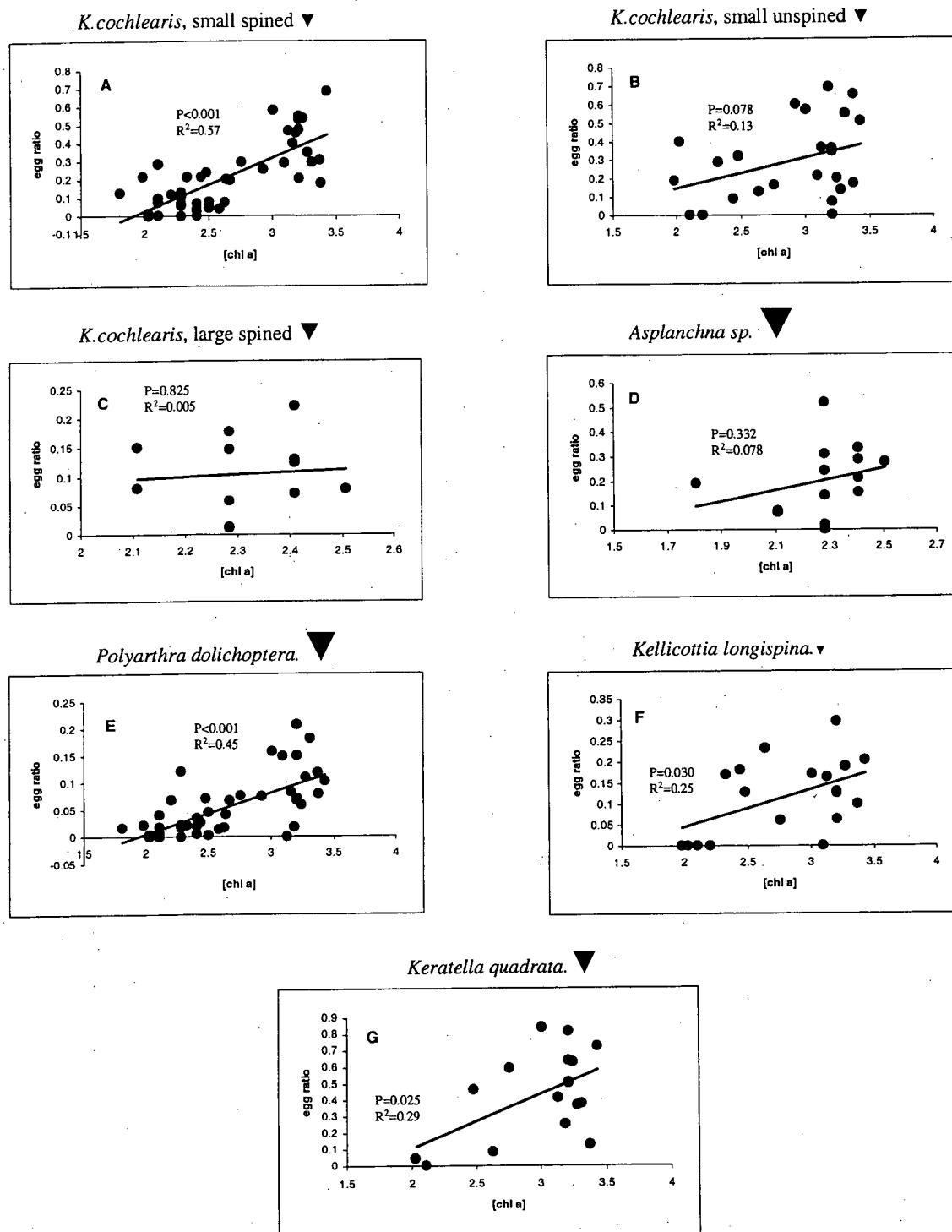
Figure 7. Regressions between the log of the concentration of cells less than 25μm in length (measured in μg/L of chlorophyll a) and egg ratio (average number of eggs/female) for seven taxa of rotifers. Triangle size represents relative rotifer body size.
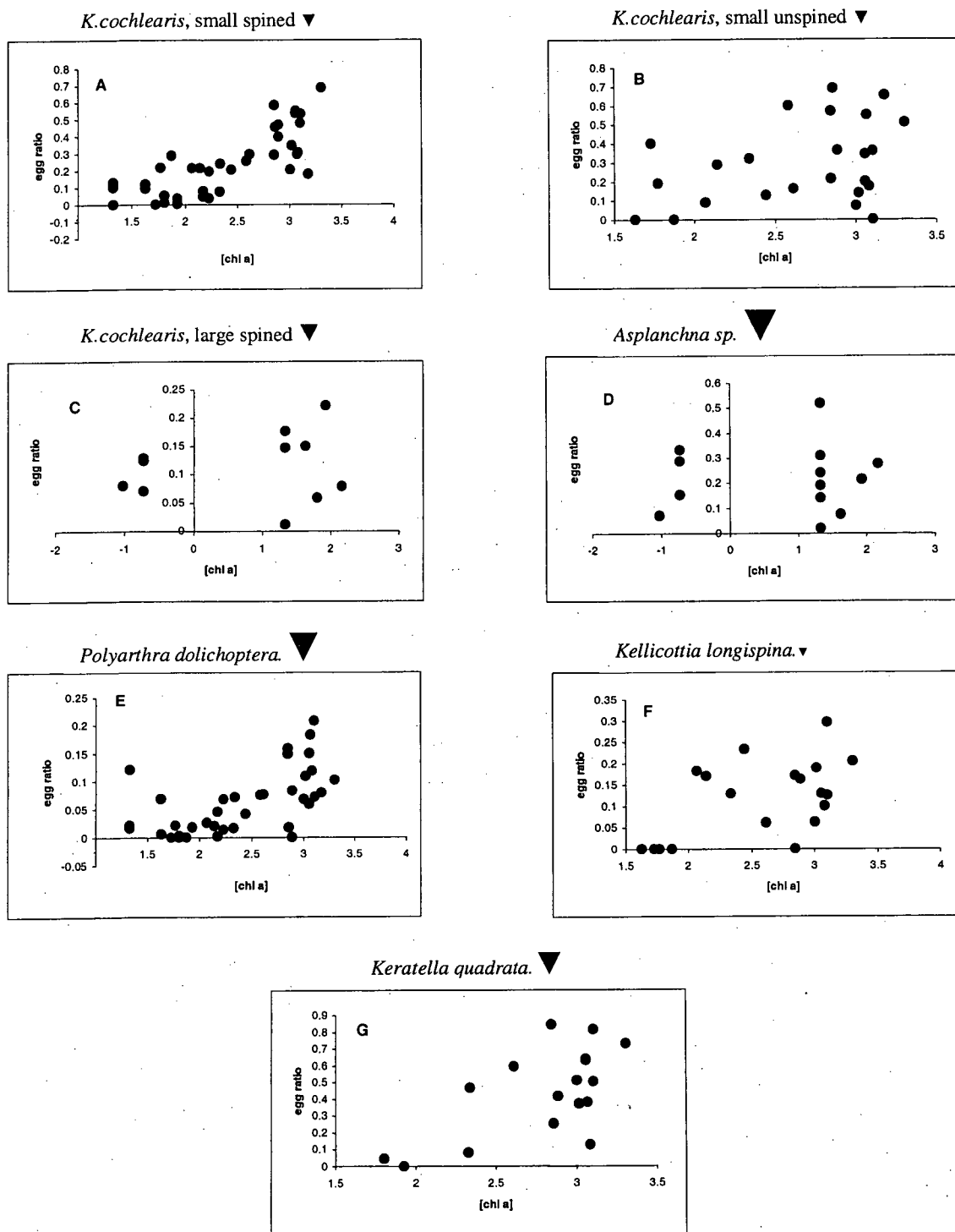
Figure 8. Relationships between the log of the concentration of cells between 8 and 25μm in length (measured in μg/L of chlorophyll a) and egg ratio (average number of eggs/female) for seven taxa of rotifers. Triangle size represents relative rotifer body size.
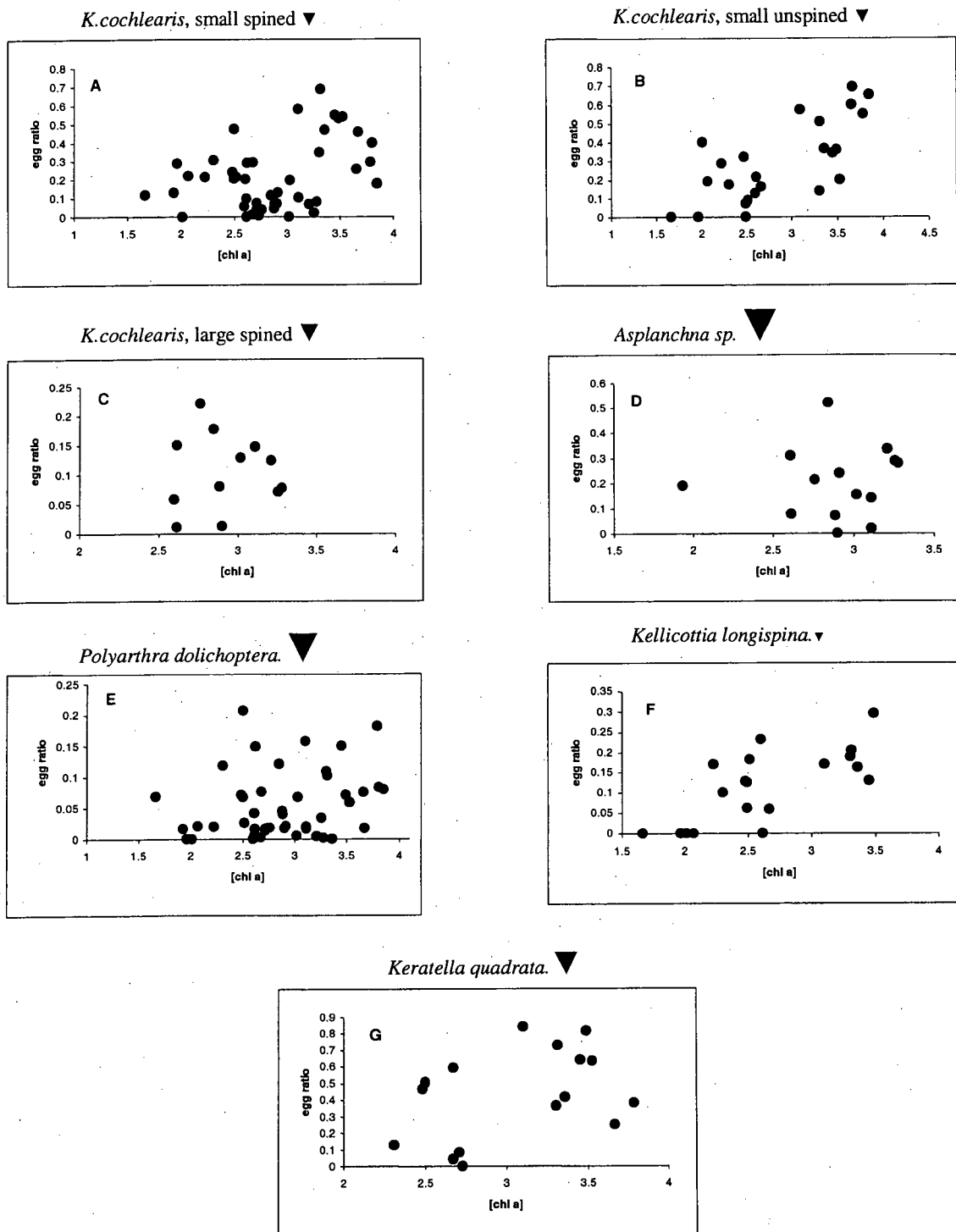
Figure 9. Relationships between the log of the concentration of cells larger than 25μm in length (measured in μg/L of chlorophyll a) and egg ratio (average number of eggs/female) for seven taxa of rotifers. Triangle size represents relative rotifer body size.
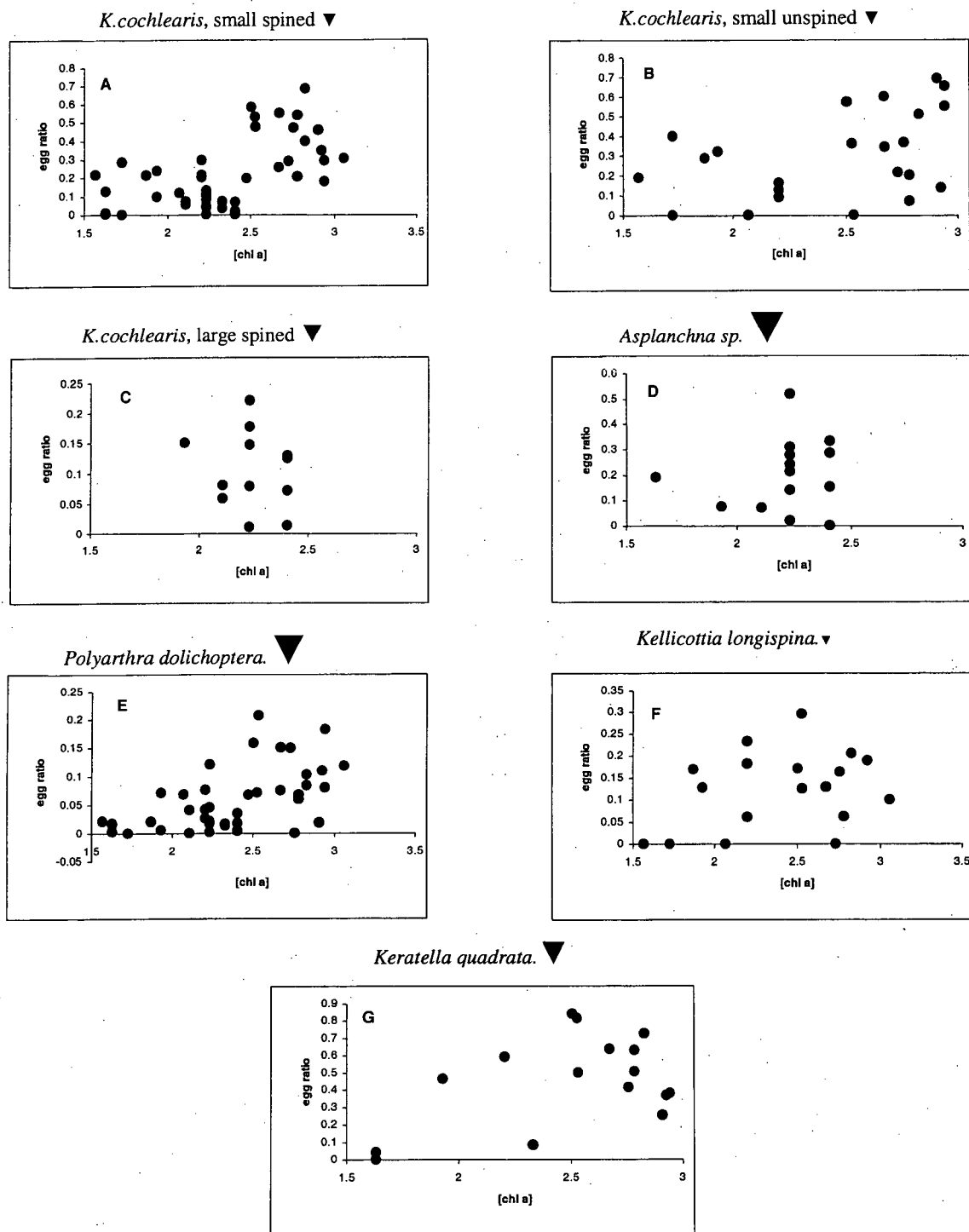
Figure 10. Relationships between the log of the concentration of cells less than 8µm in length (measured in µg/L of chlorophyll a) and egg ratio (average number of eggs/female) for seven taxa of rotifers. Triangle size represents relative rotifer body size.
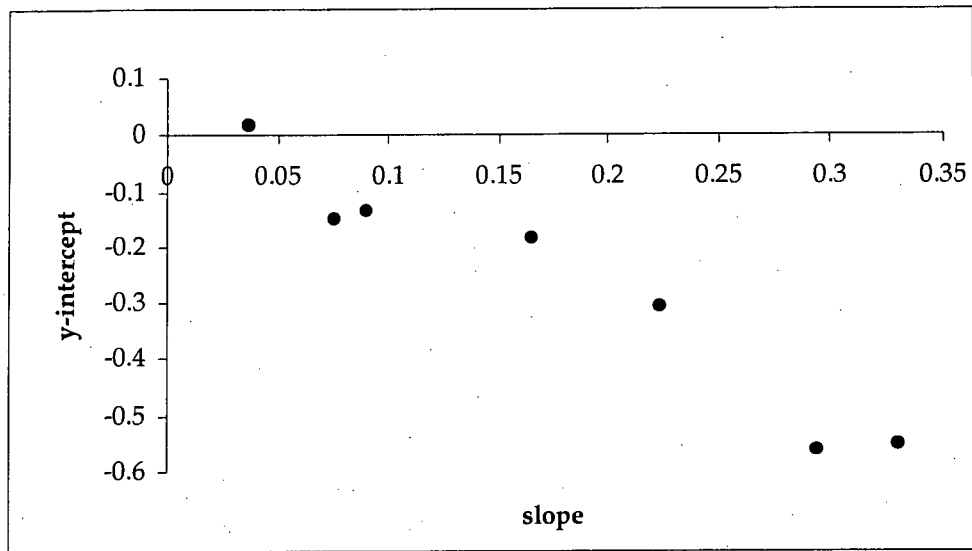
Figure 11. Inverse relationship between the y-intercept and the slope of regression equations relating egg ratio and food concentration, for seven rotifer taxa.
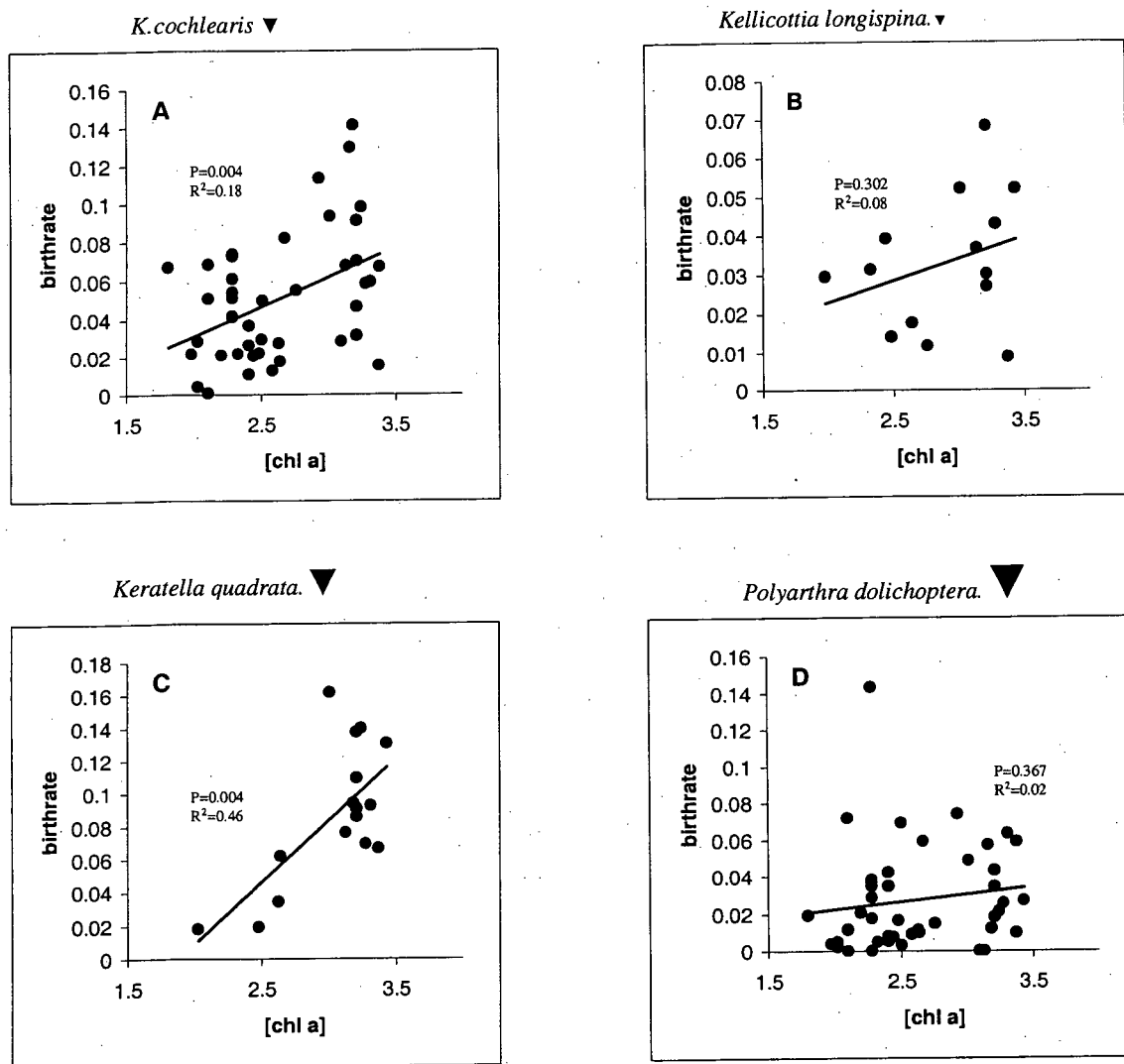
Figure 12. Regressions between the log of the concentration of cells (<25µm length), measured in µg/L of chlorophyll a, and the birthrate (females/female/day) for 4 taxa of rotifers. Triangle indicates relative rotifer body size.
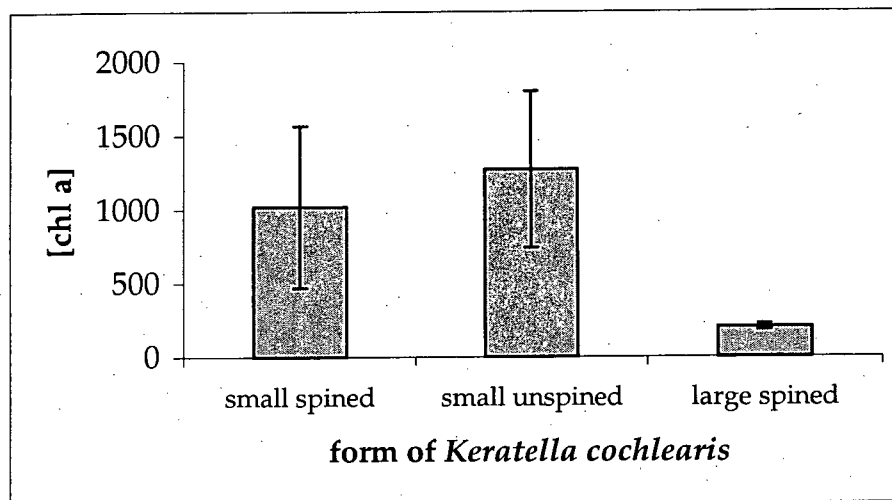
Figure 13. The food concentration (measured in µg/L) of chlorophyll a, of cells less than 25µm in length, at which three different forms of *Keratella cochlearis* produce more than 0.1 eggs/female. Bars indicate 95% confidence intervals.

DISCUSSION

The egg ratios for Deer Lake rotifers with attached eggs rose with the concentration of chlorophyll a (Figures 7-10). Based on laboratory studies (Stemberger and Gilbert 1985), I had hypothesized that the rate and manner of this increase should depend on body size. I predicted that small species would exhibit higher reproductive levels at low food concentration but that large species would have higher reproductive potential at high food concentrations (Figure 2). This follows directly from the threshold-food level hypothesis which claims that the food concentration for which population growth rate is zero is positively related to body mass. The higher the value of the y-intercept in these regression equations relating food concentration to egg ratio, the higher should be the egg ratio at zero or near zero food levels. Therefore, small species should be expected to have a higher y-intercept than large species. In addition, I had expected that the slope of these regression lines would be higher for larger rotifer taxa, a prediction of both the size-efficiency and the threshold food concentration hypothesis.

However, there appears to be no relationship between body size and the value of the y-intercept. In fact, the confidence intervals for the intercepts of all seven species overlap widely (Table 3). This indicates that there are no significant differences in the egg ratios of Deer Lake rotifers at extremely low food conditions, measured as the concentration of chlorophyll a in cells <25μm.

For example, the three species with the lowest y-intercepts fall into the size categories of small, medium and large, but the values of the intercepts do not follow this order (Table 3). The analysis of covariance showed that although some species differed in their y-intercepts, there are not many species that differ. *Asplanchna*, a large bodied rotifer, has a lower y-intercept than do some small, medium and medium-large rotifers: *Kellicottia*, the large morph of *K. cochlearis*, and *Polyarthra*. The ANCOVA also showed the smaller *K.cochlearis* (large morph) to have a higher intercept than the larger *Polyarthra*. Although these trends are in the direction that I had predicted, most of the species I observed in Deer Lake do not differ in their y-intercepts. This leads me to conclude that my evidence for higher reproduction at low food in smaller species is weak.

In addition, there appear not to be any body-size trends in the slope of these lines. The slopes of the regression lines relating egg ratios to food concentration are not significantly different from one another, based on overlap of 95% confidence intervals (Table 3). Both hypotheses predict that large species have higher reproductive potential at high food concentration than smaller-bodied ones. However, I found no evidence for this trend in the rotifer community that I studied. For example, the species with the highest change in egg ratio for a given change in food concentration are *K.quadrata* and small, spined *K.cochlearis*, a medium and a small-bodied rotifer (Table 3). The analysis of covariance revealed that although some species differed in their slopes, there was no particular body-size pattern in these differences in the value of the slope.

For example, *Kellicottia* (small-bodied) and *Polyarthra* (medium-large bodied) both had higher slopes than small and medium-bodied rotifers (unspined *K. cochlearis*, *K. quadrata*, and spined *K.cochlerais* (small morph)).

Nevertheless, it does appear that Deer Lake rotifers are exhibiting a trade-off between the amount of change in egg ratio for a unit change in food concentration, and the ability to maintain reproduction at extremely low food conditions (Figure 11). Although I have assumed equilibrium food and reproductive conditions in my analysis, this trade-off is reminiscent of the classical "velocity" versus "affinity" trade-off. However, this result may be an artifact of repeatedly sampling a set of points which all fall along the *same* regression line; if the slope was underestimated, the intercept was overestimated, and vice-versa. More analysis is necessary to determine whether this effect is real or not.

Sommer (1984) defines "affinity specialists" as species with slow responses in egg ratio to increases in food concentration. In contrast, he described "velocity specialists" as those species with high maximum population-growth rates (r_{max}) that respond to sudden increases in resource abundance with rapid increases in population density. My study assumed steady-state food conditions; I investigated the *magnitudes* of responses to various food concentrations, rather than the *rates* of these responses. However, I was unsuccessful in uncovering a correlation between the change in chlorophyll concentration from one sampling date to the next, and the strength of the response in egg ratio. I had expected that

the rate of change in egg ratio would be highest for large species, which theoretically respond most strongly to big increases in food concentration. This is because high levels of resource abundance tend to be present only during a brief window of time and require a quick reproductive response in order to be exploited successfully.

The subset of species for which birthrates could be calculated reveals a very similar pattern in the relationship between food concentration and reproductive rate (Figure 12). In addition to wide overlap of all 95% confidence intervals, there are no trends in y-intercepts that relate to body size. The smallest (*Kellicottia*) and the largest (*Polyarthra*) taxa have similarly high y-intercepts (Table 4). The largest species, *Polyarthra dolichoptera* does not appear to have higher reproductive rate than the other species, based on an inspection of the slopes relating birthrate to food concentration (Table 4). Therefore, there seems to be neither an effect of body size on the potential for reproduction at low food concentrations nor on the potential of large species for reproduction at high food concentrations.

Within a single species, there appears to be some evidence for the size-efficiency hypothesis. The large form of spined *K. cochlearis* carried more than 0.1 eggs/female at a significantly lower food concentration than either of the other two forms (Figure 13) suggesting that larger size allowed reproduction at lower food concentrations. This is in accordance with the argument of Hall et al. (1976), who elaborated on the size-efficiency hypothesis to show that the optimal size

increases with decreasing food concentration due to both greater efficiency of food collecting and somewhat greater metabolic economy.

The small, unspined form of *K. cochlearis* reproduced at a higher food concentration than the small, spined form, but this difference is not stastically significant (Figure 13). The spineless variety of *K. cochlearis*, often called *K.cochlearis* f. tecta is generally considered one of the best indicators of eutrophy (Ruttner-Kolisko 1972, Pejler 1980). This effect appears to be quite independent of temperature. Pejler (1962) found that at roughly equal temperatures, oligotrophic lakes contained only spined individuals , while forms without spines dominated in the eutrophic.

I found no evidence for either hypothesis relating food to reproductive rate in the direction of change in the average size of the rotifer community with the concentration of <25μm food (Figure 4). This indicates that there is no shift in the size-composition of the rotifer community with changing food concentration. Size does not appear to be a reliable indicator of the competitive ability and numerical dominance of rotifer species at a given phytoplankton concentration.

Reproductive rate may not be related to food abundance in the same manner as would be expected from the laboratory results of Stemberger and Gilbert (1985) for a variety of reasons. Recent research suggests that threshold food levels are not species-specific constants and may change along several environmental gradients. Achenbach and Lampert (1997) demonstrated that at temperatures above 20C, the threshold food level increased for all four

cladoceran species studied. Stelzer (1998) investigated how the threshold food

levels of three different planktonic rotifers (*Asplanchna priodonta, Brachionus*

calyciflorus, and *Synchaeta pectinata*) change along a temperature gradient of 12-

28C. He found that at 12C, *Brachionus* required a higher food concentration than

Synchaeta for zero population growth, while at 20C, the threshold food level for

both *Synchaeta* and *Asplanchna* surpassed that of *Brachionus*. In addition,

Stemberger and Gilbert's 1985 experiments calculated the food concentration as

algal dry mass using food of the cell sizes and types most highly preferred by the

rotifer species. In a natural zooplankton community such as that in Deer Lake,

the preferred food type will only be available to a subset of the rotifer species

because of inter-specific differences in food preference, and seasonal variation in

the occurrence of phytoplankton taxa. Feeding of rotifers on non-preferred

phytoplankton food decreases the clearance and ingestion rates (Gilbert and

Bogdan 1984). Therefore, a higher concentration of suboptimal cell types is

required to achieve the threshold food concentration. This may result in lowered

reproductive rates at food concentrations which, if composed of the preferred

cell type, could support zero population growth.

I am unable to conclude anything definitive about the impact of the

phytoplankton species composition on rotifer reproductive rates in my study.

Phytoplankton species identification was primarily of taxa >50μm in length, a

size category not grazable by most rotifers. The literature is filled with evidence

that planktonic rotifers differ greatly from each other in the taxa they choose to

or are able to ingest, and the fitness consequences of these choices. Rotifers are able to distinguish between prey items of similar size (Starkweather 1980, Gilbert and Bogdan 1984, Bogdan and Gilbert 1987, Rothhaupt 1990), and between nutritional states of the same food type. To further complicate matters, food preferences may not be a good indicator of the contribution of those items to growth and reproduction. For example, Sierszen (1990) reported that reproduction of *Keratella taurocephala* on its preferred food item is no higher than its reproduction on a less preferred food item, although it is possible that other life-history components such as survival are affected.

Despite the fact that all rotifers seem to discriminate amongst available food items, some do so more than others. Gilbert and Bogdan (1984) found that *Polyarthra* and *Synchaeta* are highly specialized on flagellates, especially *Cryptomonas*. The two peaks in *Synchaeta* abundance in Deer Lake appear to correspond roughly to the time periods following the blooms of *Cryptomonas* in late winter and late spring/early summer. However, I found no such pattern in the abundances of *Polyarthra* (Appendix 4).

CHAPTER 3: ROTIFER COMMUNITY STRUCTURE IN DEER LAKE

Introduction

The rotifer fauna is an ideal example of the ability of a group of species to coexist while utilizing the same pool of resources. Rotifers concentrate small particulate matter with currents generated by coronal cilia. Although diverse families of rotifers have dissimilar types of mastax, there are many examples of co-existence of rotifers of the same genus with the same type of mastax (Miracle 1974, Stemberger et al. 1979, Herzig 1987). This suggests that other niche dimensions besides food are important in organizing these communities.

Rotifer life-history strategy depends on rapid reproduction and development that exceeds the rates of crustacean zooplankton (Allan 1976). The rates of these processes are highly dependent on temperature and oxygen (Mikschi 1989, Hofmann 1977, Berzins and Pejler 1989). At the same time, rotifers must compete for phytoplankton food with the more efficient cladoceran suspension-feeders, and avoid consumption by predators and damage or death in the feeding currents of large cladocerans (Stemberger and Evans 1984, Gilbert and Stemberger 1985). Therefore, the strategy-space within which a rotifer species, and indeed any species, exists is defined by dimensions which include its competitive ability, its resistance to predation, and its reproductive ability. Certainly, these competing goals and alternative energy drains require that species make trade-offs in their life-histories, morphology and behavior, which

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allow them to increase under certain combinations of ecological conditions

(Cody 1974). In this view, community composition is influenced by the

combination of (1) a species' ecological "ability" along the axes of competitive

ability, resistance to predation, and reproductive/colonization ability, and (2) the

opportunities that the other species in the community provide. In the first part of

my study of a natural rotifer community in a eutrophic lake in British Columbia,

I attempted to explain the seasonal succession of occurrence by examining in

detail success along one axis of the strategy-space: competition for

phytoplankton food. In this chapter, I now analyze the effects of this niche axis

in the context of other demands, including temperature, competition with

cladocerans, and predation, in an attempt to formulate some hypotheses about

the relative importance of these structuring factors and the ways in which they

interact to affect seasonal distribution and abundance of rotifer species .

Temperature

As early as 1943, Carlin demonstrated that temperature and food strongly

influences the maximal occurrence of various rotifer species, with some species

identifiable as perennial and others as seasonal. A regression analysis showed

that the reproductive rates of all three rotifer species studied by Edmonson

(1965) in the field were strongly related to temperature. Those rotifer species

considered seasonal generally occur either (1) in winter or early spring, or (2) in

warm water during summer. Hutchinson (1967) studied several examples of

seasonal successions and found that seasonal species are of two general types: (a) cold stenotherms that develop greatest populations in winter and early spring, and (b) warm stenotherms that develop maxima in summer, often with two or more maxima, especially in late summer in conjunction with the development of certain types of cyanobacteria. For many rotifer species, the temperature at which maximal population abundance is recorded or the species is observed in the plankton is similar between lakes of different trophic status, morphometry, and geographic region (Hutchinson 1967). This lends support to the idea that differing temperature tolerances and/or optima permit some rotifers to occupy niches that are both spatially (metalimnion, hypolimnion) and seasonally unsuitable for other rotifers.

The embryonic development time of every rotifer species has a characteristic temperature response. The development time is quite independent of the type and quantitative nutrition of the adult female (King 1967). Development times decrease curvilinearly with increasing temperature, and regression equations describing this relationship have been calculated for various species. Species that occur in cold waters tend to have relatively short development times at low temperature, and longer development times than their warm stenothermous counterparts at high temperature (Herzig 1983). Temperature is a crucial factor in determining occurrence and fertility, particularly in stenothermal species (Hofmann 1977), and therefore it is not surprising that since the early part of the century, investigators have consistently

considered temperature to be the strongest force in structuring rotifer communities (Hofmann 1977, Berzins and Pejler 1989). Although observational studies on rotifer community composition are correlational and do not imply causation, there nevertheless seems to be a consensus that the seasonal succession of rotifers in lakes of the north temperate regions depends mainly on changing temperatures and different species-specific adaptations to temperature.

Competition between rotifers and cladocerans

Rotifers and cladocerans usually have similar food niches, but body sizes that may differ by several orders of magnitude. Neill (1984, 1985) suggested that the rotifers and *Daphnia rosea* in Gwendoline Lake, B.C., were competing almost exclusively through exploitation for limiting food resources, although other workers (Burns and Gilbert 1986) have established that large *Dahpnia pulex* may also kill rotifers by mechanical interference. For example, *Keratella cochlearis* is entrained in *Daphnia*'s feeding current and physically damaged, leading to the complete exclusion of this species from laboratory cultures (Gilbert and Stemberger 1985). Schneider (1990) found that at both high and low food levels, *K. cochlearis* is strongly affected by interference competition with large *Daphnia* but not by exploitative competition, and *K. crassa* shows no evidence of suppression by *Dahpnia* through interference competition.

Rotifers are more likely to get swept into the feeding current of large cladocerans, such as *Daphnia* than of small cladocerans such as *Ceriodaphnia* or

Bosmina. MacIsaac and Gilbert (1991) suggest that interference competition should favor invulnerable rotifer species, many of which are large bodied. They believe that exploitative competition should favor rotifer species with low food requirements, which tend to be small-bodied, though this idea is not supported by my data presented in Chapter 1.

Predation

As small-bodied zooplankton, rotifers are subject to predation from invertebrate predators. Neill (1985) found that the survival of the first two instars of *Chaoborus* in Gwendoline Lake, British Columbia, is strongly correlated with mid-summer densities of its primary food source, solitary rotifers. Soft-bodied, small rotifers such as *Synchaeta*, and some soft-bodied evasive forms like *Polyarthra major* are particularly susceptible to copepod predation (Williamson 1983). Stemberger and Evans (1984) suggest that succession from a spring community dominated by susceptible species to a summer community dominated by resistant species is partially related to differential mortality caused by variation in the abundance of cyclopoid predators. Additionally, there is much evidence that some rotifers, in response to predator exudates or a reliable environmental cue, can either lengthen or grow additional spines, and that these spines are effective in preventing capture and ingestion by some types of predators (Gilbert and Williamson 1978, Gilbert 1980, Stemberger and Gilbert 1984). These studies suggest that predation by

invertebrate predators is important as a selective pressure for many rotifer populations.

Objectives

The purpose of this part of the study was to use multivariate methods, specifically, principal components analysis, in order to form hypotheses about ecological processes that influence rotifer community structure. This method allowed me to identify a reduced number of axes onto which most of the variability in species composition could be projected. I wanted to determine whether particular groups of species tended to occur together to form ecological entities either in terms of (1) their abundances, (2) their rates of increase, or r, and (3) their egg ratios. My aim was to organize species data into functional or strategic groupings that did not necessarily conform to chronological groups, or any other imposed structure. I used ordination to group together species that perform in a similar manner, and then to look for features (such as body size, defense mechanisms, taxonomic relationships) that might be responsible for their like occurrences.

I predicted that even though population parameters did not show an effect of food availability on mean body size in Deer Lake, chlorophyll concentration may play an important role at the community level in determining the density and timing of occurrence of species of various body sizes. However, I expanded my analysis to other processes and factors that had been shown in

the literature to have large impacts on rotifer survival, development, and reproduction. In particular, I considered the temperature-dependent embryonic development rates of the rotifer species occurring in Deer Lake, and examined how these related to seasonal patterns of occurrence. I also considered patterns of occurrence and co-occurrence in terms of the abundance of cladoceran competitors and copepod predators, and related these to attributes of various rotifer species that conferred resistance or vulnerability.

RESULTS

Species diversity

The diversity of the Deer Lake rotifer community, measured using Simpson's index, steadily decreased from 4 to approximately 1.5 between January and mid-April at which time it increased and fluctuated between 3.5 and 1 (Figure 14a). Diversity did not seem to vary with the concentration of chlorophyll a (shown in Figure 14b as the size fraction of cells less than 25μm in length); there was considerable variation in species diversity for any one phytoplankton concentration.

Ordination of species abundances

A principal components ordination of log (x+1) transformed rotifer abundance data from zooplankton samples between January and August was successful in explaining a large proportion of the variation in between-sample differences in species abundance. Component 1 accounted for 32.85% of the variance, and component 2 explained 23.93% of the total variation. The rotifer samples I collected seem be arranged seasonally in principal components space (Figure 15a). The trajectory of samples on the principal components plot is circular, such that early-season samples occur at low values of both PC 1 and PC 2, and early summer samples are found at intermediate positive values of both

PC 1 and PC 2. By late summer, the position of the samples returns to a position similar to that of the winter samples.

The winter species, *K. quadrata*, *Kellicottia longispina*, and the small unspined form of *K. cochlearis* are negatively correlated with component 1, whereas *Polyarthra*, *Asplanchna*, *Conochilus*, *Trichocerca*, and large *K. cochlearis* have highly positive loadings on this axis. The spined, small form of *K. cochlearis*, *Polyarthra*, and *Synchaeta* have the highest loadings on the second principal component axis; *Conochilus*, the large *K. cochlearis*, and *Trichocerca* have negative loadings (Figure 17). Bonferroni corrections for multiple comparisons reduced the critical significance level to 0.001. Table 7 summarizes correlations between species in the Deer Lake samples, and their significance levels. It appears that *Conochilus sp.*, *Asplanchna sp.*, large *Keratella cochlearis*, small spined *K. cochlearis*, and *Polyarthra dolichoptera* are significantly correlated with one another in principal components space; the log abundance of each of the members of this group is significantly correlated with at least two other members. Small, unspined *Keratella cochlearis*, *Keratella quadrata* and *Kellicottia* form a second grouping of species; *K. quadrata* is significantly correlated with both *Kellicottia* and small, unspined *K. cochlearis*.

In addition, a principal components ordination of presence/absence rotifer data yielded nearly identical results to the ordination on log-transformed abundances. This indicates that my results were not affected by any potential non-normality in the principal components.

Temperature

I ranked the five species found in Deer Lake for which temperature-development time regression equations exist by relative development speed (1 as the fastest and 5 as the slowest for 30 temperatures ranging from 0 to 30C. Species that had positive slopes had faster development at lower temperature, and were labeled cold stenotherms, while those that had a relatively faster reproduction at higher temperature had negative slopes and were labeled warm stenotherms. The higher the value of the slope, the stronger is the preference for either cold or warm temperature. Table 8 summarizes the slopes of the equations relating temperature to development time rank for each of the taxa. The slopes of all regression equations were significantly different from zero ($p < 0.02$).

Species	slope of the regression equation
Keratella quadrata	0.08
Keratella cochlearis	0.06
Synchaeta pectinata	-0.02
Conochilus sp.	-0.07
Polyarthra dolichoptera	-0.03

Table 8. Slopes of regression equations relating temperature (on x-axis) to relative development speed (from fast to slow, on y-axis) of 5 rotifer species for which temperature-development equations exist.

In the principal components ordination of the log-transformed rotifer abundances, the first principal component is highly correlated with temperature

(df=46, F=111.81, p<0.001, R^2=0.71) (Figure 16a). Therefore, low loadings on the first component axis correlate with occurrence at low temperature, and high loadings correlate with high temperatures. When the slopes given in table 8 are plotted against their loading on the PC-1 axis, a strong negative correlation results (Figure 16b).

In the regression equations of the form $D = a(t-b)^c$ derived from the literature, which relate temperature to development time, the constant c describes the overall relative development speed, because it regulates the proximity of the curve to the temperature (x) axis . At higher values of c, overall development time is faster than for species with regression equations containing a lower value of c (Herzig 1983). Figure 16c shows that the number of samples in which a species occurs increases as the overall relative development speed rises (R^2=0.59).

Correlation of the principal components with predators, competitors and food

The second principal components axis is strongly correlated (df=46, F=21.81, P<0.001, R^2=0.33) with log cyclopoid abundance, whereas the first principal components axis is not correlated so strongly with these predators (P=0.05, R^2=0.08), (Figure 17c and d). Figure 18 shows the relationship between the seasonal fluctuations in abundance of cyclopoid copepods, which is closely tracked by the change in abundance of spined *Keratella cochlearis*, but not by the unspined form of this species.

The log of *Daphnia* abundance explains 48% of the variation in factor 1 (p<0.001), but only 24% of the variation in factor 2 (P=0.0005) (Figure 17a and b). Chlorophyll a levels tend to decrease as factor 1 increases; chlorophyll a increases with factor 2 (Figure 19). The size fractions 8-25μm and <25μm are those most highly correlated with the value of factor 1 on that sampling date (R^2=0.32, p<0.001 and R^2=0.28, p<0.001 respectively). Factor 2 appears to be correlated only with chlorophyll a that is >25μm in size (R^2=0.29, p=0.000).

Ordination of rates of increase

An ordination of *r*, the instantaneous rate of population increase, was capable of explaining 26.9% and 23.8% of the variation in the first and second components, respectively. Figure 20 shows the loadings of the rotifer species on the first and second components. The hard-bodied rotifers, except for the large *K. cochlearis* have high loadings on the second principal component. All hard-bodied species with lorica, except for large *K. cochlearis* (which, while not significantly positively correlated with the hard-bodied group, was negatively correlated with the soft-bodied group) are significantly correlated with one another (P<0.001, Bonferroni correction, Table 9). The soft-bodied rotifers, *Polyarthra*, *Synchaeta*, *Trichocerca*, *Asplanchna*, and *Conochilus*, have negative loadings on the second principal component axis. The correlation matrix in table 8 shows that *Asplanchna*, *Conochilus*, and *Tricocerca* are significantly correlated with one another (P<0.001, Bonferroni correction for multiple comparisons).

There was no clear pattern in the sampling dates with respect to r-values of the rotifers (Figure 20). I found no relationship between either of the first two principal components and temperature, *Daphnia* abundance, cyclopoid copepod abundance, or the concentration of any size fraction of chlorophyll a.

Ordination of egg-ratios

The results of a principal components analysis of egg ratios of rotifer species which carry their eggs are shown in Figure 21. Early season samples (January through April) generally have positive loading on the first principal components axis, whereas late season samples (April through August) had negative loadings on this axis. The loadings on these axes clearly separate into two groups: *Asplanchna* and large *Keratella cochlearis*, which have high loadings on factor 2 and low loadings on factor 1, and the other five taxa (spined and unspined *Keratella cochlearis, K. quadrata, Kellicottia,* and *Polyarthra*), which have high loadings on factor 1 and lower loadings on factor 2). The species in these groupings are significantly positively correlated with one another (Table 10). As in the ordination of r-values, the factors 1 and 2 in this PCA were not correlated with any physical or biological factors that I measured: temperature, chlorophyll concentrations, competitors or predators.

		Asplanchna	K.c.large	K.c.small	K.c. unspined	Kellicottia	K.quadrata	Polyarthra	Conochilus	Synchaeta	Trichocerca
Correlation	Asplanchna sp.	1.00	0.433*	0.468*	-0.29	0.01	-0.18	0.74*	0.44*	0.12	0.34
	K. cochlearis (large)	0.43*	1.00	-0.04	-0.429*	-0.23	-0.36	0.38	0.40	0.22	0.691*
	K. cochlearis (small, spined)	0.468*	-0.04	1.00	0.23	0.13	0.29	0.782*	-0.10	0.481*	-0.25
	K. cochlearis (small, unspined)	-0.29	-0.429*	0.23	1.00	0.08	0.426*	-0.18	-0.19	0.27	-0.32
	Kellicottia longispina	0.10	-0.23	0.13	0.08	1.00	0.442*	-0.11	-0.16	-0.20	-0.18
	Keratella quadrata	-0.18	-0.36	0.29	0.426*	0.442*	1.00	-0.22	-0.17	0.18	-0.27
	Polyarthra dolichoptera	0.74*	0.38	0.782*	-0.18	-0.11	-0.22	1.00	0.15	0.41	0.18
	Conochilus sp.	0.44*	0.40	-0.10	-0.19	-0.16	-0.17	0.15	1.00	0.08	0.572*
	Synchaeta pectinata	0.12	0.22	0.481*	0.27	-0.20	0.18	0.41	0.08	1.00	0.10
	Trichocerca sp.	0.34	0.691*	-0.25	-0.32	-0.18	-0.27	0.18	0.572*	0.10	1.00

Table 7. Correlation matrix of log-transformed rotifer abundances. Asterisks indicate significance at the $P<0.001$ level.

		Asplanchna	Conochilus	K. c. large	K. c. spined	K. c. unspined	K. quadrata	Kellicottia	Polyarthra	Synchaeta	Trichocerca
Correlation	Asplanchna sp.	1.00	0.812*	- 0.508*	0.08	-0.01	0.00	0.03	0.11	0.18	0.37
	Conochilus sp.	0.812*	1.00	- 0.519*	0.18	0.00	0.00	0.00	0.14	0.27	0.454*
	K. cochlearis (large)	- 0.508*	- 0.519*	1.00	-0.07	0.00	0.01	-0.16	-0.04	-0.17	-0.29
	K. cochlearis (small, spined)	0.08	0.18	-0.07	1.00	0.483*	0.585*	0.558*	0.18	0.05	0.00
	K. cochlearis (small, unspined)	-0.01	0.00	0.00	0.483*	1.00	0.32	0.18	0.08	-0.07	-0.01
	Keratella quadrata	0.00	0.00	0.01	0.585*	0.32	1.00	0.552*	-0.38	-0.03	-0.02
	Kellicottia longispina	0.03	0.00	-0.16	0.558*	0.18	0.552*	1.00	0.09	-0.23	-0.08
	Polyarthra dolichoptera	0.11	0.14	-0.04	0.18	0.08	-0.38	0.09	1.00	0.12	-0.02
	Synchaeta pectinata	0.18	0.27	-0.17	0.05	-0.07	-0.03	-0.23	0.12	1.00	0.25
	Trichocerca sp.	0.37	0.454*	-0.29	0.00	-0.01	-0.02	-0.08	-0.02	0.25	1.00

Table 9. Correlation matrix of r-values of rotifer species in Deer Lake. Asterisks indicate a significance level of P<0.001.

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| Correlation	Asplanchna	K. c. large	K. c. spined	K. c. unspined	Kellicottia	K. quadrata	Polyarthra
Asplanchna sp.	1.00	0.62*	- 0.41*	-0.39	-0.32	-0.33	-0.18
K. cochlearis (large)	0.62*	1.00	-0.41	-0.36	-0.30	-0.31	-0.22
K. cochlearis (small, spined)	- 0.41*	-0.41	1.00	0.59*	0.61*	0.81*	0.61*
K. cochlearis (small, unspined)	-0.39	-0.36	0.59*	1.00	0.34	0.49*	0.37
Kellicottia longispina	-0.32	-0.30	0.61*	0.34	1.00	0.62*	0.33
Keratella quadrata	-0.33	-0.31	0.81*	0.49*	0.62*	1.00	0.55*
Polyarthra dolichoptera	-0.18	-0.22	0.61*	0.37	0.33	0.55*	1.00

Table 10. Correlation matrix of egg-ratios of rotifer species in Deer Lake. Asterisks indicate a significance level of $P<0.002$.
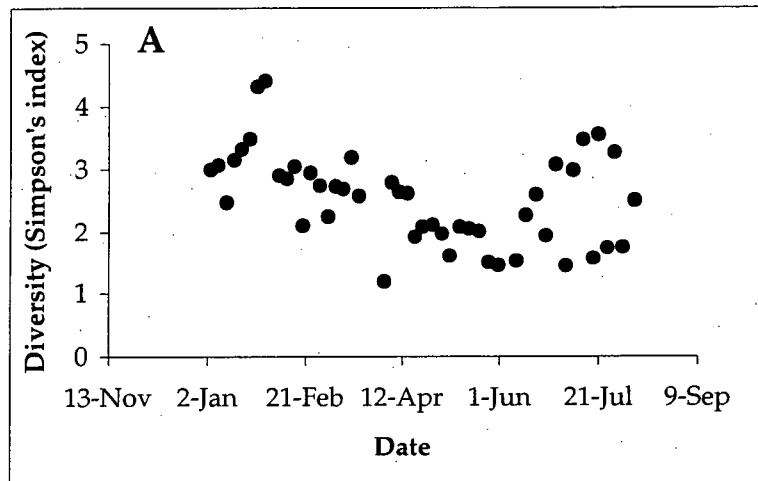
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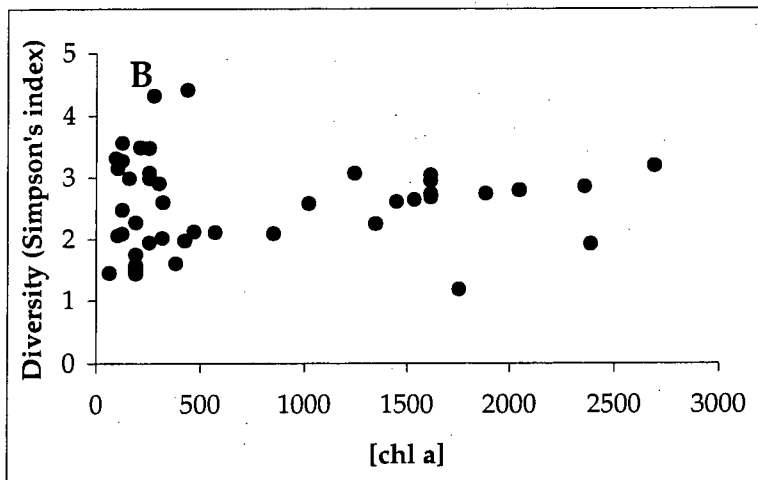
Figure 14. The relationship between Simpson's diversity index and (a) sampling date (b) chlorophyll a concentration (µg/L) of cells < 25µm in length.
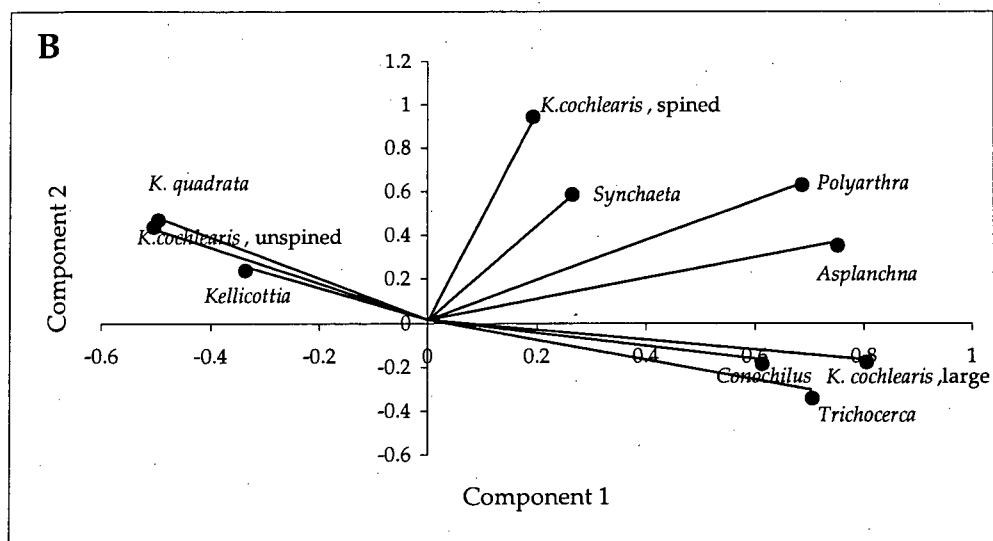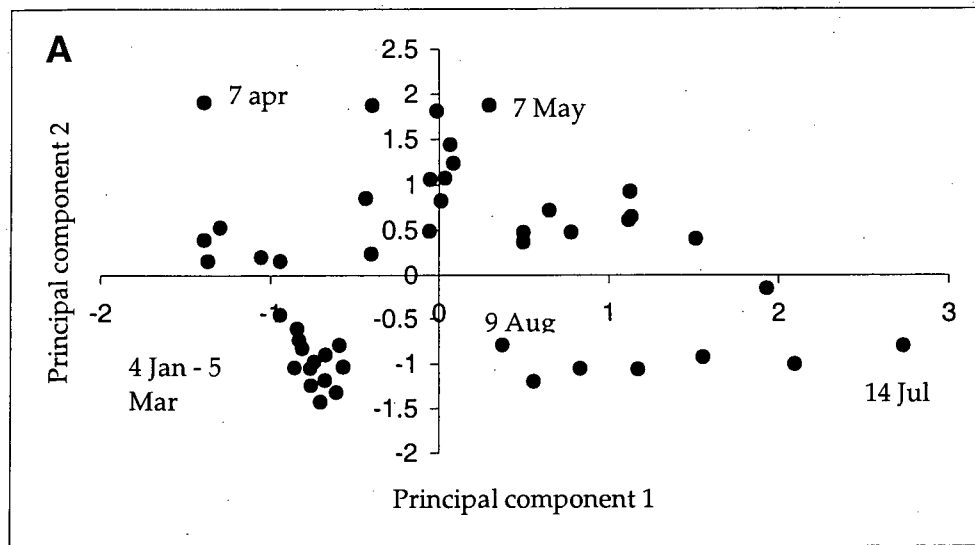
Figure 15. A) Principal components ordination of similarities in rotifer species composition of samples between early January and early August. Each point represents a sampling date, and abundances were log-transformed in the analysis. B) Species loadings of the first two principal components.
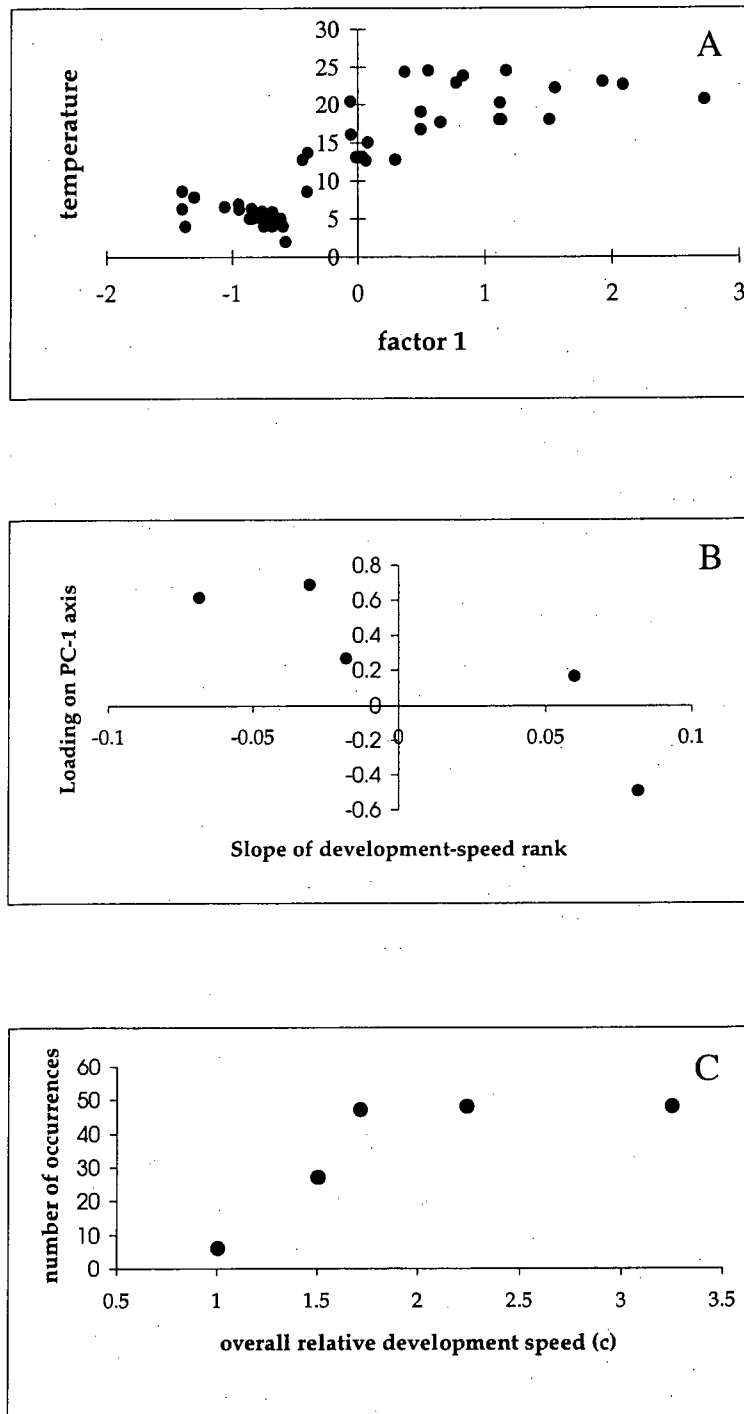
Figure 16. A) Water temperature and position along the first principal components axis of rotifer species-abundance samples collected between January and August. B) Loading along the first principal components axis and the rate of change of development speed with temperature (negative value on x-axis indicates a warm stenotherm, positive slope indicates a cold stenotherm) of five rotifer species. C) Frequency of occurrence in zooplankton samples and the development speed (c in the equation $D=a/(t-b)^c$) for five rotifer species.
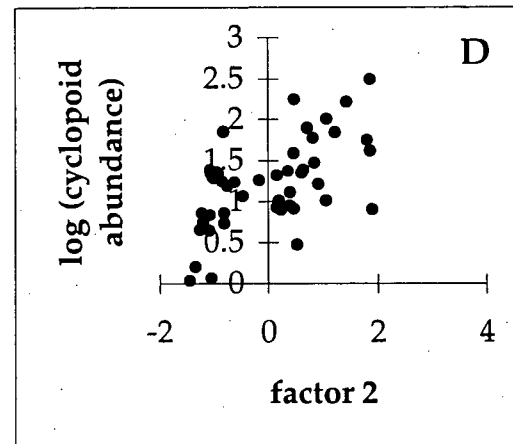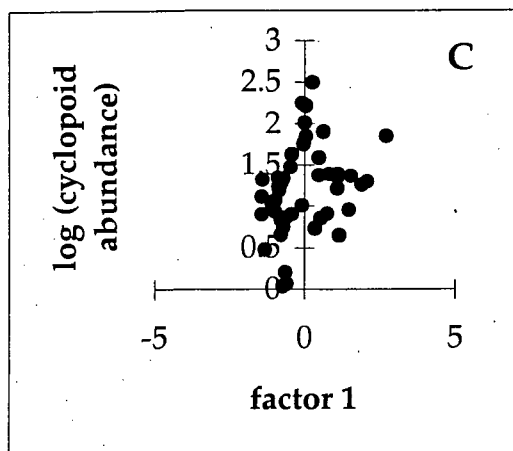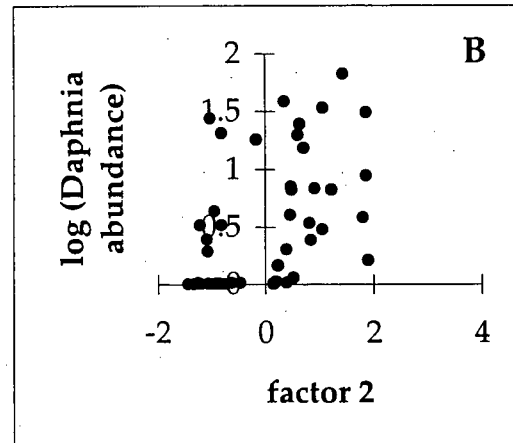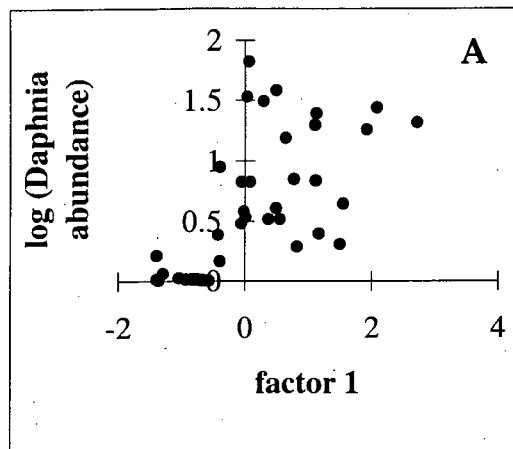
Figure 17. Position along the first and second principal components axes and the log-transformed abundances of *Daphnia* and cyclopoid copepods.
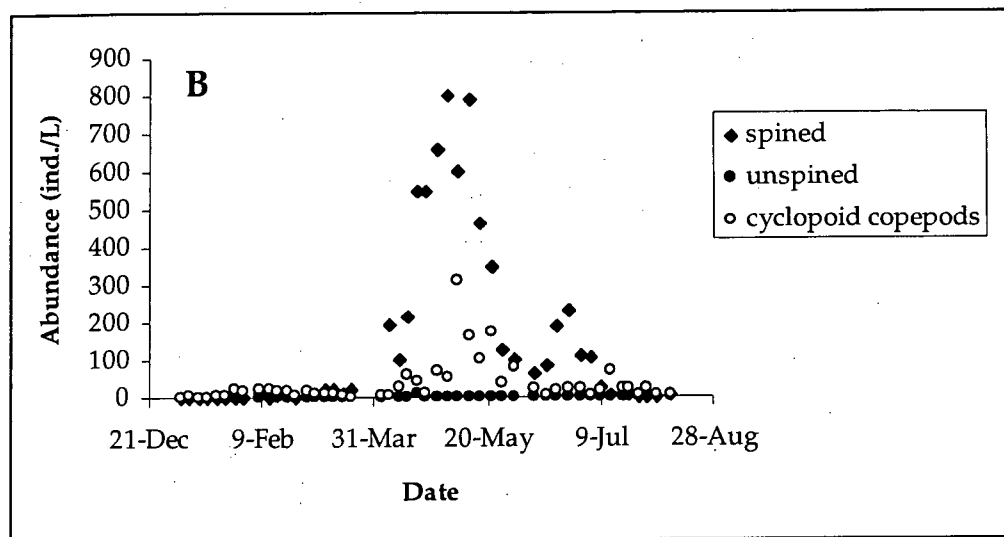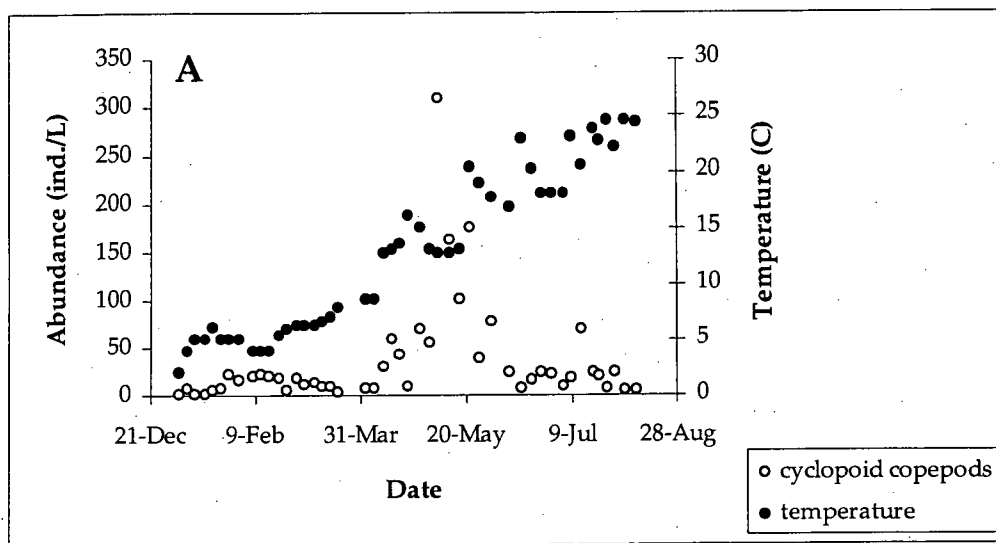
Figure 18. A) Changes in the abundance of cyclopoid copepods and temperature with sampling date in Deer Lake. B) Changes in the abundance of spined and unspined *Keratella cochlearis* and cyclopoid copeods with sampling date in Deer Lake.
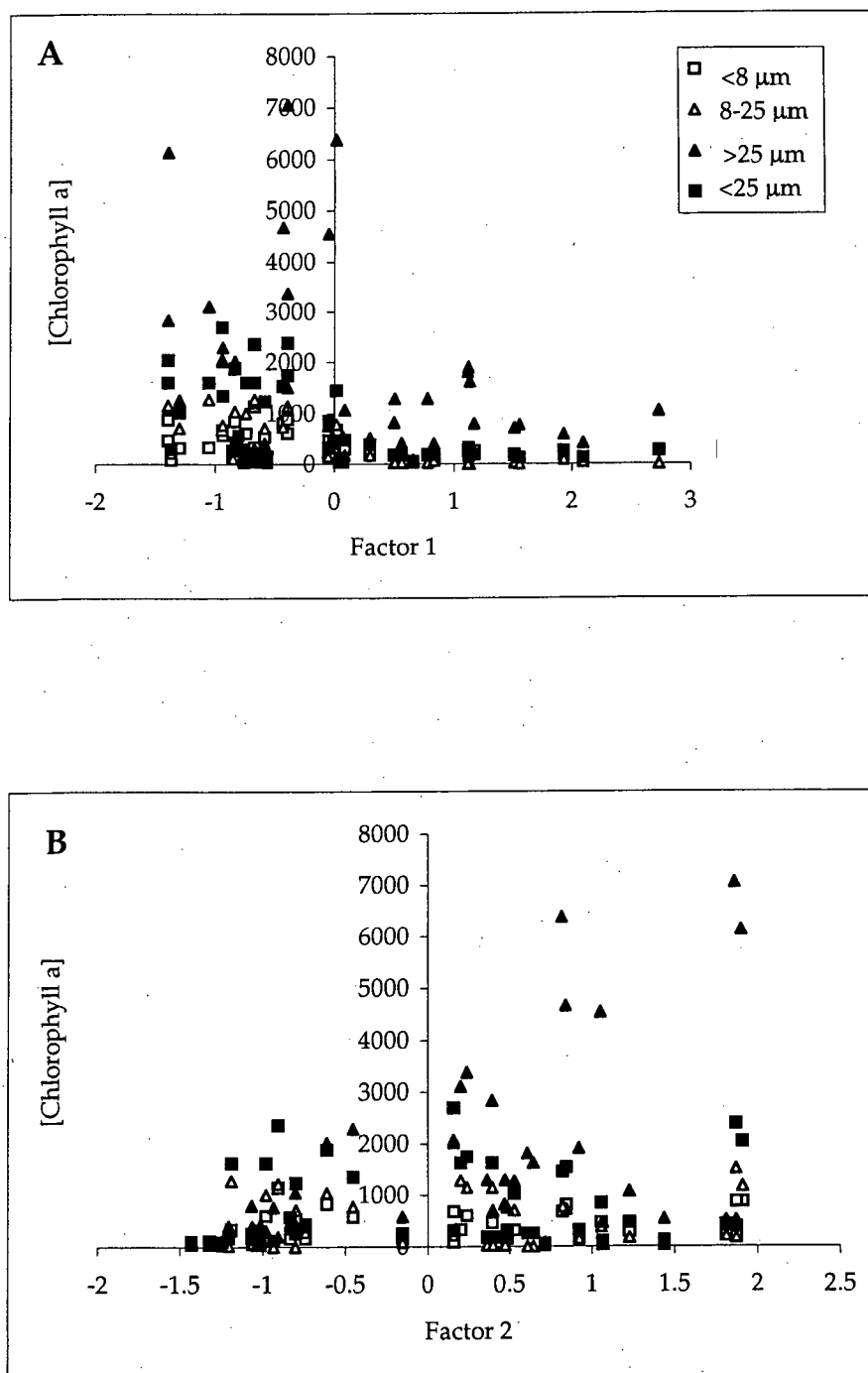
Figure 19. Correlations between chlorophyll a concentration (µg/L) and position along principal components axes 1 and 2, for each sampling date on which chlorophyll a was measured.
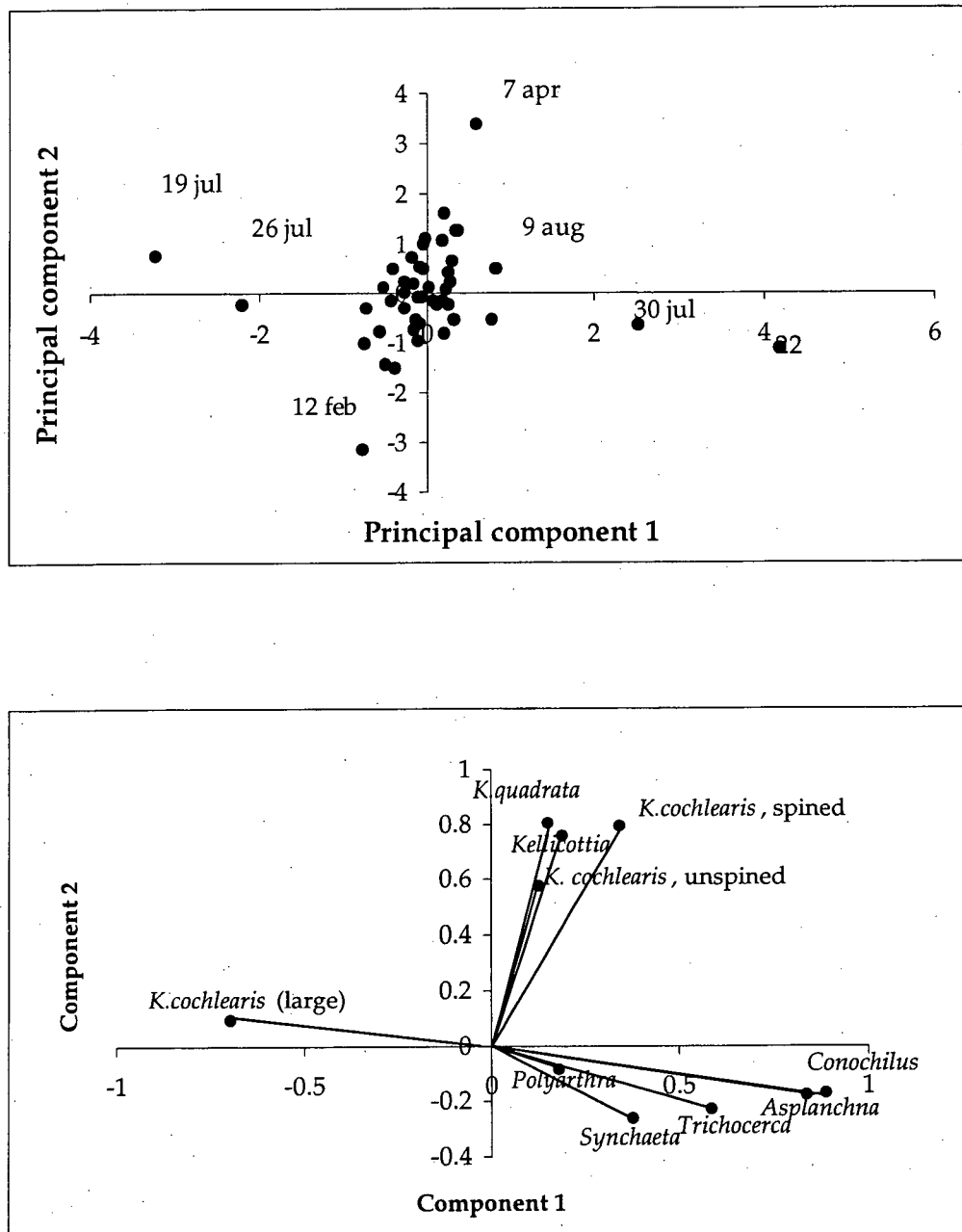
Figure 20. Top panel displays the principal components ordination of *r* (intrinsic rate of population increase) of rotifers collected from Deer Lake between January and August; each point is a separate sampling date. Bottom panel shows the species loadings for the first two principal components axes.

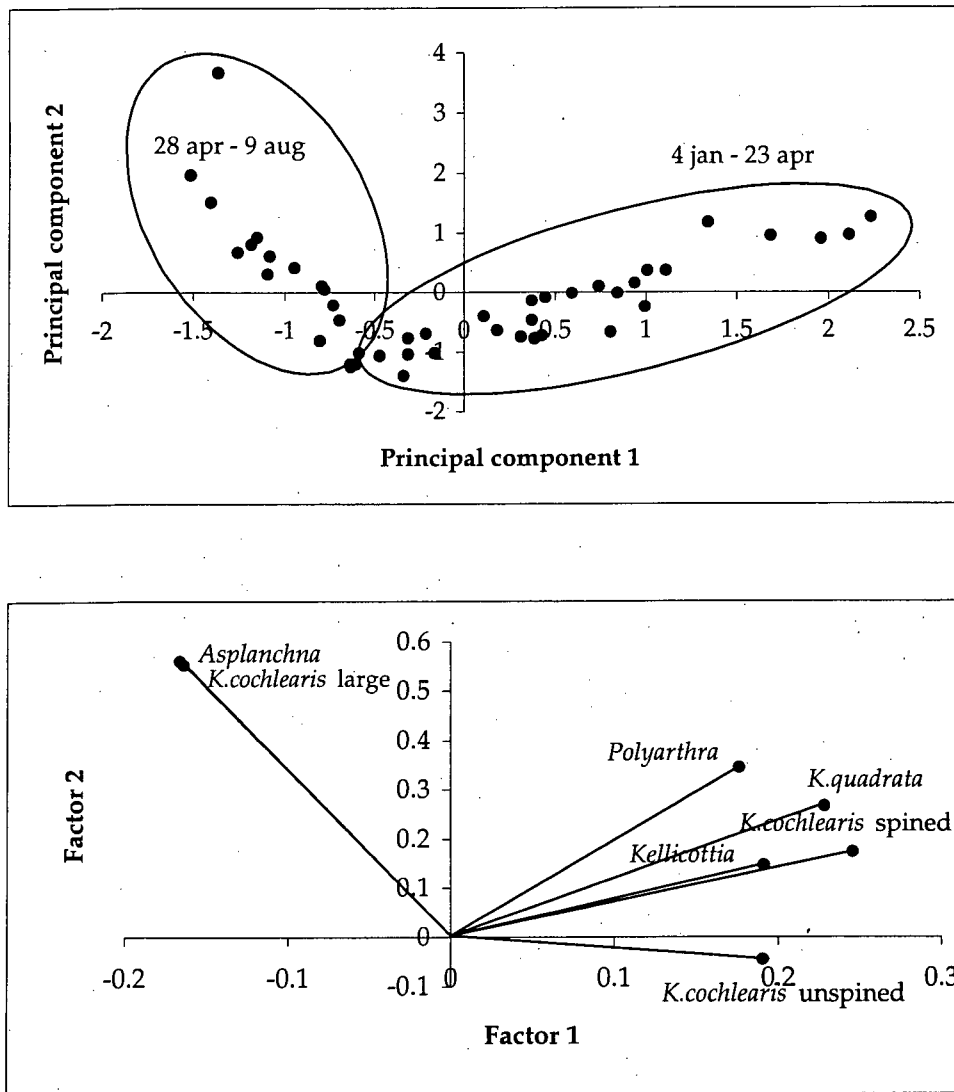Figure 21. Top panel displays the principal components ordination of egg ratios (average number of eggs per female) of rotifers collected from Deer Lake between January and August; each point is a separate sampling date. Bottom panel shows the species loadings for the first two principal components axes.

DISCUSSION

Species diversity

Perhaps the most fundamental descriptor of any community is species diversity.
I found some variation in rotifer diversity in the lake over my sampling period
(Figure 14a), but it did not correspond to my measure of food availability,
chlorophyll a (Figure 14). Given the rich literature on the relationship between
productivity and species diversity, I would have expected diversity to be highest
at intermediate levels of food abundance.

My data did not show any clear directional change in species diversity
with chlorophyll concentration (Figure 14). The literature is not definitive about
the direction of the relationship between productivity and the diversity of
consumer species. Many studies provide support for the idea that diversity rises
as resource availability increases. For example, Brown and Gibson (1983)
demonstrated that chydorid diversity is positively related to total primary
productivity. Similarly, Devetter (1997) found that maximal species diversity in
the rotifer community of a eutrophic reservoir occurred during the spring
phytoplankton bloom; lower rotifer diversity coincided with the lower summer-
autumnal phytoplankton peaks. Rutherford et al. (1999) report that
foraminiferal diversity peaks at middle latitudes (intermediate productivity) in
all oceans. Furthermore, Leibold (1999) suggest that species richness is a
declining function of nutrient levels in lakes. Perhaps I would have detected
some type of directional or unimodal pattern of diversity with chlorophyll

concentration had I extended my data collection to several years and/or measured primary productivity instead of the standing crop of chlorophyll.

Principal components analysis on abundances

Temperature

I found that temperature is important in the timing of occurrence and the relative abundances of rotifers in Deer Lake. The first principal component in the ordination of rotifer abundance data is strongly correlated with temperature (Figure 16). *K.quadrata* and *K.cochlearis* behaved as cold-stenotherms in Deer Lake, consistent with their physiological response of development time to temperature (Table 8). Development time is closely related to rotifer success because this group relies on rapid development time to compensate for small broods (Allan 1976). Similarly, *Conochilus* and *Polyarthra dolichoptera* had high loadings on the PC axis positively correlated with temperature and tended to have relatively fast development in warm water. I therefore considered these species as warm stenotherms. In this scheme, eurythermal organisms are not correlated with high or low temperature. This pattern is consistent with the relative limits of tolerance for animals of differing thermal preferences, in which eurytherms have wide tolerance limits with an activity optimum at intermediate temperatures.

Predation and competition

Temperature may not directly influence occurrence through physiological tolerance limits, as most rotifer species have extremely wide temperature ranges within which they occur (Berzins and Pejler 1989). Rather, the influence of temperature is mainly indirect, enhancing or retarding development and interacting with other biotic and abiotic factors. One such biotic factor is likely to be predation risk from invertebrate predators. Whereas small size confers protection from fish predation, large size may provide this protection for organisms susceptible to invertebrate predators (Black and Hairston 1988). Nevertheless, the relative contributions of physiological (Buns and Ratte 1991, Lehman 1988) and predation risk-reducing mechanisms which result in changes in body size, are not well understood.

Both *K. cochlearis* and *P. dolichoptera* increased in size with increasing temperature over the sampling period (Figure 6). Cyclopoid predators are a major source of predation mortality for planktonic rotifers (Stemberger and Evans 1984). Temperature may be a cue for increased predation risk, or rotifers may respond directly to predator exudates. In Deer Lake, there is good correspondence between cyclopoid density and the size of small *K. cochlearis*. Body size of this rotifer increased most rapidly in April and May, when cyclopoid densities increased 200-fold, and exhibited no further increases in June and July, when cyclopoids again became less abundant (Figure 18).

Since the increase in body size in *K. cochlearis* was the result of an increase in spine length (Figure 6), spines may have allowed for the persistence of the spined variety of *K.cochlearis* and the disappearance of the unspined form during the period of high cyclopoid abundance (Figure 18). Spine induction in a laboratory clone of *K. cochlearis* was promoted by a water soluble factor released by the copepods *Tropocyclops prasinus* and *Mesocyclops edax* (Stemberger and Gilbert 1984). Therefore, differential selection on phenotypes of different spine and body lengths could have an important effect on the observed seasonal trends in *Keratella cochlearis* phenotypes.

However, the principal components analysis did not support the idea that either predation or competition are important in structuring whole rotifer communities in Deer Lake. The increase in log (cyclopoid abundance) with an increase in the score on the second PC axis did not result in higher loadings of typically predation-resistant taxa such as *Conochilus*, *Polyarthra* (Gilbert and Williamson 1978) and *Kellicottia* on this axis than of soft-bodied or susceptible taxa (Stemberger and Evans 1984) such as *Synchaeta* and unspined *Keratella cochlearis* (Figure 15). However, as discussed above, spined small *Keratella cochlearis* are associated with higher cyclopoid abundance (Figure 18, 17d), and this trend is seen as well in the principal components plot of Figure 15. Therefore, although there is no detectable community response to cyclopoid predation, there may be a response within a single species.

Large body size may prevent some rotifers from entering the feeding chamber of cladocerans, or from becoming damaged in the process. The association between a species' PC-loading on factor 1 (Figures 17a, 15) with high cladoceran density cannot be explained by body size, because species loadings along the factor 1 axis show no patterns of either increasing or decreasing size (Figure 15). However, the rapid escape response of *Polyarthra* may allow it to avoid the feeding currents of *Daphnia*, and this may explain its association with higher *Daphnia* densities.

Because factor 1 is significantly inversely correlated with chlorophyll a <25μm in length, (Figure 19), it appears that *K. quadrata*, *K. cochlearis* (unspined), and *Kellicottia* are associated with high food availability (Figure 15). The same figure shows that *Polyarthra*, *Asplanchna*, large *K. cochlearis* and Trichocerca occur at low food concentration. Nevertheless, a Student's t-test shows that the body size occurring at low food concentrations is no different from that occuring at high food concentration (df=3, t=-1.045, p=0.186). Because of the range of potential factors that could influence species abundance, the number of species in each size class may not have been large enough for the body-size-food availability relationship to emerge from all the noise in the data. Furthermore, mortality may have obscured abundance measurements in such a way that species with high growth rates did not have high abundance.

PCA on r-values and egg-ratios

The PCA analysis of r-values separates the loadings of the hard-bodied and the soft-bodied rotifers (Figure 20). I speculate that this is due to differential mortality on rotifers with and without a hard lorica. Although I did not find find an association between the component 2 axis and cyclopoid densities, it is possible that predation was having a significant impact on the rotifer community, and that it was not measured adequately or at a scale that affected rotifer survival. Alternatively, laboratory studies on the susceptibility of various rotifers to predation may not apply in field situations in Deer Lake. The ordination of egg ratios, marked by sampling date, is also largely uninformative in the sense of a lack of correlation of PC-axes with biological processes. *Asplanchna* and large *Keratella cochlearis* either cannot, or are not forced to, compete with the other rotifer species in terms of reproduction; the reproductive efforts of these two groups are well-separated in time and in ordination space (Figure 21).

SUMMARY AND CONCLUSIONS

• Rotifer egg ratios increased with food concentration (measured as chlorophyll a), despite wide intra-specific variability in the egg ratio observed at any given food concentration.

• Egg ratios were a useful surrogate measure of birthrate, when developmental rates of all species were not known.

• For all size fractions of chlorophyll a, slopes and y-intercepts of regression equations relating food concentration and reproductive output showed no patterns with respect to rotifer body size. Thus I have no evidence for either size-efficiency or the threshold-food concentration hypothesis.

• Three morphologically distinct forms of *Keratella cochlearis* occurred within my sampling period in Deer Lake.

• Within the species *Keratella cochlearis*, I found some evidence for the size-efficiency hypothesis; large *K. cochlearis* were able to sustain an intermediate level of reproduction at a lower food concentration than either of the two smaller forms.

• Total body length in *Keratella cochlearis* increased with temperature due to elongation of the posterior spine; total body length for *Polyarthra dolichoptera* likewise increased with temperature.

• The weighted average body size of the rotifer community did not change seasonally or with chlorophyll concentration.

• Principal components analysis of log-transformed abundances showed that temperature is important in structuring the rotifer community of Deer Lake; seasonal occurrence of species was correlated with the physiological response of development time to temperature.

• The occurrence of the spined form of small *Keratella cochlearis* was seasonally related to the occurrence of cyclopoid predators.

• Although the first and second principal component axes were significantly correlated with *Daphnia* and cyclopoid abundance respectively, I did not find that species with high loadings on these axes had morphological attributes which conferred resistance to interference competition or predation. .

• A principal components ordination of egg ratios yielded a separation of early season and late season samples; however, neither this ordination nor a principal components analysis of r-values resulted in significant correlation of component axes with the physical or biological factors I measured.

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Genus	Calculation formula	Simplified formula when:	then:	
Polyarthra	v=abc	b=0.7a c=0.4a	v=0.28a^3	
Keratella cochlearis	v=0.13(ab^2)	b=0.4a	v=0.02a^3	
Keratella quadrata	v=abc	b=0.7a c=0.33a	v=0.22a^3	
Kellicottia	v=0.26(ab^2)	b=0.33a	v=0.03a^3	
Synchaeta	v=0.26(ab^2)	b=0.6a c=0.6a	v=0.1a^3	
Asplanchna	v=0.52(ab^2)	b=c=0.7a	v=0.23a^3	
Trichocerca	v=0.52(ab^2)	a:b has to be measured	v=0.52(ab^2)	

Appendix 1. Formulas for calculation of rotifer body volumes (um^3) for various genera; a=length, b=width, and c=height (from Ruttner-Kolisko 1977)
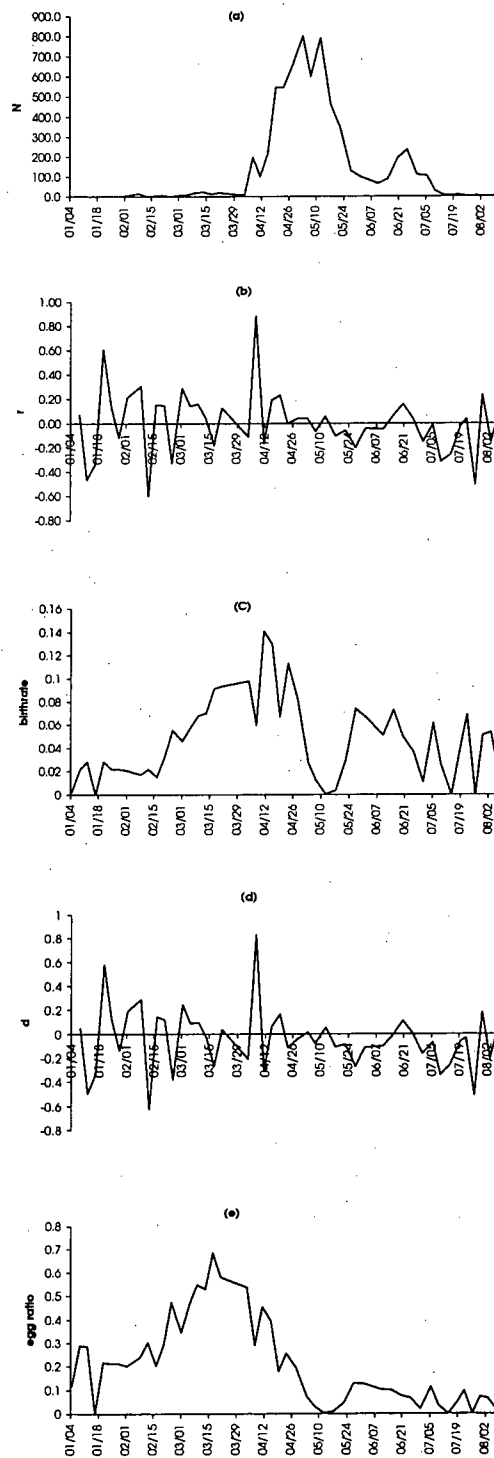
Appendix 2. Population characteristics of small, spined *Keratella cochlearis:* (a) abundance (b) rate of increase (C) birthrate (d) death rate (e) egg ratio
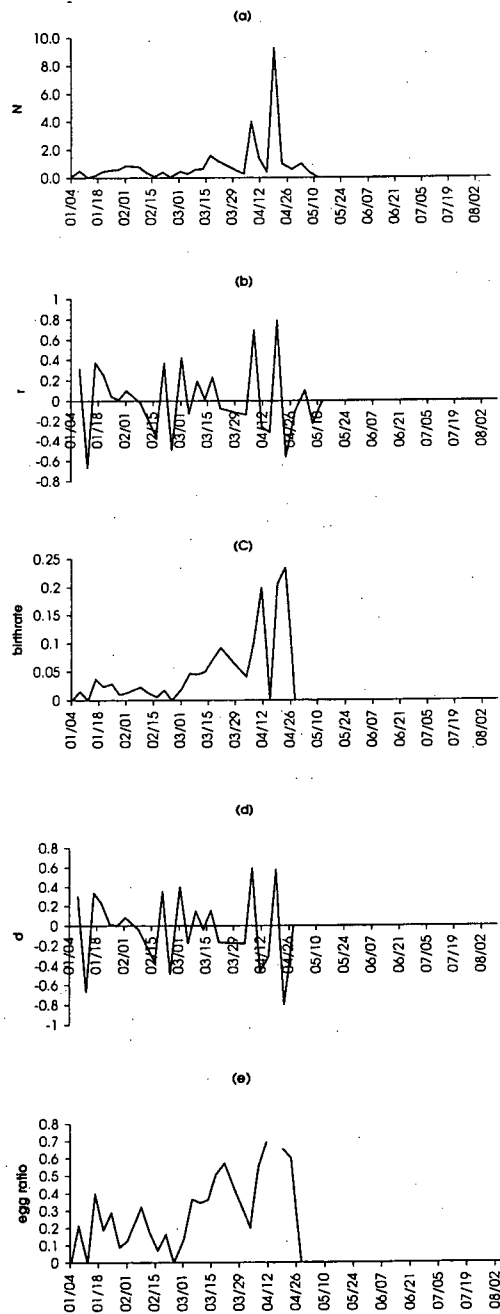
Appendix 3. Population characteristics of small, unspined *Keratella cochlearis:* (a) abundance (b) rate of increase (C) birthrate (d) death rate (e) egg ratio.
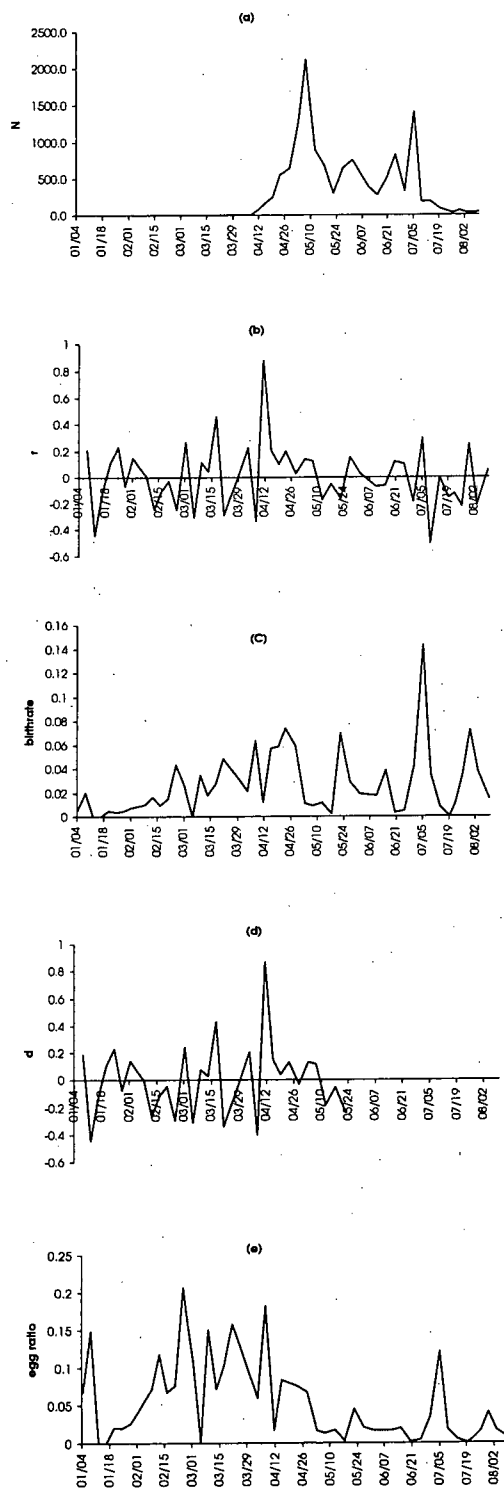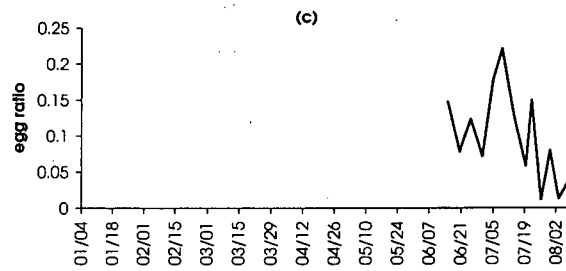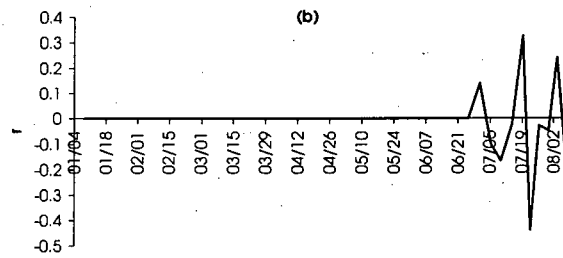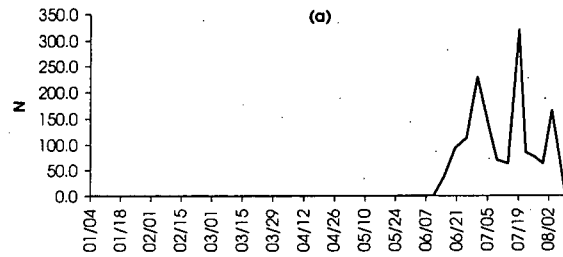
Appendix 4. Population characteristics of *Polyarthra dolichoptera*: (a) abundance (b) rate of increase (C) birthrate (d) death rate (e) egg ratio.
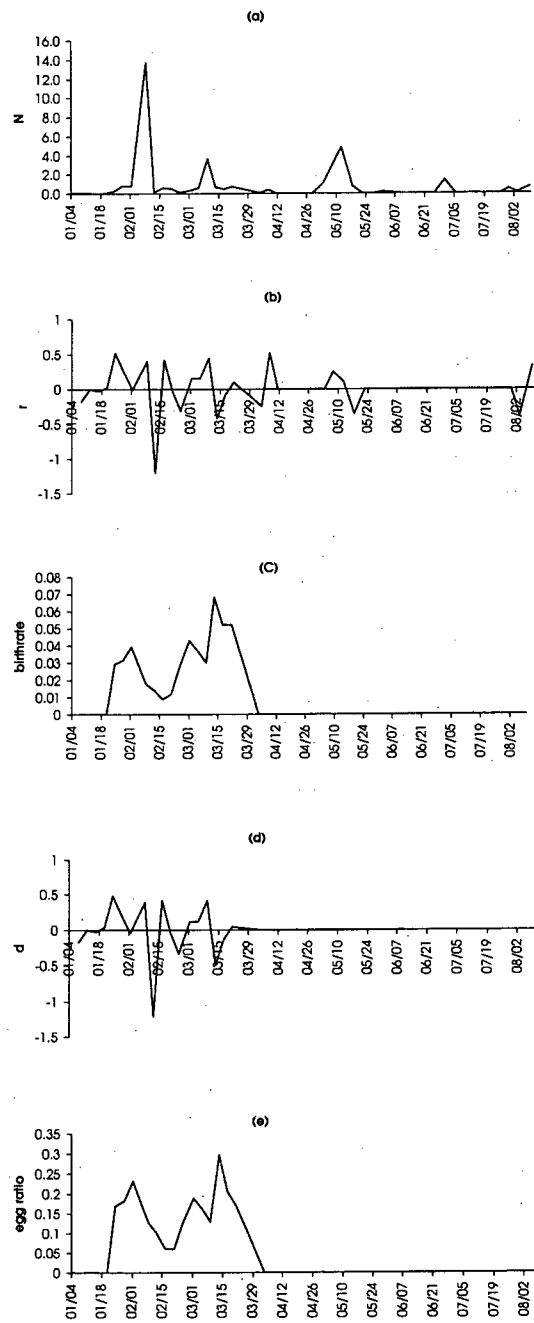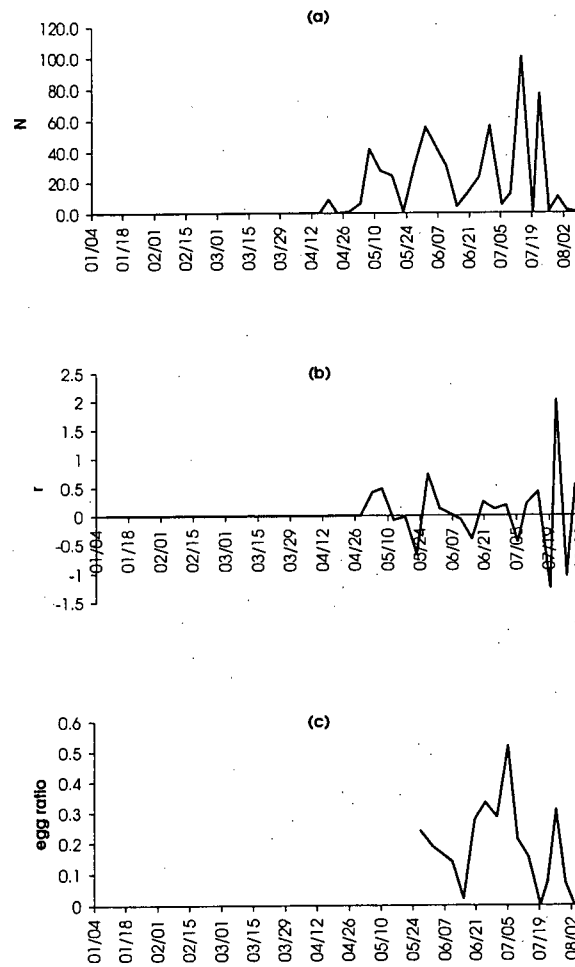
Appendix 5. Population characteristics of *Kellicottia longispina:* (a) abundance (b) rate of increase (C) birthrate (d) death rate (e) egg ratio.
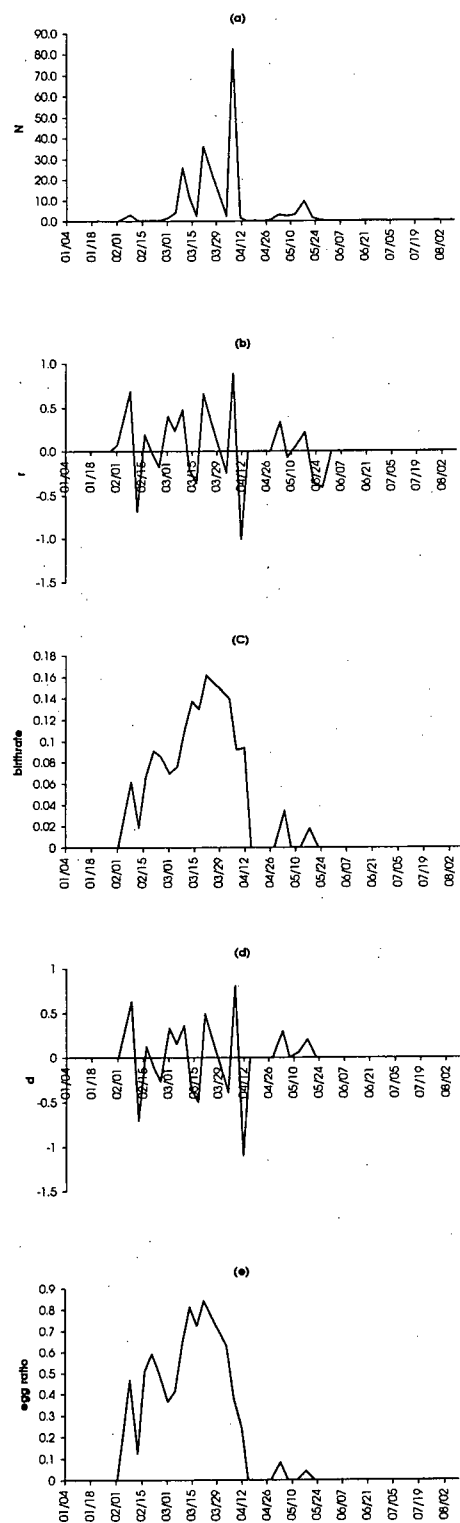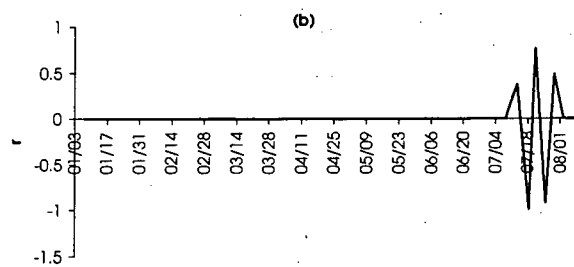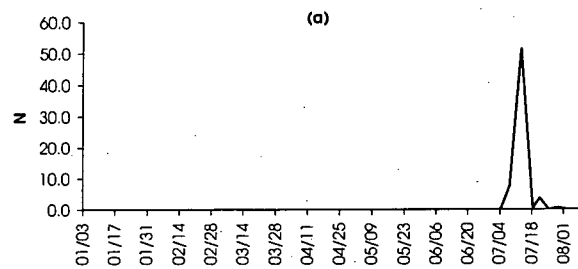
Appendix 6 Population characteristics of *Keratella quadrata:* (a) abundance (b) rate of increase
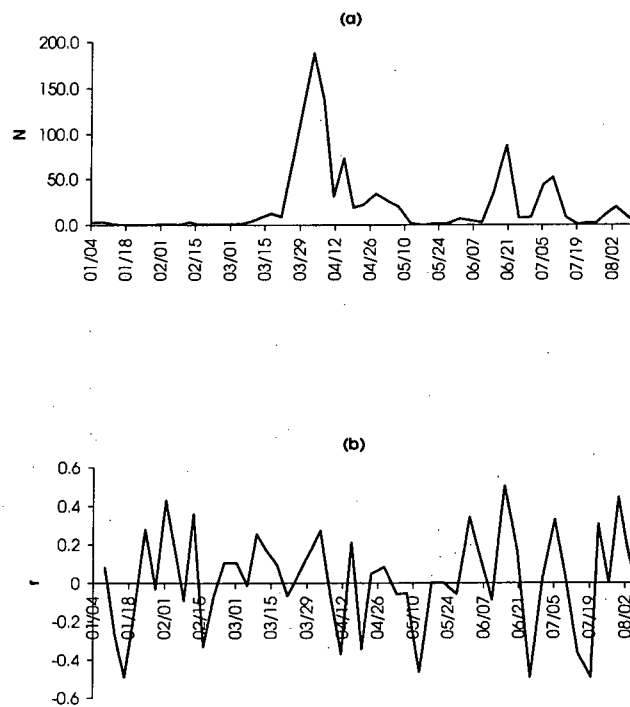(C) birthrate (d) death rate (e) egg ratio.

Appendix 7. Population characteristics of large *Kertatella cochlearis:* (a) abundance (b) rate of increase (C) egg ratio
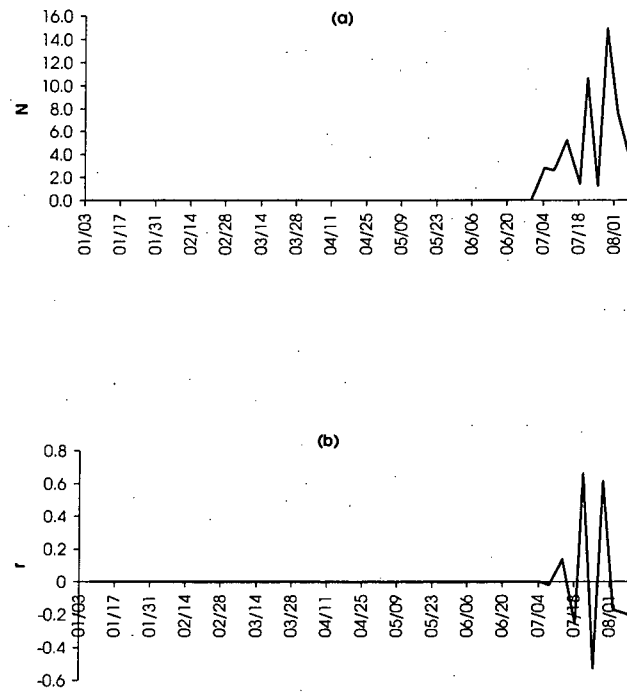
(a)

(b)

(c)

Appendix 8. Population characteristics of *Asplanchna sp.:* (a) abundance
(b) rate of increase (C) egg ratio

Appendix 9. Population characteristics of *Conochilus sp.*: (a) abundance (b) rate of increase.

(a)

(b)

Appendix 10. Population characteristics of *Synchaeta pectinata*: (a) abundance (b) rate of increase.

(a)

(b)

Appendix 11. Population characteristics of *Trichocerca sp.*: (a) abundance (b) rate of increase.