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UNIVERSITY OF ALBERTA

TROPHIC INTERACTIONS IN FISHLESS ALPINE LAKES OF THE CANADIAN ROCKY MOUNTAINS

by

Andrew J. Paul

A thesis submitted to the Faculty of Graduate Studies and Research in partial fufillment of the requirements for the degree of MASTERS OF SCIENCE.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1994

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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of graduate studies and research for acceptance, a thesis entitled TROPHIC INTERACTIONS IN FISHLESS ALPINE LAKES OF THE CANADIAN ROCKY MOUNTAINS submitted by Andrew J. Paul in partial fulfillment of the requirements for the degree of Master of Science.

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Date: 11 January 1994

Abstract

Numerous fishless alpine lakes have been stocked with trout and char to improve their recreational potential since the early part of the 20th century. In small lakes (<16 ha), stocked fish usually eliminate Hesperodiaptomus arcticus, the top pelagic predator under fishless conditions. I quantified the effects of predation by H. arcticus on rotifers, cyclopoid copepods, and phytoplankton in large in situ enclosure experiments (2250 L) using 2 levels of predator (present/absent) and 2 levels of nutrient addition (ambient, 4X). Standing [illegible] phytoplankton in several taxonomic groups were assessed using [illegible] performance liquid chromatography of algal pigments. The abundance and biomass of rotifers were significantly reduced in the presence of H. arcticus, regardless of nutrient additions. Densities of the soft-bodied rotifer Polyarthra dolichoptera were reduced 2-3 orders of magnitude and the loricate rotifer Keratella quadrata 1 order of magnitude relative to predator-free enclosures. In 69 lakes from the Canadian Rocky Mountains, the presence of Keratella or Polyarthra was negatively correlated with increasing Hesperodiaptomus densities (using maximum likelihood logistic regression); furthermore, the probability of Polyarthra occurring as Hesperodiaptomus densities increased declined more rapidly than that of Keratella. Densities of the cyclopoid copepod Diacyclops bicuspidatus thomasi were too low in the enclosures to quantify except for their nauplii; nauplii were, however, significantly reduced by H. arcticus predation. Under natural nutrient conditions H. arcticus had little effect on algal biomass, possibly due to high rates of nutrient recycling by grazers. Rotifer, cyclopoid nauplii and phytoplankton biomass all responded positively to nutrient additions. Nutrient addition increased algal standing crop 2-4 fold and changed dominance from diatoms and chrysophytes to blue-green algae. *H. arcticus* accelerated these changes by eliminating herbivory by rotifers. These results suggest that in the absence of increased nutrient flux, significant net predation effects from *H. arcticus* are strong but limited to adjacent food web levels in ultra-oligotrophic alpine lakes.

Preface

The structure of the thesis follows the paper format as outlined by the Faculty of Graduate Studies and Research, University of Alberta, October 1992. The research component of the thesis is presented in two manuscripts, chapters 1 and 2. The introductory and concluding chapters are intended to briefly outline my research, give an overview to mountain lake environments and present areas of further study. I have made an effort to keep repetition to a minimum. However, common aspects that underlie the research will unavoidably be repeated.

Acknowledgements

I would like to thank my supervisor D.W. Schindler for his commitment to research in the Canadian Rocky Mountians and continued attention to the endless drafts of my research. As well, the input from my committee members, P.R. Leavitt, W.M. Tonn and M. Hickman, was greatly appreciated. R.S. Anderson, P.J. Curtis and S. Lamontagne provided helpful comments on individual manuscripts within this thesis. I also thank S. Lamontagne, R. Vitic, B. Parker, P. Leavitt, A. Hardie, and the assitance of various students for their help in the field and Parks Canada for permitting this research. R.S. Anderson and D. Donald provided me with their unpublished data and archived samples. This work was supported by a Canadian Circumpolar Institute Boreal Research grant and a Natural Sciences and Engineering Research Council of Canada post-graduate scholarship to myself, an NSERC operating grant (#89673) to D.W. Schindler, and my wife.

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Introduction

The stocking of mountain lakes to create recreational fisheries has long been practiced. Alpine lakes of the Austrian Tyrol were stocked with Arctic char (*Salvelinus alpinus*) as far back as the late 15th century (Pechlaner 1984). The first recorded stocking of mountain lakes in the western United States and Canada are for the early part of the 20th century (Donald 1987, Larson & Liss 1991, Bahls 1992). Despite its late start, stocking with fish has dramatically reduced the number of pristine mountain lake ecosystems in both countries (Bahls 1992, Schindler et al. in review). The purpose of this study was to discern the indirect effects of fish stocking on fishless alpine lakes of the Canadian Rocky Mountains.

Direct Effects of Fish Stocking on Plankton

Planktivorous fish can reduce or eliminate large zooplankton species (Hrbàček et al. 1961, Brooks and Dodson 1965, Hall et al. 1976, Zaret 1980). Large zooplankton are selectively preyed upon by fish because they are both easier to locate by visually-feeding fish and retain in their gillrakers than smaller forms (O'Brien 1987) and optimize foraging strategies (Werner & Hall 1974). The predatory effects of fish on zooplankton in temperate lakes are well documented in the literature (for review see Zaret 1980, Northcote 1988). However, the effects of fish predation in alpine lakes have been much less documented. Reimers (1958), Anderson (1972) and Walters & Vincent (1973) provide direct evidence for the reduction of large zooplankton species in the presence of fish for alpine lakes.

Predicting effects of fish stocking in fishless lakes requires prior knowledge of the pristine planktonic (and benthic) community. Unfortunately, many alpine lakes were stocked without any knowledge of the original community (Bahls 1992, Schindler et al. in review). In these cases, paleoecological methods may be the only key to determine pre-stocking communities in mountain lakes (Lamontagne 1993, Lamontagne & Schindler in press, Leavitt et al. in review).

Description of Alpine Lakes in the Canadian Rockies

Alpine lakes are situated in the alpine eco-region based on terrestrial vegetation; this is the region at or above treeline. The minimum elevation of the alpine region in the Canadian Rocky Mountians varies between 2 125 m and 2 350 m depending on numerous factors such as latitude and aspect (Luckman 1990, Holland & Coen 1983). Typical terrestrial vegetation includes the yellow heather (*Phyllodoce glanduliflora*), white mountain heather (*Cassiope mertensiana*) and lichens, all of which reflect the harsh environmental conditions (Holland & Coen 1983). The alpine vegetation found near Snowflake Lake, Banff National Park (where I conducted most of my research; see chapter 1) can be grouped into 8 typical vegetation zones (Beder 1967). The dominant species characteristic of each zone are white heather (*C. tetragona*), yellow heather (*P. glanduliflora*), arctic willow (*Salix arctica*), two zones dominated by different sedges (*Carex* spp. and *Kobresia myosuroides*), wild rye (*Elymus innovatus*), white mountain aven (*Dryas hookeriana*) and lichens (Beder 1967).

Lakes in the alpine region also reflect the inclement environment. They remain frozen for approximately 8½ months each year, with the ice-free season lasting from around late June to early October (Anderson 1970a). Maximum summer surface water temperatures rarely exceed 12°C and thermal stratification is weak (Rawson 1942, Anderson 1970a). The low temperatures of alpine lakes are likely a combination of both direct climatic conditions and rapid water renewal, with snow and glacial meltwater, which can be significant sources of heat loss (Anderson 1970a). Cold temperatures and low concentrations of dissolved nutrients (Anderson 1970a) are responsible for the ultra-oligotrophic nature of alpine lakes.

Biotic Communities of Alpine Lakes in the Canadian Rockies

In both the western United States and Canada, an estimated 95% of mountain lakes (includes montane, subalpine and alpine lakes) were naturally fishless (Donald 1987, Bahls 1992). The absence of fish in these lakes may be due to physical barriers preventing their colonization since the retreat of the late Wisconsin glaciation around 13 ka BP (Pechlaner 1984, Osborn and Luckman 1988). Furthermore, lack of suitable spawning habitats and poor environmental conditions may have prevented fish from establishing populations in lakes where colonization was not impeded by physical barriers (Donald 1987).

The diversity of zooplankton species in alpine lakes is low (Patalas 1964, Anderson 1974, Starkweather 1990). Low species diversity may be attributed to low temperatures which could inhibit growth and reproduction of some planktonic species (Anderson 1971, Lamontagne 1993). Anderson (1971, 1974) hypothesized that low zooplankton species diversity in alpine lakes may also be the result of a uniform environment that provides few ecological niches. Finally, zooplankton in alpine lakes are often dominated by large species, especially large calanoid copepods (Patalas 1964, Anderson 1971, Stoddard 1987, Starkweather 1990). The large size of zooplankton in alpine lakes is likely a function of the lack of vertebrate predators, which selectively feed on large zooplankters (Hrbàček et al. 1961, Brooks and Dodson 1965, Zaret 1980, O'Brien 1987). Large zooplankton may subsequently reduce smaller species by either competition (Brooks and Dodson 1965, Hall et al. 1976) or predation (Dodson 1974, Zaret 1980).

The zooplankton of pristine alpine lakes from the Canadian Rocky Mountains are dominated by *Diaptomus* (subgenus: *Hesperodiaptomus*) *arcticus* (Marsh 1920) and 1 species of large *Daphnia*, usually *D. middendorffiana* or *D. pulex* (Anderson 1971). Other species of zooplankton may include cyclopoids or rotifers; however, they are usually rare or absent when *Hesperodiaptomus* is present (Anderson 1971, 1977, 1980). *H. arcticus* are large (2-3 mm) calanoid copepods that are also found in arctic ponds and temporary ponds of the prairies (Edmondson 1959, Hammer & Sawchyn 1968, Anderson 1974, Wilson & Hebert 1993). *H. arcticus* prey on a variety of zooplankton including cyclopoids, rotifers and cladocerans (Anderson 1970b, Wilson & Hebert 1993). The congeneric species *H. shoshone*, common to fishless alpine lakes of the western United States (Patalas 1964, Pennak 1978, Stoddard 1987), is also found in the Canadian Rockies but not as frequently as *H. arcticus*. *H. shoshone* also preys on smaller zooplankton (Anderson 1970b, Dodson 1974, Starkweather 1990).

Objectives

The primary objective of this study was to assess the role of *Hesperodiaptomus arcticus* in structuring pelagic communities in alpine lakes. *H. arcticus* was eliminated, following fish stocking during the 1960's, from three lakes (Bighorn, Snowflake and Pipit) in Banff National Park (Anderson 1972). *H. arcticus* has remained absent from two of these lakes (Bighorn and Snowflake) 25 years later (Schindler et al. in review, pers. obsv.); even though fish are believed to have dissappeared from all the lakes by the early 1980's (D. Donald, Environment Canada, 2365 Albert Street, Regina, Sask., S4P 4K1, unpubl. data). These past fish stocking practices may have long-lasting implications on entire alpine lake communities, especially if *H. arcticus* are important in structuring pelagic communities.

Hesperodiaptomus arcticus predation may regulate the composition and abundance of rotifers and other smaller zooplankton in alpine lakes. Furthermore, phytoplankton composition and biomass may be affected indirectly through trophic linkage (Miller & Kerfoot 1987). I directly tested these hypotheses using large in situ enclosure experiments. The direct and indirect effects of invertebrate predators in aquatic systems have rarely been studied (e.g. Vanni & Findlay 1990) and never in alpine systems.

The ability for invertebrate predators to regulate the abundance of their prey is variable (Neill & Peacock 1980, Neill 1984, Yan et al. 1991) and depends on net rates of predation and productivity of prey (Yan et al. 1991). Neill (1984) determined that prey populations (rotifers) were affected by predators (*Diaptomus leptopus* and *D.*

kenai) only if prey production was resource limited. The potential for *Hesperodiaptomus* to regulate rotifer prey may be a function of extreme resource limitation in ultra-oligotrophic alpine lakes. I tested this hypothesis by fertilizing enclosures both with and without predators.

The last objective of this study was to promote interest in mountain lake research. The lack in knowledge of basic community structure for mountain lakes, including many which have already been stocked (Bahls 1992, Schindler et al. in review), is probably due to logistic constraints. Most alpine lakes do not accomodate much of today's limnological "necessities" (such as power boats) because they are situated far from nearby roads.

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Chapter 1 - Regulation of Rotifers by Predatory Calanoid Copepods (subgenus:Hesperodiaptomus) in Lakes of the Canadian Rocky Mountains

(a version of this chapter has been accepted for publication. Paul, A.J. & D.W. Schindler. Canadian Journal of Fisheries and Aquatic Science)

Introduction

The ability of invertebrate predators to regulate planktonic rotifer communities has been debated. Dodson (1974) predicted that invertebrate predators can control zooplankton community structure, keeping small zooplankton scarce by selectively preying on them. Several publications have supported these predictions (Dodson 1974, Hebert and Loaring 1980, Luecke and O'Brien 1983, Vanni 1988); however, all were studies of invertebrate predation on crustacean zooplankton. Although numerous invertebrate predators are known to prey on rotifers (McQueen 1969, Anderson 1970a, Federenko 1975, Hillbricht-Ilkowska et al. 1975, Williamson 1983, Neill 1984, Moore and Gilbert 1987, Yan et al. 1991), their importance in controlling rotifer abundance is either insignificant or unknown. Havens (1990) established that *Chaoborus punctipennis* preyed selectively on rotifers but it had a minimal effect on rotifer community size and structure, most likely because of the high reproductive output of rotifers. In contrast, predation on rotifers by some invertebrates (predacious rotifers, copepods and *Chaoborus*) has been predicted to be important from empirical studies (Anderson 1977, 1980, Foran and King 1982, Hofmann 1983, Stemberger and Evans 1984), from consumption rate estimates (Brandl and Fernando 1979, Williamson 1983, Elser et al. 1987) and enclosure experiments (Arnott & Vanni 1993).

The role of competitors in limiting populations of herbivorous rotifers has been better studied. There is little doubt that large *Daphnia* can control rotifer populations (see Gilbert 1988 for a review). Neill (1984) determined that rotifer biomass was more strongly regulated by the presence of the competitor (*Daphnia*) than by predacious calanoid copepods; in fact, Chaoborus trivittatus predation on Daphnia enhanced rotifer biomass through competitive release, even though C. trivittatus is also known to prey on rotifers (Neill and Peacock 1980). Predators may only "fine tune" rotifer abundance when rotifers are already constrained by a low food limit set by crustacean grazing (Neill 1984).

The importance of invertebrate predation on rotifer populations is dependent on rotifer production (Yan et al 1991). Generation time and brood size (from 1 to 2 amictic eggs) of rotifers has been shown to be directly related to food supply (Makarewicz & Likens 1979). Consequently, predators might be able to control rotifer abundance if rotifer reproduction is food-limited. I hypothesized that low food availability in ultra-oligotrophic alpine lakes might lower the reproductive rates of rotifers enough to allow control by invertebrate predators.

The goals of my study were threefold. First, I tested the hypothesis that Diaptomus (subgenus: Hesperodiaptomus) arcticus (Marsh 1920), a large (2-3 mm) predatory calanoid copepod, can regulate rotifer populations in alpine lakes of the Canadian Rocky Mountains. Anderson (1977,1980) has previously shown a negative correlation in the distribution of Hesperodiaptomus and rotifers in these lakes indicating the potential for predatory regulation. Second, I tested whether elevated nutrient supplies could indirectly decrease the ability of Hesperodiaptomus arcticus to control rotifer populations by increasing food availability for rotifers. These two hypotheses were tested in enclosures by manipulating predators and nutrients. Enclosure experiments were carried out in Snowflake Lake (51°35' N 116°50' W) in

Banff National Park. Finally, our findings from the enclosure experiments were compared to the distribution and of *Hesperodiaptomus* and rotifers in 69 lakes of the Canadian Rockies.

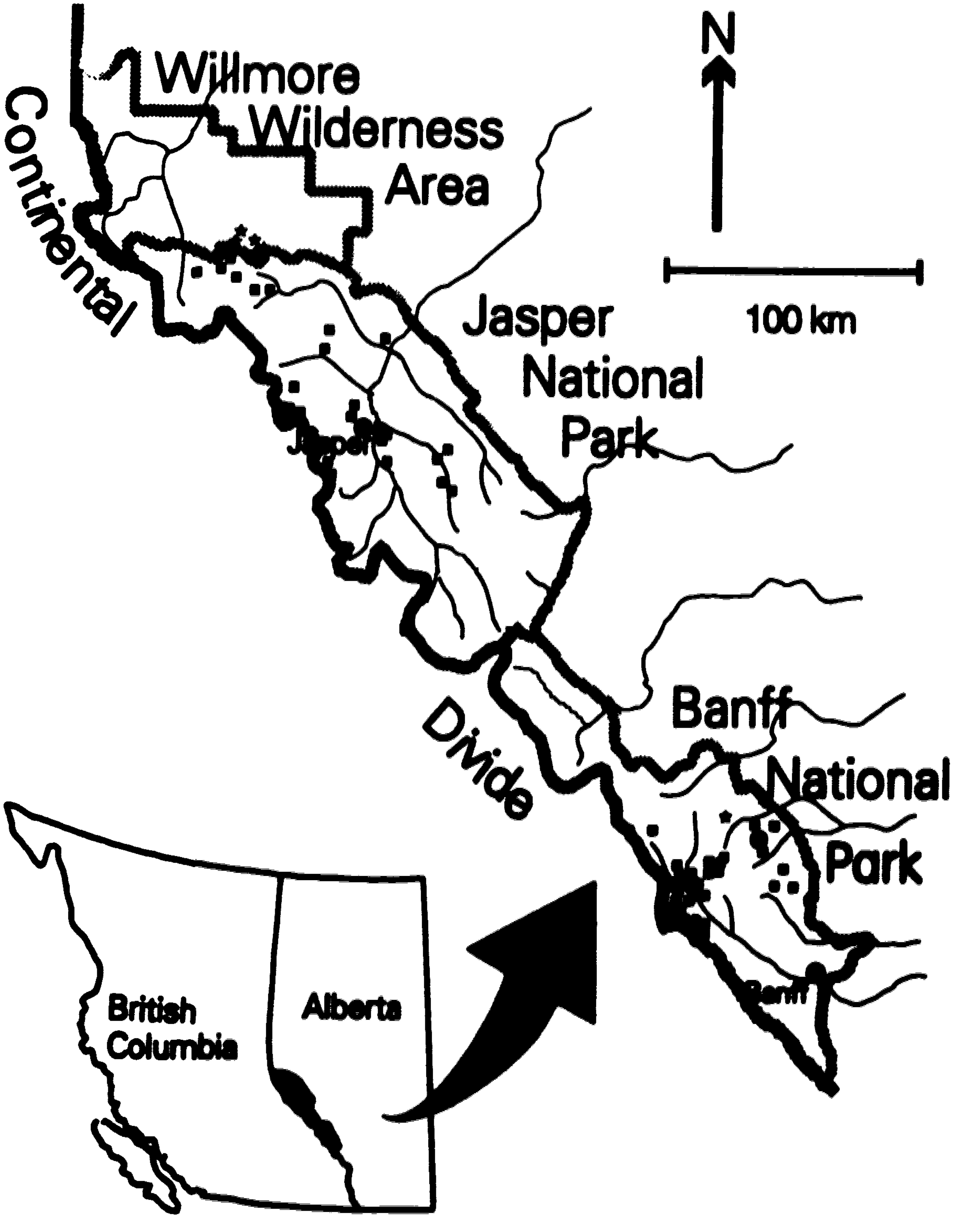
Methods

Study Lakes

The sixty nine lakes are situated in the Canadian Rocky Mountains east of the continental divide within Willmore Wilderness Area, Jasper National Park and Banff National Park (Fig. 1.1). Previous data were available for 63 of these lakes (Anderson 1971, 1974, Donald 1987, and D. Donald, Environment Canada, 2365 Albert Street, Regina, Sask. S4P 4K1, unpubl. data). The lakes ranged in elevation from 1024 m to 2423 m, in maximum depth from 1.5 m - 96 m, and in area from 0.2 ha - 2066 ha. Forty-five of the lakes were known to have been stocked with fish during the 20th century. Most of these lakes were initially fishless. The fate of stocked fish in the lakes varied from successful introductions to complete failures (Donald 1987). The remaining 24 lakes were never stocked and only four of these have natural fish populations.

Snowflake Lake is a relatively small (7.13 ha), deep (12.5 m) and alpine (elev. 2320 m) lake located between the Vermilion and Bare ranges of the Rocky Mountains in Banff National Park (Fig. 1.1). Prior to 1960, the zooplankton community consisted of *Hesperodiaptomus arcticus* and *Daphnia pulex* with small numbers of *Diaptomus tyrelli*, *Acanthocyclops vernalis*, and rotifers (*Kellicottia longispina*)

Figure 1.1- Study area showing location of lakes. ⊗ Snowflake Lake (site of enclosure experiments) and ★■ lakes used for distributional data (★-lakes sampled in this study ■-lakes from other reports).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(Anderson 1972). From 1960 to 1966 the lake was stocked with rainbow trout (*Oncorhynchus mykiss*),brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Oncorhynchus clarki*) (Anderson 1972). Large crustaceans (*H. arcticus* & *D. pulex*) were eliminated by fish predation and smaller copepods (*A. vernalis*, *D. tyrelli* and *Diacyclops bicuspidatus thomasi*) and cladocerans (*Chydorus sphaericus*) increased in density shifting the size structure of the zooplankton community toward much smaller species (Anderson 1972, Anderson 1974). The fish did not reproduce and were believed to have completely disappeared from the lake by the late 1970's or early to mid 1980's (D. Donald, Environment Canada, 2365 Albert Street, Regina, Sask. S4P 4K1, pers. comm.). *D. pulex* had returned to the plankton by 1974 and was collected in subsequent years; however, *H. arcticus* has not returned and the size structure of the pelagic community remains dominated by small species, with *D. pulex* being the only large species present (unpubl. data).

Distribution of *Daphnia* and Rotifers in Snowflake Lake

Densities of *Daphnia pulex* and the dominant rotifers were determined during the ice-free season of Snowflake Lake for 1991 and 1992. Weekly collections were made using a plankton net (25 cm dia., 64 µm mesh) towed vertically 5 times from 11 m to the surface in Snowflake Lake. Samples were preserved in formalin and sucrose (Prepas 1978). Zooplankton were enumerated from separate sub-samples using a dissecting microscope for *D. pulex* and an inverted microscope for rotifers. No fewer than 4 sub-samples for both *Daphnia* and rotifers were counted; the volume of each sub-sample ensured that at least 50 individuals of the dominant species were present. A random distribution of sub-sample counts was determined using a χ^2-test of the variance to mean ratio (Prepas 1984). The coefficient of variation was < 20% for each species counted, except when a species was rare. Plankton net efficiency was set at 20% from values calculated by Anderson (1970b) using a similar net in lakes of Jasper National Park. I stress that the densities obtained for rotifers are subject to inaccuracies associated with plankton nets and rotifer sampling (Green 1977). My density estimates likely only represent changes in order of magnitude and even at this level soft-bodied species, such as Polyarthra, may be underestimated (Green 1977).

Enclosure Experiments

During 1991 I used 6 enclosures to test the effect of Hesperodiaptomus arcticus predation on the plankton community of Snowflake Lake. The enclosures were square woven polyethylene enclosures (0.9m X 0.9m X 3m) closed at the bottom with a volume of 2250 L when filled (Appendix A). Enclosures were suspended from floating frames constructed from ABS plastic piping (Appendix A). H. arcticus were added to triplicate enclosures (predator addition enclosures) to achieve a density of 1.6 individuals$\cdot$L^{-1}, while 3 enclosures received no H. arcticus (reference enclosures). The density of H. arcticus stocked in the enclosures (1.6 ind.$\cdot$L^{-1}) is less than the mean density (3.2 ind$\cdot$ L^{-1}) for 20 lakes with Hesperodiaptomus in the Rockies (D. Donald, Environment Canada, 2365 Albert Street, Regina, Sask. S4P 4K1, unpubl. data). One enclosure for the predator addition was lost in a storm. H. arcticus were collected from Pipit Lake (2 km north of Snowflake Lake) and transferred to appropriate enclosures in Snowflake Lake 5 days after ice-out, on the 15th of July (Day 0 of the experiment). H. arcticus were removed from Pipit Lake using a coarse mesh (1 mm) large diameter (36 cm) zooplankton net. The coarse mesh separated the large bodied zooplankton H. arcticus, Gammarus lacustris (> 5mm) and Daphnia middendorffiana (~3mm) from smaller forms. The latter two species occurred at low densities (< 0.01 ind$\cdot L^{-1}$) and were easily removed by further filtration through a 3 mm mesh and hand picking. The duration of the experiment was 36 days. Enclosures were sampled at approximately 4 day intervals.

In 1992 I tested the effect of Hesperodiaptomus arcticus predation and nutrient additions on the planktonic community of Snowflake Lake. The experimental design was a 2 X 2 factorial analysis with 3 replicates (total of 12 enclosures). The treatments were addition or no addition of H. arcticus (predator addition), nutrients (N + P) or both. H. arcticus were collected from Pipit Lake in a manner similar to the 1991 experiment, except that a larger collecting net was used (120 cm diameter). This allowed us to stock H. arcticus in the enclosures at densities similar to the mean for 20 mountain lakes with Hesperodiaptomus (3.2 ind.$\cdot L^{-1}$). Nutrients were added as NH_4NO_3 and H_3PO_4 (30:1 N:P by atomic ratios) to increase total phosphorus (TP) by a factor of 4; natural TP and total nitrogen in Snowflake Lake are ~4 $\mu g \cdot L^{-1}$ and ~120 $\mu g \cdot L^{-1}$, respectively. Concentrations were maintained at constant values by weekly analyses, followed by additions of NH_4NO_3 and H_3PO_4. Both nutrients and H. arcticus were added to the enclosures on the 27th of June (Day 0) approximately 1 ice out. The experiment ran for 36 days and the enclosures were sampled at weekly intervals.

Water samples were collected from the enclosures and the lake (near the enclosures) for 1991 and 1992 using a clear polyvinylchloride tube 2.75 m in length and 0.05 m inner diameter (DeVries & Stein 1991). The tube was dropped vertically into each enclosure or the lake, plugged at the top, removed quickly, and emptied into a bucket. The procedure was repeated once removing approximately 10.5 L of water, or about 0.5% of the enclosure volume. From the 10.5 L, aliquots were taken for algal pigment analysis (0.5-1 L) and TP (0.25 L). The remaining volume was used for enumeration of rotifers and crustaceans. Zooplankton were concentrated through a 10 μm mesh, washed into vials and preserved in a sucrose-formalin solution (Prepas 1978). The minimum detectable limit for plankton using the tube sampler (assuming a Poisson distribution and a 95% probability of detection) is 0.12 $ind \cdot L^{-1}$. Larger samples were not taken to minimize depletion effects on enclosure populations.

Zooplankton species were identified using keys from Edmondson (1959), Chengalath et al. (1971), Ruttner-Kolisko (1974), Grothe & Grothe (1977) and Pennak (1978). Zooplankton were enumerated by settling the entire sample and counting all individuals on an inverted microscope. Algal biomass was inferred from concentrations of chlorophyll a (chl a) quantified by high performance liquid chromatography (Leavitt and Carpenter 1990). Rotifer densities were compared between treatments using one way or two way repeated measures analysis of variance with fixed effects (Sokal & Rohlf 1981). Rotifer densities were $\log_{10}$-transformed before statistical analysis because means increased exponentially and were positively correlated with variance (Sokal & Rohlf 1981). Exponential growth was determined by linear regression of transformed data. Statistical significance for tests was set at $\alpha = 0.05$, probabilities are given for all tests.

Geographic Distribution Data

We related the occurrence of rotifers to the density of *Hesperodiaptomus* in 69 lakes of the Canadian Rockies (Fig. 1.1). Plankton samples in all cases were collected with a plankton net (0.25 m dia., ≈64 µm mesh) towed from 1 m above the bottom to the surface over the deepest area of each lake. Densities of *Hesperodiaptomus*, averaged over ice free months (June-September), were corrected for net efficiency using coefficients from Anderson (1970b). Only the presence or absence of rotifers was determined because of the inaccuracy involved in quantitative assessments of rotifers especially when using plankton nets (Green 1977).

Maximum likelihood logistic regressions (Pindyck and Rubinfeld 1981) were used to model the presence or absence of rotifers as a function of *Hesperodiaptomus* density. This analysis was chosen over least squares regression analysis because the dependent variable (presence/absence of rotifers) is dichotomous (Reckhow et al.1987). Parameters from the regression analysis were fit to the logistic model:

$$P(y) = \frac{1}{1+e^{-(a+b(x))}} \tag{1.1}$$

where P(y) is the probability of the rotifer species being present, x is the density of Hesperodiaptomus ($\log_{10}$ of density + 0.01), a is the intercept, and b the slope. The statistical validity of the model was tested using χ^2 goodness-of-fit (SAS 1988), with α=0.05.

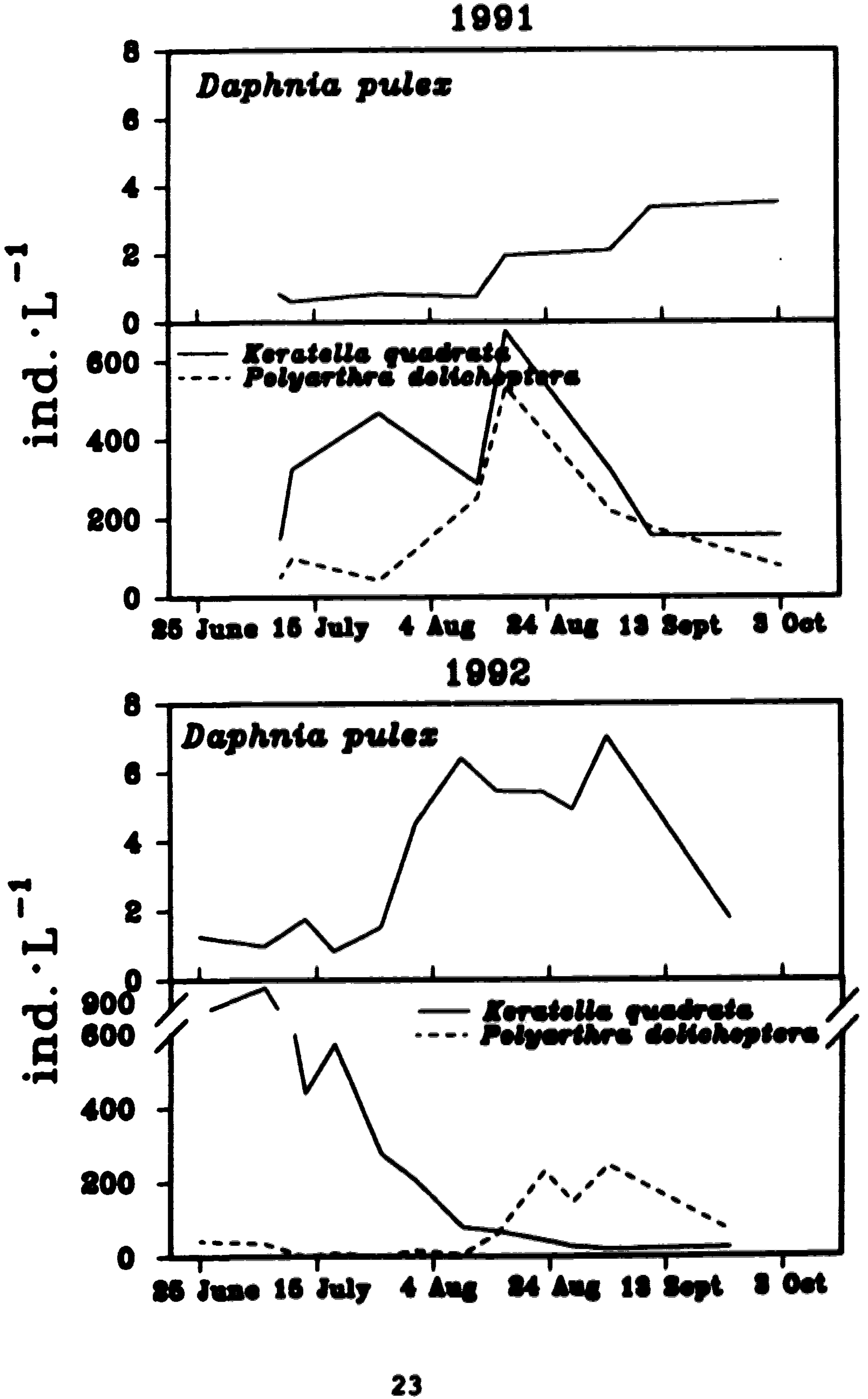
Results

Distribution of *Daphnia* and Rotifers in Snowflake Lake

The zooplankton in Snowflake Lake during 1991 and 1992 consisted largely of Diacyclops bicuspidatus thomasi, Diaptomus tyrelli, Daphnia pulex and rotifers. These three crustacean species were reported by Anderson (1972, 1974) to be present in Snowflake Lake at some point following fish stocking. The dominant planktonic rotifers in Snowflake Lake were Polyarthra dolichoptera (Idelson 1925; 120 X 76 µm) and Keratella quadrata (Müller 1786; 126 X 72 µm). Other rotifer species include Keratella cochlearis, Synchaeta spp., Notholca spp., Testudinella spp. and Kellicottia longispina. The genera Keratella, Polyarthra, Notholca and Testudinella have not previously been reported from Snowflake Lake (Anderson 1972).

Densities of D. pulex did not exceed 1 individual$\cdot$L^{-1} until late July to mid-August of each year (Fig. 1.2). The maximum density of D. pulex was ≈3-4 ind.$\cdot$L^{-1} in 1991 and ≈6-7 ind.$\cdot$L^{-1} in 1992. Densities of the dominant rotifers (K. quadrata and P. dolichoptera) tended to decrease as D. pulex increased (Fig. 1.2); however, the peak densities of P. dolichoptera and D. pulex in 1992 occurred simultaneously (Fig. 1.2).

Figure 1.2- Densities of dominant rotifers and Daphnia pulex in Snowflake Lake for the ice-free seasons of 1991 and 1992. Densities estimated from samples collected with a plankton net at the deepest point in Snowflake Lake.


1991
Daphnia pulex
8
6
4
2
0
ind.·L⁻¹
600
400
200
0
Keratella quadrata
Polyarthra dolichoptera
25 June
15 July
4 Aug
24 Aug
13 Sept
3 Oct
1992
Daphnia pulex
8
6
4
2
0
ind.·L⁻¹
900
600
400
200
0
Keratella quadrata
Polyarthra dolichoptera
25 June
15 July
4 Aug
24 Aug
13 Sept
3 Oct

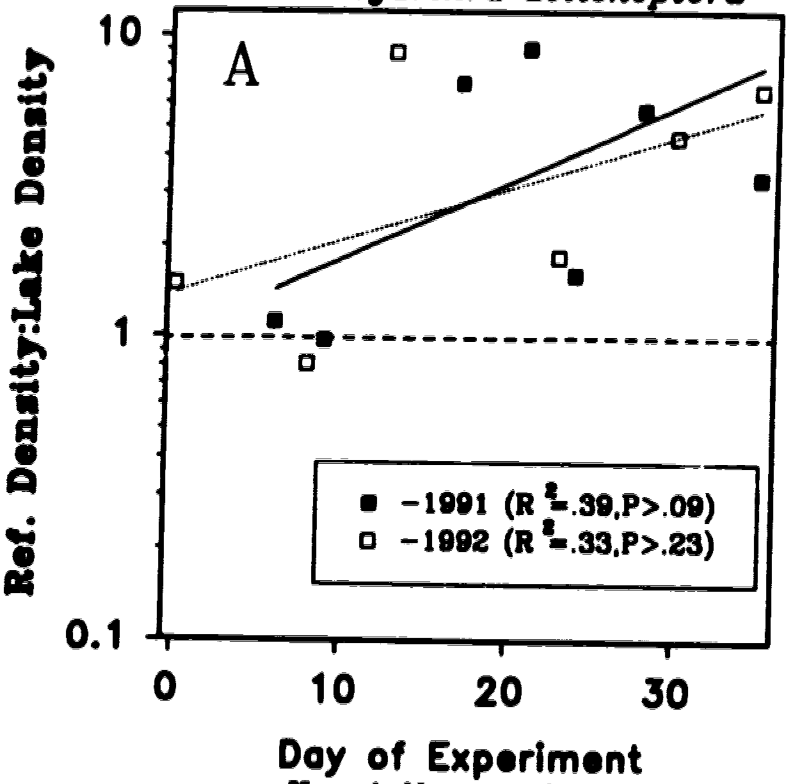
Enclosure Experiments

Rotifer densities in the reference enclosures (no predators and no fertilizer) and Snowflake Lake followed similar trends. The two dominant pelagic rotifer species were always present at densities greater than 0.12 ind.· L^{-1} in the reference enclosures and Snowflake Lake. The ratios of mean density in reference enclosures to lake samples for *Polyarthra dolichoptera* and *Keratella quadrata* were not significantly related to time in 1991 or 1992 (Fig. 1.3). If rotifers in the enclosures and the lake did not follow similar growth patterns (ie. one increased at a greater rate), then the ratios of mean reference enclosure density to lake density would have increased or decreased over time. *P. dolichoptera* and *K. quadrata* did reach higher densities for both years in the enclosures than in lake samples; however, the difference was always less than an order of magnitude, except for *K. quadrata* on one date in 1992 (Fig. 1.3).

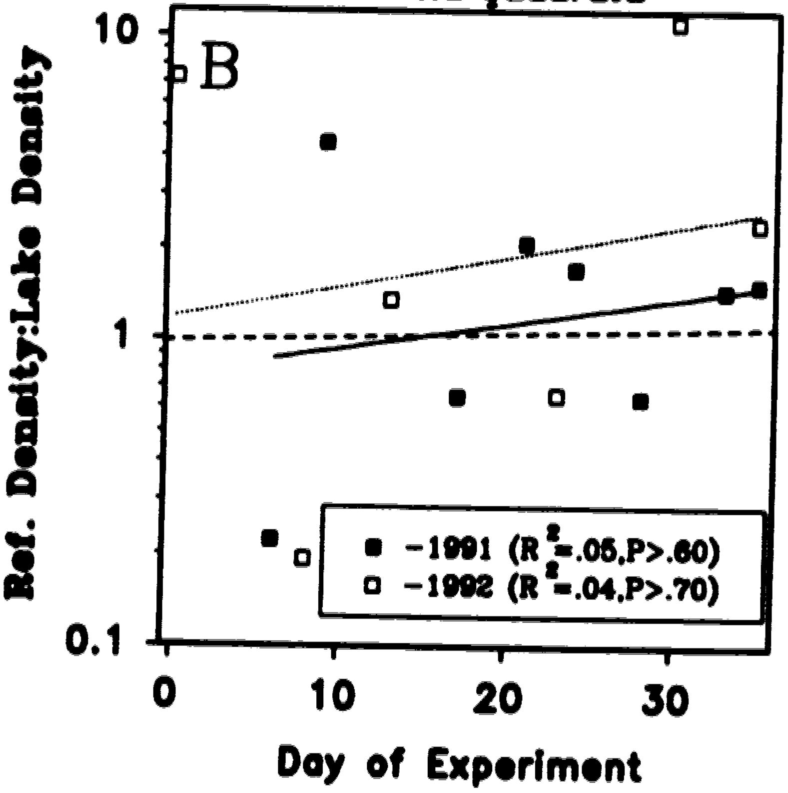
Crustacean zooplankton and non-dominant rotifers were rare in our small samples and accurate estimates of density were not possible for these species; therefore, they were excluded from quantitative analysis. Cyclopoid nauplii did occur at densities above detectable levels in the reference enclosures but only for the last day of the experiment in 1992. Naupliar stages of *Hesperodiaptomus arcticus* were collected infrequently and copepodids were never detected in any of the enclosures for both 1991 and 1992. Therefore, any change in net *H. arcticus* predation rates represented a functional response of the predator and not a numerical response.

Figure 1.3- Ratio between mean rotifer densities for reference enclosures (no predators or nutrients) and Snowflake Lake for 1991 and 1992. Densities are equal when the ratio is 1 (dashed line). Linear regression lines and coefficients of determination were calculated for both years (solid-1991; dotted-1992). A- Polyarthra dolichoptera. B- Keratella quadrata.

Polyarthra dolichoptera



Keratella quadrata



Predator Effects

In the 1991 experiment, enclosures with *Hesperodiaptomus arcticus* (predator addition) had significantly lower densities of *Polyarthra dolichoptera* than reference enclosures (Table 1.1 & Fig. 1.4). *P. dolichoptera* rarely exceeded densities > 0.12 ind$\cdot$ L^{-1} in predator addition enclosures but increased exponentially with time in the reference enclosures (Fig. 1.4a, R^2= 0.97,df= 7, P< 0.0001). *K. quadrata* densities did not differ significantly in reference and predator addition enclosures (Table 1.1, Fig. 1.4b).

Predator additions in 1992 again significantly lowered *P. dolichoptera* densities (Table 1.2 & Fig. 1.5). *P. dolichoptera* densities remained low when the predators were present, regardless of nutrient additions (Fig. 1.5a). In contrast, exponential growth of *Polyarthra dolichoptera* occurred in both fertilized (R^2= 0.90, df= 4, P< 0.004) and unfertilized (R^2= 0.97, df= 4, P< 0.0005) enclosures without predators (Fig. 1.5a).

In 1992 predator additions significantly reduced the densities of *Keratella quadrata* in all enclosures (Table 1.2 & Fig. 1.5b). Predators reduced densities up to an order of magnitude in both fertilized and unfertilized enclosures (Fig. 1.5b). *K. quadrata*, however, did increase exponentially in fertilized treatments with predators (R^2= 0.78, df= 4, P< 0.02), as well as in both fertilized (R^2= 0.90, df= 4, P< 0.004) and unfertilized (R^2= 0.89, df= 4, P< 0.005) enclosures without predators (Fig. 1.5b).

Table 1.1- Repeated measures analysis of variance for log-transformed densities of Polyarthra dolichoptera and Keratella quadrata from enclosures in 1991. Treatment refers to presence or absence of the predator Hesperodiaptomus arcticus.

TEST	SOURCE	df	MS	P
Polyarthra dolichoptera	TREATMENT	1	62.143	0.002
	ERROR	3	.535	
Keratella quadrata	TREATMENT	1	7.344	0.226
	ERROR	3	3.176	

P= probability of committing a type I error

Figure 1.4- Mean densities of the dominant rotifers in enclosures with or without _Hesperodiaptomus arcticus_ from 1991. Samples taken on day zero were lost so there are no data points for day 0. **A-** _Polyarthra dolichoptera_. **B-** _Keratella quadrata_.

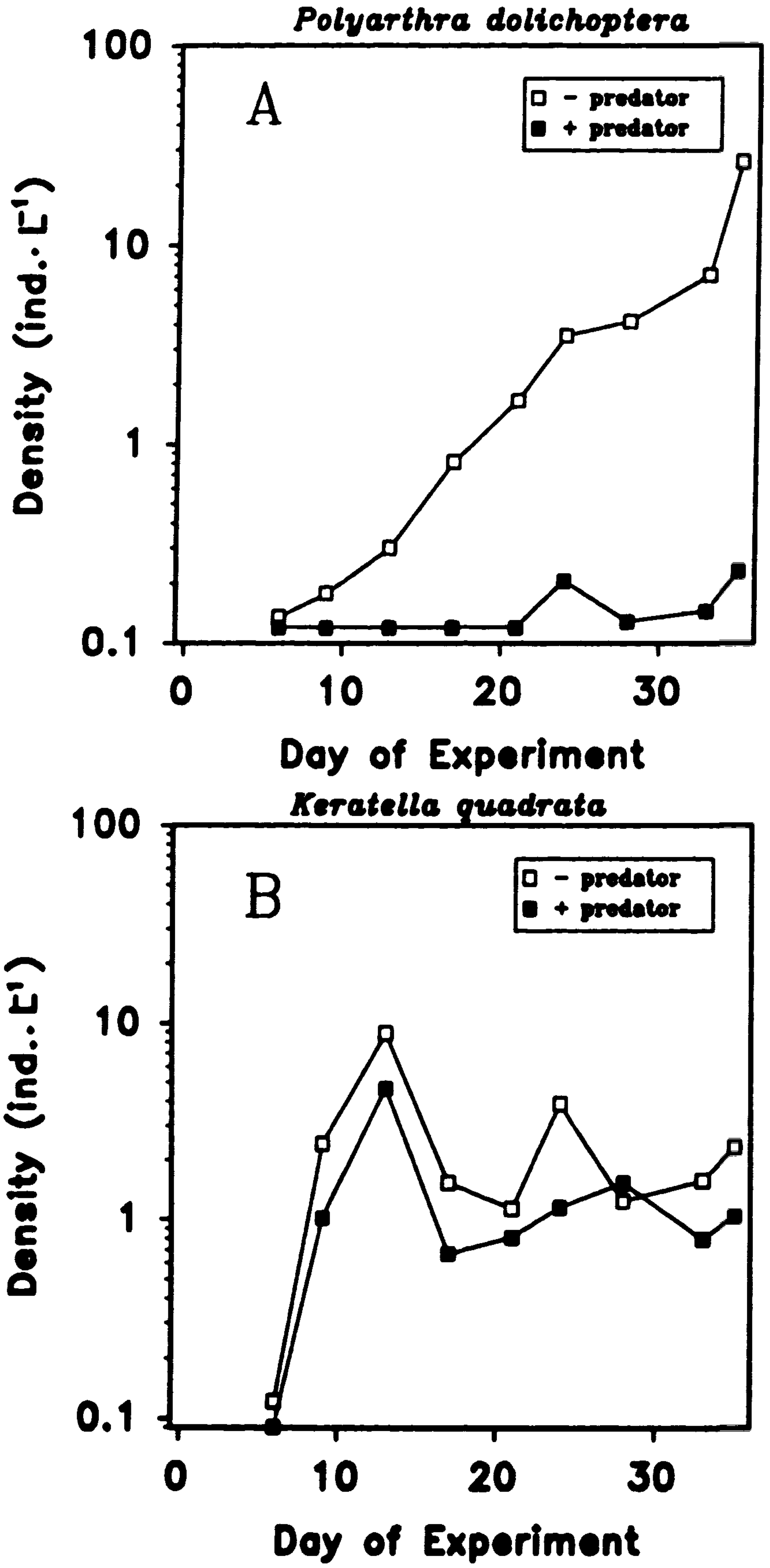
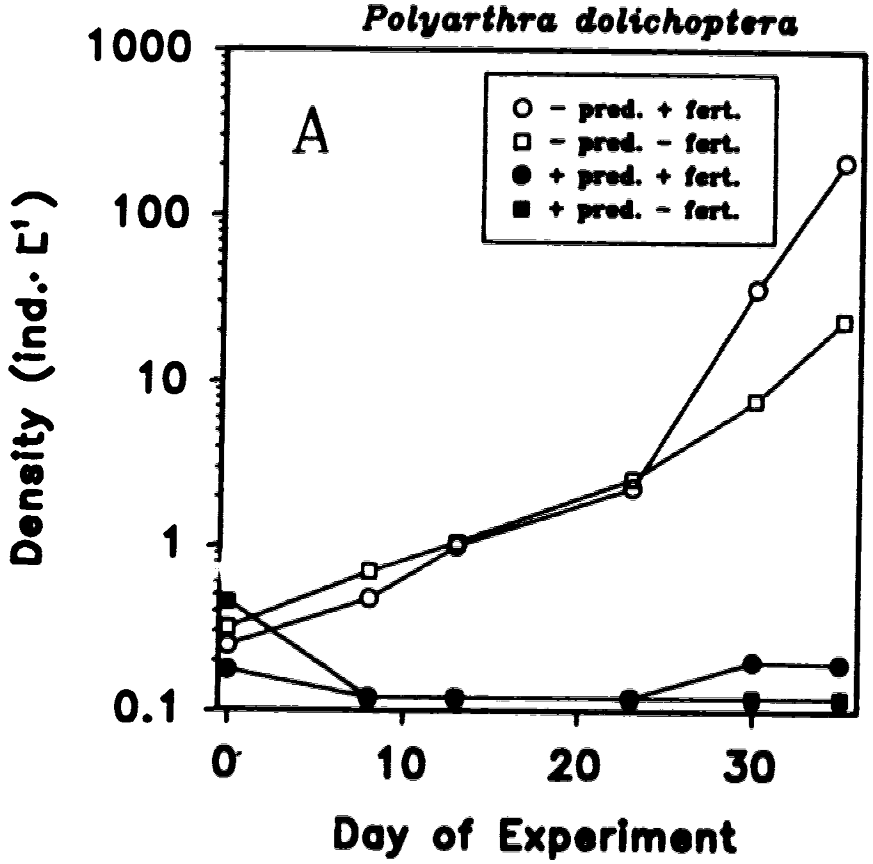

Polyarthra dolichoptera
A
□ - predator
■ + predator
100
10
1
0.1
Density (ind.·L⁻¹)
0
10
20
30
Day of Experiment
Keratella quadrata
B
□ - predator
■ + predator
100
10
1
0.1
Density (ind.·L⁻¹)
0
10
20
30
Day of Experiment

Table 1.2- Repeated measures two way analysis of variance for log-transformed densities of Polyarthra dolichoptera and Keratella quadrata from enclosures in 1992. The two treatments were presence/absence of the predator Hesperodiaptomus arcticus and addition/no addition of fertilizer.

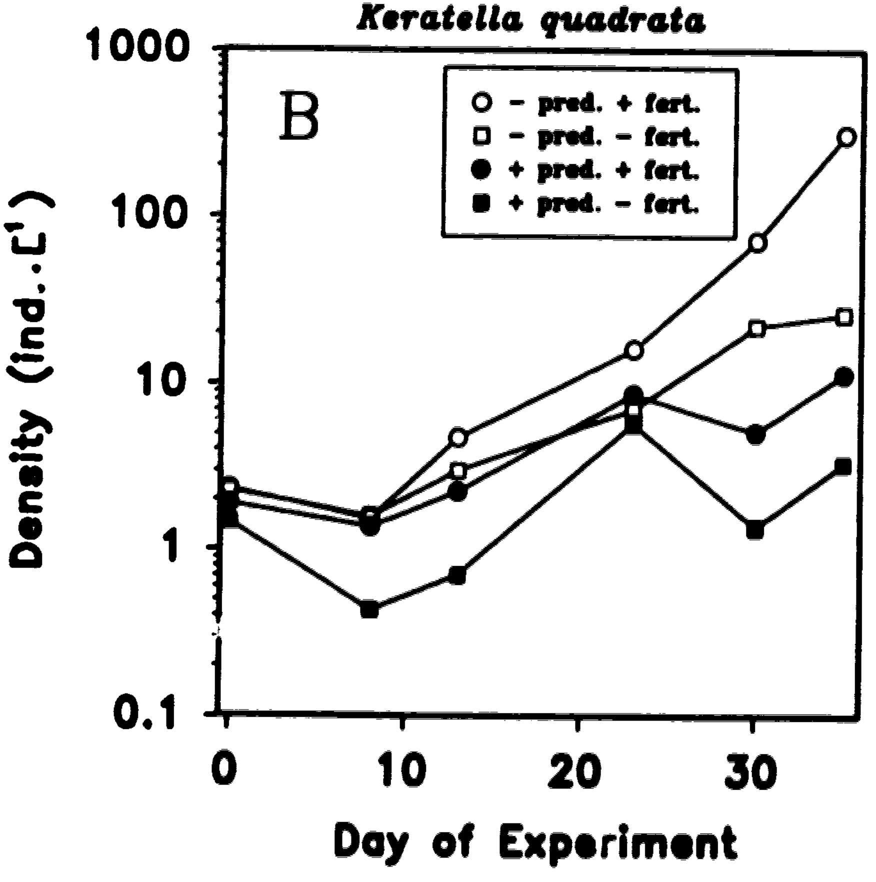
TEST	SOURCE	df	MS	P
Polyarthra dolichoptera	TREATMENTS			
	Hesperodiaptomus	1	25.8	0.0001
	Fertilization	1	.22	0.28
	interaction	1	.20	0.30
	ERROR	8	.16	
Keratella quadrata	TREATMENTS			
	Hesperodiaptomus	1	3.87	0.006
	Fertilization	1	6.91	0.02
	interaction	1	.05	0.77
	ERROR	8	.50	

P= probability of committing a type I error

Figure 1.5- Mean densities of dominant rotifers in enclosures with or without Hesperodiaptomus arcticus or fertilizer addition from 1992. A- Polyarthra dolichoptera. B- Keratella quadrata.



Polyarthra dolichoptera



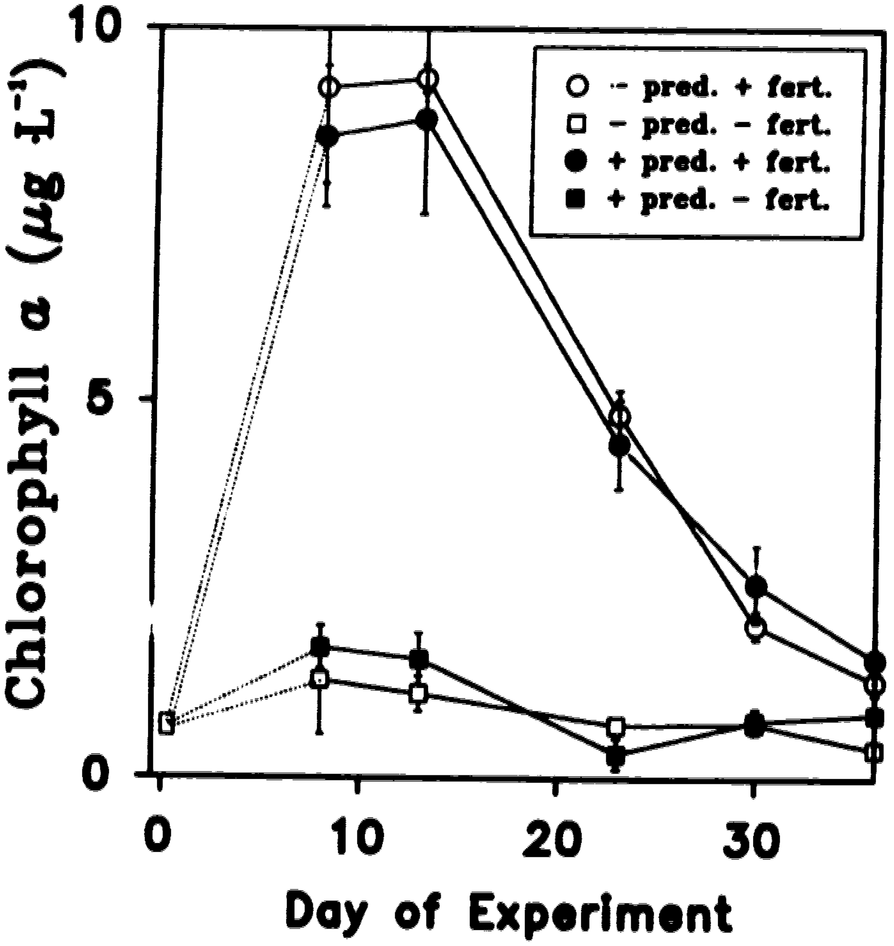
Keratella quadrata

Nutrient Effects

Nutrient (fertilizer) additions in 1992 increased mean TP to 17-21 $\mu g \cdot L^{-1}$ (mean= 18.25 SD= 2.46) in fertilized enclosures compared to 4-7 $\mu g \cdot L^{-1}$ (mean= 6.55 SD= 0.83) in reference enclosures. Standing stocks of algae (measured as chl a) increased significantly (repeated measures two-way analysis of variance, F= 136.39, df= 1,8, $P< 0.0001$) in the fertilized enclosures (Fig. 1.6). Differences in chl a between fertilized and unfertilized enclosures were greatest (4 fold) 14 days after the start of the experiment then steadily declined in the fertilizer addition treatments until on the last day (35) there was only a marginal difference between treatments (Fig. 1.6). Further results of phytoplankton dynamics (using algal pigments) from fertilization and predator treatments will be presented elsewhere.

Nutrient additions increased rotifer densities (Fig. 1.5). Densities of Keratella quadrata increased significantly in the fertilized enclosures (Table 1.2 & Fig. 1.5b). K. quadrata increased approximately 1 order of magnitude in response to fertilizer additions in both enclosures with or without predators (Fig. 1.5b). Mean densities of Polyarthra dolichoptera increased by an order of magnitude from day 23 to the end of the experiment in the enclosures without predators (Fig. 1.5a), but the overall treatment effect was not statistically significant (Table 1.2). A similar but much smaller increase in P. dolichoptera was also observed in the fertilized enclosures with predators (Fig. 1.5a).

Figure 1.6- Mean concentrations of chlorophyll a ($\mu g \cdot l^{-1}$) in enclosures with or without Hesperodiaptomus arcticus or fertilizer for 1992. Day 0 represents lake concentrations and not means from enclosures. Error bars represent 1 standard error of the mean.



Chlorophyll a (μg L⁻¹)
10
5
0
0
10
20
30
Day of Experiment
○ – pred. + fert.
□ – pred. – fert.
● + pred. + fert.
■ + pred. – fert.

Geographic Distribution

In 69 Canadian Rocky Mountain lakes the proportion of lakes containing *Keratella* or *Polyarthra* (the dominant rotifer genera from Snowflake Lake) decreased as the density of *Hesperodiaptomus* increased (Fig. 1.7). At low *Hesperodiaptomus* densities ($< 0.01 \cdot L^{-1}$) *Polyarthra* occurred more frequently than *Keratella*. When densities of *Hesperodiaptomus* were high ($> 1 \cdot L^{-1}$) both rotifers occurred less frequently, but *Keratella* was the more common of the two (Fig. 1.7).

Logistic regression models for both rotifer genera predict that the probability of rotifers occurring decreases with increasing densities of *Hesperodiaptomus* (Fig. 1.8). Parameters for the model (a and b in equation 1.1) were significant for both rotifer species (Table 1.3). At *Hesperodiaptomus* densities > 0.30 ind$\cdot L^{-1}$ *Keratella* has a greater chance of occurring than *Polyarthra*, and at densities < 0.30 ind$\cdot L^{-1}$ *Polyarthra* has a higher chance.

Discussion

Predation by invertebrates can regulate rotifer populations in alpine lakes. Rotifer abundance was dramatically reduced in the enclosures containing *Hesperodiaptomus arcticus* regardless of nutrient conditions; and the distributions of both *Keratella* and *Polyarthra* were negatively correlated with *Hesperodiaptomus*. This negative relation with *Hesperodiaptomus* also applies to other rotifer genera in Rocky Mountain lakes (Anderson 1977, 1980). In contrast, studies from other systems have found that predation does not control rotifer populations (McQueen 1969, Neill 1984, Havens 1990, Yan et al. 1991).

Figure 1.7- Percent occurrence of two rotifer genera in mountain lakes with varying densities of <u>Hesperodiaptomus</u>.

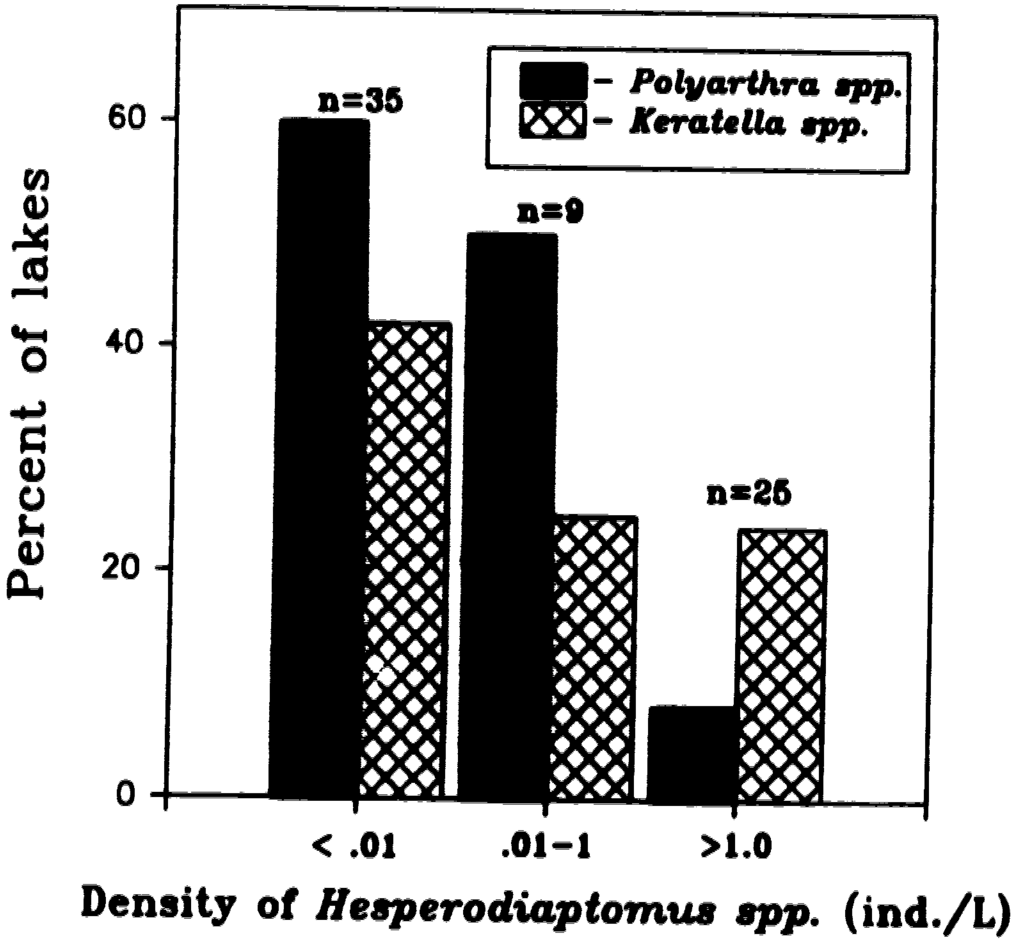

■ - *Polyarthra spp.*
▨ - *Keratella spp.*
n=35
n=9
n=25
60
40
20
0
Percent of lakes
< .01
.01–1
>1.0
Density of *Hesperodiaptomus spp.* (ind./L)

Figure 1.8- Probability of occurrence for two rotifer genera in mountain lakes as a function of *Hesperodiaptomus* density using logistic regression analysis. The range in density of *Hesperodiaptomus* represents the observed density range from 69 Canadian Rocky Mountain lakes.

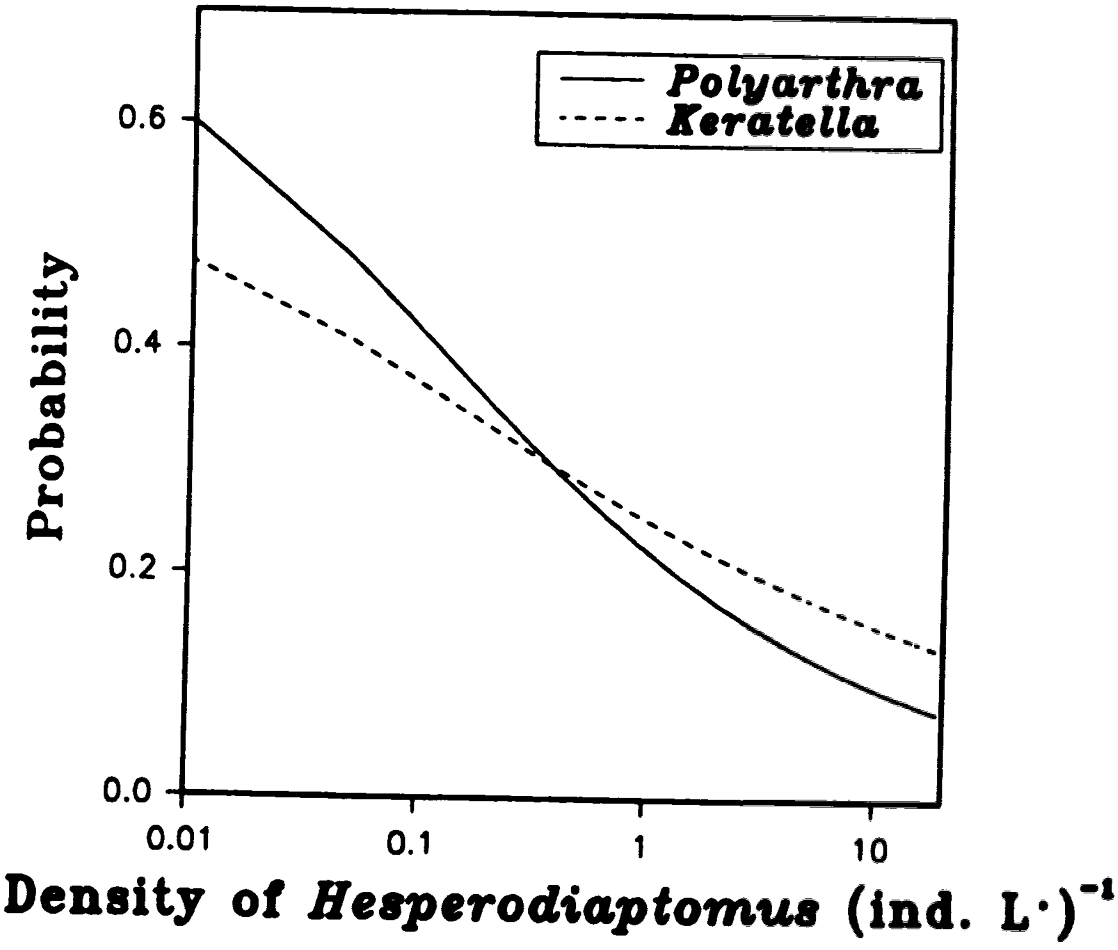

Polyarthra
Keratella
Probability
0.0
0.2
0.4
0.6
0.01
0.1
1
10
Density of Hesperodiaptomus (ind. L·)⁻¹

Table 1.3- Logistic regression estimates and χ^2 statistics from the presence/absence of <u>Keratella</u> and <u>Polyarthra</u> as a function of log-transformed densities of <u>Hesperodiaptomus</u>.

TEST	PARAMETER	ESTIMATE	χ^2	P
<u>Polyarthra</u>				
	a	-1.21	6.58	0.01
	b	-.95	12.36	0.0004
<u>Keratella</u>				
	a	-1.10	6.57	0.01
	b	-.59	5.69	0.02

P= probability parameter estimate is equal to zero

Invertebrate predators may be particularly effective in alpine lakes where low algal standing crop and cold water combine to reduce rotifer population growth. The high intrinsic growth rate of rotifers may allow them to outstrip predatory regulation in temperate eutrophic lakes (Havens 1990), acidified fishless lakes (Yan et al. 1991) and in oligotrophic montane lakes (Neill 1984). In alpine lakes nutrient inputs and algal abundance are very low and rotifer growth may be food limited. Low reproductive rates may facilitate predatory regulation by Hesperodiaptomus. However, even though fertilization produced significant increases in chl a and rotifer abundance (Keratella only), predation from H. arcticus elicited a strong response for both rotifer species with or without fertilization (predation X fertilization interaction term was non-significant, Table 2). Higher fertilization levels, a longer experimental duration or increased water temperatures might have allowed rotifers to outstrip their predators; and I am investigating these possibilities.

Predatory regulation of rotifers in Rocky Mountain lakes may be a function of temperature. Snowflake Lake and most of the lakes from the survey have a short ice-free season and low mid-summer surface water temperatures, 6-12°C (Anderson 1974, Lamontagne 1993). Edmondson (1965) reported that egg development times for Polyarthra dolichoptera and Keratella quadrata had a Q_{10} of 0.49 and 0.45, respectively. This means that for a 10°C increase in temperature the time required for an egg to develop is reduced by almost a half. Lower reproductive rates of rotifers in alpine lakes may enable predators to significantly deplete their populations.

Therefore, regulation of rotifers by *Hesperodiaptomus* predation may be facilitated through abiotic factors (low temperature regime). Community level experiments where predators, temperature and food can be varied independently are needed to test the efficiency of these variables.

Daphnia pulex in our experiments were < 0.12 ind.· L^{-1}; therefore, I saw no evidence of the regulation of rotifers through competition with *D. pulex*. Large *Daphnia* can suppress rotifer populations through both exploitative competition of similar food niches and interference competition at densities > 1 ind.· L^{-1} (Gilbert 1988). Interference competition occurs when rotifers are swept into the branchial chamber of *Daphnia* where they may be ingested, rejected in a damaged condition or have eggs detached (Gilbert and Stemberger 1985). My experiments were done immediately after ice-out during a period when large *Daphnia* were present at low densities. Increased densities of *Daphnia* later in the season in Snowflake Lake did correspond to lower densities of rotifers, especially *Keratella*. However, the co-occurence of density maxima for *Polyarthra* and *Daphnia* in 1992 indicates that these species may be able to coexist. Small rotifers (such as the dominant species in Snowflake Lake) may be able to compete with large *Daphnia* in food-limited environments because they can reproduce at lower food levels than larger rotifer species (Stemberger and Gilbert 1985, Gilbert 1988). Co-existence may be further facilitated if the rotifers can actively escape interference competition (Gilbert 1988).

Competition from *Daphnia* may be less important than *Hesperodiaptomus* predation in excluding rotifers from alpine lakes. Adult *Hesperodiaptomus* are present year-round in some Rocky Mountain lakes (Anderson 1974 and unpubl. data) or for much of the ice-free season in others (Anderson 1967, Anderson 1974). Therefore, rotifer populations are subject to predation throughout the year or at least most of the ice-free season. Furthermore, *Daphnia* are abundant (> 1 ind.· L^{-1}) for approximately only 1 month during the latter part of the ice-free season, when environmental conditions likely become more favourable for their growth (Fig. 2). These observations are consistent with the theory that the importance of competition and predation can be related to abiotic conditions (Menge & Sutherland 1987, Arnott & Vanni 1993). Arnott & Vanni (1993) proposed that in high stress environments (e.g. extreme temperatures in alpine lakes) large herbivores are reduced in abundance and their importance in regulating smaller zooplankton diminishes while the importance of invertebrate predators increases.

Altogether, evidence indicates that in alpine lakes predation by *Hesperodiaptomus*, rather than competition with large *Daphnia* is the major determinant of rotifer populations. First, the number of new rotifer genera in Snowflake Lake has increased since fish stocking; even though *D. pulex* had returned to the lake by 1974. Secondly, densities of *D. pulex* are low for a significant proportion of the ice-free season in Snowflake Lake (and likely other alpine lakes) providing a substantial time period for rotifer growth in the absence of competitive pressure from *Daphnia*. Finally, the strong impact of *Hesperodiaptomus arcticus* predation on rotifers shown here, coupled with the fact it is the most common planktonic species in alpine lakes of the Canadian Rocky mountains (Anderson 1971), suggests that Hesperodiaptomus is the key species in determining rotifer abundance and composition.

Planktonic rotifers have several defences against predation including morphological, behavioral, physiological and reproductive characteristics (Stemberger and Gilbert 1987). Keratella have rigid armoured loricas that could protect them from both capture and ingestion by copepods (Stemberger and Gilbert 1987). In contrast, Polyarthra is unarmoured but capable of rapid movements in response to a predator, avoiding predation by active escape (Gilbert 1980, Gilbert 1985).

My results indicate that Keratella may be better able to withstand Hesperodiaptomus predation than Polyarthra, even though both are of similar sizes. One prey species may be selected over another if it is "easier" to catch, the handling time for the predator is less or it is easier to ingest. The armoured lorica of Keratella likely decreases the probability of the predator successfully capturing or ingesting an individual. Other feeding experiments (Anderson 1970a) also showed that the soft-bodied rotifer Synchaeta was selected by Hesperodiaptomus over Kellicottia, a genus that has a spined lorica. Furthermore, H. arcticus predation in arctic ponds indicate that Daphnia pulex with short tail spines are more susceptible to predation than genotypes with longer spines (Wilson & Hebert 1993). Significant reductions of Keratella by Hesperodiaptomus in 1992, while it was relatively unaffected in 1991, may be explained by higher predator densities and corresponding prey shortages. I conclude that Hesperodiaptomus is able to regulate abundance and distribution of both genera of rotifers through predation; but, Keratella is better suited to withstand copepod predation due to its armoured lorica.

The different responses of Keratella and Polyarthra to nutrient additions might be explained by their relative investments in defence. The cost of having a spined hard lorica may be an increase in threshold food requirements (Stemberger and Gilbert 1987). Therefore, Keratella may have responded more strongly to nutrient additions because limitation by food was greater due to investments in predator defence. This hypothesis is supported from our model of distributional data. When predators are rare or absent, Polyarthra may be more likely to occur than Keratella because it is better able to utilize food resources for reproduction. As predator density increases Keratella begins to benefit from its investment in defence and its probability of occurrence surpasses Polyarthra's. Further studies addressing costs and benefits of investments in defence are needed to substantiate the above hypotheses.

Elimination of Hesperodiaptomus by stocking with trout and char (Anderson 1972, Donald 1987) should change zooplankton community composition by allowing the colonization (or increase in abundance) of rotifers. The recolonization of a lake by Hesperodiaptomus would markedly decrease rotifer abundance and possibly exclude them. It seems unlikely that this relation will change with increased nutrient loads alone; however, I hypothesize that climatic changes (warming trends) could increase rotifer reproduction and possibly weaken the ability of Hesperodiaptomus to limit rotifers.

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Chapter 2- Direct and Indirect Effects of Predation by a Calanoid Copepod Diaptomus (subgenus: Hesperodiaptomus) arcticus and of Nutrients in Fishless Alpine Lakes

(a version of this chapter will be submitted for publicationl. Paul, A.J., P.R. Leavitt, D.W. Schindler & A.K. Hardie)

Introduction

Determining the interactions between resources and consumers is a major objective of freshwater community ecology. The positive relationship between phytoplankton and nutrient supply has long been acknowledged in the scientific literature (Vollenweider 1968, Dillon & Rigler 1974, Schindler 1978). As well, food-web theory (Carpenter et al. 1985) predicts that a change in abundance of higher order consumers can be transmitted down the food web to eventually alter production, biomass and composition of phytoplankton (Hrbàček 1961, Shapiro & Wright 1984, Carpenter & Kitchell 1988, Mazumder et al. 1990). Since the theories of "top-down" consumer and "bottom-up" resource control are not mutually exclusive (Carpenter et al. 1985, Persson et al. 1988, Carpenter et al. 1991), ecologists need to discern the conditions (either biotic or abiotic) under which predators or resources dominate trophic interactions (Hunter and Price 1992).

Food-web studies have broader implications for freshwater systems than theoretical considerations or management of water quality. Colonization of freshwaters by non-native species may have caused more biotic impoverishment than any other anthropogenic stress (Schindler 1990). The introduction (whether intentional or accidental) of exotic fish into aquatic systems throughout the world has had disastrous effects on native food webs (Frey 1969, Villwock 1972, Barel et al. 1985, Moyle 1986, Kaufman 1992). Despite the growing number of studies documenting exotic species introductions and their consequences to communities, the further destruction of aquatic systems by these means continues (Balon & Bruton 1986).

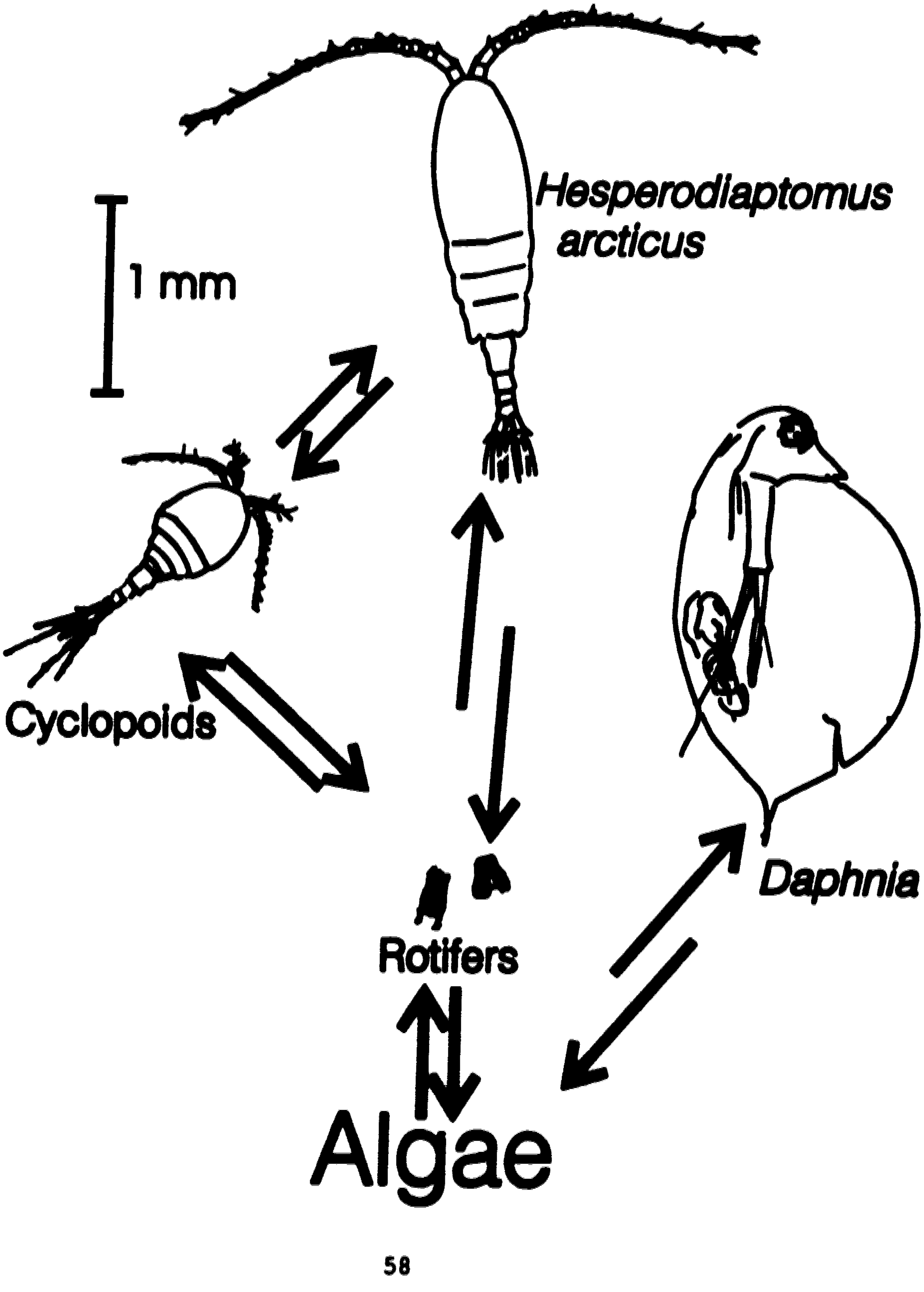
An estimated 95% of mountain lakes in western Canada and the United States were naturally fishless (Donald 1987, Bahls 1992). However, since 1900 many of these lakes have been stocked with the intention of creating a recreational fishery (Donald 1987, Bahls 1992). Approximately, 60% of the mountain lakes in the western United States (Bahls 1992) and 20% of the lakes in seven Canadian mountain national parks (Banff, Jasper, Waterton Lakes, Yoho, Kootenay, Glacier and Mount Revelstoke) have been stocked with fish (Donald 1987). Introduction of another trophic level is expected to have great impacts on lower trophic levels. However, there are few studies of long-term effects of fish stocking in mountain lakes (Liss & Larson 1991, Schindler et al. in review).

The introduction of fish into mountain lakes can directly eliminate large planktonic invertebrates and shift the size-structure of the plankton towards smaller species (Reimers 1958, Anderson 1972, Walters and Vincent 1973, Northcote & Clarotto 1975 and Northcote et al. 1978, Schindler et al. in review). Paleolimnological studies have recorded the disappearance of large Chaoborus after fish stocking in lakes of Jasper National Park (Lamontagne 1993). Analyses of fossil pigments in alpine lake sediments from Banff National Park have suggested that algal biomass has increased 10-fold after salmonid introductions (Leavitt et al. in review.). However, it is uncertain if the increases in algae were a result of herbivore elimination or increased recycling of nutrients by the stocked fish (Leavitt et al. in review). Before we can determine the relative importance of direct and indirect effects of fish on these pristine communities, we need to delineate the trophic interactions of the fishless food-web.

Planktonic communities of fishless alpine lakes in the western United States and Canada have low species diversity (Patalas 1964, Anderson 1971). Large calanoid copepods, often *Diaptomus* (subgenus: *Hesperodiaptomus*) *arcticus* or *H. shoshone* are usually the top pelagic predator (Fig. 2.1; Patalas 1964, Anderson 1971, Stoddard 1987). Anderson (1971) determined that alpine lakes in western Canada are most often dominated by *H. arcticus* and large *Daphnia*, usually *D. middendorffiana*. Smaller zooplankton (cyclopoid copepods and rotifers) are less abundant or absent (Anderson 1980, chapter 1). *H. arcticus* can prey on small zooplankton (Anderson 1970) and significantly limit rotifer abundance in large enclosures (chapter 1).

The objective of this study was to determine the trophic interactions between *Hesperodiaptomus arcticus* (Marsh 1920), cyclopoid copepods, rotifers, algae and nutrient supply (Fig. 2.1). The effect of *Daphnia* on the community is currently being investigated and will be presented elsewhere. Predators (*H. arcticus*) and nutrient supply were manipulated in large enclosure experiments to determine the effect each has on the biomass of other populations. These interactions were then used to help interpret sediment records of pigments, allowing us to evaluate long-term effects of fish stocking on these lakes (Leavitt et al. in review).

Figure 2.1- Potential food web for fishless alpine lakes. Zooplankton species are drawn to scale. Arrows illustrate that food-web processes are composed of both resource and consumer interactions.


Hesperodiaptomus arcticus
1 mm
Cyclopoids
Daphnia
Rotifers
Algae

Methods

Study Lake

Experiments were conducted in Snowflake Lake (51°35' N 116°50' W) an alpine lake (2320 m) located in Banff National Park (see Anderson 1972 and chapter 1). Prior to 1960 the lake community contained large zooplankton (Hesperodiaptomus arcticus and Daphnia pulex) were present (Fig. 2.1; Anderson 1972). From 1960 to 1966 Snowflake Lake was stocked with rainbow trout (Oncorhynchus mykiss), brook trout (Salvelinus fontinalis) and cutthroat trout (Oncorhynchus clarki) (Anderson 1972). Soon after fish stocking, large zooplankton were eliminated and the size structure of the community shifted toward smaller species (Anderson 1972, Schindler et al. in review). The fish never reproduced and are believed to have died out by the late 70's to mid 80's (chapter 1). Currently, the planktonic community is dominated by cyclopoid copepods (Diacyclops bicuspidatus thomasi), rotifers (Keratella quadrata and Polyarthra dolichoptera) and Daphnia pulex (chapter 1). H. arcticus has not been collected from Snowflake Lake since its last report in the early 60's (Schindler et al. in review).

Enclosure Experiments

Experiments were conducted bettween 27 June and 2 August 1992. The experimental design was a 2 x 2 factorial analysis with 3 replicates (total of 12 enclosures). Each enclosure was 0.9m x 0.9m x 3m and enclosed ≈2250 L of lake water. Further details of the enclosures and experimental design are given elsewhere (Appendix A, chapter 1). In brief, the treatments were addition or no addition of predators (Hesperodiaptomus arcticus), nutrients (N + P) or both. H. arcticus were collected from nearby Pipit Lake and added to the enclosures at densities (mean= 3.2 ind.$\cdot$L^{-1} SD= .64) similar to the mean density (mean= 3.2 ind.$\cdot$L^{-1} SD= 1.51) in 20 alpine lakes containing Hesperodiaptomus (chapter 1). Nutrients were added as NH_4NO_3 and H_3PO_4 (30:1 N:P by atomic ratios) to increase total phosphorus (TP) by a factor of 5; natural TP and total nitrogen in Snowflake Lake are ≈4 µg$\cdot$L^{-1} and ≈120 µg$\cdot$L^{-1}, respectively. TP concentrations were measured weekly and maintained at nearly constant values by weekly additions of H_3PO_4 and NH_4NO_3 (at the same ratio as above). Both nutrients and H. arcticus were added to the enclosures on the 27th of June (Day 0) approximately 1 week after ice out. The experiment ran for 36 days and the enclosures were sampled weekly.

Water samples were collected from the enclosures and the lake using a clear PVC tube 2.75 m in length and .05 m inner diameter (DeVries & Stein 1991). The tube was dropped vertically into each enclosure or the lake, plugged at the top, removed, and emptied into a bucket. The procedure was repeated, removing approximately 10.5 L of water per enclosure. No more than 10.5 L (0.5% of total enclosure volume) were collected to minimize sampling depletion from the enclosures. Aliquots were taken for algal pigment analysis (0.5-1 L), TP (0.25 L) and the remaining volume used for enumeration of zooplankton. Zooplankton were concentrated on a 10 μm mesh and preserved in sugared formalin (Prepas 1978). The entire zooplankton sample was settled for 24 hours and then counted using an inverted microscope and keys from Edmondson (1959), Pennak (1978), Chengalath et al. (1971) , Ruttner Kolisko 1974 and Grothe & Grothe (1977).

Rotifer biomass was calculated for *Keratella quadrata* and *Polyarthra dolichoptera* only. Other rotifers (*Keratella cochlearis*, *Synchaeta spp*., *Notholca spp*. and *Kellicottia longispina*) were collected infrequently and contributed very little to overall rotifer biomass (see chapter 1). The mean individual biomass of *K*. *quadrata* or *P*. *dolichoptera* was calculated by averaging individually estimated weights from each measured rotifer (Bird & Prairie 1985). Weights were estimated using the length-mass regression of Stemberger and Gilbert (1987). The mean lengths of *K*. *quadrata* and *P*. *dolichoptera* were 126 μm (range 100-150 μm) and 120 μm (range 90-140 μm), respectively. Total rotifer biomass was calculated from species abundance because mean lengths of both *K*. *quadrata* and *P*. *dolichoptera* did not change between enclosures or over time.

Daphnia pulex and *Diacyclops bicuspidatus thomasi* copepodids and adults occurred infrequently using our sampling methods and could not be assessed quantitatively. However, early stage cyclopoid nauplii (N1-N3) increased to detectable levels in all enclosures during the last day of the experiment. Therefore, our analysis on the effects of *Hesperodiaptomus* and nutrients on cyclopoids will be limited to their nauplii and for one date only. Mean nauplii biomass was calculated in a similar manner to rotifers using the length-weight regression of Bottrell et al. (1976) for *Cyclops scutifer* nauplii. This regression equation was chosen because the range of the nauplii used in the regression analysis for *C. scutifer* (140-290 µm, Bottrell et al. 1976) was very close to the mean length of cyclopoid nauplii in the enclosures (137 µm, range 100-180 µm). It is important that the length used to calculate biomass is within the range of the original regression (McCauley 1984). Total nauplii biomass was also calculated from their abundance because all nauplii were at a similar size between enclosures.

I tested if clutch sizes of *Diacyclops bicuspidatus thomasi* increased in response to fertilizer additions. In order to obtain a large enough sample size of ovigerous females, I pooled samples into either fertilized or unfertilized treatments for days 30 and 35 of the experiment. The unfertilized treatments also included samples taken from the lake. I did not use results from the predator-present treatments because adult *D. b. thomasi* and *Hesperodiaptomus arcticus* may compete for similar food resources (Anderson 1970). I restricted analyses to days 30 and 35 to allow female *D. b. thomasi* the longest exposure to higher resource levels. Clutch size was determined by detaching and dissecting egg sacs, and counting individual eggs.

Standing stocks of total algae and major algal groups (Cyanophyta, Cryptophyta, Chlorophyta and Chrysophyta) were quantified using the biomass of characteristic photosynthetic pigments estimated from reverse-phase high performance liquid chromatography (HPLC; Leavitt and Carpenter 1990). Briefly, pigments were extracted from plankton concentrated on Whatman GF/F filters using acetone, methanol and water (80:15:5 by vol.) for 24 hours at 12°C. The extract was filtered through 0.2 μm acropore membrane filters, dried and stored under nitrogen. Extracts were dissolved in 200 μl of acetone, ion-pairing reagent (tetrabutyl ammonium acetate, ammonium acetate and water), methanol (70:25:5 by vol.) and Sudan II (a standard dye). Pigments were separated on a Rainin C-18 column at 2000 psi. Each pigment was identified and quantified by scanning for absorbance at 430 nm. Total algal standing stocks were assessed using chlorophyll a (chl a), a pigment common to all photosynthetic plants. Cyanophyta (blue-green algae) and Chlorophyta (green algae) were quantified together using lutein and zeaxanthin, 2 inseparable xanthophylls in green and blue-green algae, respectively (Reynolds 1984). Cryptophyta (cryptomonads) and Chrysophyta (chrysophytes and diatoms) were quantified using alloxanthin and fucoxanthin, respectively (Reynolds 1984). We also quantified chlorophyll b (chl b) pigments to determine if increases in lutein-zeaxanthin could be attributed to green or blue-green algae. Chl b is only present in green algae, euglenoids and higher plants.

Rotifer and pigment biomass data were statistically analyzed using repeated measures two-way analysis of variance with fixed effects (Sokal & Rohlf 1981). Rotifer biomass was $\log_{10}$-transformed before statistical analysis because means increased exponentially and were positively correlated with variance (Sokal & Rohlf 1981). Cyclopoid nauplii biomass was analyzed using two-way analysis of variance with fixed effects on untransformed data. Multiple comparisons among means were conducted _a posteriori_ for rotifer and nauplii biomass using Studentized Newman-Keuls methods (Prepas 1984, SAS 1988). Statistical significance for tests was set at $\alpha = 0.05$, probabilities are indicated for all tests.

Results

Rotifers

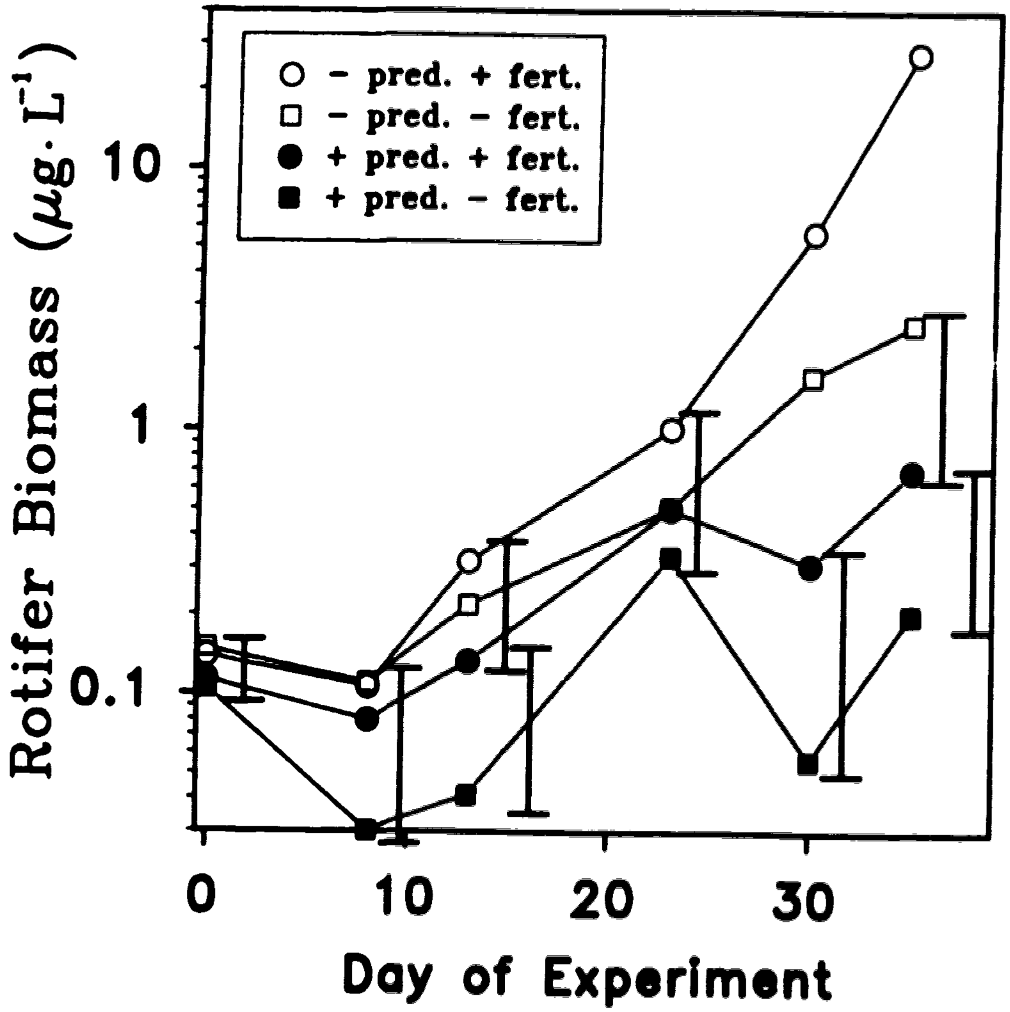
Biomass of rotifers (_Keratella quadrata_ and _Polyarthra dolichoptera_) was significantly affected by both _Hesperodiaptomus arcticus_ (predator) and nutrient additions (Table 2.1). Rotifer biomass was reduced in the presence of predators and increased with the addition of nutrients (Fig. 2.2). There was no significant interaction between the two treatments (Table 2.1). Mean rotifer biomass did not differ significantly between treatments until day 13 of the experiment when unfertilized predator present treatments were significantly different from both predator absent treatments (Fig. 2.2). Biomass between the fertilized and unfertilized predator present treatments never differed significantly (Fig. 2.2). However, in the absence of predators, biomass between fertilized and unfertilized treatments differed significantly by the end of the experiment (days 30 and 35). Rotifers reached their greatest biomass (27.7 $\mu g \cdot L^{-1}$, day 35) in the fertilized enclosures without predators and their lowest biomass in the unfertilized enclosures with predators (0.03 $\mu g \cdot L^{-1}$, day 8).

Table 2.1- Repeated measures analysis of variance for rotifer biomass and pigment concentrations from enclosures. The two treatments were presence/absence of the predator *Hesperodiaptomus arcticus* and addition/no addition of fertilizer. Rotifer biomass was $\log_{10}$ transformed.

TEST	SOURCE	df	MS	P*
Rotifer Biomass				
	TREATMENTS			
	Hesperodiaptomus	1	8.15	0.002
	Fertilization	1	2.45	0.04
	interaction	1	0.02	0.82
	ERROR	8	0.41	
Chlorophyll *a*				
	TREATMENTS			
	Hesperodiaptomus	1	4.11	0.36
	Fertilization	1	584.97	0.0001
	interaction	1	0.68	0.70
	ERROR	8	4.29	
Fucoxanthin				
	TREATMENTS			
	Hesperodiaptomus	1	0.06	0.77
	Fertilization	1	332.16	0.0001
	interaction	1	0.78	0.3175
	ERROR	8	0.69	
Alloxanthin				
	TREATMENTS			
	Hesperodiaptomus	1	0.07	0.04
	Fertilization	1	0.61	0.0001
	interaction	1	0.07	0.04
	ERROR	8	0.01	
Lutein and Zeaxanthin				
	TREATMENTS			
	Hesperodiaptomus	1	0.48	0.003
	Fertilization	1	7.45	0.0001
	interaction	1	0.30	0.009
	ERROR	8	.03	
Chlorophyll *b*				
	Hesperodiaptomus	1	0.0001	0.50
	Fertilization	1	0.0037	0.003
	interaction	8	0.0002	0.38
	ERROR		0.0002	

*P= probability of committing a type I error

Figure 2.2- Mean rotifer biomass (dw = dry weight) from enclosures with or without _Hesperodiaptomus_ _arcticus_ or fertilizer. Solid symbols (● ■) represent enclosures with _H_. _arcticus_ and open symbols (○ □) enclosures without _H_. _arcticus_. Fertilized enclosures are shown by circles (○ ●) and unfertilized enclosures by squares (□ ■). Vertical bars indicate treatment means that are not significantly different using Studentized Newman-Keuls method.



○ − pred. + fert.
□ − pred. − fert.
● + pred. + fert.
■ + pred. − fert.
Rotifer Biomass ($\mu g \cdot L^{-1}$)
10
1
0.1
0
10
20
30
Day of Experiment

Rotifer biomass increased at an exponential rate in all enclosures except the unfertilized enclosures with predators (Table 2.2). The slope of the regression equation (Table 2.2) is a measure of the rate of increase in rotifer biomass. For each nutrient treatment I estimated the instantaneous removal rate of rotifer biomass by predation as the difference in the rates of increase between the predator absent and predator present treatments. This assumes that predation is the sole reason for the observed differences in rotifer growth. Slopes (or estimates of growth) that were not significantly different from zero were set to zero. The rate of removal of rotifer biomass by Hesperodiaptomus arcticus was between 0.09 and 0.10$\cdot$ d^{-1} in both fertilized or unfertilized enclosures suggesting that the proportion of prey removed per predator was relatively constant between fertilized and unfertilized enclosures.

Cyclopoids

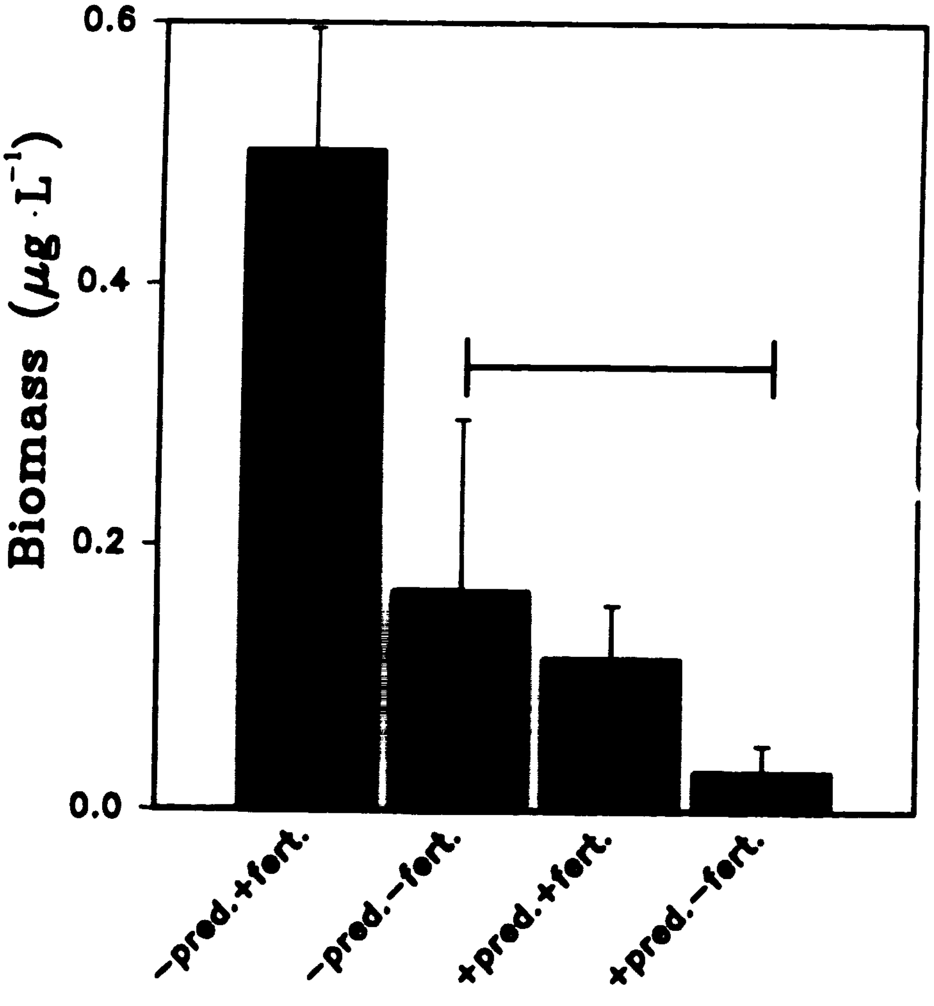
Biomass of cyclopoid nauplii responded positively to fertilization and negatively to predator additions in the enclosures (Fig. 2.3). Nauplii biomass on day 35 was greater in the fertilized enclosures than in the unfertilized enclosures (Fig. 2.3, F= 6.644, df= 1,8, $P< 0.033$). Enclosures with Hesperodiaptomus arcticus present had a lower biomass of nauplii than those without predators (Fig. 2.3, F=10.166, df=1,8, $P<.013$). There was no significant interaction between the two treatments (F= 2.207, df= 1,8, $P> 0.17$). However, a comparison of the means a posteriori indicates that the

Table 2.2- Results from linear regression analysis of $\log_{10}$ transformed rotifer biomass as a function of time. Results given for fertilized and unfertilized enclosures with(+) or without(-) predators.

TEST	R^2	SLOPE	df	P*
Fertilized				
+ Predator	.79	.0581	4	0.018
- Predator	.90	.155	4	0.0035
Unfertilized				
+ Predator	.18	.0294	4	0.40
- Predator	.91	.0915	4	0.0033

*P=probability slope is equal to zero

Figure 2.3- Mean densities of Diacyclops bicuspidatus thomasi nauplii for day 35 of the enclosure experiments. The treatments were presence/absence (+/-) of the predator Hesperodiaptomus arcticus and addition/no addition (+/-) of fertilizer. Error bars show 1 standard error of the mean. Horizontal bar indicates treatment means that are not significantly different using Studentized Newman-Keuls method.



Biomass (μg · L^{-1})
0.6
0.4
0.2
0.0
-pred.+fert.
-pred.-fert.
+pred.+fert.
+pred.-fert.

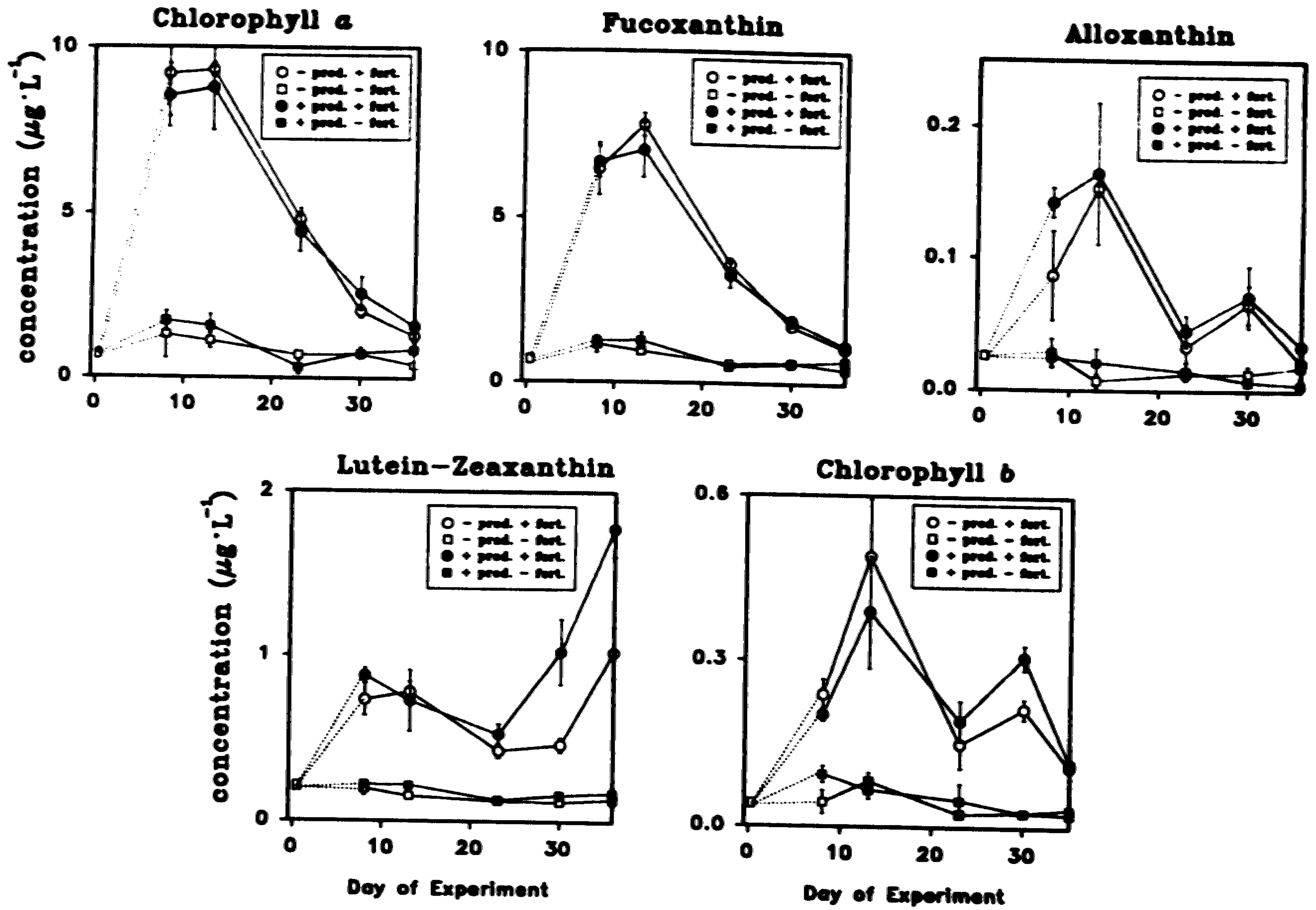
predator-absent unfertilized treatments were not significantly different from the mean biomass in either of the predator-present treatments (Fig. 2.3).

The clutch size of Diacyclops bicuspidatus thomasi increased significantly (32%) in response to fertilization (Mann-Whitney U-test, $n_{1,2}$= 11,10, P< 0.005). The mean clutch size for fertilized treatments was 45 eggs (median= 48,n= 11) compared to 34 eggs (median= 32.5,n= 10) in unfertilized enclosures or the lake.

Algae

Concentrations of all pigments (chl a, fucoxanthin, alloxanthin, lutein-zeaxanthin) increased rapidly in response to fertilizer additions (Table 2.1 and Fig. 2.4). Lutein-zeaxanthin pigments also showed a significant positive response to predator additions (Table 2.1). Lutein-zeaxanthin reached the greatest concentrations at the end of the experiment in the fertilized enclosures with predators (Table 2.1 and Fig. 2.4). Lutein-zeaxanthin pigments in the unfertilized enclosures were unaffected by predator additions (Fig. 2.4). Because lutein-zeaxanthin responded to predator additions only in the fertilized treatments, the interaction between predators and fertilizer was significant (Table 2.1). Alloxanthin (cryptophytes) also showed a positive response to predator additions in the fertilized treatments (Fig. 2.4). However, the response was only marginally significant (Table 1) and the greatest difference occurred only 8 days after the start of the experiment (Fig. 2.4). Chl a (total algae)

Figure 2.4- Mean concentrations of algal pigments from enclosures with or without *Hesperodiaptomus arcticus* (predator) or fertilizer. Solid symbols (● ■) represent enclosures with *H. arcticus* and open symbols (○ □) enclosures without *H. arcticus*. Fertilized enclosures are shown by circles (○ ●) and unfertilized enclosures by squares (□ ■). Error bars represent 1 SE of the mean. Error bars less than the size of the symbol not shown.

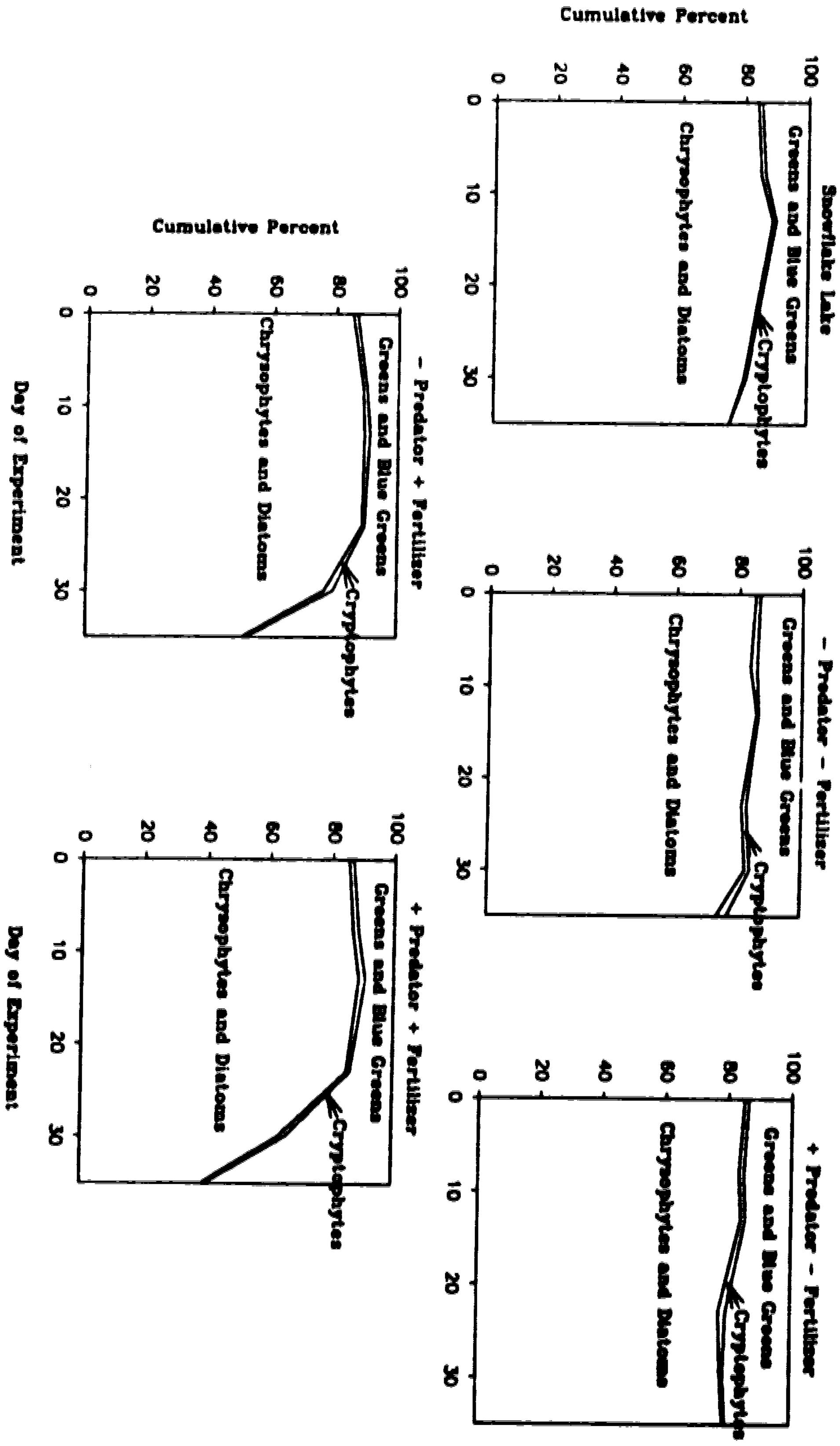

Chlorophyll *a*
Fucoxanthin
Alloxanthin
Lutein–Zeaxanthin
Chlorophyll *b*
concentration ($\mu g \cdot L^{-1}$)
concentration ($\mu g \cdot L^{-1}$)
○ - pred. + fert.
□ - pred. - fert.
● + pred. + fert.
■ + pred. - fert.
0
5
10
0.0
0.1
0.2
0
1
2
0.0
0.3
0.6
0
10
20
30
Day of Experiment
Day of Experiment

and fucoxanthin (chrysophytes and diatoms) were significantly affected by the fertilizer treatment only (Table 2.1). These two pigments increased with fertilizer addition but were unaffected by the presence or absence of the predator (Fig. 2.4).

Chl b increased significantly in the fertilized enclosures (Table 2.1 & Fig. 2.4). Therefore, the increase in lutein-zeaxanthin at the start of the experiment can be at least partially attributed to green algae. However, chl b did not show a significant response to predator treatments (Table 1) and declined in concentrations toward the end of the experiment (Fig. 2.4). In contrast, lutein-zeaxanthin showed a significant response to predators and continued increasing in concentration throughout the experiment (Fig. 2.4). Higher concentrations of lutein-zeaxanthin after day 23 suggest increased levels of blue-green algae. Furthermore, the significant response of lutein-zeaxanthin to predator treatments must also have been attributed to changes in unicellular cyanophytes because large colonial blue-greens were never present during the counting of zooplankton samples at 100X magnification.

Because changes in relative proportions of water column pigments are related to algal composition (Ridout and Morris 1985), cumulative percentages of fucoxanthin, alloxanthin and lutein-zeaxanthin were plotted (Fig. 2.5). Unfertilized enclosures and Snowflake Lake were dominated by chrysophytes and diatoms throughout the experimental period (Fig. 2.5). Relative algal composition was similar among all treatments early in the experiment; however, after day 20 green and blue-green algae

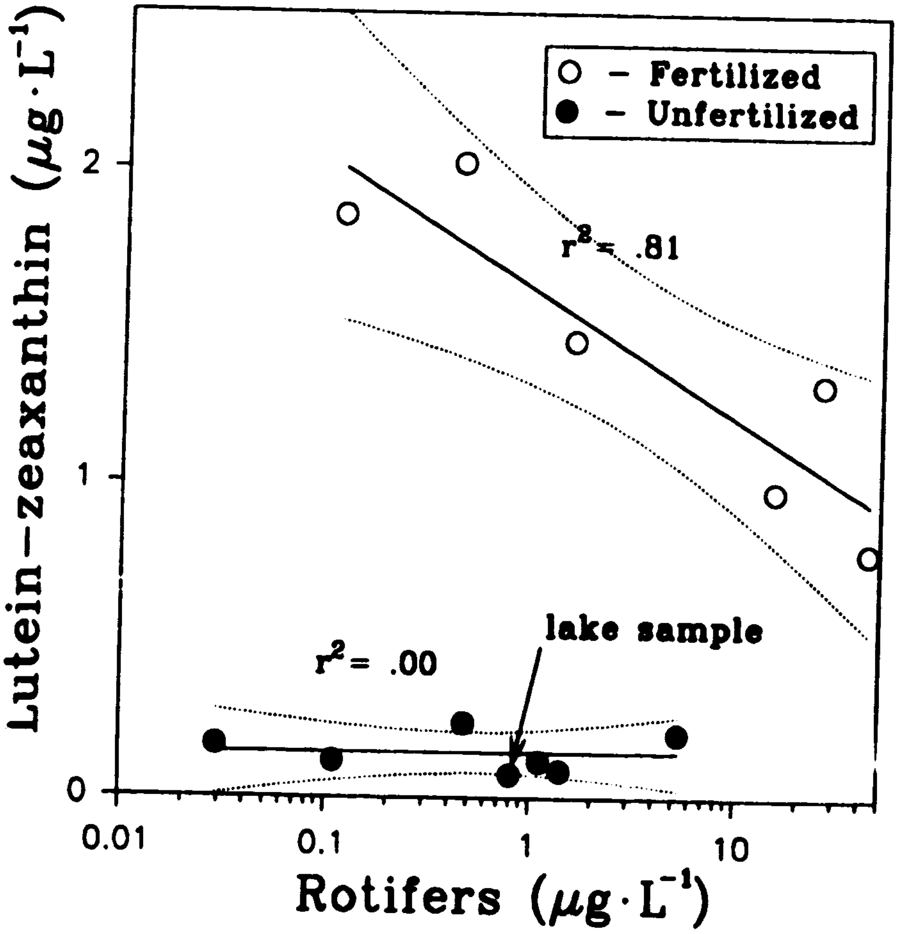
Figure 2.5- Relative proportions of algal taxa as indicated by their representative xanthophyll pigments. Greens and blue-greens are represented by lutein and zeaxanthin, cryptophytes by alloxanthin, and chrysophytes and diatoms by fucoxanthin.


Cumulative Percent
100
80
60
40
20
0
Snowflake Lake
Greens and Blue Greens
Cryptophytes
Chrysophytes and Diatoms
0
10
20
30
- Predator - Fertilizer
+ Predator - Fertilizer
- Predator + Fertilizer
+ Predator + Fertilizer
Day of Experiment

increased at the expense of diatoms and chrysophytes in the fertilized enclosures (Fig. 2.5). This shift towards greens and blue-greens occurred earlier and was greater in the presence of predators (Fig. 2.5). Cryptophytes accounted for a constant low proportion of the algal composition in all enclosures and Snowflake Lake throughout the experimental period (Fig. 2.5).

The relationship between standing stocks of blue-green algae and rotifer biomass was examined by plotting concentrations of lutein-zeaxanthin as a function of rotifer biomass for day 35 of the experiment. Although the nauplii of cyclopoids are herbivorous, they were not an important grazer during the experiment because their biomass was insignificant compared to rotifers' biomass (Fig. 2.3). Each enclosure was plotted as a separate system and a straight line was fitted to the data using linear regression analysis. Rotifer biomass was negatively correlated with, and explained a large portion of the variation in, lutein-zeaxanthin concentrations ($R^2 = 0.81$, N=6) for the fertilized enclosures (Fig. 2.6). However, in the unfertilized enclosures rotifer biomass explained none of the variation in lutein-zeaxanthin concentrations ($R^2 = 0.00$, N=7) (Fig. 2.6), albeit that in the unfertilized enclosures lutein-zeaxanthin concentrations were low.

Figure 2.6- Lutein and zeaxanthin concentrations plotted with respect to rotifer biomass (dw = dry weight) for day 35 of the experiment. The solid symbols (●) represent unfertilized enclosures and a lake sample while the open symbols (○) represent fertilized enclosures. Regression lines (solid line) were drawn through the points for both fertilized and unfertilized enclosures (including lake sample). 95% confidence interval (dotted line) and squared correlation coefficient are shown for each regression line.



○ – Fertilized
● – Unfertilized
r^2 = .81
r^2 = .00
lake sample
0
1
2
0.01
0.1
1
10
Lutein-zeaxanthin ($\mu g \cdot L^{-1}$)
Rotifers ($\mu g \cdot L^{-1}$)

Discussion

Predator and Nutrient Effects on Rotifers

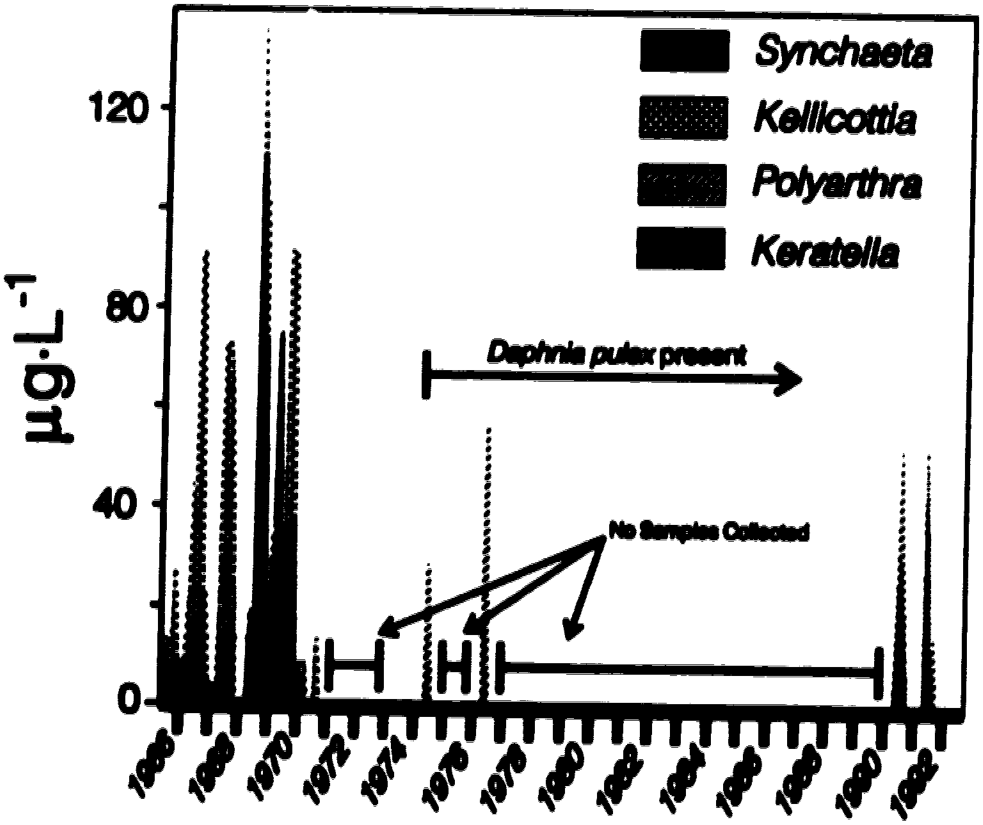
Hesperodiaptomus arcticus predation on rotifers is important in determining the composition (Anderson 1980, chapter 1) and biomass of rotifer communities in alpine lakes. H. arcticus preys selectively on certain rotifer species (Anderson 1970, chapter 1) and has a strong negative effect on total rotifer biomass.

Hall et al. (1976) predicts that as prey densities increase, invertebrate predation rates will saturate before prey densities are significantly reduced. Our results indicate that Hesperodiaptomus arcticus removed a constant proportion of prey over different biomass and did not show saturation. Furthermore, the response of H. arcticus to prey was functional (Hollings 1959) as juvenile stages of H. arcticus were limited to small naupliar forms, which are likely herbivorous. The cold thermal regime of Snowflake Lake and other alpine lakes may keep productivity and biomass of rotifers below saturation levels of their predators, regardless of enhanced nutrient levels (chapter 1). Therefore, the strong functional response of H. arcticus towards its prey coupled with a numerical response in subsequent years could effectively reduce rotifer biomass in alpine lakes. This prediction is supported for both Keratella quadrata and Polyarthra dolichoptera by the manipulative experiments and empirical models (chapter 1).

Increased nutrient levels caused rotifer biomass to increase. Rotifers probably indirectly benefited from fertilization treatments by grazing on increased standing stocks of suitable algae. Our results suggest that unicellular blue-green algae, and not green algae, were the important component of rotifer's diet in the fertilized enclosures. Although, unicellular and filamentous blue-green algae can inhibit growth in *Daphnia* (Arnold 1971, Lamr 1981) rotifers can grow in cultures consisting solely of filamentous (Starkweather & Kellar 1983) or unicellular (Pourriot & Rougier 1975) blue-green algae. In fact, populations of the littoral rotifer *Brachionus dimidiatus* grown on the unicellular blue-green algae *Synechoccus cedrorum* reached higher growth rates than those grown using the green algae *Chlamydomonas* sp. or *Diogenes* sp. (Pourriot & Rougier 1975). Unfortunately, nutritional requirements of many planktonic rotifers are unknown and may vary between isolated populations of the same species (Stemberger 1981).

Increased rotifer abundance following fish stocking in Snowflake Lake (Fig. 2.7) was facilitated by reduced invertebrate predation (Anderson 1972, chapter 1); however, actual rotifer biomass attained may have been a function of algal abundance and lack of competitors (ie. *Daphnia pulex*). Standing stocks of the major algal taxa increased 4-10 fold following fish stocking and declined in subsequent years (Leavitt et al. in review). Furthermore, *D. pulex*, a strong competitor of herbivorous rotifers (Gilbert 1988), was absent from the plankton between 1966 and 1975 (Fig. 2.7). During the period of high algal stocks and no *D. pulex* (late 60's) rotifer biomass was greatest (Fig. 2.7). Rotifers reached their maximum biomass in 1969 (139 $\mu g \cdot L^{-1}$, Fig. 2.7) shortly after estimated peak levels of phosphorus excretion from introduced fish (Leavitt et al. in review). *Synchaeta oblonga* (mean length= 220 μm)

Figure 2.7- Mean monthly biomass (dry weight) of dominant rotifers from Snowflake Lake. Years when no data was collected are indicated. Data are from Anderson (1972), D. Donald (Environment Canada, 2365 Albert Street, Regina, Sask. S4P 4K1, unpubl. data) and chapter 1. All data were collected using a similar net towed over the deepest part of Snowflake Lake (chapter 1). Biomass was calculated as described in methods (see text) from the length-mass regression of Stemberger & Gilbert (1987) and measured lengths.


Synchaeta
Kellicottia
Polyarthra
Keratella
μg·L⁻¹
120
80
40
0
Daphnia pulex present
No Samples Collected
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992

replaced Kellicottia longispina (mean length= 160 μm) as the dominant rotifer in 1969 (lengths measured from 1969 Snowflake Lake samples collected by R.S. Anderson and archived in the Zoology Musuem, University of Alberta, Edmonton, Canada). As algal stocks diminished and D. pulex returned to the plankton, rotifer biomass decreased (Fig. 2.7). Currently, Polyarthra dolichoptera and Keratella quadrata dominate in Snowflake Lake reaching a combined maximum biomass of approximately 50 μg· L^{-1} in 1991 and 1992 (Fig. 2.7).

Predator and Nutrient Effects on Cyclopoid Copepods

Reduction in the biomass of cyclopoid nauplii from predation (by Hesperodiaptomus arcticus) could have been related to the fecundity of adults, the survivorship of nauplii or both. Hesperodiaptomus predation could have directly reduced nauplii and ovigerous adults (Anderson 1970) resulting in an observed decrease in nauplii biomass. However, predation on adult cyclopoids would have been lower than on nauplii because Hesperodiaptomus predation rates are inversely related to prey size (Anderson 1970).

Increased cyclopoid nauplii biomass from fertilization could also be related to adult fecundity, nauplii survivorship or both. Fertilization increased the clutch sizes of Diacyclops bicuspidatus thomasi. Similar observations have been made for the same species in oligotrophic montane lakes (Peacock 1982), as well as for other cyclopoids (Smyly 1970) and diaptomids (Chow-Fraser & Maly 1991). However, the 3-fold increase in nauplii biomass in the fertilized compared to the unfertilized enclosures (Fig. 2.3) can not be explained solely by the 32% increase in clutch sizes of *D. b. thomasi*. The observed increase in nauplii must also have been a result of higher numbers of ovigerous females or increased nauplii survivorship. Peacock (1982) determined that fertilization did not increase the proportion of ovigerous *D. b. thomasi* at a given time of egg production; but it did increase the survivorship of nauplii. Therefore, the observed increase in nauplii biomass from fertilization is likely a result of larger clutch sizes coupled with increased nauplii survivorship. Unfortunately, we could not determine the independent effects of fertilization (or *H. arcticus*) on ovigerous adults and nauplii survivorship because of our small sample size and the absence of nauplii until the end of the experiment.

Cyclopoid predation in alpine lakes does not likely control rotifer populations (Anderson 1980). Although, cyclopoids are known to prey on rotifers (McQueen 1969, Anderson 1970, Stemberger 1985), their presence in lakes of the Canadian Rocky Mountains apparently does not suppress rotifer abundance (Anderson 1980). The inability of cyclopoids to limit the abundance of rotifer prey in these lakes may be due to the trophic nature of cyclopoids and lack of alternate prey resources. Predacious cyclopoids are more obligate predators (Fryer 1957) than *Hesperodiaptomus*, which can be omnivorous (Anderson 1970). Hodgkin & Rippingale (1971) predict that facultative copepod predators are more likely to eliminate prey species than obligate predators because alternate resources can maintain predator abundance even when prey become rare.

Predation by Diacyclops bicuspidatus thomasi may be important in regulating abundance of zooplankton with generation times ≥ 1 year. However, predation by adult Hesperodiaptomus and poor nutrient regimes of alpine lakes will limit the number of cyclopoid nauplii that reach adult stage. Enhanced nutrient levels and reduced predation pressure (as predicted from fish stocking) will increase a cohort of cyclopoid nauplii. If this strong cohort reaches its predacious stages (as a copepodid or adult) it could regulate the abundance or presence of other zooplankton with long generation times, such as H. arcticus, by preying on their juvenile stages (Anderson 1970, Leavitt et al. in review). This is analogous to the predator "bottleneck" described by Neill (1975) and Neill & Peacock (1980) for other aquatic systems.

Predator and Nutrient Effects on Algae

The major algal taxa in Snowflake Lake are strongly nutrient limited as reflected by the rapid response in algal pigments (alloxanthin, fucoxanthin and lutein-zeaxanthin) to fertilizer treatments. Other investigators (Sprules & Munawar 1986, Watson & McCauley 1988, Richman & Sager 1990) have found that the proportion of nanoplankton biomass to total algal biomass is inversly related to nutrient levels. They suggest zooplankton biomass increased with nutrient levels leading to higher grazing losses of nanoplankton in the more productive systems (Watson & McCauley

1988, Sager & Richman 1991). My observation that [illegible] greens increase in nutrient enriched treatments appeared to contradict theory and suggests further study is required.

The ability of zooplankton to reduce algal standing stocks depends on the community grazing rates for specific algal assemblages. Community grazing rates depend on numerous factors including herbivore biomass and their taxonomic composition (Peters & Downing 1984, Cyr & Pace 1992). Low herbivore biomass (due to the oligotrophic nature of Snowflake Lake) and absence of large Daphnia (due to the timing of the experiment, see chapter 1) may have allowed small algal species to substantially increase in the nutrient enriched enclosures. These results are supported by models of phytoplankton communities (Carpenter & Kitchell 1984) that incorportate both losses (due to grazing) and gains (from nutrient recycling by grazers). These models predict that small algae will dominate in zooplankton communities characterized by low biomass of small grazers (Carpenter & Kitchell 1984, Berquist et al. 1985).

Indirect effects of Hesperodiaptomus arcticus predation on algal biomass may be dependent on nutrient availability. Algal growth can be maintained or even enhanced in the prescence of grazers due to excretion of nutrients in a form available to algae (Berquist & Carpenter 1986, Sterner 1986, Elser & Goldman 1990). Furthermore, rotifers recycle nutrients at high mass-specific rates and in forms available to algae (Ejsmont-Karabin 1983). This compensatory effect is important for small edible (by zooplankton) algae if zooplankton abundance is low and the algae are nutrient limited (Berquist & Carpenter 1986). When nutrient levels are saturated (*ie*. further increase in nutrients do not increase algal growth) nutrient recycling is no longer significant and grazers can have only a negative effect on algal growth (Lehman 1980, Lehman & Sandergren 1985). Therefore, the negative relation between concentrations of lutein-zeaxanthin and rotifers in the fertilized but not the unfertilized enclosures may have been possible because algal growth was nutrient saturated in the fertilized enclosures.

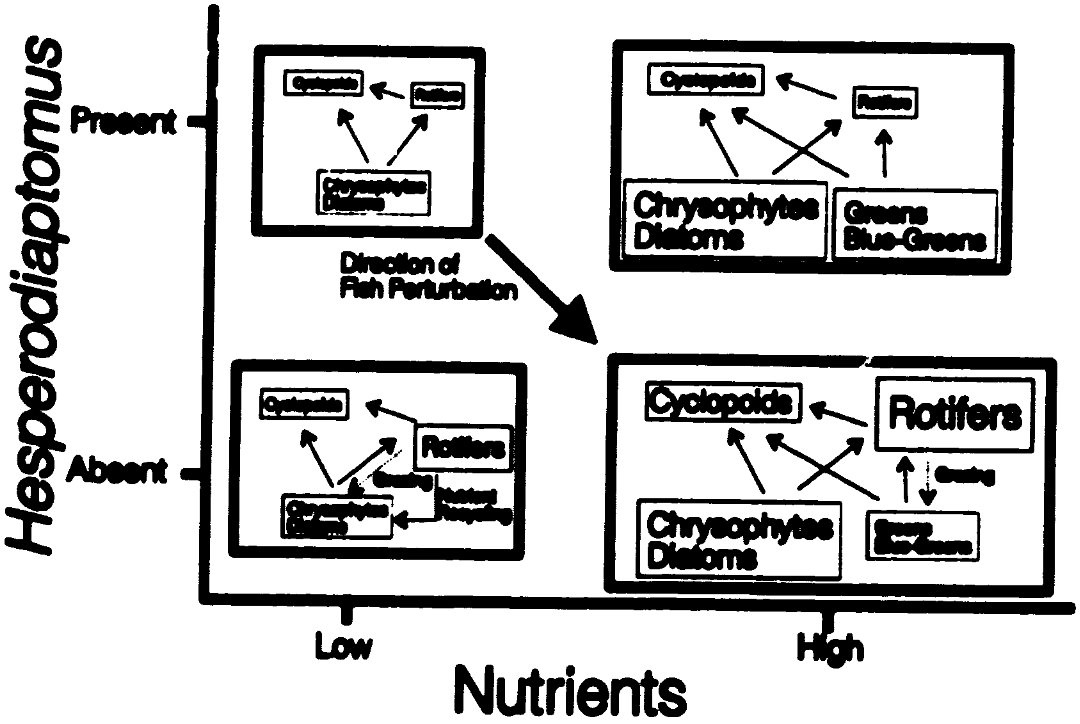
Experimental Design

I feel the enclosure experiments accurately represented lake processes. First, oligotrophic lakes are well suited to enclosure experiments as periphyton edge effects are minimal (Neill 1988). Second, reference enclosures (no predators or fertilizer added) did not differ from Snowflake Lake for either rotifer populations (chapter 1) or algal composition (Fig. 2.5). We did not assess cyclopoid populations because of our small sample sizes. Lastly, the magnitude of our treatments represented the estimated effects of the fish manipulation in Snowflake Lake, a 3-4 fold increase in phosphorus (Leavitt et al. in review) and absence of *Hesperodiaptomus arcticus* (Anderson 1972).

Implications for Alpine Food Webs

The four treatments in this experiment form a community matrix with distinct cells that differ in both the biomass and interactions of rotifers, cyclopoids and algae (Fig. 2.8). The matrix can be used to illustrate discrete changes in alpine lakes following fish stocking. The pristine lake is represented by the presence of Hesperodiaptomus and low nutrients (Fig. 2.8). The stocking of fish will eliminate Hesperodiaptomus (Anderson 1972, Walters and Vincent 1973) and increase nutrient concentrations (Leavitt et al. in review) pushing the system into the bottom right corner of the matrix (Fig. 2.8). If fish fail to reproduce and stocks diminish, nutrient levels will decrease to premanipulation levels (Leavitt et al. in review) and the system will move to the bottom left corner of the matrix (Fig. 2.8). The final step following stocking would be the recolonization by Hesperodiaptomus, returning the system to premanipulation conditions. However, recolonization by Hesperodiaptomus is variable (Schindler et al. in review) and may depend on the magnitude of fish stocking (Schindler et al. in review, Leavitt et al. in review), the abundance of cyclopoids (Anderson 1970, Leavitt et al. in review), lake morphometry and the presence of refugia (Donald et al. in press), or chance reintroductions (Schindler et al. in review).

Figure 2.8- Food-web interactions between cyclopoids, rotifers and algae with or without predators (*Hesperodiaptomus arcticus*) or added nutrients. Arrows represent the important interactions between components, solid lines show positive and dashed lines negative interactions. Box size estimates biomass of its component.


Hesperodiaptomus
Present
Absent
Cyclopoids
Rotifers
Chrysophytes
Diatoms
Direction of
Fish Perturbation
Cyclopoids
Rotifers
Chrysophytes
Diatoms
Greens
Blue-Greens
Cyclopoids
Rotifers
Grazing
Nutrient
Recycling
Chrysophytes
Diatoms
Cyclopoids
Rotifers
Grazing
Chrysophytes
Diatoms
Greens
Blue-Greens
Low
High
Nutrients

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General Discussion

Hesperodiaptomus arcticus are important in structuring the pelagic community of alpine lakes. Rotifers and cyclopoids are directly reduced in abundance or eliminated by H. arcticus. Biomass and composition of the major algal groups are not significantly affected by H. arcticus alone. However, composition within these taxonomic groups may be altered by reduced herbivory (Schindler et al. in review).

Because H. arcticus is a keystone predator in alpine lakes, its removal following fish stocking will affect community structure. Therefore, long-term effects of fish stocking in these lakes will be signficant if H. arcticus are extirpated. Smaller zooplankton will increase in abundance and certain phytoplankton species may be reduced by increased grazing from the smaller zooplankton (Schindler et al. in review).

Alpine Lakes: Endangered Ecosystem?

The preservation of lakes in their natural state is now regarded as an important management goal in Canadian National Parks (Schindler et al. in review). Such a decision could not come too soon. Estimates from the western United States indicate that less than five percent of the larger (>2 ha surface area), deeper (>3 m max. depth) mountain lakes remain in a pristine fishless condition (Bahls 1992). The percentage of lakes in the Canadian Cordillera that remain in pristine fishless conditions is unknown.

However, it is estimated that 20% of the lakes in seven Canadian National Parks (Banff, Jasper, Waterton, Kootenay, Yoho, Glacier and Mt. Revelstoke) have been stocked with fish (Donald 1987).

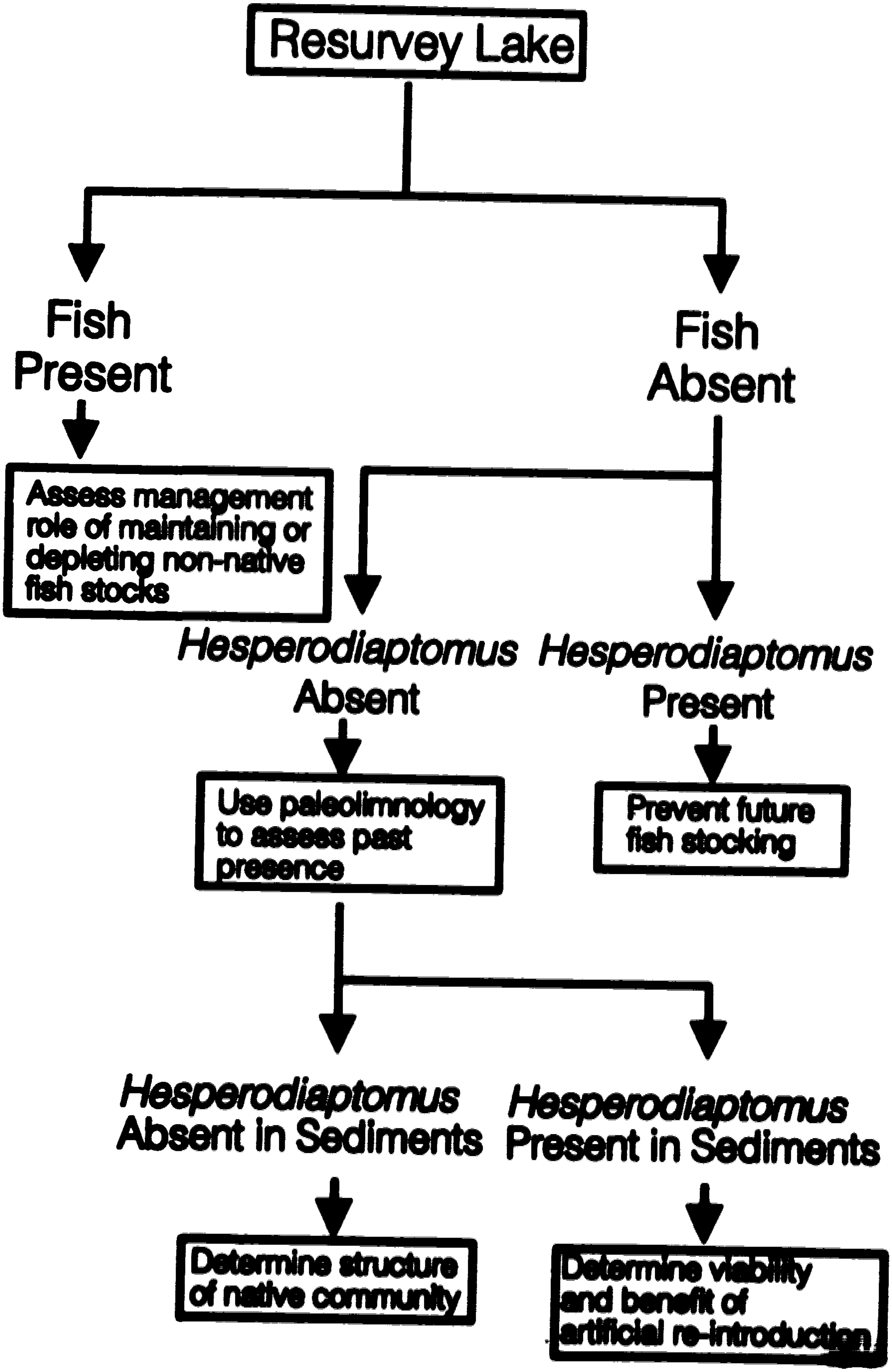
The indiscriminant stocking of mountain lakes has resulted in the demise of indigenous fish (Schindler et al. in review), amphibians (Liss & Larson 1991) and invertebrates (Reimers 1958 Anderson 1972).

Lake Recovery

Before we can evaluate the recovery of lakes (following fish stocking and failure), it is necessary to have knowledge of the original lake community. Because many mountain lakes were never surveyed prior to fish stocking, paleolimnological analysis will be the key in gathering this information (Schindler et al. in review).

Twenty-five percent of a 112 lakes surveyed in Banff and Jasper National Parks may have had Hesperodiaptomus extirpated by fish stocking (Appendix B). The list of lakes in Appendix B provides managers with a starting point from which to carry out further work. Although the likelihood of a lake previously having Hesperodiaptomus may be predicted (Appendix B), the certainty of past presence will require more study. A procedure that can be followed is outlined in Figure 3.1. The flow chart (Fig. 3.1) integrates fisheries, limnology and paleolimnology into a method

Figure 3.1 - A flow chart illustrating a procedure that could be followed in determing the past and current status of Hesperodiaptomus populations and their management.


Resurvey Lake
Fish Present
Fish Absent
Assess management role of maintaining or depleting non-native fish stocks
Hesperodiaptomus Absent
Hesperodiaptomus Present
Use paleolimnology to assess past presence
Prevent future fish stocking
Hesperodiaptomus Absent in Sediments
Hesperodiaptomus Present in Sediments
Determine structure of native community
Determine viability and benefit of artificial re-introduction

to assess the current status (in reference to Hesperodiaptomus) of a previously stocked lake.

The use of paleolimnology to determine past presence of Hesperodiaptomus in mountain lakes (Fig. 3.1) has two shortcomings. First, copepods are difficult to assess from sediment records because they leave few diagnostic fossil remains. A suitable technique must be developed to confirm the presence of Hesperodiaptomus in mountain lakes by paleolimnology. Some possibilities that need exploring are the use of copepod spermatophores (Warner 1989) or copepod resting eggs (eggs may be diagnostic by size for Hesperodiaptomus). Secondly, low productivity and high sedimentation of inorganic matter in mountain lakes necessitate that large amounts of sediments be concentrated before invertebrate subfossils may be used (Lamontagne 1993). Fortunately, these techniques would be aimed at determining the presence of the species and not its abundance. Therefore, only 1 identifiable spermatophore or resting egg need be distinguished.

The re-establishment of Hesperodiaptomus following its extirpation by fish is variable among lakes. Three lakes in Banff National Park (Snowflake, Pipit and Bighorn) all had H. arcticus eliminated by fish stocking in the 1960's (Anderson 1972). Fish did not successfully reproduce in any of the lakes; however, H. arcticus has naturally recolonized only Pipit Lake (Schindler et al. in review, pers. obsv.). There are a number of possible variables that may influence the re-establishment of H. arcticus in these stocked lakes (see chapter 2). In lakes where H. arcticus has not recolonized years after the disappearance of fish, artificial re-introduction of *H. arcticus* may be required to return lakes to a condition similar to their pristine state (Fig. 3.1).

Future Research

Numerous areas of future research have been mentioned throughout the thesis. However, there are some specific areas I feel are of special concern.

Trophic interactions in alpine lakes may be limited by their thermal regime. Warming trends could alter these interactions by allowing phytoplankton and prey production to increase. Enclosure experiments with temperature as a controlled treatment would be ideal to answer these questions. However, these would be costly and difficult to implement. Alternatively, reciprocal enclosure experiments could be used in similar lakes with different thermal regimes.

Consumption rates of predators and production rates of prey could also be modelled as functions of temperature (see Yan et al. 1991). This would require good data for both *H. arcticus* (biomass, respiration, growth, assimilation and food selectivity) and prey (biomass and growth rates) from alpine lakes as values obtained from more temperate systems or laboratories do not account for acclimation of individuals to their environment (Armitage & Lei 1979).

The life history of *Hesperodiaptomus arcticus* is not known for alpine lakes. Sawchyn & Hammer (1968) described the life history of *H. arcticus* in prairie ponds of Saskatchewan; in these ponds, H. arcticus hatch from resting eggs early in the spring, develop into adults and have dissappeared in 6 weeks. The persistence of H. arcticus throughout the year in some alpine lakes (Anderson 1974, pers. obsv.) indicates a very different life history than in prairie ponds. The timing of egg production, egg release and development of juvenile stages may depend on such factors as algal standing stocks, presence of predacious cyclopoids, water renewal rates or temperature (Ravera & Tonolli 1956, Anderson 1970). The life history of Hesperodiaptomus arcticus and its relation to abiotic and biotic factors should be determined for a variety of mountain lakes.

Large invertebrate species other than Hesperodiaptomus (e.g. Gammarus lacustris or Branchinecta paludosa) may also be important pelagic predators in alpine lakes (Anderson & Raasveldt 1974). Like Hesperodiaptomus these species would also be highly susceptible to fish predation. Therefore, events similar to those recorded in Snowflake and Pipit Lake following fish stocking (Anderson 1972, Leavitt et al. in review) may have occurred in lakes dominated by other invertebrate predators. A review of historical records, current species distribution and paleolimnology could be used to assess the past presence of these predators in stocked lakes (see Lamontagne 1993); as well, similar experiments to the ones I performed could be used to assess their importance in alpine lakes.

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Appendices

Appendix A- A Compact Lightweight Enclosure Design

Background

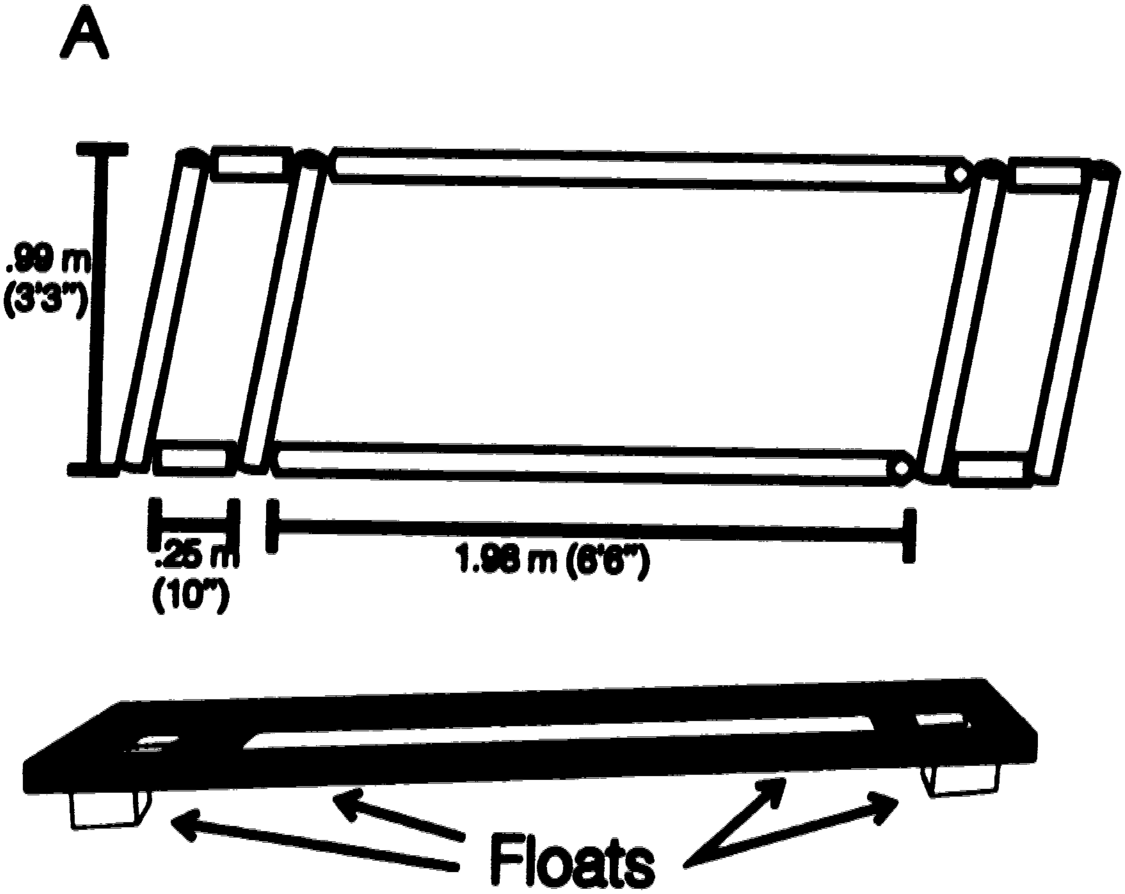
Enclosure experiments can be a useful tool when investigating interactions in aquatic systems (Mazumder et al. 1990). Two advantages of using enclosures are they can be replicated and may be more feasible to work with than whole lake experiments. Enclosure experiments have enabled researchers to study various community interactions across an assortment of aquatic systems (Neill 1981, Vanni 1986, Post & McQueen 1987, Mackay et al. 1990, Turner & Mittlebach 1992, Christoffersen et al. 1993 and many others).

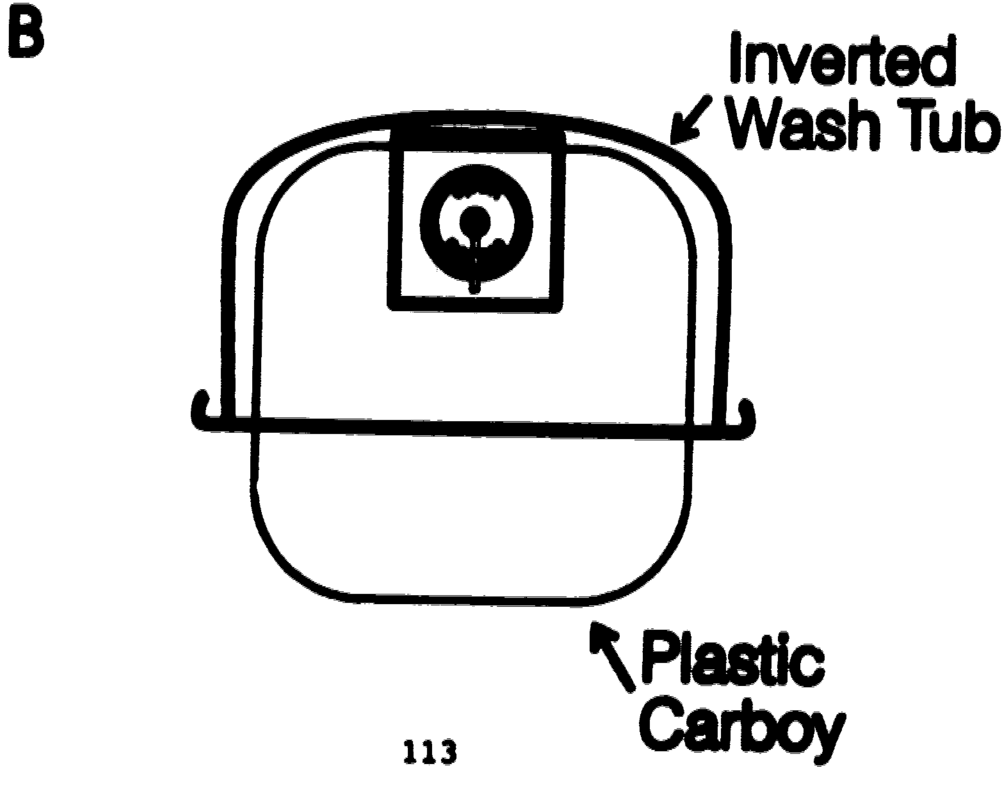
Enclosure experiments may be of particular use in systems where community structure and interactions have been little studied (Schindler et al. in review). However, many such systems are located in remote areas making commonly used enclosure designs of wood for frames (Neill 1981, Vanni 1986, 1988, Mackay et al. 1990) and polystyrene for floatation (Neill 1981, Vanni 1986, 1988) impractical, for they are not easily transported when access is limited to helicopter or foot. Here I present a compact lightweight frame design useful in areas where access is difficult.

Design

The floating frame supports the enclosures and keeps them in a fixed position. I used 2½" i.d. ABS plastic tubing for the frame structure (Fig. A.1a). All ABS

Figure A.1- A.) Diagram of the frame structure. B.) Diagram of the float. Spigot protrudes through a section cut-away from the wash tub.


A
.99 m
(3'3")
.25 m
(10")
1.98 m (6'6")
Floats


B
Inverted
Wash Tub
Plastic
Carboy

tubing was pre-cut and fitted prior to assembly in the field. Clean and dry sections were glued together at the field site using ABS solvent cement. Air temperatures at time of drying were 10°C and all joints dried securely. Flotation for each frame (Fig. A.1a) was provided by four 20 L collapsible plastic water carboys (manafactured by Reliance®). Each carboy was suspended in an inverted plastic wash basin (Fig. A.1b). The spigot of the carboy protruded through an opening cut out of the wash basin (Fig. A.1b). Each float was securely attached to one corner of the frame (Fig. A.1a). The floats were attached on 3 sides using plastic electrician's ties that ran around the ABS piping and through the plastic wash basin. Carboys were inflated by opening the spigot (Fig. A.1b), inflating by mouth and then closing securely. This floating frame provides enough support and space for two enclosures 1 m in diameter or 1 m square. A complete inventory of the materials used in 1 frame is provided in Table A.1.

The enclosures I used were constructed by CanFab, Edmonton, Alberta from sealed woven polyethylene . Their size was 0.9m x 0.9m x 3m, closed at the bottom and with hems sewn on both the top and bottom. The enclosures were kept square at the bottom with a frame (0.9m x 0.9m) of 1" inner diameter (i.d.) ABS plastic piping attached to the hem. The top of the enclosure was kept square with two 1.2 m lengths of 1" i.d. ABS pipe run through opposite hems and securely attached to the flotation frame.

The enclosures were filled and attached to the frame from a boat. The procedure involved folding an enclosure like an accordion with the open end secured

Table A.1- Inventory of materials required in 1 floating frame.

Description	Size/Type	Quantity
2½" i.d. ABS Tubing	1.98m(6'6")	2
2½" i.d. ABS Tubing	.99m(3'3")	4
2½" i.d. ABS Tubing	90° Joint	4
2½" i.d. ABS Tubing	T Joint	4
20 L Plastic Carboy	Reliance®	4
Plastic Wash Tub	to Fit Carboy	4
ABS Glue	250 ml	1
Plastic Electrical Ties	.2 m	12

to a small frame (0.9 m x 0.9 m) tethered to the boat by a 4 m cord. Weights were added to the folded enclosure sinking it to about 4 m. When the enclosure had reached 4 m the weights were tied off to the boat and the tethered frame (attached to open end of the enclosure) was raised to the surface. The enclosure was fully filled using this procedure; in fact, some water had to be expelled allowing the top of the enclosure above the water line to be attached to the main frame. Once secured to the main frame the weights and small tethered frame were removed and used to inflate the next enclosure.

Discussion

The lightweight frame design and enclosures have been successfully used over three summers (1991, 92, 93) in Snowflake Lake, Banff National Park (Schindler et al. in review, chapter 1 & 2, unpublished data). Snowflake Lake is located 38 km from the nearest road and access is restricted to helicopter, hiking or horse packing. All 3 modes of transportation have been used during different summers to move both frames and enclosures to Snowflake Lake. The use of ABS tubing kept the weight of the frames to a minimum. The use of plastic carboys for flotation instead of polystyrene floats significantly reduced the bulk of materials that needed to be transported.

Enclosure experiments (lasting >30 days) and lakes have yielded similar results for the effects of planktivorous fish, Daphnia and copepod predation on community structure (Mazumder et al. 1990, Sarnelle 1992, chapter 1). However, some community interactions (especially those involving large vertebrate predators) may require spatial and temporal scales that make enclosures inappropriate or impractical (Schindler 1987). It is important for the designer of enclosures to consider the temporal and spatial scales necessary for the hypothesis being tested (Frost et al. 1988, Carpenter & Kitchell 1988). The lightweight frame presented here can easily be modified to the dimensions of different experimental designs.

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Appendix B- Lakes in Banff and Jasper National Park from which *Hesperodiaptomus* may have been Extirpated by Fish Stocking.

I have compiled a table of lakes in Jasper and Banff National Parks where *Hesperodiaptomus* may have been extirpated by fish stocking (Table B.1). The data for 112 lakes used to create the table are from unpublished reports of the Canadian Wildlife Service (D. Donald, Environment Canada, 2365 Albert Street, Regina, Sask. S4P 4K1). These reports were produced for Parks Canada by the Canadian Wildlife Service from data collected in the 1970's and early 80's.

Several criteria were used to build the table. First, a list of the lakes that do not contain *Hesperodiaptomus arcticus* or *H. shoshone* was comprised. From this list, all lakes were deleted that either had never been stocked or had native fish populations. Lakes that had uncertain histories (*ie*. it was not known if fish were native) were also deleted. The final table listed lakes that were naturally fishless, stocked at least once and did not have *Hesperodiaptomus* at the time of last sampling.

It was then necessary to determine which of these lakes was likely to have had populations of *Hesperodiaptomus* before fish were stocked. *Hesperodiaptomus* are cold stenotherms (Anderson 1971) restricted to higher elevation lakes (Anderson 1974, Maly 1988), arctic lakes and ponds (Edmondson 1959, Wilson & Hebert 1993) and prairie lakes and ponds during the spring season only (Sawchyn & Hammer 1968,

Table B.1- List of lakes in Banff National Park (BNP) and Jasper National Park (JNP) that Hesperodiaptomus may have been extirpated by fish stocking. Temperature is mid-summer surface water temperature (MSSWT). Probability (using logistic model) of H. arcticus presence based on the MSSWT is shown.

Lake	Park	Alt. (m)	Temp.(°C)	Probability
Upper Consolation	BNP	1951	5	0.72
Lower Consolation	BNP	1951	5	0.72
Bighorn	BNP	2347	8	0.51
Chalet	JNP	1976	8.5	0.47
Geraldine #2	JNP	1690	9	0.43
Hidden	BNP	2271	9	0.43
Snowflake	BNP	2320	10	0.36
Temple	BNP	2179	10	0.36
Harvey	JNP	1617	10	0.36
Agnes	BNP	2118	10.5	0.33
Lower Geraldine	JNP	1600	11	0.29
Tilted	BNP	2210	11	0.29
Upper Caribou	JNP	1788	11	0.29
Edwards	JNP	1228	12	0.24
Hostel Pond	JNP	1560	12.5	0.21
Twintree	JNP	1558	13	0.19
Maligne	JNP	1675	13	0.19
Horseshoe	JNP	1230	14	0.15
Beatrix	JNP	1646	14	0.15
Lower Caribou	JNP	1767	14	0.15
Boom	BNP	1893	14	0.15
Mud	BNP	1600	14	0.15
Sassenach #2	JNP	1851	14	0.15
Kingfisher	BNP	1539	15	0.11
Lower Colfair	JNP	1355	15	0.11
Upper Colfair	JNP	1355	16	0.09
Little Herbert	BNP	1570	16	0.09
Herbert	BNP	1600	16	0.09
Medicine	JNP	1442	16	0.09

Anderson 1974). Therefore, it was likely that the distribution of *Hesperodiaptomus* was related to water temperature in mountain lakes.

The distribution of *Hesperodiaptomus* was related to mid-summer surface water temperatures (MSSWT; Fig. B.1) for the 112 lakes in Banff and Jasper National Parks. The occurence of *H. arcticus* decreased as MSSWT increased over 10°C; and it was never present in lakes with a MSSWT >16°C (Fig. B.1). Using MSSWT, presence/absence data for *Hesperodiaptomus* and logistic regression analysis (see chapter 1) a statistical model was developed. This model predicts the probability of *Hesperodiaptomus* being present in a given lake based on its MSSWT. Parameter values for the model (equation 1.1, Table B.2) were highly significant.

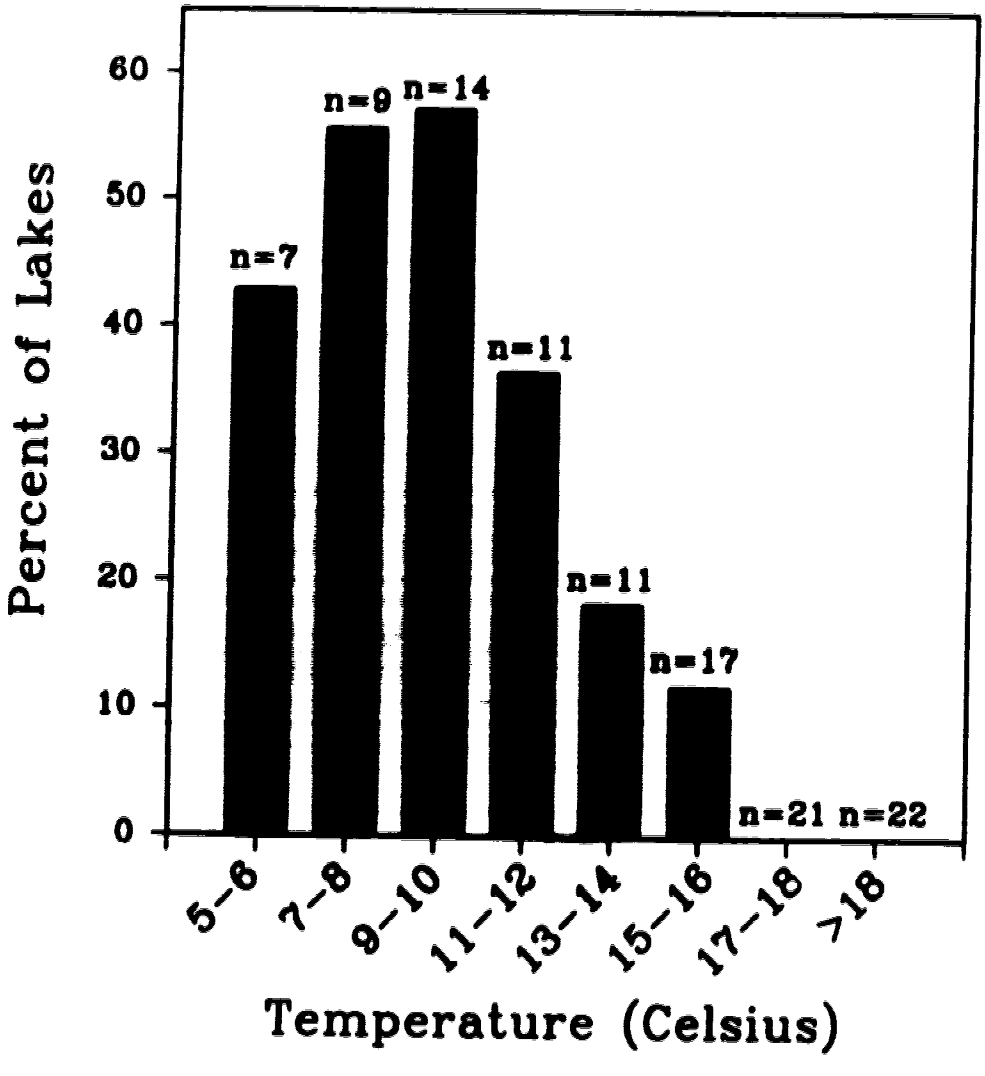
Of the 112 lakes surveyed in Banff and Jasper National Parks 29 may have had *Hesperodiaptomus* present before they were stocked (Table B.1). The probability of *Hesperodiaptomus* occurring based on MSSWT is included in the list of lakes (Table B.1). Lakes with a MSSWT of ≤16°C were listed because *H. arcticus* was never found in any lakes with a MSSWT >16°C (Fig. B.1). The list only represents those lakes (112) for which data were available.

Table B.2- Logistic regression estimates and Chi-square statistics for the presence/absence of Hesperodiaptomus arcticus as a function of mid-summer surface water temperatures (MSSWT).

PARAMETER	ESTIMATE	CHI-SQUARE	P
a	2.4165	8.49	0.004
b	-.2990	17.96	0.0003

P= probability parameter estimate is equal to zero

Figure B.1- Percent occurrence of Hesperodiaptomus arcticus in mountain lakes with different mid-summer surface water temperatures (MSSWT).


Percent of Lakes
0
10
20
30
40
50
60
n=7
n=9
n=14
n=11
n=11
n=17
n=21
n=22
5–6
7–8
9–10
11–12
13–14
15–16
17–18
>18
Temperature (Celsius)

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