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TROPHIC INTERACTIONS IN EUTROPHIC BOREAL PONDS IN RELATION TO FISH PREDATION PRESSURE

by

Mariola E. Janowicz ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of Master of Science.

in
Environmental Biology and Ecology
Department of Biological Sciences

Edmonton, Alberta

Spring 1999

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Date: 16 April 1999

A lake is the landscape's most beautiful and
expressive feature. It is the earth's eye;
looking into which the beholder measures
the depth of his own nature.

Walden
Henry David Thoreau

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **TROPHIC INTERACTIONS IN EUTROPHIC BOREAL PONDS IN RELATION TO FISH PREDATION PRESSURE** submitted by **Mariola E. Janowicz** in partial fulfillment of the requirements for the degree of **Master of Science** in **Environmental Biology and Ecology**.

William M Tonn

Dr. W. M. Tonn, Supervisor

Dr. C. A. Paszkowski, Committee Member

Dr. D. A. Craig, External Examiner

Date: 15 April 1999

Dedication

This thesis is dedicated with love to my family, Mark and Kasia

Abstract

How does the density of an omnivorous fish affect the structure of aquatic ecosystems? Both top-down and bottom-up processes, as well as density-dependent mechanisms acting within the fish population, could be important. To investigate these processes, I examined the direct and indirect effects of fathead minnow (*Pimephales promelas*) density on zooplankton communities, phytoplankton biomass (Chl *a*), and water quality in small eutrophic ponds; simultaneously, I examined feeding habits of fatheads and trophic relationships in these ponds by integrating stomach content and stable isotope analyses. Variations in structure and composition of zooplankton communities were associated with fish predation pressure even when effects of abiotic variables were accounted for. High fish densities resulted in dramatic decreases in macrozooplankton and increases in microzooplankton densities. In contrast, fish effects were less evident at the phytoplankton and nutrient levels. At high densities, fatheads attained the highest trophic position, indicated by $\delta^{15}N$, apparently as a result of increased cannibalism on eggs and larvae.

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Chapter 1. GENERAL INTRODUCTION

Lake food webs

Lake communities are made up of limnetic, littoral and benthic food webs. Limnetic communities occupy the offshore water column. Littoral organisms inhabit the zone between the shore and the offshore boundary of rooted macrophytes. Benthic communities include organisms that dwell in the bottom sediments in littoral or profundal zones of a lake. Although these organisms occupy different habitats within lakes, resulting in spatially complex food webs (Crowder et al. 1988), interactions among organisms of the littoral, benthic and limnetic zones occur through seasonal and diel migrations and contribute to the exchange of the nutrients and energy flow among these habitats (Crowder et al. 1988).

Despite the fact that such interactions result in highly dynamic food web processes, food webs are often presented as static and most of them are described by seasonal averages in one particular location (Crowder et al. 1988). However, organisms within a north-temperate lake are continually subjected to seasonal changes in controlling environmental factors, such as temperature, dissolved oxygen, water levels or nutrient inputs (Mills and Forney 1988). These seasonal environmental changes contribute to seasonal succession in phytoplankton (Sommer et al. 1986), zooplankton, and to recruitment variability in fishes (Mills and Forney 1988). Fish, in turn, are relatively long-lived organisms, and occupy and use different habitats throughout their life. As they develop and move through various habitats, their top-down effects shift from one food web to another (Sommer et al. 1986, Mills et al. 1987). To understand the food web dynamics in north-temperate systems, knowledge of food web dynamics is needed in relation to the complex spatial structure.

Bottom-up vs. top-down control of lake food webs

Traditionally, lake ecosystems have been studied from two distinct perspectives, bottom-up and top-down control of food webs. Bottom-up viewpoints concentrate on physical and chemical factors and their direct relationships to lower trophic levels (Dillon and Rigler 1974, Schindler 1978). Top-down approaches (the cascade hypothesis), on the other hand, focus more research attention on fishes and their effects on lower trophic levels (Carpenter et al. 1987). Since the theories of top-down and bottom-up control of food webs are not independent (Carpenter et al. 1985, Carpenter et al. 1991, Persson et al. 1988), it is important to determine which kinds of factors (e.g., biotic or abiotic) dominate interactions in aquatic food webs (Shapiro and Wright 1984, Mc Queen et al. 1986, Persson et al. 1988).

Top-down control of zooplankton community composition, abundance and biomass by planktivores has been widely documented (e.g. Hrbacek et al. 1961, Brooks and Dodson 1965, Hall et al. 1976, Zaret 1980). Large-bodied zooplankton are selectively preyed upon by fish because they are both easier to locate by visually-feeding planktivorous fish (O'Brien 1987) and optimize the foraging efficiency of these fish (Werner and Hall 1974). Intense zooplanktivory by fish often results in a zooplankton community dominated primarily by small species, which, in turn, is associated with high phytoplankton biomass (Lynch and Shapiro 1981, Carpenter et al. 1987). Fish planktivory may also decrease invertebrate predation (Dodson 1974, Paine 1980) and intensify competitive interactions among small zooplankton species (DeMott 1989).

Planktivorous fish can also strongly affect the morphology, physiology, biochemistry, or behavior of prey without actually consuming them. Since behavioral responses to predation often involve changes in prey species' distributions, they can potentially be transmitted through the food web in a manner similar to changes in consumer abundances (Paine 1980, Abrams 1984, Carpenter et al. 1985).

High predation pressure of planktivorous fish may enhance algal populations by decreasing zooplankton grazing (Shapiro and Wright 1984, Carpenter and Kitchell 1988). Furthermore, phytoplankton biomass may increase due to increased nutrient recycling by zooplankton. Because small zooplankton have higher mass-specific nutrient excretion rates than large zooplankton (Bartell 1981, Carpenter and Kitchell 1984), small-bodied zooplankton communities that dominate under intense zooplanktivory may recycle nutrients for phytoplankton uptake at a greater rate than large-bodied zooplankton communities (Vanni and Findlay 1990). Algal growth may also be enhanced by the nutrients (primarily nitrogen and phosphorus) excreted by fish (Lamarra 1975, Nakashima and Leggett 1980, Braband et al. 1990), through feeding, metabolism and death (Drenner et al. 1986, Therkeld 1987, Schindler 1992).

Even water transparency and turbidity can be influenced by foraging activities of fish. These activities can substantially contribute to decreases in transparency by resuspension of sediments (Meijer et al. 1990), through the feeding activities of fish on the bottom of the lake or by selective filter-feeding on large (> 60 μm) phytoplankton cells (Drenner et al. 1984, Drenner et al. 1986). Although some filter-feeding fish that feed on wide range of phytoplankton cells have been found to increase water clarity (Carruthers 1986), others have no impact on turbidity, suggesting that water clarity is mediated more by effects on nutrients than by trophic cascade effects (Threlkeld 1987).

While the 'trophic cascade' from planktivorous fish has been demonstrated repeatedly (for review see Zaret 1980, Northcote 1988), the mechanisms responsible for lake system responses to omnivorous fish are not as clear. Omnivorous fish (feeding at several trophic levels) not only suppress macrozooplankton but also act as 'nutrient pumps', whereby they consume benthic nutrients in form of periphyton, sedimented detritus, and benthic macroinvertebrates, and then excrete the nutrients in dissolved form into the water column (Lamara 1975, Brabrand et al. 1990). Nutrients transported into the water column then become available to phytoplankton communities. Therefore, omnivorous fish can enhance phytoplankton by both nutrient pumping activities (Drenner et al. 1996) and zooplankton suppression (Lynch and Shapiro 1981, Vanni 1987). As a result, omnivorous fish may regulate aquatic food webs via complex 'middle-out' processes that affect both higher and lower trophic levels simultaneously (Stein et al. 1995). If so, then responses of the ecosystem to omnivores may be more complex than predicted by the trophic cascade theory (Carpenter et al. 1985).

Use of stable isotopes in food web studies

Trophic interactions in freshwater food webs involving fish have been traditionally determined from experimental studies (mesocosms, enclosures, ponds), observations of the presence of organisms within a system, evaluation of predator-prey interactions, and by analyzing diets using stomach content analysis (SCA) (Crowder 1990). Each approach has its advantages and limitations; in particular, species composition of stomach contents can provide detailed yet incomplete information on trophic interactions (Yoshioka et al. 1994). Stomach content data provide a 'snapshot' of food items consumed over a short time period, between ingestion and digestion, which in fish is generally measured in hours, and the assimilation of ingested food is not considered (Kling et al. 1992). If assimilation rates arc not accounted for, it may lead to underestimation of easily digested food items and cause errors in determination of food selectivity (Gannon 1976, Hyslop 1980). Recently, stomach content analyses are being complemented or replaced by stable isotope analyses (SIA). Unlike SCA, SIA not only provide information on the long-term diet of an animal under study but also on the food ingested and assimilated over the period of tissue turnover (Hesslein et al. 1993).

The complementary use of two or more biologically important elements in SIA, such as carbon and nitrogen, has been employed in tracing trophic relationships in aquatic food webs (Fry 1988, Hamilton et al. 1992, Keough et al. 1996). Stable carbon ($^{13}C/^{12}C$) and stable nitrogen ($^{15}N/^{14}N$) isotope ratios have been increasingly used in ecological studies to examine dietary patterns and species positioning in trophic levels within food webs (Peterson and Fry 1987, Hesslein et al. 1991, Cabana and Rasmussen 1996), respectively.

Various primary producers process carbon differently as part of their photosynthetic pathways (O'Leary et al. 1992, Hecky and Hesslein 1995). Because carbon isotopes fractionate at low rates in organisms, the $^{13}C/^{12}C$ of consumers reflect the isotopic composition of the original plant or carbon source (De Niro and Epstein 1978). For example, in a freshwater system, the isotopic ratio of organic carbon of terrestrial origin differs from the autochthonous carbon sources (Rau and Anderson 1981, Rosenfeld and Roff 1992). As well, pelagic algae usually have lower $^{13}C/^{12}C$ values than benthic algae (Hecky and Hesslein 1995). Thus, zooplankton that feed exclusively on pelagic algae, and fish that feed on these zooplankton, will be also more isotopically depleted of the heavier isotope than fish feeding on benthic invertebrates using littoral plant sources. By analyzing carbon isotope ratios, therefore, it is often possible to discriminate between pelagic-feeding and littoral (or benthic)-feeding organisms, and so provide information on the original source of carbon and energy flow in the food web (Peterson and Fry 1987).

In contrast to carbon isotopes, nitrogen isotopes consistently fractionate in organisms, as ^{14}N is selectively excreted by consumers and ^{15}N incorporated in body tissues; thus, with each successive trophic level, $^{15}N/\ ^{14}N$ values in the tissue of an organism tend to increase (Minagawa and Wada 1984, Peterson and Fry 1987). The average enrichment in $^{15}N/\ ^{14}N$ from prey to predator is 3.2 to 3.4 ‰ (Minagawa and Wada 1984, Peterson and Fry 1987, Fry 1991, Kidd 1996). Therefore, $^{15}N/\ ^{14}N$ provide a continuous measure of an organism's trophic positioning.

In simple systems, e.g., pelagic food webs or where dietary habits cannot be determined with conventional methods, stable carbon and nitrogen ratios are particularly useful for delineating trophic relationships (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1995). However, in complex ecosystems (e.g., with many omnivores that have overlapping isotopic signatures), stable isotope analysis should be complemented with other data, such as stomach content analysis of consumers (Gearing 1991).

Rationale for study

Lakes in the Boreal Plain Ecoregion of Alberta are typically small, shallow, and have relatively longer water residence times than most lakes of other regions of Canada

(Chambers and Prepas 1988). Many of these lakes are isolated from rivers and have only intermittent inlet and/or outlet streams because of low topographic relief and high evaporation-to-precipitation ratios. In Alberta, about 50 % of the hardwater lakes are eutrophic to hypertrophic (Mitchell and Prepas 1990) with high internal phosphorus loading from the bottom sediments (Shaw and Prepas 1990). High total phosphorus concentrations often lead to algal blooms, whose decomposition can lower dissolved oxygen concentrations below levels required for survival by aerobic organisms such as fish.

Because of severe oxygen depletion in the winter (Babin and Prepas 1985), shallow Alberta lakes are subjected to frequent and severe winterkills of fish. This contributes to the relatively few fish species found in Alberta lakes compared with other areas in north-central North America (Tonn and Magnuson 1982, Robinson and Tonn 1989). These small lakes are often dominated by two distinct fish assemblage types, those dominated by (i) large-bodied carnivores, including northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), and (ii) small-bodied fish, such as fathead minnows (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) (Robinson and Tonn 1989). Although fathead minnows are tolerant of low-oxygen conditions, they are not invulnerable (Klinger et al. 1982) and often experience high winter mortality that results in large, year-to-year variability in fish population density in small Alberta lakes (W. M. Tonn, personal communication). Because the omnivorous fatheads are often the top "predators" but feed at all trophic levels, these large fluctuations in fish densities could affect the entire structure of food webs.

Small lacustrine ecosystems, like north-temperate lakes and ponds, offer ideal systems to study the structure and function of food webs. Detecting complex interactions often requires tracing the effect of a perturbation in one component of the community (e.g., winterkill of fish) as it spreads to other parts of the community. It is much easier to track such perturbations in small lakes than in large lakes; perturbations attenuate through spatial heterogeneity and distant physical boundaries in large systems (Neill 1988). Limnetic communities in small lakes may also be more strongly influenced by interactions with littoral and benthic habitats than large lakes (Wetzel 1983) thereby increasing the chances for detecting explicit trophic, spatial, and life cycle interactions. Yet few, if any, food web interaction studies have been conducted in small lakes of Alberta.

The objectives of my study were to (1) determine the effects of fathead minnow density on zooplankton communities, phytoplankton biomass (Chl *a*) and water quality in ponds, (2) describe dietary patterns of fathead minnows in relation to different fish densities, and (3) determine the potential for trophic interactions between fathead minnow (*Pimephales promelas*) and organisms at lower trophic levels.

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Chapter 2. DIRECT AND INDIRECT EFFECTS OF FATHEAD MINNOW (*Pimephales promelas*) DENSITY ON ZOOPLANKTON COMMUNITIES, PHYTOPLANKTON BIOMASS (Chl *a*) AND WATER QUALITY IN EUTROPHIC PONDS IN ALBERTA.

INTRODUCTION

Perturbations of fish density (either natural or anthropogenic) have been shown to have strong effects on the function and structure of aquatic ecosystems (Kerfoot 1987). The cascading effects of fluctuations in planktivorous fish densities, in particular, have been demonstrated repeatedly (for reviews see Zaret 1980, Northcote 1988). However, the mechanisms accountable for system responses to facultative planktivores (filter-feeding omnivorous fish that feed at many trophic levels) are not clear.

Omnivorous fish not only suppress macrozooplankton directly, but also act as 'nutrient pumps', whereby they consume benthic nutrients in the form of periphyton, sedimented detritus, and benthic macroinvertebrates, and then excrete nutrients in dissolved forms back into the water column (Lamara 1975, Brabrand et al. 1990). These dissolved nutrients are readily available to phytoplankton communities. As a result, omnivorous fish can enhance phytoplankton by both nutrient pumping activities (Drenner et al. 1996) and zooplankton suppression (Lynch and Shapiro 1981, Vanni 1987). In this way, omnivorous fish may regulate aquatic food webs via complex 'middle-out' processes that affect both higher and lower trophic levels simultaneously (Stein et al.

1995). Consequently, the responses of ecosystems containing omnivores may be more complex than those predicted by the trophic cascade theory (Carpenter et al. 1985).

In the boreal region of north-central Alberta, fish species richness is generally low, due to climatic severity, and the small sizes and isolation of lakes (e.g., large distances from a river or absence of outlets) (Robinson and Tonn 1989). Fish assemblages are often limited to only one or two small-bodied fish species, particularly fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*). The omnivorous fathead minnow (consumers of zooplankton, benthic invertebrates, plants and detritus) is commonly found across Alberta, which represents the northwestern limit of its distribution (Scott and Crossman 1973, Nelson and Paetz 1992). These fish, although tolerant of low-oxygen conditions, frequently experience winterkills (Klinger et al. 1982) that result in year-to-year variations in population sizes (W. M. Tonn, unpublished data). These interannual variations in fish populations, whether caused by density dependent mechanisms such as those acting on recruitment rates of young-of-the-year (YOY) (Vandenbos 1996) or density independent processes, e.g., winterkill, should affect lower trophic levels. Still, although omnivory has been found to be important in freshwater systems elsewhere (Vadas 1990), studies on these small boreal systems are almost nonexistent.

The goals of my study are threefold, (1) examine if fathead minnow (*Pimephales promelas*), an omnivorous fish, can directly and indirectly affect zooplankton communities in small ponds of the boreal region of north-central Alberta, (2) if so, do the effects vary with the density of fathead minnows, and (3) determine whether different fathead minnow predation regimes affect phytoplankton standing crop (represented by

Chl *a*) and a number of water quality variables. These three objectives were tested by manipulating fathead densities in experimental ponds at Meanook Biological Research Station (MBRS) and comparing observed patterns to two reference ponds (with and without fathead minnows).

METHODS

Study sites

During each of two field seasons, two reference ponds and three experimental ponds were used for this study. All ponds are located in the boreal mixed-wood forest of Alberta (Figure 2.1). The reference ponds [Tempo (1994) and Meanook (1995); without fish, Beaver (1994-1995); with fathead minnow] are all small, shallow and naturally productive (Table 2.1) and thus are representative of the north-central region of Alberta. The three experimental ponds, located at MBRS, were used for experimental fish density manipulations (Table 2.1).

The reference ponds were studied to observe natural variation in zooplankton communities and phytoplankton biomass (Chl a) during the study period, whereas effects of fish density were examined in experimental ponds.

Pond manipulations

Fish density manipulations were conducted in 1994 and 1995 (May-September). The three ponds (Table 2.1) were divided in half by impermeable polyvinyl curtains supported by wooden stakes extending 1m above water level. The bottoms and sides of the curtains were attached to metal sheets that were secured in the substrate. Prior to the experiment, each pond was drained, cleared of vegetation, planted with cattails (*Typha* spp.) along the shores, and then refilled with water. Ten fence boards (1.5 m long) per pond were attached by twine to weights and allowed to float at the water surface to provide nesting substrates, which allowed successful reproduction of fathead minnows in the ponds.

Fathead minnows used in the experiment were collected from nearby lakes. The fish were classified into three categories based on external morphological characteristics: mature males (the presence of tubercles, total length (TL) ≥ 70 mm), mature females (apparent ovipositor, TL ≥ 63 mm) and juveniles (no visible secondary sexual characteristics, 40 ≤ TL ≤ 56 mm). The ponds were stocked in equal proportions of males, females and juveniles at two densities in triplicates. Each pond was given both treatments, low density (LD, 1 fish/ m^2) and high density (HD, 4 fish/ m^2), on opposite sides of the curtain. The stocking densities were based on natural population estimates of fathead minnows in Beaver Pond (the reference pond) (Figure 2.2).

Field collections and laboratory analyses

In all ponds or pond halves, fish densities were surveyed monthly. Zooplankton, phytoplankton (Chl *a*), and water samples were collected every two weeks from May through August of 1994 and 1995.

Fish - To track the stocked fish in experimental ponds, fish were marked with a fluorescent elastomer injection in 1994 (Northwest Marine Technology Inc. Shaw Island, WA) and with a distinct combination of fin clips for each fish category in 1995. Young-of-the-year (YOY) fish appeared during the first month of the experiment and were distinguished from the stocked fish by their small size and lack of markings. To monitor fathead densities, five minnow traps were set overnight along the shore of each experimental pond half. Captured fish were sorted into categories, counted and returned to the ponds.

To assess population size of fatheads in Beaver Pond, fish were censused in the spring, before fathead minnows had spawned, by multiple mark-recapture methods using minnow traps and fin-clipping. Thirty traps were randomly set along the perimeter of the pond. Young-of-the-year were not included in the censuses. Data collected were used to calculate abundances and densities (fish/m^2) of each life-history category (males, females, and juveniles) using Schnabel's (1938) technique. Because fathead minnows almost exclusively inhabit the littoral zone at this time of the year (W. Tonn, University of Alberta, personal communication), the area of Beaver Pond ≤ 2 m (2.25 ha) was used in density calculations. To monitor fish densities throughout the summer, monthly samplings were done using the same capture procedure.

Zooplankton - To assess the impact of fish densities on the zooplankton community dynamics, I sampled zooplankton in all ponds and pond halves with a 10-L Schindler-Patalas trap fitted with a 64 µm mesh net bucket. Samples were taken from four inshore and four offshore stations in each reference pond and from two inshore and two offshore sites in experimental ponds. Inshore samples were taken at a water depth of 0.5 m and 1- 2 m from the shore. Offshore samples were taken in the middle of experimental ponds and in the pelagic zone of reference ponds at a water depth of 1m. All zooplankton samples were collected outside macrophyte beds. Samples were preserved in a 4 % chilled sugared formalin solution.

Cladoceran and copepod zooplankton (macrozooplankton) identifications were made with taxonomic keys of Edmondson (1959), Pennak (1989), Clifford (1991), and

Thorp and Covich (1991). Rotifers (microzooplankton) were identified with keys of Chengalath et al. (1971), Ruttner-Kolisko (1977), Grothe and Grothe (1977), and Clifford (1991).

For each sample, the number of individuals per taxon was estimated by counting all individuals in three 1-5 mL subsamples, depending on density, extracted with an Eppendorff pipette, representing 20-50 % of the total sample volume. Estimated densities were expressed as number of individuals per liter. Rotifers were settled in counting chambers for 24 hours and counted on an inverted microscope. Cladocerans and copepods were counted on a dissecting microscope.

Subsamples of cladocerans and copepods (30 individuals per taxon) were measured using a drawing tube and digitizing tablet. Rotifers were measured using the fitted micrometer in the ocular of the inverted microscope. The mean dry mass of each taxon was calculated by averaging individually estimated masses from measured individuals. Masses of crustaceans and rotifers were estimated using length-mass regressions (Bottrell et al. 1976, Stemberger and Gillbert 1987).

Chlorophyll a and water quality - Secchi depth was measured at the two deepest stations using a 30-cm diameter disk between 10 and 12 h. Water samples were collected at the same stations as for zooplankton. Samples taken from all sites in each pond were pooled into a composite sample representing a particular pond. All water samples were taken with a 3-L Van Dorn sampler (0.5 m height) at depths of 0.5 m (inshore) and 1 m (offshore). All water samples were stored immediately in coolers and then refrigerated at 4 °C in the laboratory until they were analyzed. Within 10 hr of collection, water samples for Chl *a*, total phosphorus (TP), and total dissolved phosphorus (TDP), were filtered under low pressure (~ 50 kPa).

For Chl *a* analyses, triplicate 250-ml aliquots were filtered through Whatman GF/C filters. The filters were wrapped in aluminum foil, placed in petri dishes and stored in a freezer. Chlorophyll *a* was determined with a spectrophotometric technique using the 95% ethanol extraction and measured after 24 h (Bergmann and Peters 1980) at 750, 665 and 649 nm; the 750 reading was used as a turbidity correction.

Samples for TP were filtered through a 250-µm Nitex net, samples for TDP analyses were filtered through prewashed 0.45-µm HAWP Millipore membrane filters and transferred to culture tubes (Prepas and Rigler 1982). Total and dissolved phosphorus were digested and analyzed by Menzel and Corwin's (1965) potassium persulfate method.

Samples for total nitrogen (TN) and total dissolved nitrogen (TDN) were analyzed within 48 hr of collection on Technicon autoanalyzer. Ammonium (NH_4) and TKN (total Kjeldahl nitrogen) were analyzed by Solorzano's (1969) phenolhypochlorite method, as modified by Prepas and Trew (1983). Nitrate and nitrite (NO_3 and NO_2) were determined using the cadmium-copper reduction method of Stainton et al. (1977). Total nitrogen was calculated as the sum of TKN, NO_3 and NO_2.

Samples for dissolved oxygen (DO) were taken in 10-mL syringe and treated in the field according to Burke's (1962) technique. Conductivity was measured with Mertohm E578 conductometer at 25 °C, pH was measured using a Mertohm E588 pH meter. Temperature was measured with the Flett thermistor.

Statistical analyses

Repeated measures analysis of variance (RM-ANOVA) was used to examine the main effects of fish on the mean densities of individual zooplankton taxa, total biomass of zooplankton and phytoplankton (Chl a), and water quality. For these analyses, the eight ponds or pond halves were blocked into four categories: high density (HD) and low density (LD) experimental treatments, and reference ponds with fish (FR) and without fish (NFR). Eight sampling periods were used for 1994 and six for 1995. Fewer sampling dates in 1995 resulted from heavy rain storms that flooded four of the experimental ponds in late July, which prevented replicate samplings on the last two dates.

Prior to analyses, data were log-transformed to ensure additivity of variances (Zar 1984). In cases in which the repeated-measures ANOVA revealed significant effects of fish, treatment means for each sampling date were compared using independent t-tests as described by Zar (1984), to determine which means were significantly different from each other. All statistical analyses were performed with SPSS, version 6.0 (1993).

To assess how variation in the abundances of major zooplankton taxa was related to a combination of fish treatments and abiotic variables, I used Redundancy Analysis (RDA), a linear multivariate technique for direct gradient analysis. This analysis constructs ordination axes that maximize the variation in overall community composition, as constrained by the combined effects of environmental variables (Jongman et al. 1987, ter Braak and Prentice 1988). Prior to RDA: (1) zooplankton abundance and environmental data were ln (x+1) transformed to correct skewed distributions (Zar 1984), and (2) detrended correspondence analysis (DCA) was performed on abundance data to determine the gradient length of the first ordination axis. For the whole data matrix, RDA was determined to be the most appropriate approach to detect patterns in zooplankton taxa and taxa – environment relationships, since DCA indicated a short gradient length

(< 2 standard deviations; ter Braak and Prentice 1988).

RDA and DCA were performed with the computer program CANOCO (version 3.12; ter Braak 1990). Inshore and offshore stations and sides of the ponds had high collinearity with other variables (i. e. variance inflation factors > 20; ter Braak 1988), therefore, these variables were excluded from further RDA. Forward selection of environmental variables was applied to determine a minimal set of variables that explained the greatest amount of variance in the zooplankton abundance nearly as well as the full set of environmental variables (ter Braak 1990). At each step of the forward selection, the variable added was tested for statistical significance with Monte Carlo permutation test (99 unrestricted permutations, $P < 0.05$). The significance of relationships between individual taxa and environmental variables was evaluated by approximate t - tests for the canonical coefficients (ter Braak 1990). For each year, the significance of the first canonical ordination axis and the overall ordination fit were then tested with Monte Carlo tests (99 unrestricted permutations, $P < 0.05$). Partial redundancy analysis was used to test whether zooplankton community structure was significantly related to fish density after removal of the influence of abiotic covariates (Monte Carlo permutation test for the significance of the sum of all eigenvalues, CANOCO program), following the procedure described by ter Braak (1990).

RESULTS

Fish

No fish were caught in the fishless reference ponds in each field season during the study period. Fish abundances in Beaver Pond (fish reference) during 1994 and 1995 were relatively low (Figure 2.2). Although fish in Beaver Pond were sampled monthly,

monthly population estimates were not possible because of low catches. Fish populations declined throughout season. However, on all sampling dates there were about three times as many stocked fish in the HD than in LD experimental treatments (Figure 2. 3). Recruitment of young-of-the-year (YOY) fatheads in both years of study was higher in LD treatment (Vandenbos 1996).

Zooplankton

Differences in fish density were reflected in the zooplankton communities. The presence of fish was generally associated with higher species richness (Table 2.2, ANOVA, $P<0.002$). Higher fish density resulted in increased relative abundance of microzooplankton (Rotifera) and reduced macrozooplankton (Cladocera and Copepoda) (Table 2.3), and increased total biomass (Figure 2.4). Fish effects were also observed in different habitats (inshore vs. offshore) within each pond (Table 2.3). Fish density, however, did not affect the mean sizes of the four major groups of zooplankton (Figure 2.5, ANOVAs, $P > 0.05$).

In 1994, relative biomass of macrozooplankton was significantly reduced in treatment with high density of fish (Figure 2.6). The mean relative contribution of macrozooplankton to total zooplankton biomass in HD was only 13 %, compared with 47 % in LD, 70 % in the reference pond without fish (Tempo), and 97 % in the reference pond with fish (Beaver) (Figure 2.6). Although results in 1995 were generally similar, a low contribution of macrozooplankton to total biomass (7 %) was observed in the new reference pond without fish, Meanook Pond. Copepods dominated the zooplankton biomass in LD and Beaver, whereas *Daphnia* was relatively important in the total biomass of the two references without fish, especially Tempo (Figure 2.6). Rotifers dominated the biomass in high density experimental ponds (HD) and the Meanook fishless pond.

Among the major taxa, densities of large-bodied cladocerans, specifically *Daphnia pulex* and *Daphnia rosea*, were significantly reduced in ponds that contained fish (LD, HD, and Beaver), and were less abundant inshore than offshore (Table 2.3, Figure 2.7). Smaller cladocerans, such as *Simocephalus*, *Sida*, *Chydorus*, *Ceriodaphnia*, and *Scapholeberis*, were, however, found at higher densities in ponds with fish (Other Cladocera; Table 2.3, Figure 2.7) than in fishless references. These small cladoceran grazers were found at higher densities inshore than offshore in all ponds. Copepods, although present in all ponds, were most abundant in the fish reference pond (RM ANOVA, $P < 0.05$), (Figure 2.7) and found in greater numbers inshore than offshore.

High fish density was also associated with increased rotifer abundances (Figure 2.7). Total rotifer densities were up to eight times higher in HD than in the reference ponds and LD (Table 2.3, Figure 2.7). Relative contributions of individual rotifer taxa differed, however, between 1994 and 1995. In 1994, *Keratella cochlearis* was predominant in all ponds until mid-July, when a more complex rotifer community developed. In ponds with fish, *Polyarthra dolichoptera*, *Philodina* and *Monostyla* were important whereas *Pomopholyx* was predominant only in the reference pond without fish (Figure 2.8). In 1995, the relative contribution of *Keratella cochlearis* remained high (> 60 % of total rotifer density) through most of field season in HD and the fishless reference pond, whereas in LD and fish reference other taxa were also important in mid- and late summer. Some rotifers, although found only at low densities, were restricted to certain ponds: *Collotheca mutabilis* and *Notomnata* spp. occurred only in HD, *Tetramastix* and *Russelettia* in reference ponds without fish, *Platyias patulus*, *Eudactylocota eudactylocota* and *Gastropus* in reference with fish.

Phytoplankton biomass estimate (Chl a)

In 1994, total algal biomass (Chl *a)* differed among ponds (Table 2.4) and was two to four times higher in the fishless pond than in ponds containing fish on most sampling dates. Chlorophyll *a* concentrations were similar in ponds with fish throughout most of the summer, although LD had a peak of Chl *a* near the end of July (Figure 2.9). In 1995, Chl *a* concentrations were not affected by fish density and were similar in all ponds. However, a different temporal pattern was observed for the fishless reference pond (Table 2.4: interaction effect), largely due to a July peak in Chl *a* concentrations (Figure 2.9).

Water transparency (Secchi depth) was significantly higher in the fish reference pond in both years than any other treatments (Table 2.4, Figure 2.9). There were, however, no differences observed between LD and HD treatments (Figure 2.9).

Water quality

A majority of the measured water quality variables were affected by fish density in one or both years (Table 2.4: treatment and interaction effect), as well as showing significant seasonal variation within each year (time effect). The temporal patterns of most of the variables were more complex in 1995 than in 1994. (Figs. 2.10 and 2.11)

Mean concentrations of total phosphorus (TP) were two to three times higher in the fishless reference pond in 1994 (Figure 2.10 *a*) than in other ponds, rising sharply in August. Within the ponds with fish, however, only on one sampling date (June) did the experimental ponds (LD and HD) differ from the fish reference pond. In 1995, when total dissolved phosphorus (TDP) was measured instead of TP, different temporal patterns of TDP were observed for each of the fish density treatments (interaction effect: $P = 0.04$). However, by late summer, TDP concentrations were higher in ponds with fish than in the fishless reference (Figure 2.10 *a*).

Mean TN concentrations in 1994 were significantly lower in LD and HD ponds than in either reference pond (RM ANOVA, $P = 0.009$). In 1995, the overall TDN concentrations were higher in LD and HD treatments than in reference ponds and the temporal patterns of total dissolved nitrogen (TDN) concentrations were complex (Table 2.4: interaction effect, Figure 2.10 *b*). The differences in TDN were mostly observed in June and August. TDN concentrations were highest in the fish reference pond in May and decreased substantially during the summer (Figure 2.10 *b*).

No significant effects of fish density were observed on the concentrations of dissolved oxygen (DO) (RM ANOVA, $P>0.05$, Table 2.4). However, the mean DO concentrations tended to be higher in LD and HD than in reference ponds (Figure 2.11 *a*). In 1994, DO concentrations followed similar patterns in all ponds; DO concentrations increased in July and decreased substantially in August (Figure 2.11 *a*). In 1995, notable fluctuations in DO concentrations were observed throughout the whole sampling period for LD and HD, sometimes in opposite directions. DO concentrations were more stable in reference than in experimental ponds in 1995.

Similar to DO concentrations, there were no observed effects of fish on pH (RM ANOVA, $P>0.05$, Table 2.4). The only observable differences were noted at the beginning and end of the summer 1994, with higher values recorded for experimental treatments (LD and HD) (Table 2.4: interaction effect). In contrast, pH values during the summer of 1995 were similar in all ponds (Figure 2.11 *b*).

Fish density influenced temporal patterns of conductivity (RM ANOVA, $p<0.001$) during both years of study. In 1994, the highest conductivity values were recorded in HD and LD ponds (Figure 2.11 *c*). Although fish treatments did not result in differences in mean conductivity values in 1995, temporal patterns in early summer were different among treatments.

Community level analysis

For the two-year study, RDA showed that zooplankton community composition (density) was strongly related to the treatment and to the measured environmental variables (Monte Carlo permutations for the first canonical axes and overall ordination, $P = 0.01$) and simultaneously explained 73 to 86 % of variance in the taxa-environment relationships (Table 2.5). The first two axes of RDA explained cumulatively 29 and 30 % of the variance in the taxa, respectively (Table 2.5).

The forward selection criteria determined that fish treatment, Chl *a*, phosphorus and nitrogen concentrations, pH, dissolved oxygen concentrations, and conductivity explained the taxa data almost as well as the original data set of 13 variables. In 1994, all selected environmental variables were correlated with either axis 1 or 2 (Table 2.5), therefore, were important in explaining large portion of the variation in zooplankton densities. In terms of fish treatment, low density, LD, and reference without fish, NFR, were correlated with both axis 1 and 2, whereas high density, HD, and fish reference, FR, were weakly correlated with axis 2. In 1995, however, fish treatments were generally more strongly correlated with the two canonical axes than environmental variables (Table 2.5). Based on partial RDA results, fish treatments explained more variance in zooplankton abundance (18 and 28%) than chemical variables (14 and 3%) in 1994 and 1995, respectively.

The RDA biplots (Figure 2.12) support earlier results indicating that macrozooplankton taxa were most abundant in ponds with low or no fish predation pressure, whereas microzooplankton were found in greater abundance in the experimental ponds. In both years, daphnids (*Daphnia pulex* and *Daphnia rosea*) had the highest abundance in the fishless reference pond, whereas the large-bodied calanoid, *Acanthodiaptomus denticornis* (Diapt), and two cyclopoids, *Dicyclops bicospidatus thomasi* and *Acanthocyclops vernalis* (Cycl) were abundant in both natural reference ponds (Figure 2.12). In addition, the occurrence and densities of macrozooplankton taxa were negatively correlated with pH, conductivity, and DO concentrations, which were positively associated with the experimental ponds. In experimental ponds high densities of rotifers and copepod naupliar stages were found to be positively correlated to the concentrations of phosphorus and nitrogen (Figure 2.12). Chlorophyll *a*, in turn, was associated with elevated phosphorus concentrations. In 1994, this was driven largely by the fishless reference pond environment rather than by any fish treatment *per se*.

DISCUSSION

This study extends earlier work of Hrbacek et al. (1961), Brooks and Dodson (1965), Carpenter and Kitchell (1988) and Pinel-Alloul et al. (1995), among others, by providing evidence that variation in the abundance and size structure of zooplankton are associated with fish predation pressure even when potentially confounding effects of abiotic variables are accounted for. Specifically, the results of this study show that different fathead minnow densities were associated with markedly different zooplankton community structure, density, and biomass, with less evident differences in phytoplankton (Chl *a*) and nutrients.

The community level analysis (RDA) demonstrated that fish treatment and selected environmental variables (phosphorus and nitrogen concentrations, conductivity, pH, and DO) were important in structuring zooplankton communities and explained 29 to 30 % of total taxa variance. Partial RDA indicated, however, that fish treatment explained more variance in zooplankton abundance than environmental variables in these small ponds.

Effects of fish density on zooplankton

Fish have a demonstrated ability to alter the structure and composition of zooplankton communities; fish predation often results in decreased abundance and production of large-bodied zooplankton species (Hrbacek et al. 1961, Brooks and Dodson 1965, Carpenter and Kitchell 1988). In my study, predation by fathead minnows led to the elimination of *Daphnia* and suppressed overall cladoceran populations in all ponds with fish. A similar observation was noted by Spencer and King (1984). Other cyprinids, such as bream (*Abramis brama*) and roach (*Rutilus rutilus*), can also reduce or eliminate cladoceran populations during summers of high recruitment (Andersson 1984, Townsend 1988) and influence the dynamics of small-bodied cladocerans (Winfield and Townsend 1991).

Rotifer densities were affected by fish in two ways, indirectly by the reduction of a dominant competitor, *Daphnia* and directly through feeding. In LD and HD, the elimination of *Daphnia* resulted in a dramatic increase in rotifer densities; actual rotifer densities achieved in the ponds may have additionally been a function of algal abundance and reduced invertebrate predation (Anderson 1970). At high densities, large *Daphnia* can suppress rotifer populations through exploitative competition for similar foods and interference competition (Gilbert 1988). Rotifer densities were however relatively lower in LD than in HD treatment. LD treatment had high recruitment of YOY, which after hatching feed primarily at rotifers (Chapter 3), and therefore, densities of rotifers in LD were reduced directly by YOY consumption.

Moreover, the elimination of *Daphnia* coincided with increases in cyclopoid copepod densities, particularly *Dicyclops bicuspiatus thomasi.* This supports previous studies that showed that the abundance and biomass of cyclopoids increase in response to intermediate and high levels of fish predation (Hamrin 1983, Kerfoot and DeMott 1984, Kerfoot 1987, Rudstam et al. 1993, Hessen et al. 1995). Positive relationships between a prey and its predator can be a result of indirect effects caused by a reduction by the predator of a dominant competitor of the prey (Paine 1966).

Reductions of *Daphnia* densities have been shown to positively affect cyclopoids (Soto 1985, Vanni 1986). Vanni suggested that the most likely cause for increased abundance of cyclopoids is reduced competition for food resources between *Daphnia* and cyclopoid nauplii. Cyclopoids have much lower clearance rates on algae than daphnids (Adrian 1991), and cyclopoid nauplii are sensitive to starvation mortality (Soto and Hurlbert 1991). Therefore, the reduction in abundance of *Daphnia* in the experimental ponds likely enhanced the juvenile survival of cyclopoids. Adult cyclopoids, e.g., *Mesocyclops*, consume rotifers (*Polyarthra, Keratella, Synchaeta and Conochillus*), small cladocerans and the dinoflagellate, *Peridinium* (Williamson 1981), all of which were found in high densities in my study ponds. Therefore, the increased availability of small prey in my study in the absence of *Daphnia* probably resulted in increased cyclopoid fecundity, juvenile survival, and density (Kerfoot 1987).

Unlike cyclopoids, calanoid copepods were negatively correlated with fish density. In experimental ponds, calanoid densities were suppressed to extremely low levels. In contrast, in Beaver Pond, a fishkill two winters prior to my study (W.M. Tonn, University of Alberta, personal communication) resulted in reduced fish densities. Low fish predation pressure, therefore, led to an increase in calanoid copepod biomass, particularly *Acanthodiaptomus denticornis*.

In the absence of fish, the zooplankton communities in Tempo and Meanook ponds both contained a relatively high biomass of large cladocerans (*Daphnia* spp.), but the relative densities of other common zooplankton groups differed between these ponds. The zooplankton community in Tempo was dominated by large *Daphnia pulex* and calanoid copepods, whereas in Meanook the zooplankton biomass was dominated by rotifers, with daphnids in smaller proportions.

Invertebrate predation probably played an important role in structuring zooplankton communities in these fishless ponds. In Tempo, two invertebrate predators, *Chaoborus* and *Gammarus*, were found in high densities, whereas in Meanook only *Chaoborus* was present and then only in smaller numbers. Invertebrates such as *Chaoborus* are size-selective predators (Zaret 1980, Moore et al. 1994), and so can dramatically alter zooplankton community structure. Unlike fish, invertebrate predators often shift the dominance in zooplankton communities to large-bodied species, with small-bodied species becoming rare (Dodson 1972, Zaret 1980, Reinertsen et al. 1990).

The late instars of *Chaoborus* are effective predators on small cladocerans and cyclopoid copepods (Riessen et al. 1984, Kerfoot and Sih 1987, Stenson et al. 1993), whereas all instars regulate the populations of rotifers (Fedorenko 1975, Pastorok 1980, Moore and Gilbert 1987). *Gammarus*, also an active carnivore, preys on small cladocerans and copepod nauplii (Anderson and Raasveldt 1974).

In Meanook Pond, the populations of small- and medium-size cladocerans and calanoid copepods were depressed in the presence of *Chaoborus* but rotifer populations were elevated. Similar findings were reported by Neill (1985) and Hanazato (1990). The early instars of *Chaoborus* preferentially feed on rotifers (Pastorok 1980, Saunders and Lewis 1988), yet their predation pressure may not have been sufficient to decrease rotifers (Shei et al. 1988, Hanazato 1990). Moreover, the late instars are effective predators on cladocerans, thereby releasing the rotifers from competition. Small rotifer species (such as the dominant species in Meanook) may, however, be able to coexist with large *Daphnia* if algal resources are not limited (Stemberger and Gilbert 1985, Gilbert 1988).

Size-selective planktivory by invertebrate and fish predators has also been hypothesized to be one of the most important factors contributing to the formation of inshore-offshore differences in zooplankton community structure (Dodson 1972, Hall et al. 1979, Zaret 1980). Inshore-offshore variation in the intensity of size-selective feeding pressure is often large, counteracting opposing forces such as the physical differences of water (and zooplankton) between the inshore and offshore region (Evans 1990). The inshore habitat is mainly inhabited by adult fathead minnows during spring when fish migrate there to spawn. The inshore region is an important habitat for young-of-the year and juvenile fish from late spring to early autumn (Price et al. 1991). Hence, most large-bodied zooplankton, such as *Daphnia* spp. and calanoid and cyclopoid copepods, are expected to be less abundant in the inshore region during the periods of high fish predation. In my study, densities of *Daphnia* spp. and calanoid cyclopoid copepods were greater in the offshore habitat, whereas small cladoceran species were more abundant in inshore habitat. Conversely, in ponds without fish, inshore and offshore habitats seem to support equal densities of major zooplankton taxa.

Despite strong effects of fathead minnow density on zooplankton community structure, density, and biomass in both inshore and offshore habitats, I did not detect effects on size within major zooplankton groups. The effects of fish on the body size of crustacean zooplankton was probably confounded by the fact that in all ponds, juvenile copepods were abundant (Sorrano et al. 1993). It was also suggested that daphnid length might be an unreliable indicator of fish predation, whereas overall cladoceran length should be a more satisfactory indicator. Although a numerical increase of small cladocerans in the presence of planktivory (LD and HD) was observed, fish predation did not affect the size of individual cladocerans taxa.

Effects of fish density on phytoplankton biomass and water quality

Unlike strong effects of fish predation on zooplankton structure, density and biomass, phytoplankton biomass (Chl *a*) was unaffected. Similar results have been found from north temperate lakes with small populations of macrozooplankton (Carpenter et al. 1985, Dettmers et al. 1996). In contrast, numerous studies in shallow enclosures or pond experiments have shown that planktivorous and omnivorous fish can affect phytoplankton biomass (Vanni 1987, Vanni and Findlay 1990, Christoffersen et al. 1993, Hansson and Carpenter 1993) directly through size-selective grazing (Drenner et al. 1986, Smith 1989) and by indirect enhancement in nutrient availability.

In many studies where the top-down effects of predation were not transmitted to lower tropic levels, the lack of responses was often attributed to bottom-up influences (McQueen et al. 1989). Bottom-up forces may also have played a role, to some extent, in Tempo Pond (the fishless reference) that experienced external nutrient loading during this study. In systems with high loadings of nutrients, algal populations may be more strongly influenced by the dynamics of nutrient supply, rather than by losses from zooplankton grazing (McQueen et al. 1989, Gulati et al. 1990). Zooplankton significantly influence phytoplankton when *Daphnia* density exceeds 40 individuals/L (Dettmers and Stein 1996). The densities of *Daphnia* in Tempo, in contrast, never reached such abundances.

Although previous studies of the effects of omnivorous fish on water quality (see Sih et al. 1985 for review) detected strong fish effects, in my study fathead minnows imposed variable effects. Fathead minnow density did affect water transparency (Secchi depth), which was markedly lower in experimental (LD and HD) than in fish reference pond, but did not enhance nutrient concentrations. Defecation and benthic foraging activities of fatheads, together with extremely high densities of rotifers, likely contributed to relatively low water transparency in the experimental ponds. Similarly, Opuszynski (1980) reported a decrease in pond water nitrogen and phosphorus levels at increasing densities of fish (silver carp), however this decline was accompanied by increased phytoplankton biomass.

McQueen et al. (1992) proposed that elevated nutrient availability through recycling by fish might be associated with a shift towards smaller algal cells; omnivorous fish usually enhance nanoplankton (2-20 um) and mesoplankton (> 200um). In my study, however, large inedible Pyrrophyta (dinoflagellates) were found at high densities in HD; *Ceratium* was the most abundant in HD ponds (>90 % of the total phytoplankton biomass), whereas smaller numbers of *Peridinium* were noted in both LD and HD (personal observations). The high abundance of dinophlagellates suggests that elevated internal nutrient loadings enhanced those large, inedible algae that require high nutrient levels (Ramcharan et al. 1995). Dinoflagellates, especially *Ceratium*, in my study were enhanced by the presence of fish and were negatively affected by increases in zooplankton biomass.

Other experimental studies have found that nutrients released by fish are in forms highly available for algal uptake; roach excretion and defecation could contribute to about 30 % of the total phosphorus supply in the water column (Brabrand et al. 1985). Kitchell et al. (1975) found that nutrient release from feces, and also from fish decomposition was important (see also Nakashima and Leggett 1980). Although post-spawning mortality of fathead minnows was high in this study (about 60 %), there was no observed evidence of increased total nutrient pools. Threlkeld (1988) has similarly shown that low biomass of dead fish (<0.9 g dry weight/m^3) does not enhance nutrient concentrations.

Few scenarios could explain the absence of fish effects on nutrient concentrations. First, fish populations might act as nutrient sinks (Kitchell et al. 1979) by incorporating phosphorus into fish tissue. In my study, fish in all treatments exhibited growth and reproduced during the two years of study. Losses of nutrients attributable to fish may account for 15 to 40 % of the daily particulate phosphorus losses from the lake

(Nakashima and Leggett 1980); the nutrient loss through fish populations is dependent upon natural sedimentation rates and feeding habits of fish.

The benthic feeding activities of omnivorous fish usually act as nutrient pumps, transferring large amounts of nutrients from sediments to the water column through their excretion (Lamara 1975, Brabrand et al. 1990). Fish feeding on benthic and littoral sources regenerate the greatest fraction of phosphorus from the lake (Nakashima and Leggett 1975, Nakashima and Leggett 1978, Nakashima 1979). Because fathead minnows feed from these habitats in ponds, thus it is probable that fatheads also redistribute particulate phosphorus tied up in prey organisms. Terrell (1975) also found no significant changes in phosphorus concentrations in ponds with or without fish, although greater concentrations of nutrients were found in the pond sediments with fish, indicating rapid uptake from water. This might be also true for the ponds in my study.

In summary, the results of my study demonstrated that fathead minnows are important in structuring the zooplankton communities in small Alberta ponds. The different levels of predation pressure by fathead minnows resulted in major differences in the plankton community structure. High density of fathead minnows resulted in decreased abundance and biomass of daphnids but increased the abundance and biomass of rotifers and small cladocerans. The results of this study also suggest a positive relationship between fathead minnow density and cyclopoid calanoids but negative effects of fatheads on the density of calanoid copepods. Although increased fathead minnow density was associated with reduced water clarity, Chl *a* and nutrient concentrations (phosphorus and nitrogen) were unaffected by fish density.

The community analysis demonstrated similarly that zooplankton communities in ponds with fatheads are structured by fish, environmental variables having only moderate influence. I suggest that biotic and abiotic factors controlling zooplankton community dynamics in lakes should be part of any evaluation of the effects of natural or anthropogenic perturbations of fish populations.

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Table 2.1. Morphometric, physical, and chemical characteristics of experimental (Low Density, LD and High Density, HD treatments) and reference ponds (Beaver, Tempo and Meanook). All water quality data are given as means (SE) for 1994 and 1995; FM indicates ponds with fathead minnows.

	1994				1995			
	LD	**HD**	**Beaver**	**Tempo**	**LAD**	**HAD**	**Beaver**	**Meanook**
Fish assemblage	FM	FM	FM	fishless	FM	FM	FM	fishless
Surface area (ha)	0.02	0.02	3.0	10.0	0.019	0.019	3.0	0.05
Maximum depth (m)	1.6	1.6	5.0	3.9	1.6	1.6	5.0	1.5
Chlorophyll *a* (μg/L)	83.2(19.0)	54.7(9.9)	56.4(9.8)	178.1(43.7)	39.1(3.6)	49.5(5.9)	32.2(5.9)	54.3(8.9)
Secchi depth (m)	1.1(0.0)	1.1(0.0)	2.4(0.2)	1.2(0.2)	1.1 (0.2)	1.0(0.2)	2.1(0.1)	1.2(0.2)
TP*/TDP** (μg/L)	42.4(8.1)	40.4(4.3)	34.7(2.9)	126.7(2.9)	14.5(2.4)	14.9(2.1)	13.8(2.3)	10.1(2.0)
TN*/TDN** (μg/L)	473.7(55.1)	484.2(35.0)	1170.2(103.2)	1567.3(55.0)	9.4(2.9)	7.8(1.6)	10.1(2.8)	13.6(3.0)
Conductivity (μS/cm)	419.2(23.1)	476.3(27.0)	272.9(9.2)	309.5(16.7)	358.3(20.0)	349.7(33.4)	272.4(13.0)	349.6(34.5)
Dissolved oxygen (mg/L)	8.7(0.3)	8.8(0.5)	6.6(0.9)	6.1(1.2)	6.0(0.5)	6..4(0.5)	5.1(0.2)	4.8(0.8)
pH	8.1(0.1)	8.0((0.1)	7.6(0.1)	7.5(0.1)	8.1(0.1)	8.2(0.1)	8.0(0.1)	7.6(0.1)

* 1994; ** 1995

Table 2.2. The occurrence of zooplankton taxa in experimental ponds, LD-Low Density and HD-High Density, and reference ponds (fish reference-Beaver Pond (BP) and fishless-Tempo Pond (TP) in 1994 and Meanook Pond (MP) in 1995).

	LD		HD		BP		TP	MP
Rotifera	1994	1995	1994	1995	1994	1995	1994	1995
Aneaouropsis spp.	x	x	x	x			x	x
Asplanchna periodonta		x	x	x	x	x	x	x
Asplanchnopus spp.		x	x		x		x	x
Brachionus diversicornis					x		x	x
Brachionus quadratienta		x		x				
Brachionus rubens	x	x	x	x	x	x		
Cephalobdella gibba		x	x	x				
Collotheca mutabilis				x				
Colurella spp.	x	x	x	x		x		x
Conochilus unicornis	x	x	x		x	x	x	
Euchlanis dilata	x	x	x	x	x	x	x	x
Eudactylocota eudactylocota						x		
Filinia longiseta	x	x	x					
Gastropus spp.						x		
Keratella cochlearis	x	x	x	x	x	x	x	x
Keratella longispina	x	x	x				x	
Keratella quadrata	x	x	x	x	x	x	x	x
Keratella serulata		x						
Lecane luna	x	x	x	x	x	x	x	x
Lepadella patella	x	x	x	x	x	x	x	x
Monostyla bulla	x	x	x	x	x	x		x
Monostyla lunaris	x	x	x	x	x	x	x	x
Monostyla quadratienta						x	x	
Mytilina vernalis	x		x	x	x	x		
Notholca acuminata	x	x	x	x	x	x		x
Notholca squamula		x						
Notomnata spp.				x				
Philodina spp.	x	x	x	x	x	x	x	x
Platyias patulus					x	x		
Pleosoma spp.				x		x		
Polyarthra dolichoptra	x	x	x	x	x	x	x	x
Pompholyx sulcata	x	x	x	x	x	x	x	x
Russelettia spp.							x	
Squatinella spp.		x	x	x				
Syncheta pectinata	x	x	x	x	x	x	x	x
Tertamastix spp.								x
Testudinella triloba	x	x	x	x	x		x	x
Trichocerca cylindrica	x	x	x	x	x	x		x
Trichotria tetractis	x	x	x	x	x	x		
Cladocera								
Alona spp.				x		x		
Alonella spp.	x		x	x	x	x		x
Bosmina longirostris					x			x
Ceriodaphnia reticulata	x		x	x	x	x	x	x
Chydorus sphericus	x	x	x	x	x	x	x	x
Daphnia pulex	x	x	x	x	x	x	x	x
Daphnia rosea	x	x	x	x	x	x	x	x
Daphnia schodleri	x				x		x	
Diaphanosoma brachyurum	x		x		x	x		
Graptoleberis testudinaria	x				x	x	x	
Pleuroxus denticulata	x			x	x	x	x	
Pleuroxus procurvulatus		x						x
Pleuroxus striatus				x				
Scapholeberis mucronata	x	x	x	x	x	x	x	x
Sida crystalina	x	x	x	x	x	x		x
Simocephalus serrulatus						x		
Simocephalus vetulus	x	x	x	x	x	x		x
Calanoida								
Acanthodiaptomus denticornis	x	x	x	x	x	x	x	x
Cyclopoida								
Acanthocyclops vernalis	x	x	x	x	x	x	x	x
Dicyclops bicuspidatus	x	x	x	x	x	x	x	x
Species richness	**37**	**38**	**38**	**40**	**38**	**40**	**29**	**33**

Table 2. 3. Results of repeated-measures ANOVA comparing zooplankton densities among the experimental ponds, LD-Low Density and HD-High Density, and reference ponds, (fish reference- Beaver and fishless-Tempo (1994) and Meanook (1995); df for 1994 are shown as the first, for 1995 as the second number in brackets.

		Fish treatment effects				Time effects					
		Treatment (df=3,3)		Station (df=1,1)		Time (df=7,5)		Treatment xTime (df=21,15)		Station x Time (df=7,5)	
Taxonomic group		F	P	F	P	F	P	F	P	F	P
Daphnia spp.	1994	29.2	0.006	122.3	0.000	36.2	0.000	165.0	0.000	56.8	0.000
	1995	27.2	0.004	1.4	0.303	1.8	0.160	2.9	0.014	0.4	0.833
Other Cladocerans	1994	115.0	0.000	14.1	0.000	86.7	0.000	11.6	0.000	5.0	0.001
	1995	6.2	0.056	0.0	0.852	15.9	0.000	32.3	0.000	35.4	0.000
Acanthodiaptomus denticornis	1994	2.0	0.231	3.3	0.010	15.0	0.012	4.0	0.000	3.6	0.070
	1995	13.1	0.016	3.6	0.131	9.4	0.000	2.7	0.021	3.6	0.017
Diaptomus nauplii	1994	42.1	0.003	1.3	0.274	10.2	0.024	1.8	0.081	3.7	0.006
	1995	1.9	0.278	0.0	0.084	0.7	0.596	1.9	0.084	0.6	0.718
Cyclops spp.	1994	10.7	0.031	15.2	0.000	44.6	0.002	6.3	0.000	0.7	0.669
	1995	33.4	0.003	14.1	0.020	3.3	0.240	0.3	0.979	0.3	0.897
Cyclops nauplii	1994	0.2	0.687	1.2	0.354	6.5	0.051	0.9	0.587	0.9	0.524
	1995	3.5	0.126	0.0	0.935	2.7	0.053	0.9	0.582	0.9	0.480
Keratella cochlearis	1994	4.8	0.093	9.1	0.000	3.7	0.102	2.2	0.024	0.6	0.760
	1995	9.2	0.029	6.0	0.070	7.5	0.000	9.2	0.000	3.8	0.015
Polyarthra delichoptera	1994	8.5	0.033	0.0	0.909	7.7	0.000	4.1	0.000	1.5	0.201
	1995	1.5	0.344	0.6	0.491	3.1	0.031	2.5	0.028	0.2	0.969
Other Rotifera	1994	6.1	0.069	2.5	0.039	5.9	0.059	2.1	0.032	0.3	0.932
	1995	0.7	0.616	0.4	0.569	0.2	0.944	0.4	0.974	0.3	0.895

Table 2. 4. Results of repeated-measures ANOVA comparing the fish treatment effects on phytoplankton biomass (Chlorophyll *a*) and selected chemical variables among the experimental ponds, LD-Low Density and HD-High Density, and reference ponds, (fish reference- Beaver and fishless- Tempo (1994) and Meanook (1995), May-August, 1994 and 1995; df for 1994 are shown as the first, for 1995 as the second number in brackets.

		Treatment (df=3,3)		Time (df=7,5)		Treatment xTime (df=21,15)	
Source		**F**	**P**	**F**	**P**	**F**	**P**
Chlorophyll *a*	**1994**	7.8	0.038	2.4	0.050	1.6	0.123
	1995	1.5	0.338	15.8	0.000	2.3	0.038
TP	**1994**	0.1	0.950	3.6	0.007	2.3	0.021
TDP	**1995**	0.4	0.750	4.2	0.009	1.3	0.282
TN	**1994**	18.4	0.080	5.8	0.000	0.7	0.794
TDN	**1995**	1.5	0.340	2.4	0.073	2.7	0.022
pH	**1994**	2.8	0.116	32.6	0.000	5.1	0.000
	1995	1.4	0.361	3.4	0.023	1.0	0.521
Conductivity	**1994**	6.3	0.053	10.6	0.000	3.7	0.001
	1995	0.9	0.528	57.4	0.000	12.5	0.000
Dissolved oxygen	**1994**	0.1	0.839	8.1	0.000	0.1	0.990
	1995	2.0	0.167	7.9	0.000	0.9	0.526

Table 2.5. Redundancy analyses (RDA) of the zooplankton taxa in experimental treatments (Low Density-LD, and High Density-HD) and reference ponds (Fish Reference-FR (Beaver Pond), and No Fish Reference-NFR (Tempo-1994 and Meanook-1995). Eigenvalues for the first two axes of the ordination were 21.1 % and 30.0 % in 1994 and 1995, respectively.

Year	Taxa data	Taxa-environment relationship	Variables	Canonical Coefficient		Correlation Coefficient	
	First 2 axes	First 2 axes		Axis 1	Axis 2	Axis 1	Axis 2
1994	28.9	73.4	*Fish treatments*				
			LD	-0.2	-0.3	-0.2	-0.3
			HD	0.0	-0.2	0.0	-0.2
			FR	-0.1	0.1	0.1	0.3
			NFR	-0.1	0.1	0.2	0.4
			Environmental variables				
			Chlorophyll *a*	0.0	0.1	0.2	0.3
			TP	0.2	0.0	0.3	0.0
			TN	0.1	0.0	0.5	0.4
			pH	-0.2	0.1	0.5	0.1
			Dissolved Oxygen	0.0	0.0	-0.2	-0.3
			Conductivity	-0.1	-0.2	-0.3	-0.4
1995	30.0	85.8	*Fish treatments*				
			LD	-0.5	0.2	-0.3	0.3
			HD	-0.6	-0.1	-0.5	-0.2
			FR	-0.1	0.0	0.3	-0.2
			NFR	0.1	0.0	0.5	0.0
			Environmental variables				
			Chlorophyll *a*	-0.1	-0.3	-0.2	-0.3
			TP	-0.1	0.1	-0.2	-0.2
			TN	0.1	-0.1	0.0	-0.1
			pH	0.2	-0.2	-0.1	-0.1
			Dissolved Oxygen	0.1	-0.1	-0.1	-0.3
			Conductivity	0.0	-0.1	0.0	0.0

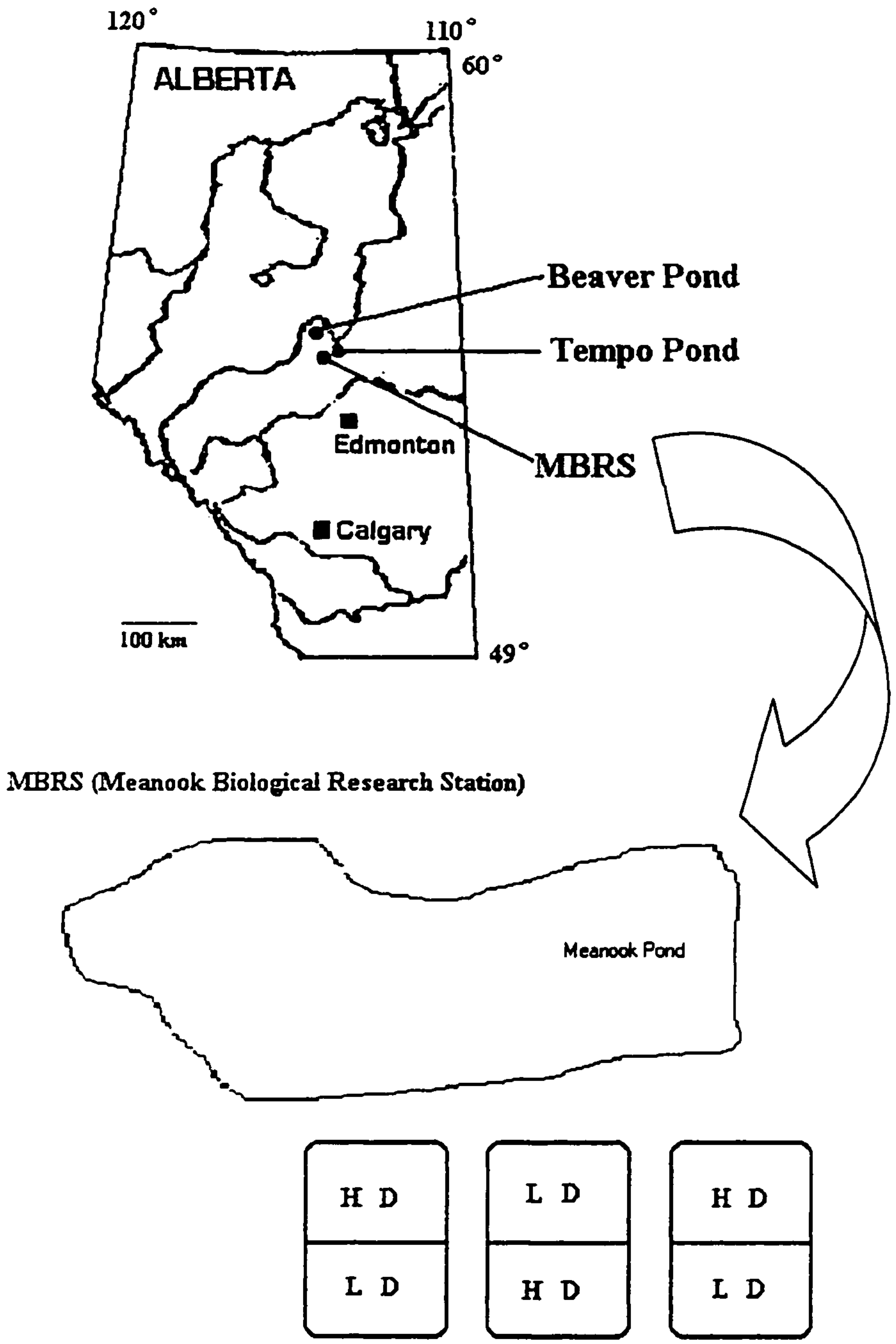

Figure 2. 1. Location of study sites and experimental design for pond manipulations (LD- Low Density and HD-High Density treatments) at Meanook Biological Research Station, Alberta. Ponds are not drawn to scale.

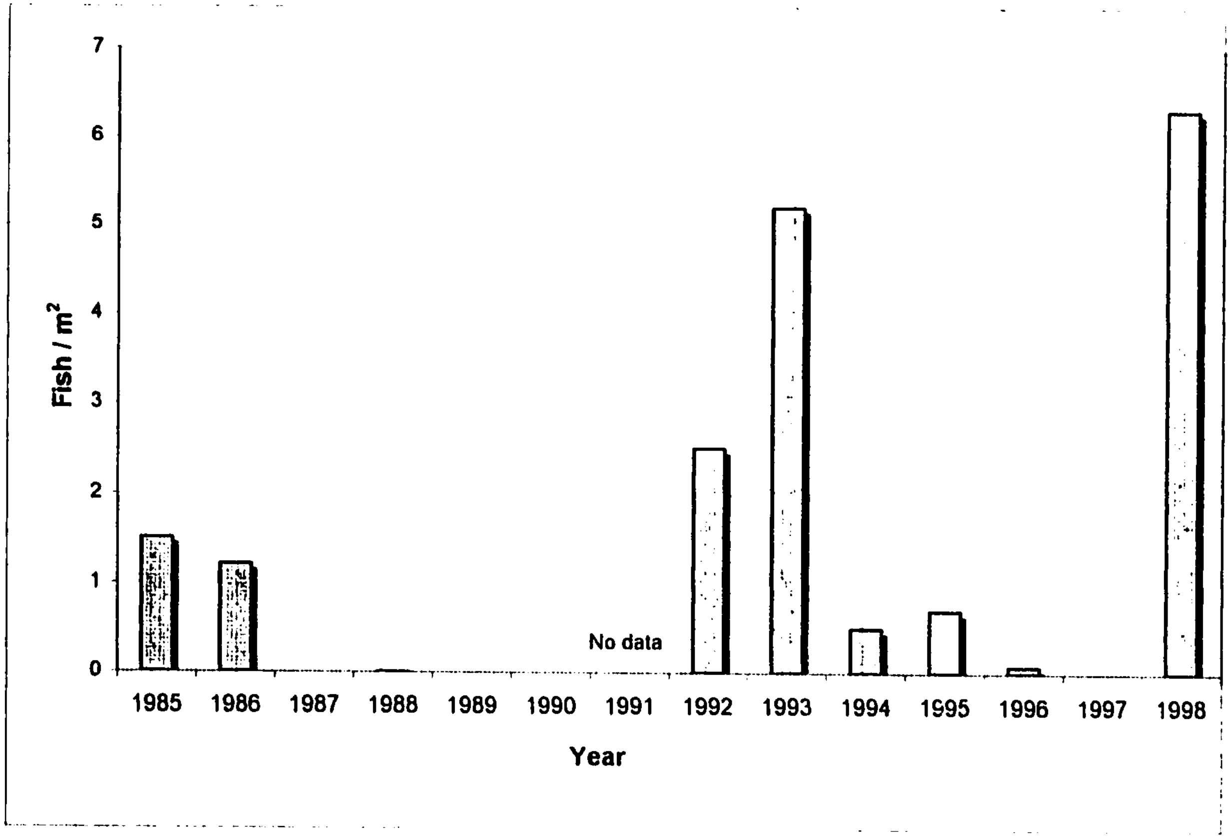

Figure 2.2. Fathead minnow density estimates (fish/m^2) in Beaver Pond (fish reference) from 1985 to 1998 (W. Tonn, unpublished data).

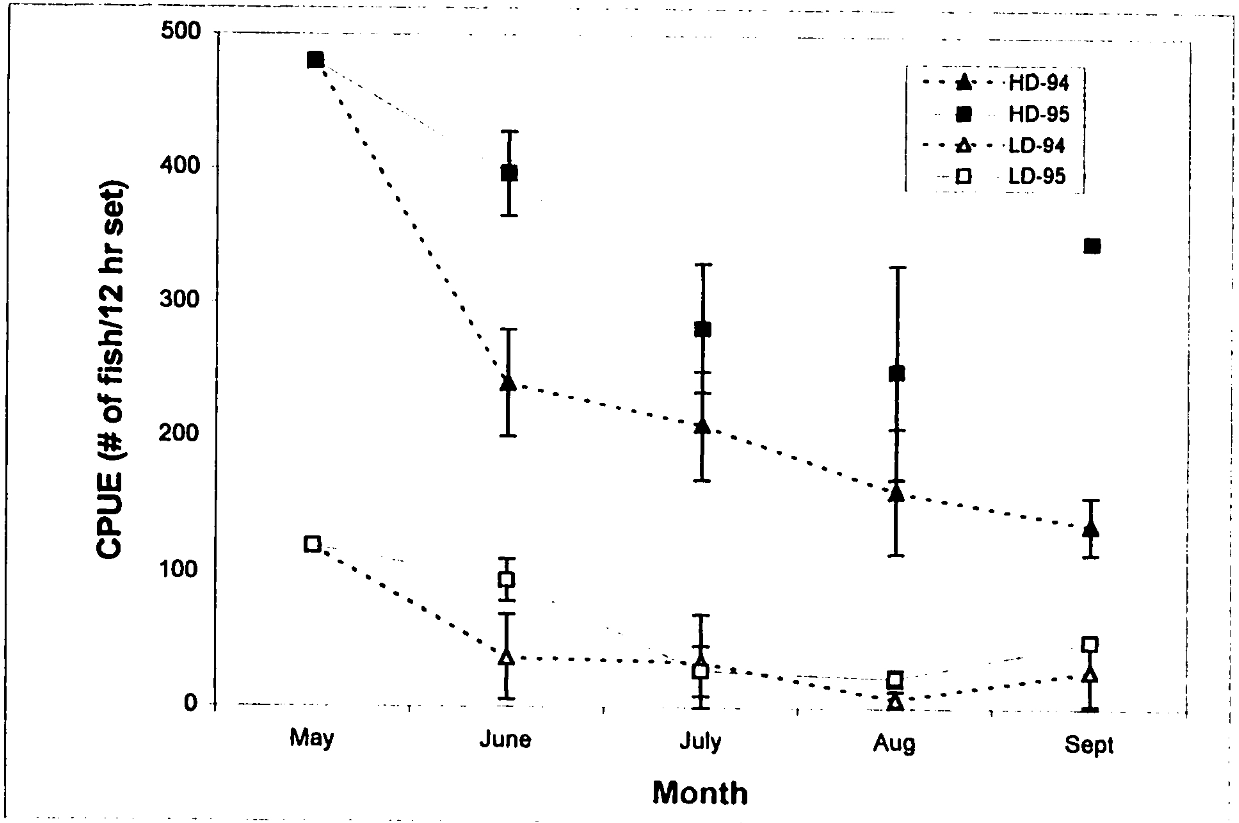

Figure 2. 3. Densities (SE) of adult fathead minnows in the experimental ponds, LD-Low Density and HD-High Density during the two-year study (1994-1995) at Meanook Biological Research Station.

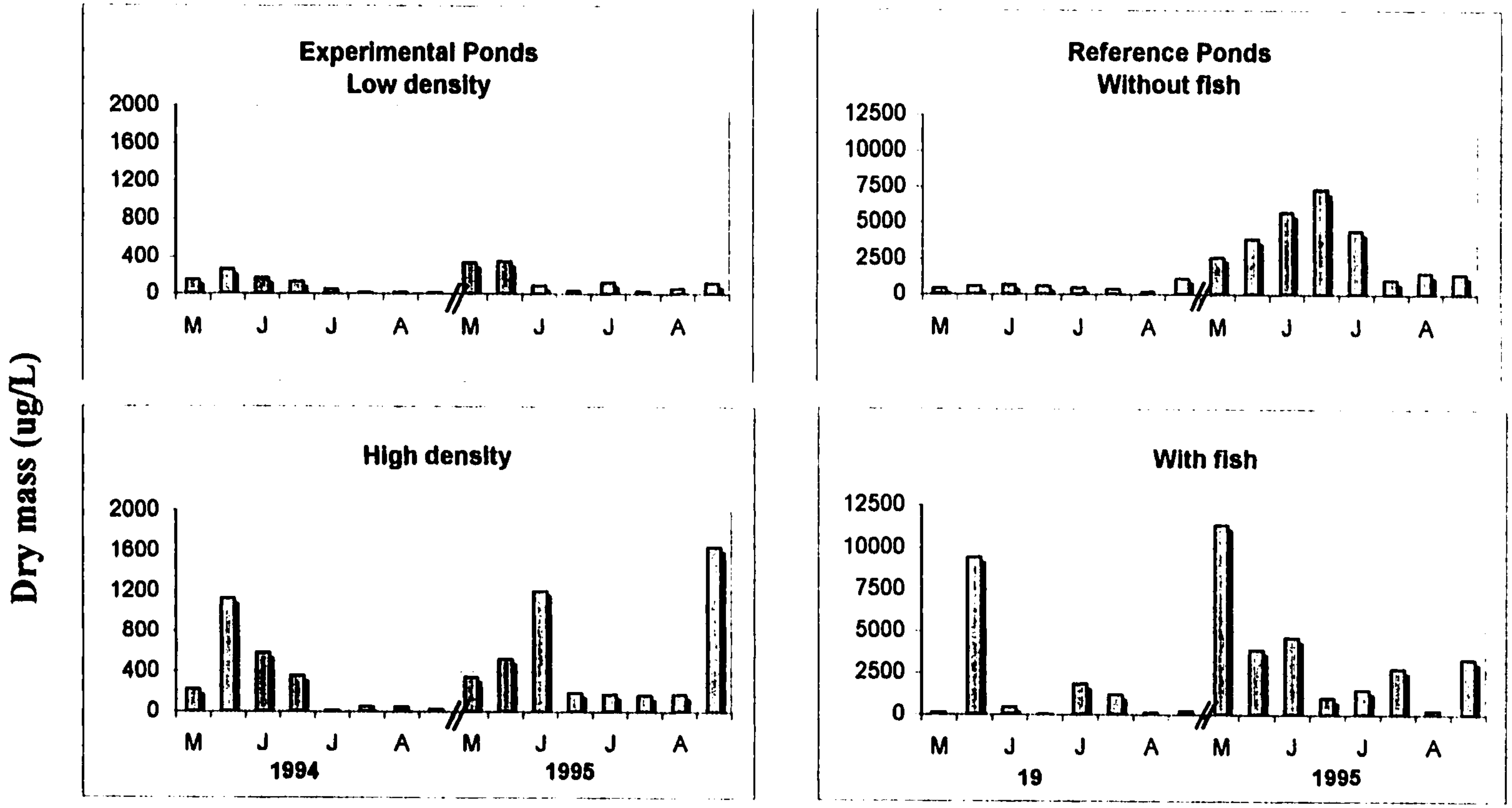

Figure 2. 4. Mean total dry mass (ug/L) of the zooplankton taxa in experimental ponds, Low Density and High Density, and reference ponds, (with fish) Beaver and without fish (Tempo (1994) and Meanook (1995). Note variation in scale of the vertical axes.

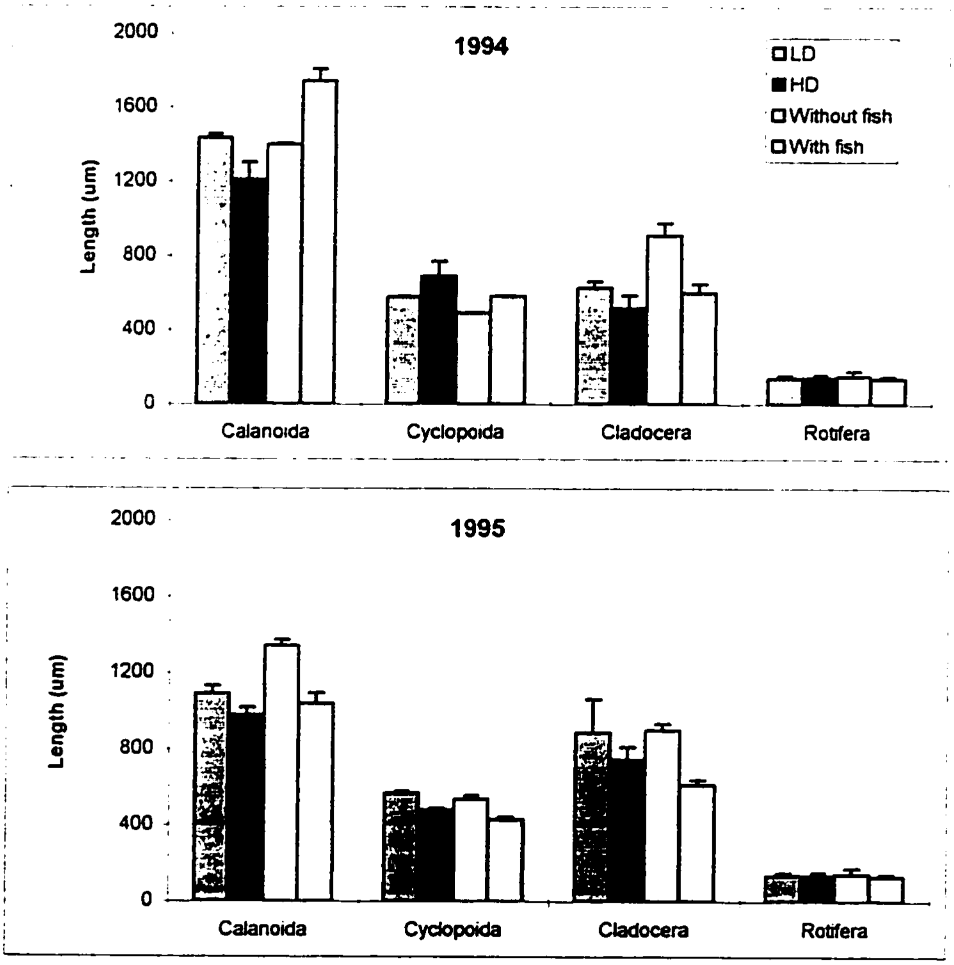

Figure 2. 5. Mean size (SE) of major zooplankton taxa in the experimental ponds (LD-Low Density and HD-High Density) and reference ponds (with fish - Beaver and without fish-Tempo (1994) and Meanook (1995).

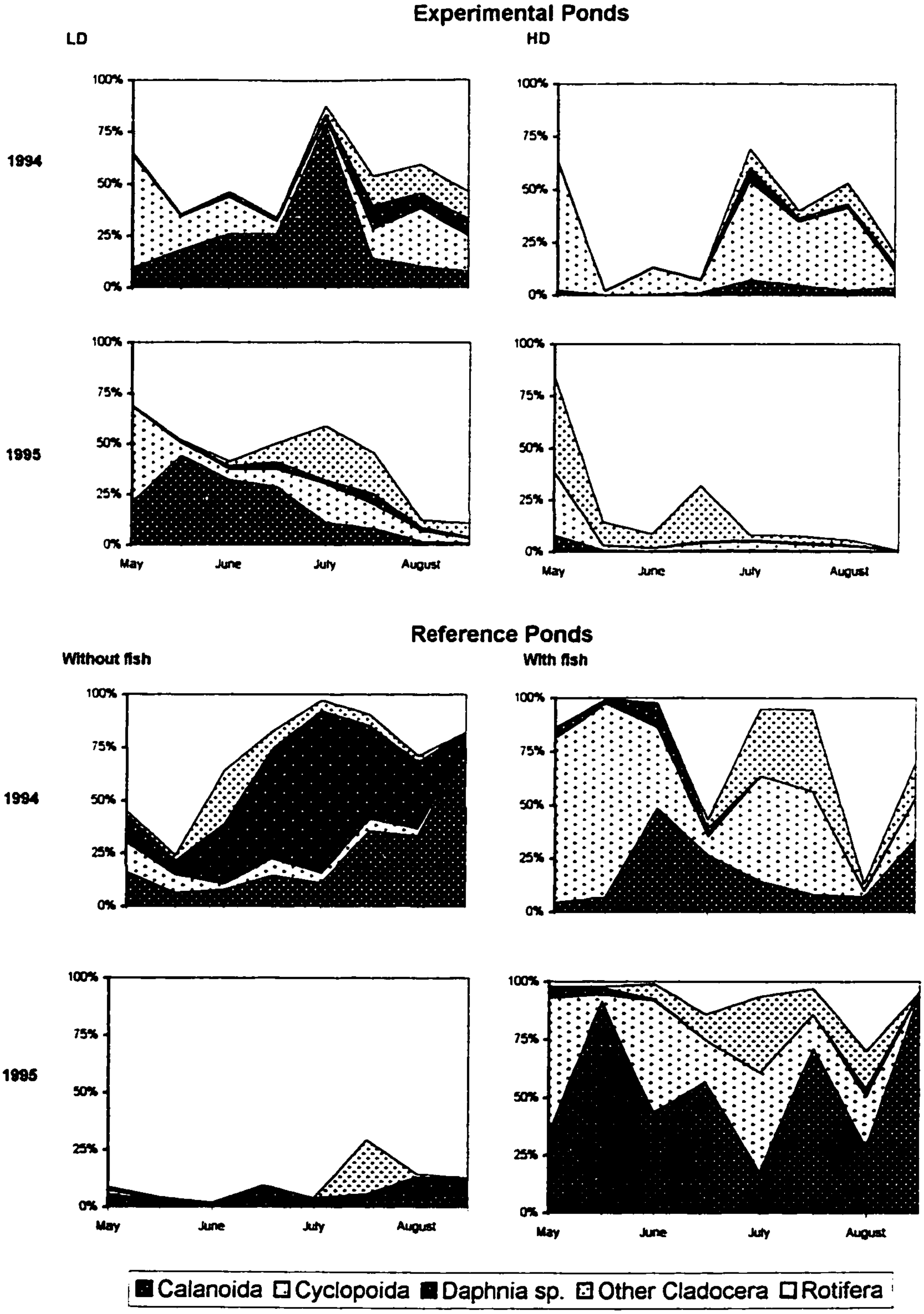

Figure 2. 6. The relative contribution of major zooplankton groups to total zooplankton biomass in experimental (LD and HD) and reference ponds (with fish-Beaver and without fish-Tempo (1994) and Meanook (1995)); May-August 1994 and 1995.

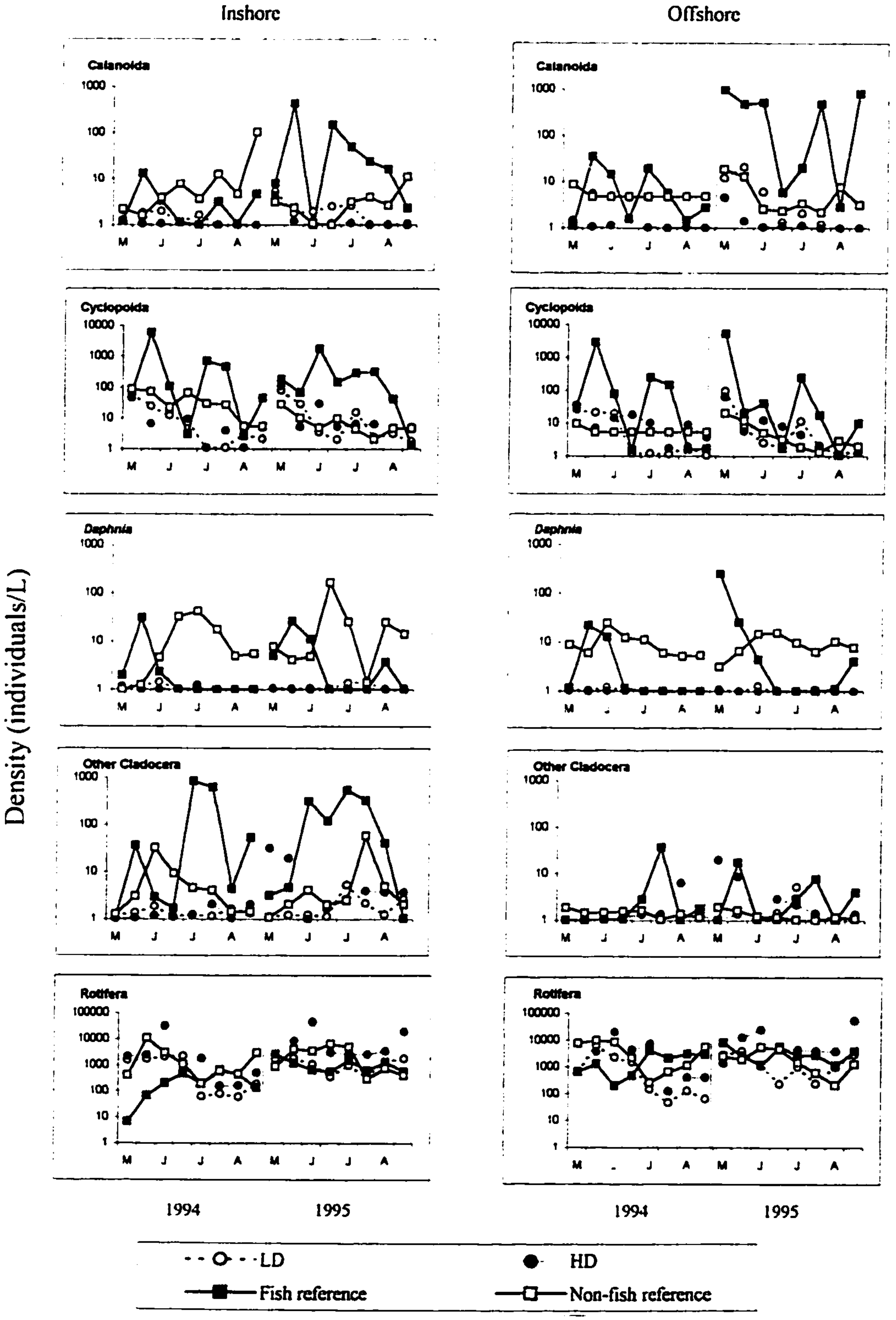

Figure 2.7. Mean densities (individuals/L) of major zooplankton taxa in the experimental and reference ponds from inshore and offshore sites, May-August, 1994 and 1995. Note logarithmic scale of the vertical axes.

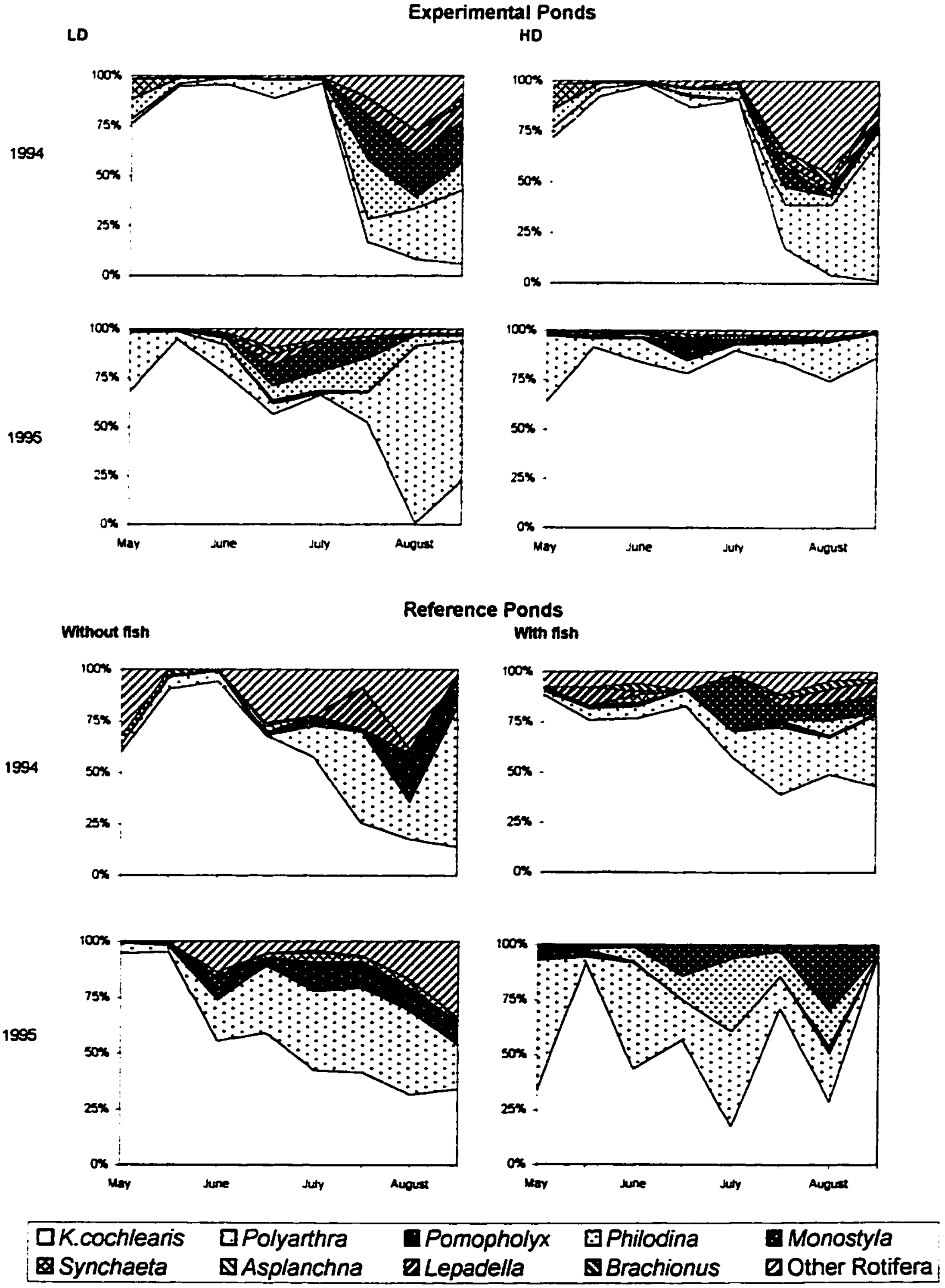

Figure 2.8. Distribution of Rotifera densities (% contribution to total Rotifera density) in experimental (LD-Low Density and HD-High Density) and reference ponds (with fish-Beaver and without fish-Tempo (1994) and Meanook (1995)).

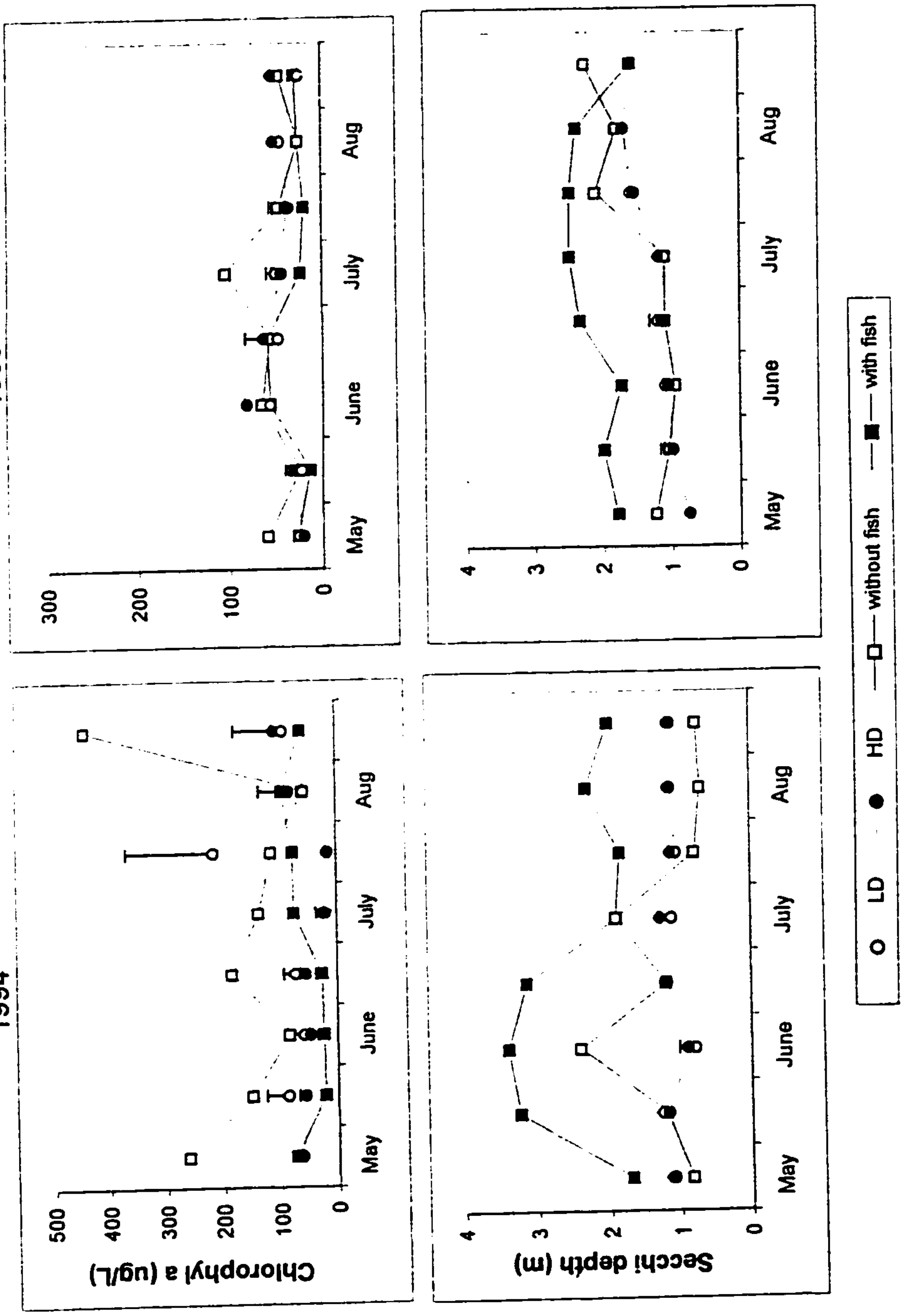

Figure 2.9. Mean (SE) Secchi depth and chlorophyll *a* concentration in the experimental (LD-Low Density and HD-High Density) and reference ponds (with fish-Beaver and without fish-Tempo (1994) and Meanook (1995)).

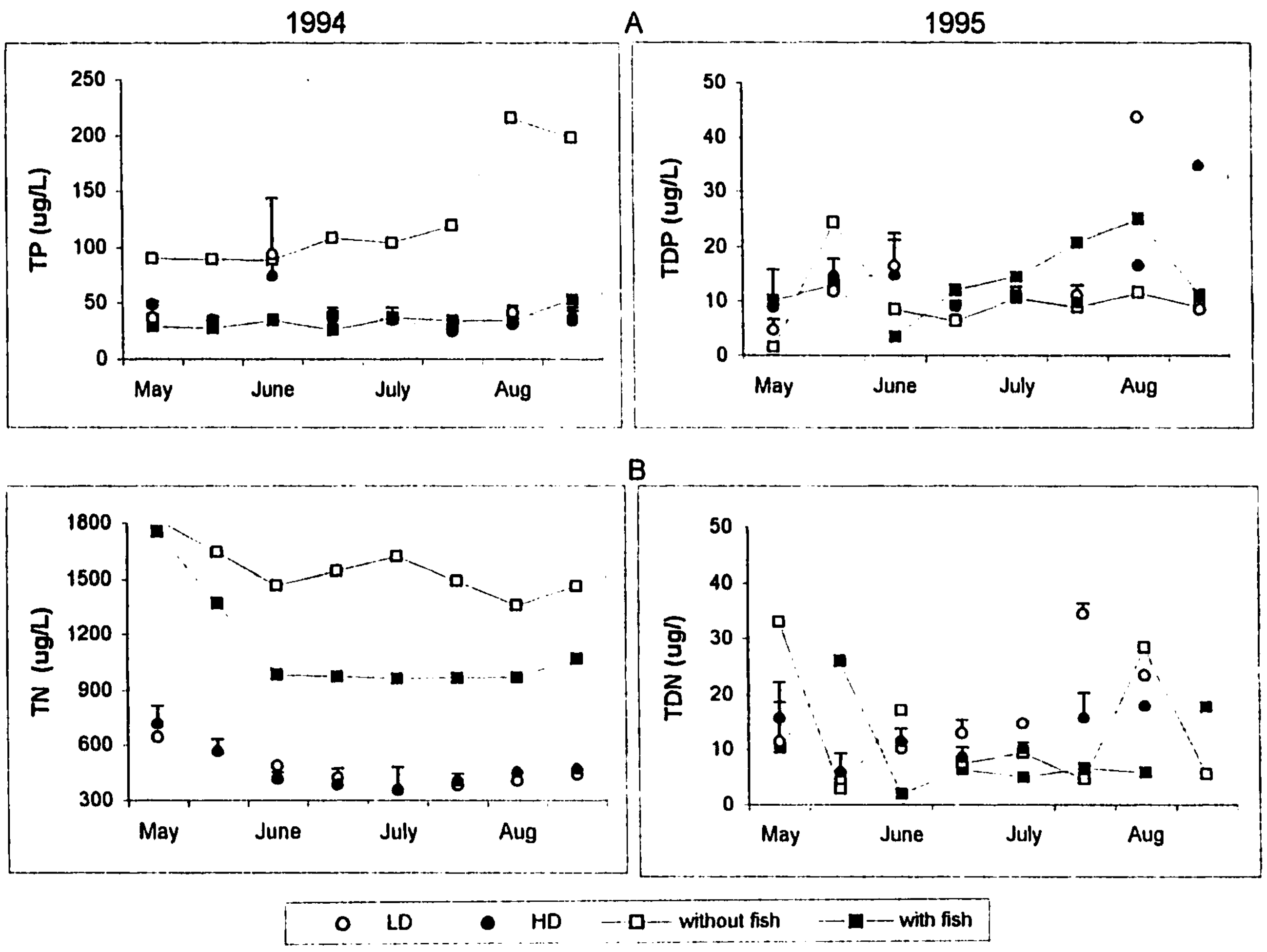

Figure 2.10. Mean (SE) phosphorus and nitrogen concentration in the experimental (LD-Low Density and HD-High Density) and reference ponds (with fish-Beaver and without fish-Tempo (1994) and Meanook (1995)). Note variation in vertical axes.

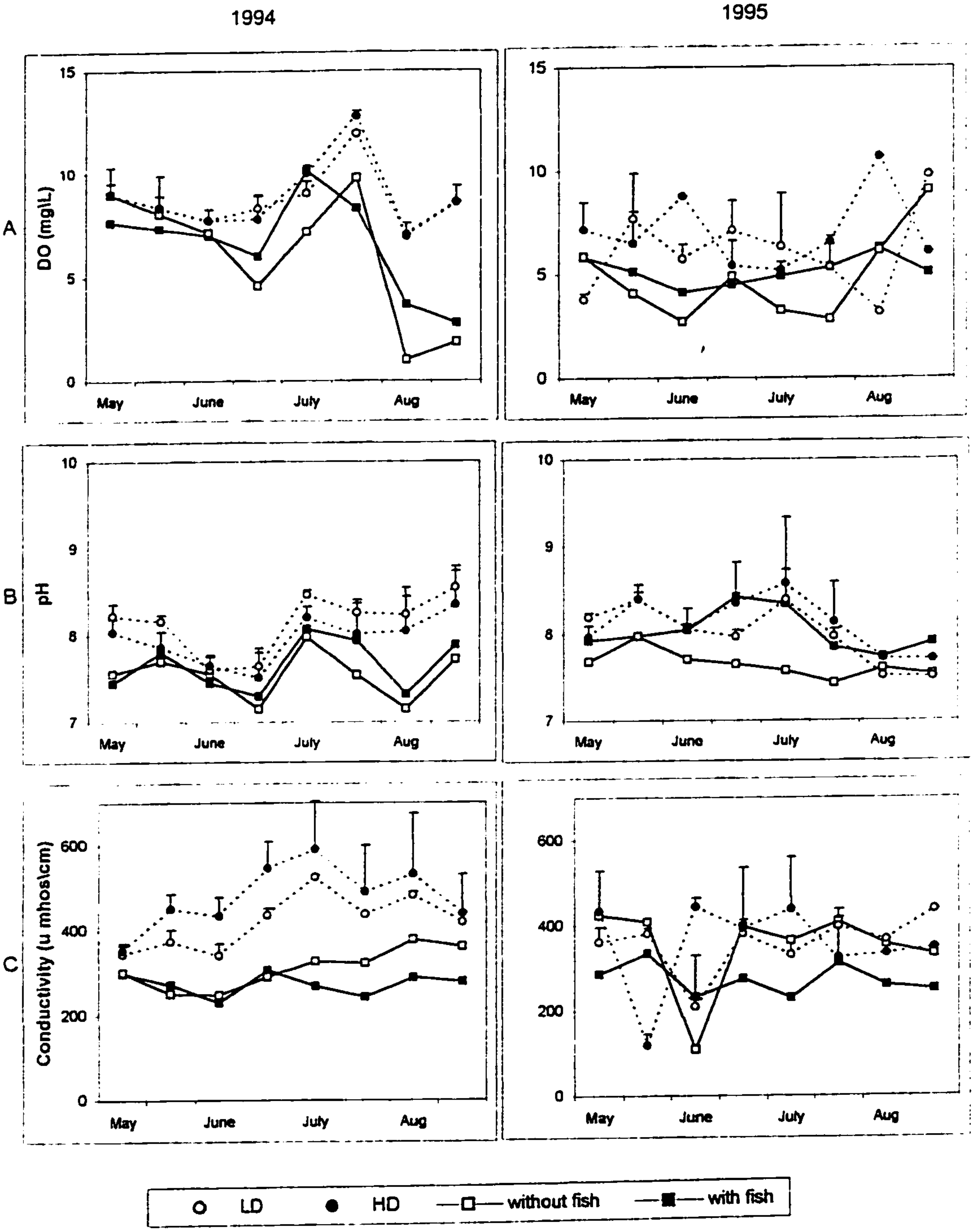

Figure 2.11. Mean (SE) dissolved oxygen (DO) concentration, pH and conductivity in the experimental (LD-Low Density and HD-High Density) and reference ponds (with fish-Beaver and without fish-Tempo (1994) and Meanook (1995)).

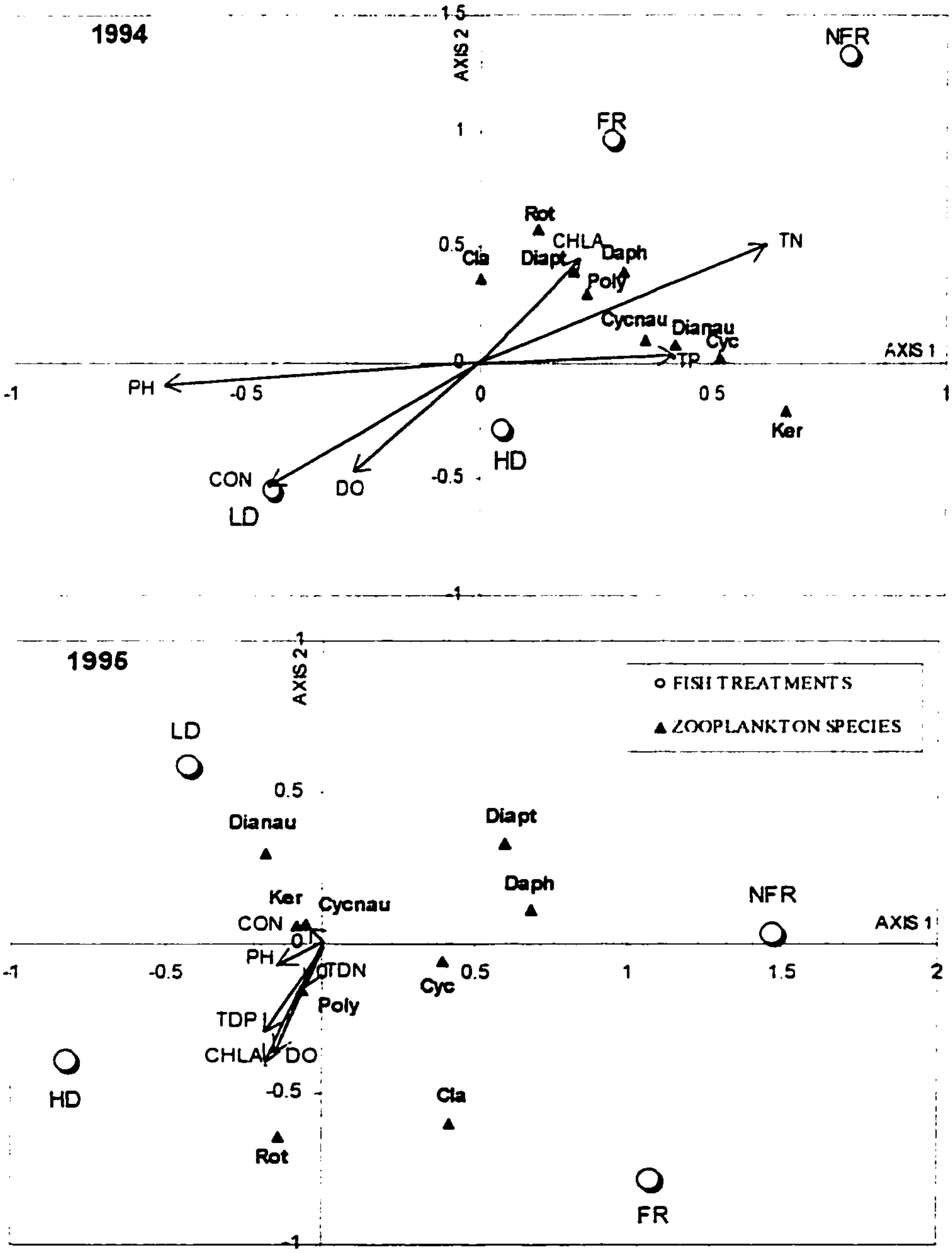

Figure 2. 12. RDA (redundancy analysis) biplots of zooplankton taxa (triangles), fish treatment centroids (circles) and environmental variables (vectors) of samples taken during 1994 and 1995 from reference ponds: fish reference (FR-Beaver and fishless reference ponds (NFR-Tempo (1994) and Meanook (1995)) and Low (LD) and High Density (HD) fish treatments in experimental ponds. TP, TDP: phosphorus; TN, TDN: nitrogen; CHLA: chlorophyll *a*; and DO: dissolved oxygen concentrations. Daph: *Daphnia pulex* and *D. longispina*; Cla: other Cladocera; Cyc: *Dicyclops bicuspidatus* and *Acanthocyclops vernalis*; Cycnau: cyclopoid nauplii; Dia: *Acanthodiaptomus denticornis*; Dianau: copoepod nauplii; Ker: *Keratella cochlearis*; Poly: *Polyarthra dolichoptera*; Rot: other Rotifera.

Chapter 3. DIET OF FATHEAD MINNOWS (*Pimephales promelas*) AND TROPHIC RELATIONSHIPS IN EUTROPHIC BOREAL PONDS

INTRODUCTION

Diet analyses are important in studies of predation, competition, trophic relationships, and food webs of aquatic ecosystems (Keast 1978, Johnson and Dropkin 1993). Such relationships can be influenced by physical, chemical, and biotic factors in conjunction with the ontogeny of the organisms within the system (Crowder et al. 1988). Environmental variability contributes significantly too, affecting primary productivity, relationships among aquatic organisms, and variability in fish recruitment (Mills et al. 1987).

A number of studies have shown that variability in fish population densities can exert strong influences on intraspecific interactions (Fox 1975, Polis 1988, Tonn et al. 1994). For example, competition for food and cannibalism are two such processes that, in turn, may contribute to density-dependent growth and mortality (Frank and Leggett 1994). Furthermore, Dong and DeAngelis (1998) revealed a strong interaction between cannibalism and competition for food. Cannibalism has been shown to be inversely related to the density of food and to increase when fish were facing starvation (see also Fox 1975, Polis 1988).

Determining trophic relationships in natural ecosystems can be difficult (Paine 1988). This is particularly true in aquatic systems, especially when using the conventional techniques such as stomach content analysis (SCA), due to a high degree of omnivory in some species. With conventional SCA, errors can arise because prey can be digested differentially or beyond recognition or stomachs can be empty (Vander Zanden and Rasmussen 1996). In addition, there can be significant discrepancy between food ingestion and actual energy assimilation (Boisclair and Leggett 1988). Stomach content data provide only a "snapshot" of food taxa eaten by an organism over a short time period immediately prior to capture. Therefore, reliable averages that integrate temporal and spatial variation require considerable investment of time, effort, and the sacrifice of large numbers of fish (Trippel and Beamish 1993).

Stable isotope analysis (SIA), conversely, can provide an integrated picture of nutritional sources used by organisms over a longer time period, i.e., the tissue turnover time. Further, because nitrogen in a consumer's tissues is derived exclusively from its diet, trophic estimates are based on assimilated, not simply ingested, food items (Hobson and Welsh 1995). The relative abundance of ^{15}N in the tissues of consumers is typically enriched over that in their prey because of preferential excretion of the lighter ^{14}N during protein transamination and deamination (Minagawa and Wada 1984). This trophic enrichment effect (increase in the ratio $^{15}N/^{14}N$ with trophic level) is relatively constant, averaging 3.4 ‰ across levels (Peterson and Fry 1987). Trophic fractionation of isotopic carbon (^{13}C), i.e., a change in $^{13}C/^{12}C$ with trophic level, is usually small (0.5 - 1 ‰) compared with ^{15}N, making $^{13}C/^{12}C$ a relatively reliable indicator of carbon sources (e.g., pelagic, littoral, or benthic) rather than trophic position (Peterson and Fry 1987). Thus, analyses of stable isotope ratios of biologically important elements, such as carbon and nitrogen, have been useful in tracing the paths of energy flow from primary producers to herbivores and higher level consumers (Estep and Vigg 1985, Fry 1991, Keough et al.

1996) and for delineating trophic linkages in aquatic food webs (Peterson and Fry 1987, Kling et al. 1992, Fry 1988).

Although stable isotope signatures are indicative of the main pathways of energy flow in a system, additional information on specific food web interactions can only be obtained from stomach content analyses (Kidd 1996). Analyses of stomach contents often provide specific information on resource utilization or food web interactions that are not detectable from isotopic analyses. Sometimes many prey species are similar in isotopic composition, making it difficult to determine if a fish feeds strictly on one prey or a combination of prey (Kidd 1996). Although these problems can be overcome to some extent by using multiple isotopes (Hesslein et al. 1991), the integrative nature of isotope signals can obscure certain food web relationships. A combination of SIA and SCA, therefore, should be useful in discerning trophic relationships in systems with high degree of omnivory and in complex food webs.

Omnivores, such as fathead minnows (*Pimephales promelas*), are widely distributed in small lakes of the boreal region of north-central Alberta (Scott and Crossman 1973, Nelson and Paetz 1992). Typical habitat includes shallow eutrophic lakes and ponds, where fathead minnows commonly experience winter hypoxia. Hypoxia eliminates other species, leaving fathead minnows as the only fish in many ponds (Klinger et al. 1982, Robinson and Tonn 1989). Such populations can occur at high densities and consist of fish in different size and life history categories. Although there are differences in feeding habits among the size categories and sexes, no distinct ontogenetic diet shifts take place (Price et al. 1991). Because diet overlap remains high among size categories, fathead minnows should be vulnerable to intraspecific competition for food (Hamrin and Persson 1986).

Few studies to date have complemented dietary information obtained from stomach content analyses, representing one-time ingestion, with stable isotope analysis of long-term dietary assimilation of fishes to determine feeding habits and discern trophic relationships (Kidd 1996), particularly in relation to varying fish densities. The objectives of my study were to integrate these two approaches to examine the diets of fathead minnows and their trophic positioning in relation to different minnow densities.

METHODS

Study Area

The study was carried out from May to September, 1995 in one reference (Meanook Pond) and three research ponds at Meanook Biological Research Station (MBRS; 54°37'N, 113°35'W) and in a second reference pond (Beaver Pond) located 15 km north (Figure 2.1). Pond characteristics are presented in Table 3.1.

Beaver Pond (54°38'N, 113°35'W) is a eutrophic pond fed by a small wetland spring with the outlet blocked by a beaver dam. Thermal stratification normally occurs during June - August. The summer Secchi depth is typically > 2 m (Chapter 2). Macrophytes are abundant, extending to a depth of ca. 2.5 m, and are dominated by *Myriophyllum* and *Potamogeton*. Fathead minnows are the only fish species present. The only piscivores observed at the pond are a pair of common loons (*Gavia immer*) and an occasional belted kingfisher (*Ceryle alcyon*) (personal observations).

Meanook Pond is a decades-old manmade, eutrophic pond that also serves as a water source for the research ponds. The pond is fishless and the invertebrate community is dominated by large zooplankton species, particularly *Daphnia* spp. (Chapter 2). The littoral zone is well developed with abundant macrophyte vegetation, mostly *Potamogeton*, extending into the center of the pond.

The experimental portion of the study, in which fish densities were manipulated, was conducted in three research ponds at MBRS. The ponds were divided in half by impermeable polyvinyl curtains supported by wooden stakes and extending 1m above the water surface. The bottoms and sides of these curtains were attached to metal sheets that were buried into the substrate. Prior to the experiment, each pond was drained, cleaned of vegetation, planted with cattails (*Typha*) along the shores, refilled and provided with nesting sites for fathead minnows (10 fence boards allowed to float at the water surface).

Fathead minnows used in the experiment were collected from nearby lakes. Based on external morphological characteristics, fish were classified into three life history categories: mature males (the presence of tubercles; total length, TL≥70 mm), females (apparent ovipositor, TL ≥ 63 mm) and juveniles (TL = 40-56 mm). Fish were stocked in equal proportions of males, females, and juveniles at two densities: low density (LD, 1 fish/ m^2) and high density (HD, 4 fish/ m^2), with three replicates of each treatment. Both treatments were applied to each pond (on each side of the curtain). The densities of fish used in this experiment were determined from annual population estimates of fathead minnows in Beaver Pond (the reference system) and a preliminary study in 1993 (W. Tonn, personal communication). To monitor survival of stocked fish in each class, fish were marked with fin clips. Young-of-the-year (YOY) fish appeared during the experiment and were distinguished from the stocked fish by their small size.

Sample collection

SCA: Fish were sampled monthly (June-September 1995) in the three research ponds and Beaver Pond using Gee minnow traps. The 30 traps in Beaver Pond and 5 in each half of the research ponds were set along the shores for 3 hr. Captured fish were sorted into life - history categories (males, females, juveniles, and YOY), counted, measured (total length, TL), and returned to the ponds. A subsample of 3 individuals from each class and trap was sacrificed and frozen shortly after collection until diet analyses were conducted.

SIA: All samples for stable isotope analyses were collected from each pond on September 15, 1995. 1-2 each of males, females, and juveniles, and 5 YOY fathead minnows were collected in the same manner as for SCA. The date for SIA sampling was determined from a 35-week laboratory-based feeding experiment in which I monitored the change in the nitrogen ratios ($^{15}N/^{14}N$) of the muscle tissue (tissue turnover) of adults, juveniles and YOY in response to a change in the nitrogen ratio of their food (*Daphnia* spp.) (Appendix, Table 5).

Benthic invertebrates were collected at several locations within each pond using sweep nets (mesh size=1 mm). Trichopterans were removed from cases in the field. Animals were washed and stored in tap water for several hours to allow for gut evacuation, identified (Pennak 1978, Clifford 1991), sorted into major taxonomic groups, and frozen until laboratory analyses.

Zooplankton samples were obtained with vertical tows of a plankton net (mesh size=64 µm). Samples were pooled into a composite sample, filtered through a 150-µm mesh net, and larger species were picked with tweezers and pipettes under a dissecting microscope. Zooplankton were also allowed to void their guts for several hours prior to freezing.

Phytoplankton were collected using a 3.1-L Van Dorn bottle, filtered first through a coarse net (mesh size 500=µm) to remove large particles, then successively with smaller meshes (250, 144, and 45-µm) to eliminate small zooplankton, and concentrated on glass fiber filters (Whatman GF/C) precombusted at 450 °C for 2 hours. Rocks and submerged snags from the littoral zones were scraped to obtain samples of periphyton.

Detritus was collected from several stations within each pond with a 4 - barrel corer. The upper layers of sediment (ca. 1 cm) were removed, pooled, and kept frozen until analyses.

Laboratory analyses

Diet analysis: In the laboratory, all fish were dissected and examined for the presence or absence of food. Contents of the anterior two - thirds of the digestive tract were preserved in sugared formalin solution (Prepas 1978). Prey taxa were identified to the lowest possible level using keys from Edmondson (1959), Pennak (1978), and Clifford (1991) for macroinvertebrates and macrozooplakton, and keys from Chengalath et al. (1971), Ruttner-Kolisko (1974), and Grothe and Grothe (1977) for rotifers. All prey taxa were counted and their biovolumes calculated.

To determine volumes of zooplankton, ca. 30 preserved individuals of each taxon were measured and the dry mass calculated using length-mass regressions (Bottrell et al. 1976, Stemberger and Gilbert 1987). Because these regressions were developed for fresh specimens, a multiplication factor of 1.37 was applied to preserved specimens to correct for loss of mass in formalin (Giguere et al. 1989). Dry masses were then converted to volumes assuming a specific gravity of 1 (1 cm^3 = 1g) and dry mass of all species being 10 % of wet mass (Bottrell et al. 1976).

Because most of the invertebrates in the guts were partially digested, whole animals collected from benthic samplings during the summer were used for volume calculations. Invertebrates were blotted and weighed (± 0.1 mg), and their biovolumes calculated using a specific gravity of 1.05 (Smit et al. 1993) and multiplied by 1.43 to account for the leaching of mass during preservation in 70 % ethanol solution (Howmiller 1972). Detritus and plant material (filamentous green algae and pieces of macrophytes) were estimated as relative percentages of total volume of food in the gut.

Diet composition and the relative importance of prey taxa were quantified for each fish life history category (males, females, juveniles and YOY) as an average of three measures: frequency of occurrence, percentage composition by number and by volume of all prey taxa (Wallace 1981). The index of Relative Importance, RI (George and Hadley 1979) was determined for a given prey taxon *i* for each fish category during each month from the absolute importance index (AI_i) as follows:

$$RI_i = 100\ AI_i \,/\, \sum_{i=1}^{n} AI_i$$

where, AI_i = % frequency of occurrence + % total numbers + % total volume for prey taxon *i*;

n = total number of prey taxa;

% frequency of occurrence = the percentage of all non-empty stomachs that contained prey taxon *i*,

% total numbers = the percentage that prey taxon *i* contributed to the total number of prey items in all stomachs,

% total volume = the percentage that prey taxon i contributed to the total volume of food in all stomachs

For detritus and plant material, no correct numerical evaluation could be made, therefore the Absolute Importance Index was calculated as:

AI_i = % frequency of occurrence + % total volume

Because prey represented by items such as fish scales could not be quantified numerically or volumetrically, they were expressed only as the frequency of occurrence and were not included in the RI calculations. Prey items that were impossible to identify due to digestion were also omitted from the RI calculations.

To determine mean summer diet breadths of fathead minnows in all ponds I used Shannon-Wiener diet breadth (H') (Colwell and Futuyma 1971):

$$H' = -\sum p_j \log p_j$$

where p_j are proportions of mean summer abundance of prey taxa j found in fathead stomachs of a particular life history category.

To determine seasonal differences in diet compositions between all fish categories within and among the ponds I used Schoener's (1974) diet overlap index (α),

$$\alpha = 1 - \left(\tfrac{1}{2} \sum_{i=1}^{n} | p_{xi} - p_{yi} | \right),$$

where p_{xi} and p_{yi} are proportions (based on RI) of prey taxa i in any pair of fish categories x and y, and n is the total number of prey taxa. The index ranges from 0 to 1, with 0 indicating no overlap and 1 complete overlap in the diets (Wallace 1981). Keast (1978) suggested that overlap was low when $\alpha < 0.3$, and high when $\alpha > 0.7$.

To determine trophic relationships in all ponds I used Stable Isotope Analysis (SIA). In ponds containing fish, I compared the results of stomach content analyses (SCA) to patterns suggested by SIA. Based on SCA for each fish category within each pond, a predicted mean summer $\delta^{15}N$ for each fish category was calculated by adding the trophic enrichment value of 3.2 ‰ (Peterson and Fry 1987) to the $\delta^{15}N$ of the prey they consumed, weighted by the mean RI of the prey for the particular fish category (Figures 3.2 to 3.4, Appendix, Tables 2 to 4). It was assumed that all species had comparable trophic enrichments of $\delta^{15}N$ and that all components of prey organisms (excluding cases and shells) were digested and assimilated into fish tissues.

For SIA, skinless, lateral muscle tissue from 5 fish each of males, females and juveniles, and 10 whole, gutless YOY were dissected for isotopic analyses. Whole zooplankton and invertebrates were analyzed from samples containing 1-10 mg of animal matter. All samples were oven dried at 60°C for 24-48 hours, then ground to a fine powder to homogenize the samples. Dry samples were placed in tin capsules (6-15 mg for nitrogen analyses, and 2-6 mg for carbon analyses) and combusted in Carlo Erba NA 1500 elemental analyzer (Research Centre at Agriculture and Agri-Food Canada, Lethbrige, AB). Sample gases were introduced into a VG Optima automated mass spectrometer with helium carrier gas. Water and CO_2 were removed cryogenically with a magnesium perchlorate and Ascarite column, respectively. The ratios of stable isotopes were measured against the reference standards BMO #1 (red spring wheat), and oxalic acid for carbon samples and BMO #1 and SQD #4 (soil) for nitrogen. A laboratory standard was run every 10 samples. Precision over several years has been 0.4 parts per million (2 SD) (analyzed by Clarence Gilbertson, Agriculture and Agri-Food Canada, Lethbrige, AB). The delta notation (δ) was used to indicate the parts per mil (‰) difference in the isotopic ratio of the sample from the standard. The ratios of stable carbon and nitrogen were calculated as follows:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ (Hobson and Welch 1995).

RESULTS

Dietary patterns

Fathead minnows in HD treatment had a significantly higher proportion of empty guts than fish in LD and Beaver Pond ($x^2 = 7.3$, df = 2, $P < 0.05$) (Appendix, Table 1). Prey diversity was highest in HD (47 taxa), followed by LD (38) and Beaver Pond (35 taxa) (Appendix, Table 1). In all ponds, fatheads had similar diet breadths (H' of 0.6-0.7), with the exception of females and YOY in Beaver Pond (H' = 0.4 and 0.9, respectively), and YOY in LD (H'=0.4) (Table 3.2).

The diet of fathead minnows in all three systems consisted of a wide variety of invertebrate taxa, which were subsequently combined into four larger categories: macroinvertebrates, cladocerans, copepods and rotifers. Overall, cladocerans (RI of 36 %, 32 %, and 36% in Beaver Pond, LD, and HD treatments, respectively) and macroinvertebrates (26 %, 24 %, and 21 %) were the most important food categories in all ponds (Figure 3.1). Among cladocerans, *Daphnia*, *Chydorus*, and *Alona* were most important in Beaver Pond (Table 3.3), whereas *Sida*, *Chydorus*, and *Alona* were predominant in diets of fatheads from LD (Table 3.4); in HD, *Chydorus* was the dominant taxa (Table 3.5). Within macroinvertebrate prey, *Chaoborus* was important only in Beaver Pond (Table 3.3), whereas Chironomidae were relatively important in all ponds. Copepods were somewhat important only in LD (Table 3.4) and HD (Table 3.5) treatments, whereas plant material (filamentous green algae, macrophytes and seeds) was important only in Beaver Pond (Table 3.3). Detritus was moderately important food item for all three populations (Figure 3.1).

Although not incorporated into calculations of Relative Importance, the frequency of fish scales in the diet of fathead minnows was variable among months, categories of fish, and treatments, but could be quite high (Table 3.6). Frequencies were highest in female diets in September and lowest among YOY in August. Frequencies for males appeared to be more consistent across months (Table 3.6).

Although diets of fatheads were variable within each particular pond, some temporal patterns were common for all ponds. The Relative Importance of macroinvertebrates was greatest in June and decreased progressively during the summer, reaching the lowest values in August (Figures 3.2 to 3.4, Appendix, Tables 2 to 4) Cladocerans as a group remained important throughout the summer in all ponds, however, they were increasingly important towards the end of the summer, reaching an RI of about 40 % in September for all fish categories. Copepods, although unimportant as prey for fatheads in Beaver Pond (Figure 3.2, Appendix, Table 2) were progressively more important toward the end of summer in LD (Figure 3.3, Appendix, Table 3) and HD (Figure 3.4, Appendix, Table 4). Rotifers were most important for YOY in July in LD (Figure 3.3) and HD (Figure 3.4), less so in August and were absent from their diets in September. The relative importance of detritus was steady for females, males, and juveniles from LD (Figure 3.3) and HD (Figure 3.4) throughout the summer, whereas its consumption in Beaver Pond varied among fish categories (Figure 3.2).

Trophic relationships

Diet overlap: During the summer of 1995, similarity in diet composition between the Beaver Pond and two experimental treatments (LD and HD) was low in the early summer but increased to a moderate degree in July and August (Table 3.7), due to a shift in the diet of minnows in Beaver Pond from *Chaoborus* toward small cladocerans, chironomids and detritus. Diet overlap of fathead minnows in LD and HD treatments was relatively high throughout the summer (Table 3.7) due to a common prey base of cladocerans, macroinvertebrates and detritus. A slight decrease in diet overlap was recorded in August when *Chydorus sphericus* was especially important for fatheads in High Density ponds.

Dietary overlap among all fish categories in Beaver Pond was moderate-to-high, 0.53 to 0.82, throughout the summer (Table 3.8), reflecting their common foraging on many of the invertebrate prey. The highest diet overlap was recorded in June, between females and juveniles, resulting mainly from the mutual consumption of *Daphnia* spp. and *Chaoborus* spp. In July, only YOY and juvenile fish were caught; they achieved a high degree of diet overlap by mutually consuming a wide variety of invertebrate taxa, detritus and plant material. In August, the diets of males and females and males and juveniles were most similar, reflecting their common foraging on many of the cladoceran species, Chironomidae, and detritus. YOY fish showed only moderate similarity to the other fish due to the higher proportions of plant material and lower importance of detritus in their diets.

A greater range of diet overlap (0.3 to 0.76) was observed for fish in LD treatments (Table 3.9). Overlap among stocked fish was moderate throughout most of the summer, 0.55 to 0.67, and reflected a common prey base of aquatic invertebrates, detritus and plant material. The highest degree of overlap was recorded in September, between juveniles and females, and juveniles and males, due mainly to mutual consumption of *Sida crystalina*, *Diacyclops bicuspidatus*, Chironomidae and detritus. Diet overlap between YOY and the stocked fish was generally moderate (0.5-0.65), except for the low overlap between YOY and females in July.

Diet overlaps in HD treatments also varied temporally and among different categories of fish (Table 3.10). Overlaps between adults and juveniles were moderate-to-high throughout the summer (0.63-0.81), reflecting the common prey base of aquatic invertebrates and detritus. The lowest overlap was documented in July between YOY and adults (Table 3.10), when YOY fish fed primarily upon rotifers. Diet overlaps between YOY and other fish increased progressively in August and September, as growing YOY fish shifted to the same invertebrate prey as older fish.

Stable Isotope Analyses: Consumers and primary producers displayed considerable differences in carbon and nitrogen isotopic ratios ($\delta\,^{13}$C and δ^{15}N) among ponds (Table 3.11). The $\delta\,^{13}$C value of macroinvertebrates from the LD and HD were consistent with mixed diets of detritus and possibly phytoplankton; in Beaver Pond with macrophytes. The $\delta\,^{13}$C of zooplankton from both LD and HD were similar to the carbon signatures of phytoplankton, whereas in Beaver Pond, $\delta\,^{13}$C of zooplankton was similar to both periphyton and phytoplankton. The δ^{15}N values of zooplankton and macroinvertebrates were less than the predicted 3.2 ‰ enrichment from their likely food sources.

The trophic relationships of minnows in Beaver Pond, as determined by SIA, were generally consistent with those revealed from the stomach analyses (Figure 3.5). All categories of fish had similar δ^{15} N values (5.3-5.6 ‰), indicating similar trophic positions within this pond (Figure 3.5). Carbon isotope analyses of both fish and prey suggested that all categories of fish derived their carbon mainly from zooplankton, phytoplankton, periphyton and detritus, although juvenile fish may have consumed macroinvertebrates in greater proportions.

The δ^{15} N signatures of male, female and juvenile fatheads from the LD treatments were 0.65-1.52 higher than YOY indicating that they occupied somewhat higher positions within the same trophic level (Figure 3.6). These δ^{15} N signatures of the older minnows suggested that they fed selectively upon prey with higher δ^{15} N relative to YOY, e.g., predacious versus herbivorous zooplankton. The δ ^{13} C values of fish indicated that most primary producer and consumer categories were potential carbon sources.

Similar to the LD ponds, δ^{15} N signatures of minnows in the HD treatment indicated that adults and juveniles occupied somewhat higher trophic positions than YOY fish (Figure 3.7), i.e., that in their diet of aquatic invertebrates, plant material and detritus (and possibly YOY), they consumed greater proportions of prey more enriched in δ^{15} N than did YOY fish. Isotopic carbon signatures (-23.4 to -24.6 ‰) indicated that the diets of all categories of fish originated from similar carbon sources that were a combination of all prey taxa measured.

For Beaver Pond fatheads, the predicted values of δ^{15} N were similar to their measured nitrogen ratios (Figure 3.5). For LD ponds, males and females had higher measured nitrogen ratios (by 1.2 and 1.4 ‰, respectively) than predicted from their gut analyses (Figure 3.6). The observed δ^{15} N for juveniles was only slightly higher than expected (0.5 ‰), whereas expected and observed isotopic nitrogen ratios were comparable for YOY fish. For HD treatment, the δ^{15} N measured signatures were approximately 2 ‰ higher for adult and juvenile fish and 1.2 ‰ for YOY than predicted from stomach contents (Figure 3.7).

The trophic relationships in the fishless Meanook Pond revealed larger differences in δ^{15} N and $\delta\ ^{13}$ C among phytoplankton, periphyton, invertebrates and zooplankton than in the ponds containing fish (Table 3.11, Figure 3.8). The highest (5.3 ‰) δ^{15} N values were found in zooplankton and indicated that these organisms' diet consisted mainly of phytoplankton (3.3 ‰). Macroinvertebrates had a lower nitrogen signature (3.8 ‰) and appeared to feed primarily upon detritus, phytoplankton, and macrophytes. The carbon isotopic signatures of primary producers varied considerably, ranging from –9.7 ‰ in periphyton to –27.7 ‰ in phytoplankton.

DISCUSSION

Diet of fathead minnows

Fatheads from Beaver Pond, LD and HD treatments were omnivorous, i.e., they exploited prey from all trophic levels. Omnivory is a common feeding strategy in which consumers complement energy and protein from animal prey with more abundant but less nutritious primary producers or detritus (Alghren 1990*a*, Bowen et al. 1995). However, with an array of prey potentially available, fatheads should selectively consume animal prey, which is higher in the protein content, to maximize their foraging efficiency (Persson 1983, Alghren 1990*b*).

Although a broadly catholic diet has been documented previously for fatheads, past studies indicate that fatheads usually focus their feeding on a few food taxa at any given time (Scott and Crossman 1973, Held and Peterka 1974, Tallman et al. 1984, Price et al. 1991). Although there was considerble seasonal variation in diet, fatheads in my study consumed numerous prey categories simultaneously throughout the whole sampling season. Moreover, the greatest diversity of prey consumed was attained in the HD treatments. This suggests that fatheads in high densities employ generalist feeding strategy when food resources are poor or depleted by conspecifics (Schoener 1969). Similarly, Hodgson and Kitchell (1987) found that bass developed generalized foraging habits in the presence of intense intraspecific competition.

Consistent with other findings (e.g., Persson et al. 1993, Tonn et al. 1994), high fish densities in my experimental treatments appeared to cause limited food resources, which resulted in significantly higher proportions of empty stomachs in HD and LD treatments than in Beaver Pond. Limited food resources result in reduced fish growth, poor condition and low overwinter survival rates in high-density populations (Holopainen and Pitkänen 1985, Tonn et al. 1994). Intense competition in both experimental treatments was indicated by the dominance of small-bodied invertebrates, both in the plankton samples (Chapter 2) and in the diet of fathead minnows. In addition, fatheads in high-density ponds consumed substantially greater proportions of cyclopoid copepods, which are generally considered difficult to catch by non-specialist zooplanktivores like cyprinids (Wright and O'Brien 1984, Winfield and Townsend 1991, Michelsen et al.

1994). However, fatheads selected for copepods with egg sacs, which may have been easier to prey upon (Hessen 1985, Winfield and Townsend 1991). Moreover, higher proportion of cyclopoids in the stomachs of fatheads in high-density treatment corresponds to higher densities of cyclopoids in these ponds (Chapter 2), and thus it suggests that fatheads simply took advantage of an abundant food.

In addition to invertebrate prey, fatheads also consumed significant amounts of detritus. Because detritus is readily available throughout the summer, searching for and feeding on detritus involves lower energetic cost than foraging for invertebrates (Michelsen et al. 1994). Although detritus is lower in protein content than animal food, it may provide sufficient energy to support somatic growth or fulfill metabolic demands. Therefore, it might be energetically beneficial for fatheads in high densities to prevent weight loss or starvation (Alghren 1990*a*, Price et al. 1991, Michelsen et al. 1994).

In contrast, a reduction in intraspecific competition should result in an increase in the importance of preferred prey and a decrease in diet breadth (Hodgson and Kitchell 1987). In Beaver Pond, a partial winterkill two winters prior to my study (Chapter 2, W.M. Tonn, University of Alberta, personal communication) resulted in reduced fish densities during my study. This low-density environment was reflected in the composition of the fatheads' diet in early summer, which consisted almost entirely of invertebrates (>95 % by R I), primarily *Daphnia* and *Chaoborus*. By mid-summer, however, the high densities of YOY fish increased pressure on food resources and resulted in diets consisting of small-bodied benthic invertebrates and cladocerans, plant material, and detritus.

Trophic relationships

To determine the trophic relationships in studied systems, I used two techniques, diet overlap index (α) among ponds and minnow life history categories based on stomach content analysis (SCA), and stable isotope analysis (SIA) that involved measuring the ratios of naturally occurring stable isotopes of carbon and nitrogen (δ^{13} C and δ^{15} N) in fish, their potential prey, and the primary producers.

Pairwise analyses of diet overlaps suggested that diets among fatheads from all ponds were generally similar throughout the summer, with the exception of June, when fatheads from Beaver Pond fed exclusively on zooplankton and macroinvertebrate prey. The comparisons within each pond revealed that the only substantial differences in diet were those between YOY fatheads and older fish, with YOY consuming relatively greater proportions of small-bodied zooplankton, particularly rotifers and small chydorids, than older fish. These results were likely due to differences in the overall body sizes and sizes of mouth and gill rakers, which can limit the size of prey that can be consumed by a fish (Eggers 1977) and contribute to considerable variations in diets (Hyatt 1979). Similarly, among the older fish, males consumed greater proportions and a wider variety of large macroinvertebrates than either females or juveniles, likely because of their larger size (Held and Peterka 1974, Scott and Crossman 1973, Price et al. 1991).

Nitrogen isotope data from my study confirmed that either experimental and reference ponds, had only three trophic levels. The highest values of δ^{15}N were observed from fish and clearly indicated that although omnivorous, fathead minnows occupied the highest trophic positions, excluding piscivorous birds. The δ^{15} N values predicted from the diet analyses of fatheads from Beaver Pond generally agreed with their observed values and indicated that fatheads consumed a combination of zooplankton, macroinvertebrates, detritus and plant material.

However, substantial discrepancies in trophic position of fatheads were found in the LD and HD treatments between the positions determined from stomach content analysis (SCA) and those measured as $\delta^{15}N$. One reason for these discrepancies could be cannibalism by adults on fish eggs and larvae, which are rapidly digested and often missed by SCA (Dionne 1985).

Nitrogen ratios ($\delta^{15}N$) suggest that a higher rate of cannibalism was attained in HD than LD treatments. The findings from my study support and extend other works that showed cannibalism to be density-dependent, with rates of cannibalism conditional on the availability of alternative food resources (Fox 1975, Tonn et al. 1994). Cannibalism increases with low absolute or relative densities of prey but high densities of small conspecifics (Smith and Reay 1991). In addition, cannibalism can improve the growth of cannibals, particularly when victim density is high (Dong and DeAngelis 1998).

In laboratory trials, YOY were easily cannibalized by adults in a size-dependent manner (larger adults were able to cannibalize larger fry than smaller adults) (Vandenbos 1996). Only fry ≥ 2 cm were able to avoid consumption by adult conspecifics (average size = 6 - 8 cm). Fatheads also cannibalized eggs. Vandenbos (1996) observed considerable egg cannibalism by older fish in the high-density treatments. On several occasions she witnessed schools of fish mobbing nest-guarding males in high-density treatments and noted that nests were cannibalized completely in each case. Egg cannibalism was likely a response to food demands by guarding or non-territorial fatheads of both sexes. Nest raiding and egg eating by non-territorial males and juveniles but also by guarding males, may maximize their reproductive output at the expense of conspecifics in populations where food is scarce (Hyatt and Ringler 1989). Nest raiding and egg eating may furthermore represent an option for minimizing the amount of time that must be spent foraging, allowing it to be allocated toward reproductive activities (Hyatt and Ringler 1989).

Despite Vandenbos' (1996) observations, cannibalism was not detected from stomach content analysis. Soft-bodied food taxa, such as eggs and newly hatched larvae, are digested more rapidly than hard-bodied invertebrates (Sutela and Huusko 1994) and may either go undetected, as in my study, or highly underestimated (Dionne 1985). Also, rates of cannibalism vary seasonally and with food availability (Fox 1975), which makes detection unlikely from monthly samplings. The absence of ingested conspecifics in gut-content analyses may explain why cannibalistic interactions have not been considered earlier in fathead minnow population studies (Held and Peterka 1974, Tallman et al. 1984, Price et al. 1991). SCA alone, therefore, is not a reliable indicator of food habits of fish species in which the occurrence of cannibalism on eggs/larvae is sporadically high as a response to fluctuations in food availability and population density.

The expected stepwise $\delta^{15}N$ enrichment from primary producers to consumers (~3.4 ‰) (Minagawa and Wada 1984, Estep and Vigg 1985, Hobson and Welch 1995, Kling et al. 1992) was detected from the fishless reference only, Meanook Pond, where zooplankton occupied the highest trophic position. In ponds that had fish, only a ~1.5 ‰ enrichment between primary producers and zooplankton and macroinvertebrates was observed. Hobson and Welch (1995) found a similar low $\delta^{15}N$ enrichment in Char Lake and suggested that the sources of nitrogen used by invertebrates may be isotopically lighter than any of the measured sources, with bacteria providing the most likely source of nutrients depleted in ^{15}N. Further, omnivory can explain enrichment between trophic levels below the expected 3.4 ‰ (Kling at al. 1992). My results, therefore, add support to studies showing that omnivory is common in aquatic communities (Sprules and Bowerman 1988, Vadas 1990, Kling et al. 1992).

In my study, $\delta^{13}C$ values of zooplankton and phytoplankton from LD and HD, and of zooplankton, phytoplankton and periphyton from Beaver Pond were similar and suggested that the zooplankton most likely derived their carbon sources from these primary producers. The carbon ratios for macroinvertebrates, lying between those of phytoplankton and macrophytes, suggest that macroinvertebrates utilized a combination of these sources of primary production. The $\delta^{13}C$ values of detritus were comparable among ponds and suggest that detritus may be primarily composed of phytoplankton.

There were inconsistencies in $\delta^{13}C$ values of consumers in Meanook Pond (the fishless reference pond). Both zooplankton and macroinvertebrates carbon ratios were too depleted of $\delta^{13}C$ to suggest that they derived their biomass carbon from any of the primary sources from this pond. These inconsistencies in $\delta^{13}C$ may be due considerable inputs of terrestrial C_3 plants (< -25 ‰) and may account for the larger $\delta^{13}C$ range in aquatic primary consumers (Angardi 1994, Peterson and Fry 1987). Also, benthic metabolism may have contributed strongly to the dissolved CO_2 pool, consequently resulting in low $\delta^{13}C$ values of plankton (Rau 1980).

In summary, SCA indicated that fathead minnows are opportunistic generalists and highly omnivorous feeders, incorporating an array of zooplankton, macroinvertebrates, algae and detritus into their diets. In response to high fish density, fatheads simultaneously consume numerous prey categories and the greatest diversity of prey consumed was attained in the HD treatments. Only modest diet differences exist among life history categories, with smaller fish (YOY) consuming mostly rotifers and adults and juveniles eating more invertebrates and detritus. However, no distinct dietary switches occur and diet overlap remains high among the fish categories over the growing and reproductive season. Short-term feeding habits of fatheads, as indicated from SCA, do not always correspond to their long-term average trophic position, as measured by $\delta^{15}N$ and $\delta^{13}C$, particularly for fish in high-density treatment. The highest trophic position was attained by fatheads in HD treatment, which appeared to be a density-dependent response to food availability, including availability of conspecifics as prey. SIA was consistent with other evidence, which indicated that this density-dependent effect was manifested as cannibalism on eggs/larvae, as well as exploitation competition among all fish categories for limited food resources. Cannibalism may be important in determining the structure and dynamics of these single-species assemblages in small, shallow, eutrophic lakes and ponds in Alberta.

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Table 3.1. Limnological characteristics of the experimental (Low Density, LD and High Density, HD treatments) and reference ponds (Beaver and Meanook). All water quality data are given as means for 1995 (SE in brackets); FM indicates ponds with fathead minnows.

	LD	**HD**	**Beaver**	**Meanook**
Fish assemblage	FM	FM	FM	fishless
Surface area (ha)	0.02	0.02	3.0	0.05
Maximum depth (m)	1.6	1.6	5.0	1.5
Chlorophyll *a* (µg/L)	39.1(3.6)	49.5(5.9)	32.2(5.9)	54.3(8.9)
Secchi depth (m)	1.1 (0.2)	1.0(0.2)	2.1(0.1)	1.2(0.2)
TDP (µg/L)	14.5(2.4)	14.9(2.1)	13.8(2.3)	10.1(2.0)
TDN (µg/L)	9.4(2.9)	7.8(1.6)	10.1(2.8)	13.6(3.0)
Conductivity (µS/cm)	58.3(20.0)	349.7(33.4)	272.4(13.0)	349.6(34.5)
Dissolved oxygen (mg/L)	6.0(0.5)	6.4(0.5)	5.1(0.2)	4.8(0.8)
pH	8.1(0.1)	8.2(0.1)	8.0(0.1)	7.6(0.1)

Table 3.2. Mean indices of diet breadth (H'), excluding detritus and plant material, based on mean number of prey eaten by fish category in Beaver Pond, Low Density (LD) and High Density (HD) treatments.

	Beaver	**LD**	**HD**
Females	0.39	0.74	0.64
Males	0.76	0.76	0.67
Juveniles	0.72	0.67	0.60
YOY	0.94	0.40	0.70
mean	**0.70**	**0.64**	**0.65**

Table 3.3. Frequency of occurrence, percentage by number and volume, and Relative Importance (RI) of prey taxa in the diet of fathead minnows from Beaver Pond during the summer of 1995; n = number of fish stomachs analyzed for RI.

Prey Taxa	% Frequency of Occurrence	% Number	% Volume	% RI n = 78
Cladocera:				**35.5**
Daphnia spp.	36.9	21.6	1.0	9.9
Sida crystalina	2.5	0.7	0.0	0.5
Alona spp.	35.1	15.5	0.1	8.8
Alonella spp.	6.3	1.2	0.0	1.1
Chydorus sphericus	40.5	16.1	0.1	9.3
Pleuroxus spp.	6.2	2.6	0.0	1.5
Other Cladocera	18.4	7.5	0.1	4.4
Copepoda:				**3.7**
Copepod nauplii	5.5	0.9	0.0	1.2
Diacyclops bicuspidatus	14.4	1.6	0.0	2.5
Rotifera:				**2.8**
Monostyla lunaris	3.5	2.0	0.0	0.9
Other rotifers	9.1	2.7	0.0	2.0
Macroinvertebrates:				**26.3**
Gastropoda	0.0	0.0	0.0	0.0
Ostracoda	5.3	1.2	0.0	1.0
Amphipoda	5.1	0.6	0.6	1.0
Ephemeroptera	7.0	0.7	1.6	1.6
Odonata	1.1	0.1	0.1	0.2
Hemiptera	0.6	0.0	0.1	0.1
Trichoptera	0.0	0.0	0.0	0.0
Coleoptera larvae	5.2	0.3	4.2	1.5
Chaoborus spp.	26.7	10.3	25.0	10.5
Chironomidae	36.3	13.1	12.7	10.1
Other Diptera	2.1	0.1	0.5	0.4
Plant Material	68.8		17.0	**15.7**
Detritus	57.2		37.0	**16.0**

Table 3.4. Frequency of occurrence, percentage by number and volume, and the Relative Importance (RI) of prey taxa in the diet of fathead minnows from Low Density treatment during the summer of 1995; n = number of fathead minnow stomachs analyzed for RI.

Prey Taxa	**% Frequency of Occurrence**	**% Number**	**% Volume**	**% RI n = 61**
Cladocera:				**31.8**
Daphnia spp.	2.5	0.4	0.0	0.4
Sida crystalina	35.4	21.5	7.6	10.2
Alona spp.	37.1	7.9	0.1	7.3
Alonella spp.	7.6	1.3	0.0	1.3
Chydorus sphericus	45.3	9.3	0.3	8.6
Pleuroxus spp.	17.2	4.2	0.0	3.4
Other Cladocera	4.2	1.9	0.1	0.8
Copepoda:				**9.3**
Copepod nauplii	5.7	0.5	0.0	0.9
Diacyclops bicuspidatus	44.5	9.5	0.6	8.3
Rotifera:				**5.3**
Monostyla lunaris	11.5	10.1	0.1	3.4
Other rotifers	10.4	1.3	0.0	1.9
Macroinvertebrates:				**24.4**
Gastropoda	8.4	0.5	0.3	1.2
Ostracoda	7.5	1.3	0.0	1.1
Ephemeroptera	6.1	0.5	0.7	0.9
Hemiptera	5.1	1.6	0.4	0.8
Trichoptera	0.9	0.1	0.7	0.2
Coleoptera larvae	3.6	1.6	1.3	0.9
Chaoborus spp.	8.2	0.6	2.1	1.6
Chironomidae	47.1	24.7	23.5	15.3
Other Diptera	5.8	1.0	7.2	2.3
Plant Material	47.3		3.8	**7.5**
Detritus	87.5		51.1	**21.7**

Table 3.5. Frequency of occurrence, percentage by number and volume, and the Relative Importance (RI) of prey taxa in the diet of fathead minnows from High Density treatment during the summer of 1995; n = number of fathead minnow stomachs analyzed for RI.

Prey Taxa	% Frequency of Occurrence	% Number	% Volume	% RI n = 127
Cladocera:				**35.9**
Daphnia spp.	1.4	0.0	0.0	0.2
Sida crystalina	17.5	1.1	2.6	3.1
Alona spp.	45.7	7.1	0.3	7.6
Alonella spp.	10.9	2.5	0.1	1.9
Chydorus sphericus	67.6	40.3	5.1	16.3
Pleuroxus spp.	28.1	9.1	0.2	5.3
Other Cladocera	8.2	1.3	0.3	1.4
Copepoda:				**13.7**
Copepod nauplii	9.4	0.2	0.0	1.4
Diacyclops bicuspidatus	64.6	19.8	1.8	12.3
Rotifera:				**6.2**
Monostyla lunaris	17.3	2.8	0.0	2.9
Other rotifers	21.2	1.9	0.0	3.4
Macroinvertebrates:				**15.3**
Gastropoda	3.2	0.4	4.5	1.1
Hydrachnidia	2.0	0.1	0.1	0.3
Ostracoda	8.6	0.9	0.1	1.3
Ephemeroptera	6.2	1.0	1.5	1.2
Odonata	2.4	0.1	1.3	0.6
Hemiptera	1.3	0.1	0.3	0.2
Trichoptera	1.6	0.1	3.3	0.7
Coleoptera larvae	0.3	0.1	1.8	0.3
Chaoborus spp.	4.4	0.1	5.6	1.5
Chironomidae	53.7	10.1	23.3	12.6
Other Diptera	3.5	0.4	4.5	1.2
Plant Material	47.9		2.9	**7.3**
Detritus	67.7		40.1	**15.5**

Table 3.6. Temporal variation in the frequency of occurrence of fish scales in the stomachs of fathead minnows from Beaver Pond, and experimental ponds with low (LD) and high (HD) density treatments during the 1995 study; n = number of stomachs analyzed, X indicates no fish collected.

		Frequency of Occurrence (%)				
		Females	**Males**	**Juveniles**	**YOY**	**mean**
Beaver P.	June	8.3	16.7	27.3	X	**17.4**
(n=78)	July	X	X	20.0	16.7	**18.3**
	August	25.0	80.0	50.0	0.0	**38.8**
	mean	**16.7**	**48.3**	**32.4**	**8.3**	
LD	June	83.3	28.6	62.5	X	**58.1**
(n=61)	July	50.0	33.3	50.0	33.3	**41.7**
	August	75.0	33.3	0.0	X	**36.1**
	September	100.0	75.0	25.0	100.0	**75.0**
	mean	**77.1**	**42.6**	**34.4**	**66.7**	
HD						
(n=127)	June	20.0	44.4	12.5	X	**25.6**
	July	33.3	75.0	X	8.3	**38.9**
	August	15.8	33.3	36.8	0.0	**21.5**
	September	50.0	30.0	14.3	33.3	**31.9**
	mean	**29.8**	**45.7**	**21.2**	**13.9**	

Table 3.7. Temporal variation in diet overlap (α) among fathead minnows in Beaver Pond (BP), Low (LD) and High (HD) density treatments.

		LD	**HD**
BP	June	0.27	0.25
	July	0.67	0.64
	August	0.62	0.66
HD	June	0.77	
	July	0.73	
	August	0.66	
	September	0.73	

Table 3.8. Temporal variation in diet overlap (α) among males, females, juveniles, and YOY fathead minnows in Beaver Pond ; X indicates no available comparison.

	Males	Juveniles	YOY
June			
Females	0.66	0.82	X
Males		0.68	X
Juveniles			X
July			
Females	X	X	X
Males		X	X
Juveniles			0.71
August			
Females	0.78	0.65	0.56
Males		0.74	0.53
Juveniles			0.56

Table 3.9. Temporal variation in diet overlap (α) among females, males, juveniles, and YOY fathead minnows in Low Density treatments; X indicates no available comparison.

	Males	Juveniles	YOY
June			
Females	0.61	0.66	X
Males		0.58	X
Juveniles			X
July			
Females	0.63	0.67	0.30
Males		0.57	0.50
Juveniles			0.50
August			
Females	0.67	0.58	X
Males		0.55	X
Juveniles			X
September			
Females	0.56	0.74	0.65
Males		0.76	0.50
Juveniles			0.50

Table 3.10. Temporal variation in diet overlap (α) among females, males, juveniles, and YOY fathead minnows in High Density treatments; X indicates no available comparison.

	Males	Juveniles	YOY
June			
Females	0.65	0.74	X
Males		0.69	X
Juveniles			X
July			
Females	0.64	X	0.38
Males		X	0.30
Juveniles			X
August			
Females	0.79	0.77	0.46
Males		0.81	0.57
Juveniles			0.57
September			
Females	0.66	0.75	0.85
Males		0.63	0.60
Juveniles			0.79

Table 3.11. $\delta\,^{15}N$ and $\delta\,^{13}C$ of prey and fish from Meanook Pond, Beaver Pond, Low (LD) and High Density (HD) treatments. For each group, all taxa were combined into composite samples before SIA.

	$\delta\,^{13}C$				$\delta\,^{15}N$			
	Meanook Pond	**Beaver Pond**	**LD**	**HD**	**Meanook Pond**	**Beaver Pond**	**LD**	**HD**
Detritus	-24.52	-26.70	-22.35	-25.51	0.87	0.52	1.68	0.58
Phytoplankton	-27.73	-27.09	-30.46	-26.84	3.28	2.04	1.38	3.61
Periphyton	-9.70	-28.11	-17.88	-18.50	0.99	4.13	-0.65	-0.08
Macrophytes	-22.01	-20.70	-20.49	-20.70	1.51	-0.64	1.29	0.15
Zooplankton	-35.53	-28.52	-30.41	-29.11	5.30	3.30	2.42	1.83
Macroinvertebrates	-30.68	-21.76	-27.75	-24.22	3.78	2.89	2.69	2.46
Fish:								
Males		-28.47	-25.26	-23.71		5.60	6.59	7.22
Females		-27.84	-26.21	-23.40		5.41	6.88	6.89
Juveniles		-26.34	-26.76	-23.93		5.29	6.01	7.03
YOY		-28.60	-26.27	-24.64		5.46	5.36	6.28

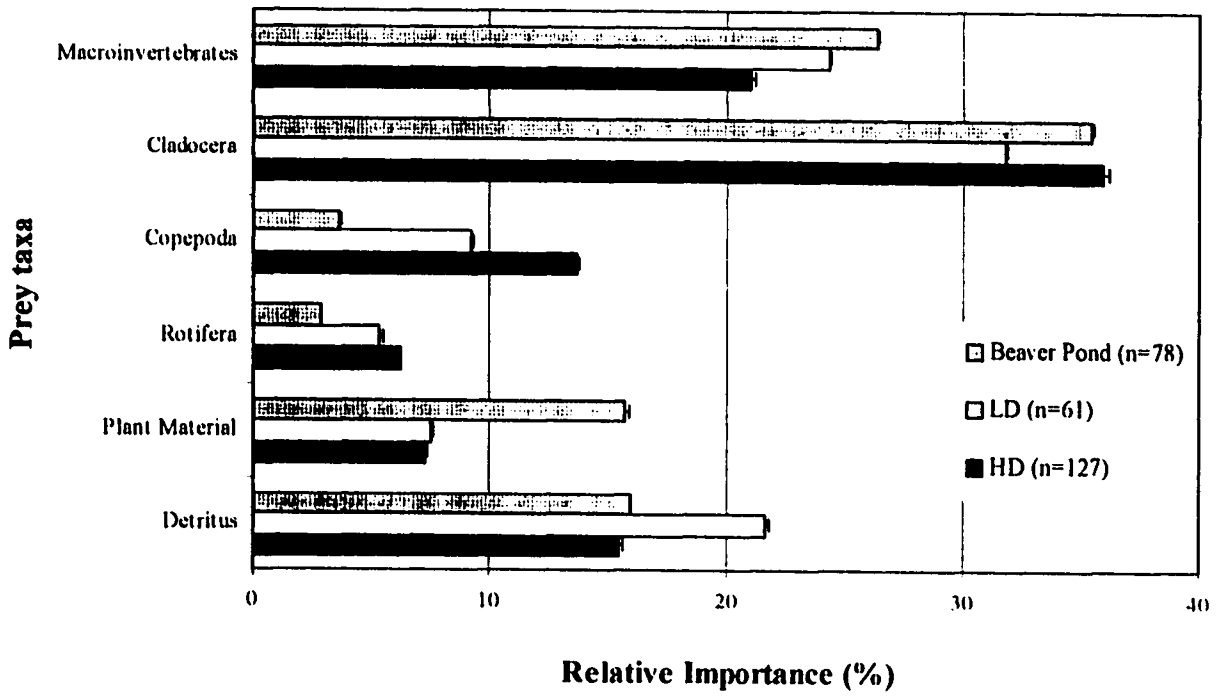

Figure 3.1. Relative Importance of major prey categories in the diets of fathead minnows from Beaver Pond (BP), and in experimental ponds with Low (LD) and High (HD) Density treatments; n = number of non-empty stomachs analyzed.

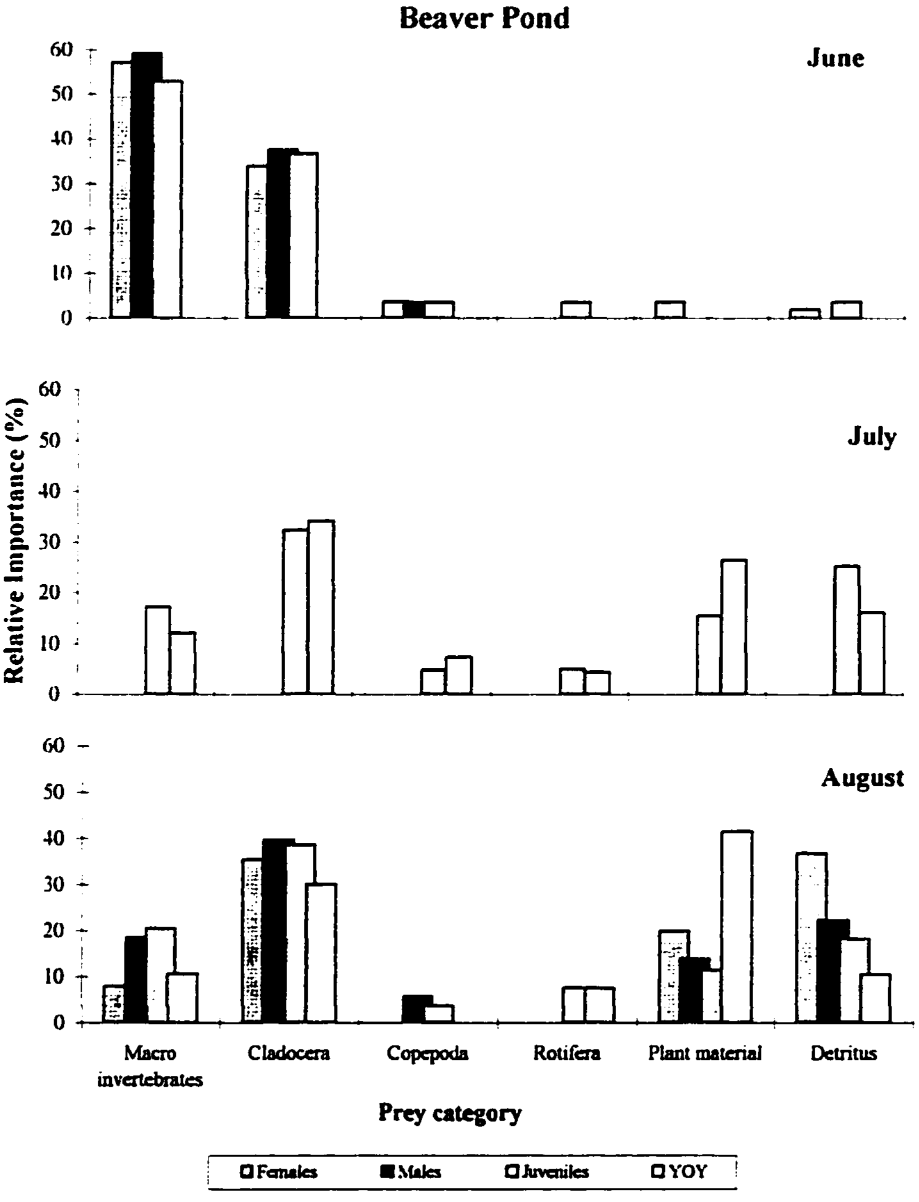

Figure 3.2. Seasonal variation in the diet composition (Relative Importance, %) of females, males, juveniles, and YOY fathead minnows from Beaver Pond during the summer of 1995. See Appendix, Table 2 for sample sizes.

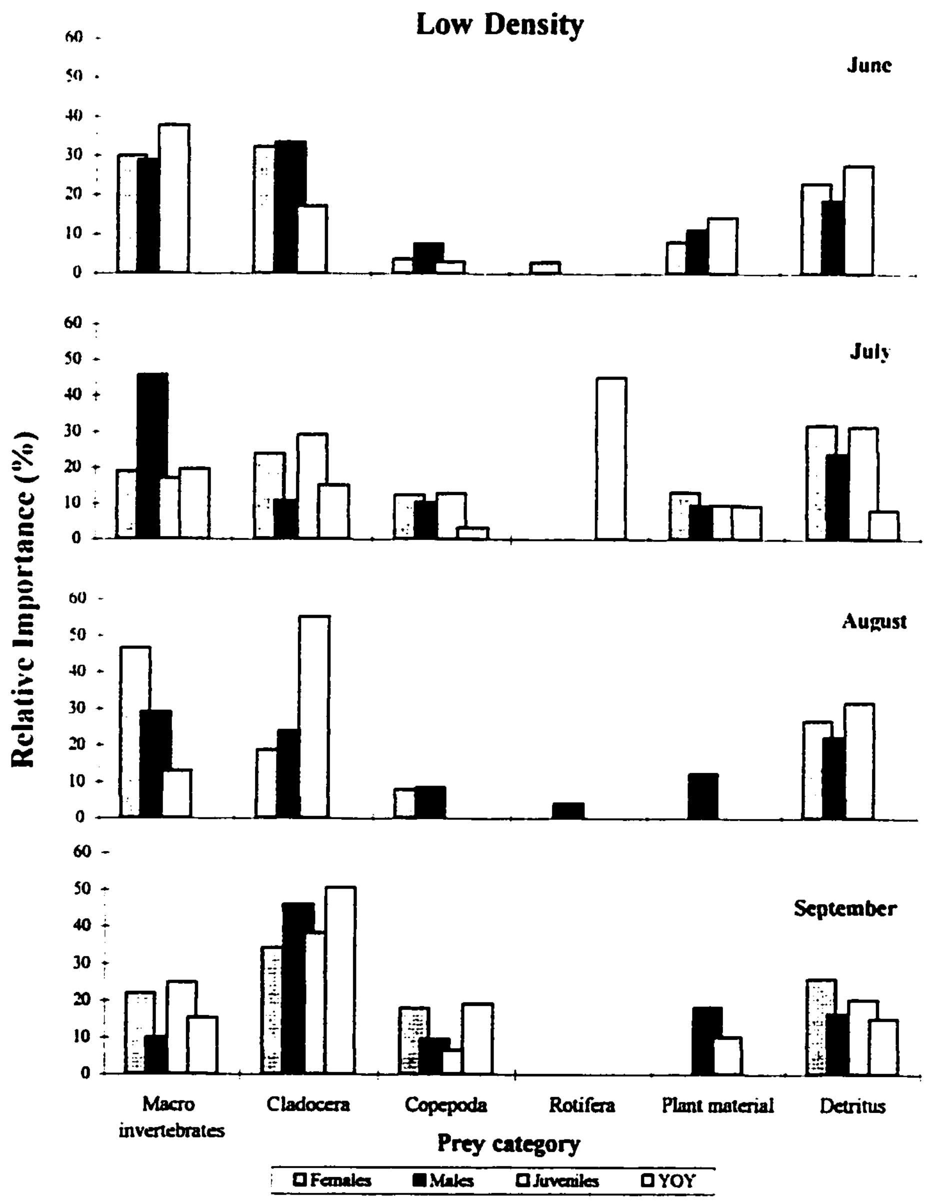

Figure 3.3. Seasonal variation in the diet composition (Relative Importance, %) of females, males, juveniles, and YOY fathead minnows from Low Density treatment during summer 1995. See Appendix, Table 3 for sample sizes.

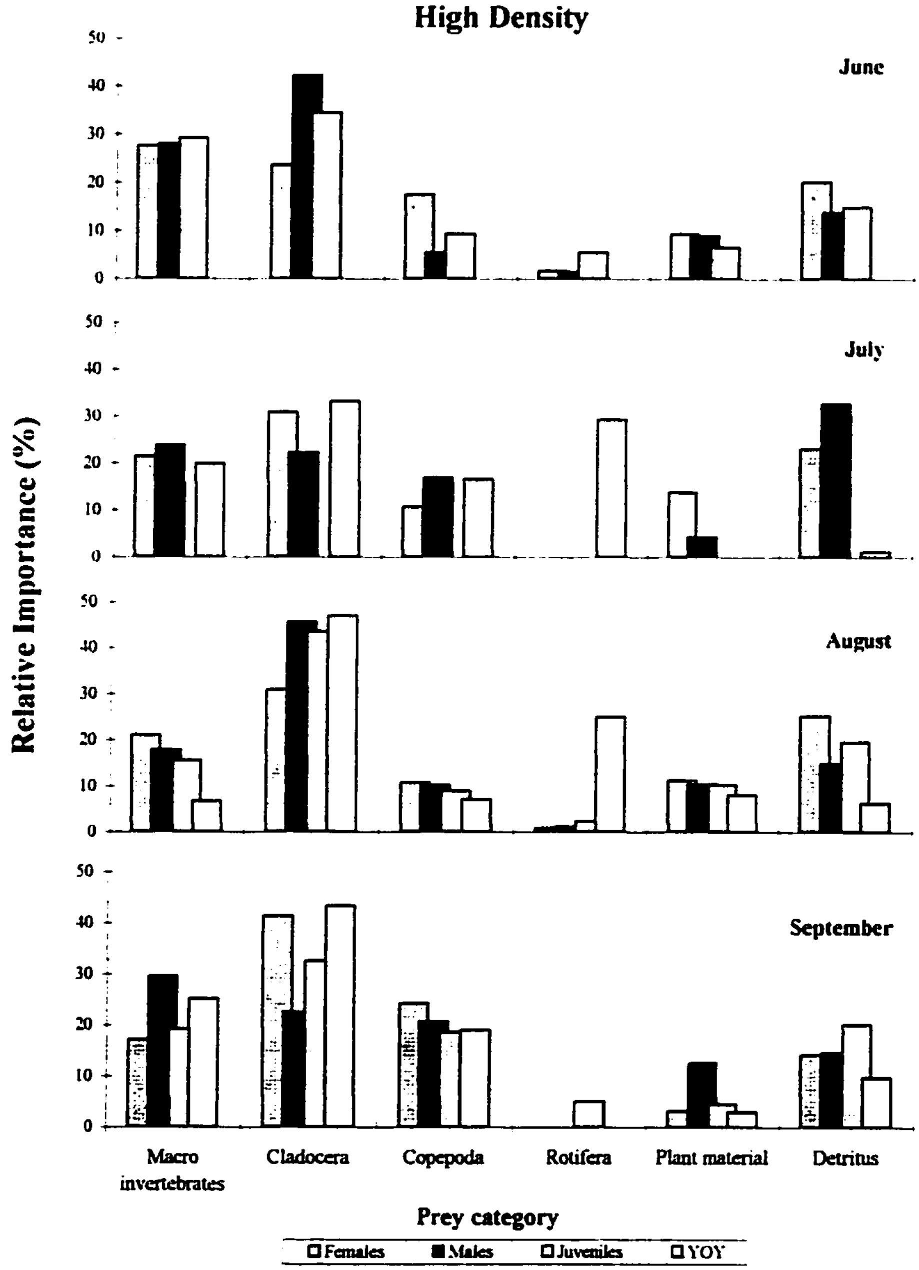

Figure 3.4. Seasonal variation in the diet composition (Relative Importance, %) of females, males, juveniles, and YOY fathead minnows from High Density treatment during summer 1995. See Appendix, Table 4 for sample sizes.

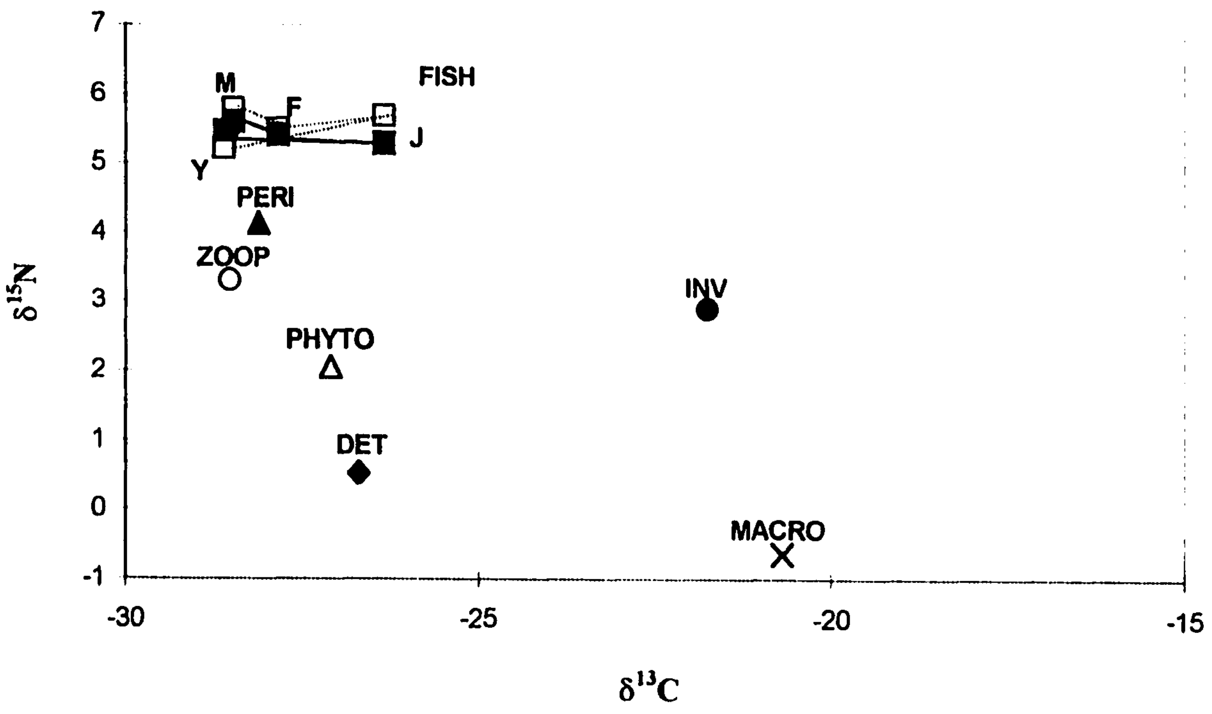

Figure 3.5. Trophic relationships in Beaver Pond, based on stable isotope analyses of carbon and nitrogen. For fish, filled squares and solid lines are observed values; open squares and dashed lines indicate values predicted from stomach content analysis (see text). F – females, M – males, J – juveniles, Y – YOY, INV – macroinvertebrates, ZOOP – zooplankton, PHYTO – phytoplankton, PERI – periphyton, MACRO – macrophytes, DET – detritus.

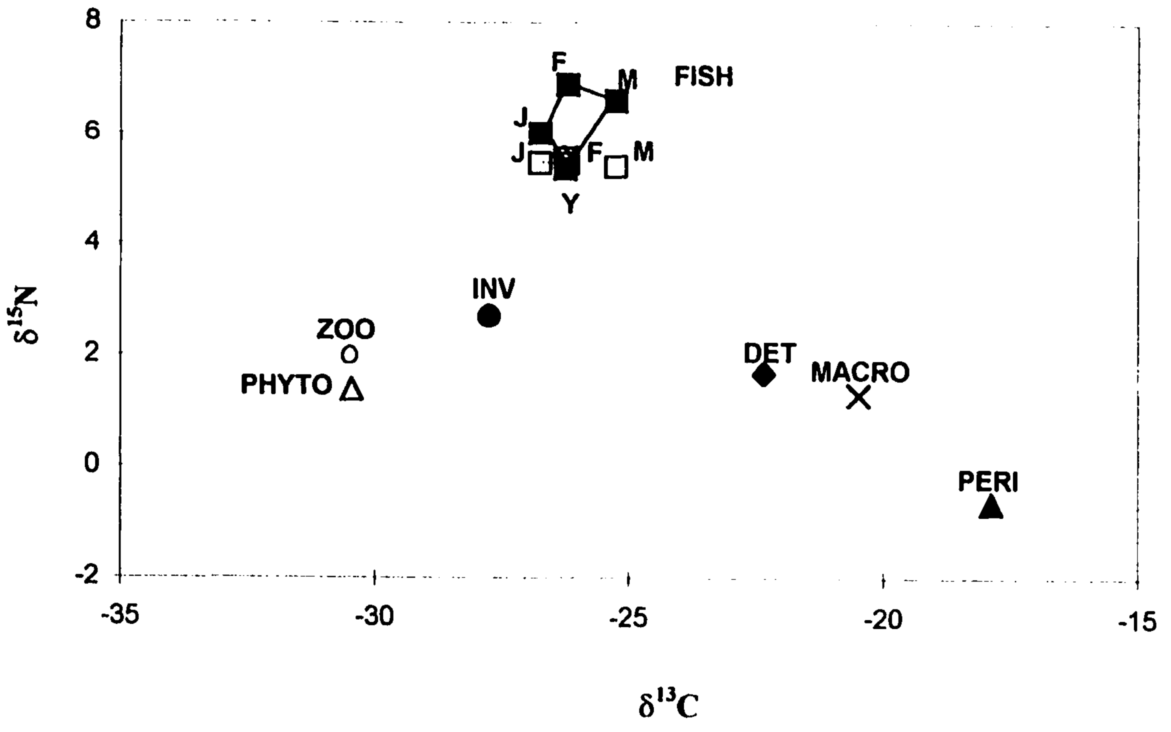

Figure 3.6. Trophic relationships in Low Density treatment, based on stable isotope analyses of carbon and nitrogen. For fish, filled squares and solid lines are observed values; open squares and dashed lines indicate values predicted from stomach content analysis (see text). F – females, M – males, J – juveniles, Y – YOY, INV –macroinvertebrates, ZOOP – zooplankton, PHYTO – phytoplankton, PERI – periphyton, MACRO – macrophytes, DET – detritus.

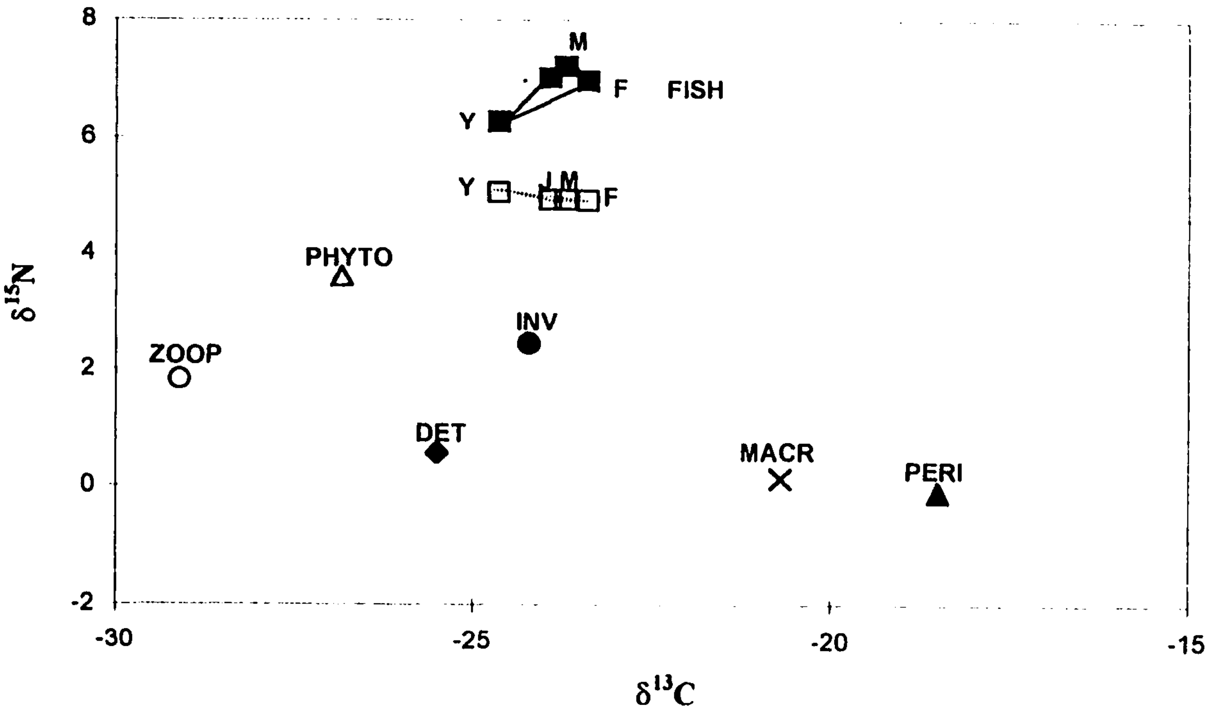

Figure 3.7. Trophic relationships in High Density treatment, based on stable isotope analyses of carbon and nitrogen. For fish, filled squares and solid lines are observed values; open squares and dashed lines indicate values predicted from stomach content analysis (see text). F – females, M – males, J – juveniles, Y – YOY, INV – macroinvertebrates, ZOOP – zooplankton, PHYTO – phytoplankton, PERI – periphyton, MACRO – macrophytes, DET – detritus.

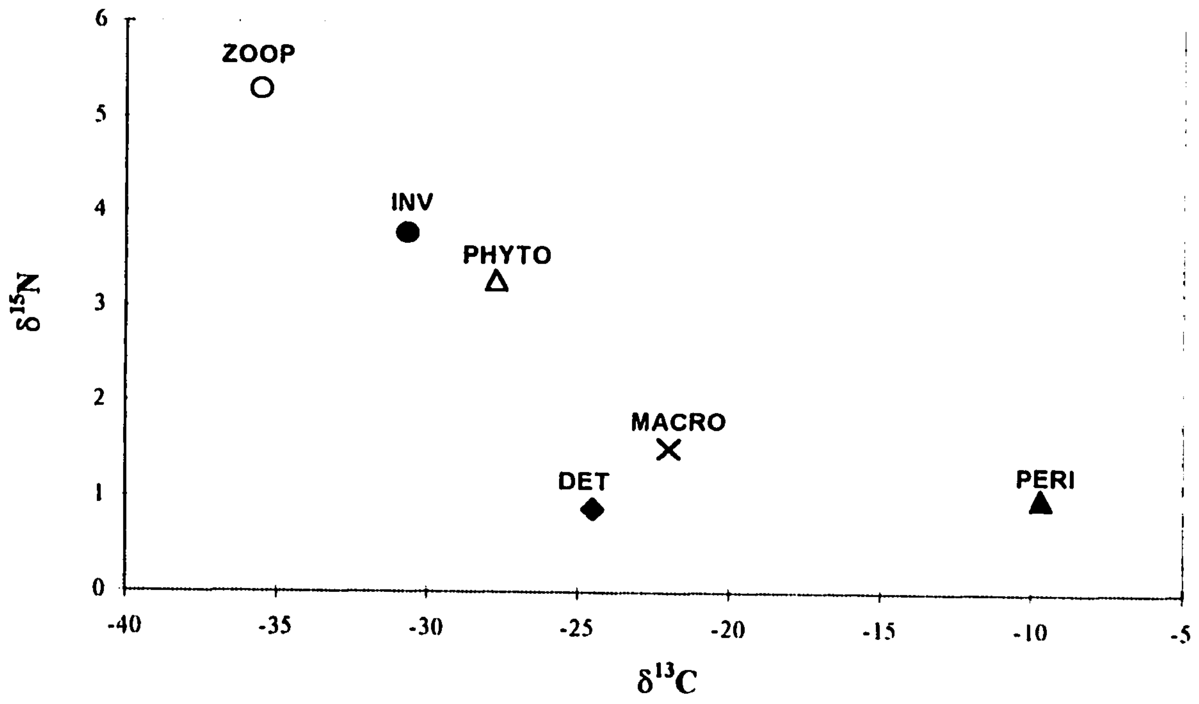

Figure 3.8. Trophic relationships in Meanook Pond, based on carbon and nitrogen ratios of primary producers and consumers. INV – macroinvertebrates, ZOOP – zooplankton, PHYTO – phytoplankton, PERI – periphyton, MACRO – macrophytes, DET – detritus.

Chapter 4. GENERAL DISCUSSION AND CONCLUSIONS

Omnivorous fathead minnows (*Pimephales promelas*) are important in structuring zooplankton communities in small Alberta ponds. I found significant fish-density effects on zooplankton community structure, density, and biomass. High fish densities in my experimental ponds resulted in increases in the relative abundance of microzooplankton (Rotifera) and decreases in macrozooplankton (Cladocera and Calanoida), and increases in total zooplankton biomass. Fathead minnows also affected the distribution of zooplankton taxa in different habitats (inshore vs. offshore) within each pond. Densities of *Daphnia* spp. and copepods were greater in the offshore habitat, whereas small cladoceran species were more abundant in inshore habitats in all ponds with fish. In contrast, in ponds without fish, inshore and offshore habitats supported similar densities of zooplankton.

Abundances of the large-bodied cladoceran, *Daphnia*, and the calanoid copepod, *Acanthodiaptomus denticornis*, were dramatically reduced in the ponds containing fish and the effects were stronger with increasing fish density. Decreased densities of macrozooplankton were likely attributable to direct predation by fathead minnows. Stomach analyses revealed that fatheads consumed numerous taxa of zooplankton, with cladocerans comprising close to 40 % (by Relative Importance) of prey in the stomachs of all life-history categories of fatheads (males, females, juveniles, and YOY). The well-documented selection of larger zooplankton by fish (e.g., Hrbacek et al. 1961, Brooks and Dodson 1965, Zaret 1980, Carpenter and Kitchell 1988) was thus the likely mechanism behind the observed effect of fish density on large-bodied zooplankton taxa.

The elimination or reduction of large zooplankton in the high-density ponds led to a dramatic shift to smaller zooplankton. In concordance with previous research (e.g., Hamrin 1983, Kerfoot and DeMott 1984, Kerfoot 1987, Christoffersen et al. 1993, Rudstam et al. 1993, Hessen et al. 1995), increased minnow density resulted in increased abundance of rotifers and cyclopoid copepods. Rotifers were only an important food for YOY and thus likely benefited from decreased competition with *Daphnia*. Cyclopoids were important prey only in high-density ponds, where they also occurred at higher densities. Thus, it appears that fatheads simply took advantage of an abundant food without directly affecting abundance.

Despite the strong effects of fish density on zooplankton, effects at the phytoplankton and nutrient level were less apparent. Fathead minnow density decreased Secchi depth without coincidental increases in chlorophyll *a* or nutrient (phosphorus and nitrogen) concentrations. Changes in phytoplankton community structure (e.g., size of algal cells) appeared to be the only response to different fish densities; large-bodied, inedible Pyrrophyta (dinoflagellates) developed at high densities. Because these large algae require high nutrient loadings (Ramcharan et al. 1995), it is possible that the internal nutrient loadings at high fish densities enhanced their growth. My results, therefore, showed that the effects of densities of fathead minnows on lower trophic levels are more complex than these predicted by the trophic cascade hypothesis (Carpenter et al. 1985). Hence, I propose that more research should be conducted to discern the relationships between omnivorous fish density and the phytoplankton community and nutrient responses.

In addition, to corroborating the importance of large-bodied zooplankton as prey of fathead minnows, stomach content analyses (SCA) revealed that fatheads also consumed macroinvertebrates, plant material, and detritus regardless of the density treatment. However, fatheads consumed the greatest number of prey taxa, had higher proportions of empty stomachs, higher proportions of detritus, and small-bodied invertebrates dominated their diets in high-density ponds. In these ponds, fatheads evidently experienced intense density-dependent exploitation competition for food. Competition, in turn, often causes reduced fish growth and poor condition (Holopainen and Pitkänen 1985, Tonn et al. 1994), which would likely contribute to higher overwinter mortality of fatheads in high-density populations, especially in the north-temperate lakes where fish are subjected to long and severe winters (Shuter and Post 1990).

The short term feeding habits, indicated from SCA, of fatheads did not always correspond to their long-term average trophic position, as measured by $\delta^{15}N$. In particular, fatheads from high-density treatment attained the highest trophic position; higher than predicted based on SCA, which was a density-dependent effect and displayed as cannibalism.

Because cannibalism was not detected from stomach content analysis, it suggests that eggs and larvae are preferentially digested and thus are hard to detect from SCA. The lack of ingested conspecifics in the analyzed guts may explain why the potential for cannibalistic interactions has not been considered earlier in fathead minnow population studies. SCA alone, therefore, is not likely a reliable indicator of food habits of fish species in which the occurrence of egg or larval cannibalism is sporadically high as a response to fluctuations in food availability and population density.

In conclusion, the complementary use of community level analysis of prey, and SCA and SIA revealed that multiple linkages and complex interactions occur in small

Alberta pond ecosystems with different fathead minnow densities. Moreover, variations in fathead minnow populations, whether caused by density-dependent mechanisms, such as cannibalism, or density independent processes, e.g., winterkill, affect lower trophic levels. Although I found that fatheads had stronger effects on zooplankton than environmental variables in these ponds, the community analyses stressed that both top-down and bottom-up factors operate simultaneously to influence the structure and function of aquatic ecosystems (Mills and Forney 1988, Carpenter et al. 1985). Such complexities will mean that accurate predictions of the effects of perturbations of fish populations are not always possible. Still my documentation of environmental and biological responses to different fathead minnow densities should help aquatic ecologists understand the complexity of lake food webs and may have implications for modeling and managing eutrophic lake systems.

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APPENDIX

Table 1. Prey items present in fish stomachs from Beaver Pond, and Low and High Density treatments in 1995 (X indicates the presence of food item).

	Beaver Pond	**Low Density**	**High Density**
# of stomachs with prey	74	61	127
# of empty stomachs	4	11	79
Cladocera:			
Alona spp.	X	X	X
Alonella spp.	X	X	X
Chydorus sphericus	X	X	X
Daphnia spp.	X	X	X
Graptoleberis spp.	X		X
Pleuroxus spp.	X	X	X
Sida crystalina	X	X	X
Simocephalus spp.	X	X	X
Copepoda:			
Diaptomus nauplii	X	X	X
Dicyclops bicuspidatus	X	X	X
Rotifera:			
Brachionus spp.	X	X	X
Conochillus spp.		X	X
Euchlanis spp.		X	X
Keratella cochlearis	X	X	X
Keratella quadrata		X	
Lecane luna	X		
Lepadella patella		X	
Monostyla bulla	X	X	X
Monostyla lunaris	X	X	X
Macrothrix spp.	X		X
Mytilina spp.		X	X
Notholca aquminata			X
Philodina spp.		X	X
Platyias spp.	X		X
Pleosoma spp.	X		X
Pomopholyx sulcata			X
Syncheata spp.			X
Testudinella spp.	X	X	X
Trichocerca spp.	X	X	X

(Table 1 continued)

Macroinvertebrates:			
Chaoborus spp.	X	X	X
Chironomidae:	X	X	X
Coleoptera	X	X	X
Diptera:			
Ceratopogonidae	X	X	X
Tipulidae	X		X
Ephemeroptera	X	X	X
Gastropoda:			
Lymnelidae		X	X
Planorbidae		X	X
Hemiptera:			
Corrixidae	X	X	X
Notonectidae		X	X
Hydrachnidia			X
Nematoda			X
Odonata	X		X
Ostracoda		X	X
Trichoptera	X	X	X
Unidentified insects	X	X	X
Plant material:			
Filamentous green algae	X	X	X
Macrophytes	X	X	X
Seeds	X	X	X
Detritus	X	X	X
Fish scales	X	X	X
Total # of prey taxa	**35**	**38**	**47**

Table 2. Temporal variation in the Relative Importance (RI) of invertebrate prey taxa in the diet of fathead minnows from Beaver Pond in 1995; n = number of fish stomachs analyzed for RI.

	Relative Importance (%)								
	Females		**Males**			**Juveniles**		**YOY**	
	June	**August**	**June**	**August**	**June**	**July**	**August**	**July**	**August**
Prey Taxa **(n)**	**12**	**4**	**6**	**5**	**11**	**15**	**6**	**12**	**7**
Cladocera:									
Daphnia spp.	32.1	0.0	27.4	0.0	34.8	2.2	1.9	5.2	0.0
Sida crystalina	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0
Alona spp.	1.8	10.2	3.3	10.4	1.7	7.1	10.3	13.6	15.0
Alonella spp.	0.0	0.0	0.0	0.0	0.0	2.4	5.7	2.3	0.0
Chydorus spp.	0.0	15.0	3.5	16.9	0.0	14.9	13.1	12.8	0.0
Pleuroxus spp.	0.0	0.0	0.0	0.0	0.0	3.5	3.7	0.0	7.5
Other Cladocera	0.0	10.2	3.3	9.1	0.0	2.2	3.9	0.0	7.5
Copepoda:									
Copepod nauplii	1.8	0.0	0.0	0.0	1.7	1.0	0.0	5.5	0.0
Diacyclops bicuspidatus	1.8	0.0	3.3	5.8	1.7	3.7	3.7	1.7	0.0
Rotifera:									
Monostyla lunaris	0.0	0.0	0.0	0.0	0.0	3.7	1.9	2.6	0.0
Other rotifers	0.0	0.0	0.0	0.0	3.5	1.2	5.7	1.7	7.5
Macroinvertebrates:									
Ostracoda	1.8	0.0	0.0	0.0	3.4	0.0	5.1	0.0	0.0
Amphipoda	1.8	0.0	0.0	3.0	3.6	0.0	0.0	0.9	0.0
Ephemeroptera	2.0	0.0	7.6	0.0	1.9	0.0	0.0	2.9	0.0
Odonata	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0
Hemiptera	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0
Coleoptera larvae	2.5	0.0	12.3	0.0	0.0	0.0	0.0	0.0	0.0
Chaoborus spp.	45.4	0.0	27.4	0.0	34.1	0.0	1.9	0.0	0.0
Chironomidae	3.6	8.0	7.8	15.5	9.8	13.9	13.6	8.2	10.7
Other Diptera	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**94.6**	**43.4**	**100.0**	**63.9**	**96.4**	**59.1**	**70.4**	**57.6**	**48.1**

Table 3. Temporal variation in the Relative Importance (RI) of invertebrate prey taxa in the diet of fathead minnows from Low Density treatment in 1995; n = number of fish stomachs analyzed.

	Females				**Males**				**Juveniles**				**YOY**	
	June	**July**	**August**	**Sept**	**June**	**July**	**August**	**Sept**	**June**	**July**	**August**	**Sept**	**July**	**Sept**
Prey Taxa **(n)**	**6**	**3**	**4**	**2**	**7**	**3**	**3**	**4**	**8**	**2**	**2**	**4**	**12**	**1**
Cladocera:														
Daphnia spp.	0.0	5.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sida crystalina	7.3	7.3	3.7	34.2	0.0	0.0	5.5	23.8	0.0	0.0	18.4	25.7	0.0	16.6
Alona spp.	10.5	5.8	3.8	0.0	5.1	5.8	4.4	3.0	6.5	16.4	14.2	0.0	3.2	14.8
Alonella spp.	7.2	0.0	0.0	0.0	5.1	0.0	4.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0
Chydorus sphericus	4.0	5.8	7.5	0.0	9.6	0.0	4.1	13.2	3.4	0.0	11.0	12.7	11.8	19.2
Pleuroxus spp.	3.3	0.0	3.8	0.0	3.6	5.0	5.9	3.1	3.4	12.8	11.6	0.0	0.0	0.0
Other Cladocera	0.0	0.0	0.0	0.0	8.4	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda:														
Copepod nauplii	0.0	5.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0
Diacyclops bicuspidatus	3.6	7.3	7.9	17.9	7.7	5.4	8.5	9.5	3.1	12.9	0.0	6.5	0.0	19.0
Rotifera:														
Monostyla lunaris	0.0	0.0	0.0	0.0	0.0	0.0	4.1	0.0	0.0	0.0	0.0	0.0	29.2	0.0
Other rotifers	2.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.9	0.0
Macroinvertebrates:														
Chaoborus spp.	10.9	0.0	3.7	0.0	1.9	0.0	0.0	3.6	0.0	0.0	0.0	0.0	2.9	0.0
Chironominidae	15.0	13.2	25.1	22.0	9.5	7.9	14.3	6.3	30.8	17.0	13.0	24.9	7.1	15.4
Ephemeroptera	4.1	0.0	0.0	0.0	2.0	5.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	5.7	0.0	0.0	0.0	9.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	3.7	0.0	5.4	5.0	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	0.0	0.0	3.7	0.0	3.4	5.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other Diptera	0.0	0.0	10.5	0.0	1.9	0.0	0.0	0.0	7.0	0.0	0.0	0.0	9.5	0.0
Hemiptera	0.0	0.0	0.0	0.0	1.9	13.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	**68.9**	**55.0**	**73.2**	**74.2**	**70.2**	**66.9**	**65.6**	**65.5**	**58.0**	**59.1**	**68.3**	**69.6**	**82.8**	**85.0**

Table 4. Temporal variation in the Relative Importance (RI) of invertebrate prey taxa in the diet of fathead minnows from High Density treatment in 1995; n = number of fish stomachs analyzed.

	Females				Males				Juveniles			YOY		
	June	July	August	Sept	June	July	August	Sept	June	August	Sept	July	August	Sept
Prey Taxa (n)	10	3	19	4	9	4	12	10	8	19	7	12	4	6
Cladocera:														
Daphnia spp.	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Sida crystalina	1.6	0.0	1.8	3.5	1.5	0.0	7.4	1.5	2.5	3.5	6.6	1.2	4.8	6.1
Alona spp.	7.8	0.0	7.3	12.8	9.7	11.7	7.2	1.4	10.5	12.0	0.0	7.5	7.2	11.7
Alonella spp.	1.8	4.8	1.2	0.0	5.8	5.3	0.0	0.0	2.9	0.8	0.0	1.1	4.1	0.0
Chydorus sphericus.	8.8	10.1	14.7	18.6	11.4	5.3	23.7	15.5	3.6	22.6	26.0	9.1	30.9	22.6
Pleuroxus spp.	3.5	11.3	6.0	6.4	10.4	0.0	6.1	1.4	9.2	3.1	0.0	12.1	0.0	2.8
Other Cladocera	0.0	4.8	0.0	0.0	2.1	0.0	1.2	2.8	5.7	1.6	0.0	1.1	0.0	0.0
Copepoda:														
Copepod nauplii	3.1	0.0	0.0	3.2	0.0	0.0	0.0	1.4	0.0	0.8	0.0	5.4	3.5	0.0
Diacyclops bicuspidatus	14.4	10.7	10.8	21.0	5.4	17.0	10.2	19.3	9.3	8.1	18.5	11.2	3.6	18.9
Rotifera:														
Monostyla lunaris	1.7	0.0	0.8	0.0	0.0	0.0	1.1	0.0	2.2	1.5	0.0	15.0	10.9	0.0
Other rotifers	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	3.2	0.8	5.0	14.3	14.1	0.0
Macroinvertebrates:														
Chaoborus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	3.3	0.0	0.0	11.8	0.0	0.0
Chironominidae	21.9	11.4	8.3	17.2	10.9	13.1	10.3	8.7	21.7	7.2	19.3	2.8	6.8	22.3
Ephemeroptera	0.0	0.0	1.5	0.0	3.0	5.6	0.0	8.4	0.0	1.0	0.0	0.0	0.0	0.0
Coleoptera larvae	0.0	0.0	1.2	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	0.0	0.0	5.8	0.0	0.0	0.0	5.2	0.0	0.0	1.0	0.0	4.1	0.0	0.0
Ostracoda	0.0	4.8	0.0	0.0	2.9	5.3	2.3	0.0	0.0	0.8	0.0	1.1	0.0	2.9
Other Diptera	0.0	5.3	1.1	0.0	4.3	0.0	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0
Hemiptera	2.0	0.0	0.0	0.0	0.4	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0
Odonata	2.1	0.0	0.0	0.0	1.5	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	0.0
Hydrachnidia	1.6	0.0	1.7	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichoptera	0.0	0.0	1.4	0.0	0.0	0.0	0.0	9.6	0.0	0.0	0.0	0.0	0.0	0.0
Total:	**70.4**	**63.1**	**63.6**	**82.7**	**77.1**	**63.1**	**74.7**	**72.8**	**78.5**	**70.2**	**75.4**	**98.9**	**85.8**	**87.4**

Table 5. Stable nitrogen ratios ($\delta^{15}N$) for adults (males and females), juveniles, and YOY fathead minnow muscle tissue obtained during the 35-week feeding experiment, June 1995-March 1996.

	$\delta^{15}N$			
		Fathead minnows		
Week	*Daphnia* spp	Adults	Juveniles	YOY
1.0	12.8	7.4	8.6	5.9
2.0	13.1	8.4	8.2	8.2
3.0	11.6	7.7	8.9	9.6
4.0	11.6	8.5	9.8	9.2
5.0	11.6	8.4	10.9	12.6
6.0	11.6	7.6	13.0	12.7
7.0	12.1	10.3	10.9	15.0
8.0	12.4	9.7	11.9	15.6
9.0	12.4	10.1	13.4	16.0
10.0	13.1	10.2	13.3	
11.0	13.1	10.8		
12.0	13.3	9.8		
13.0	12.8	10.0		
15.0	12.7	11.1		
18.0	13.1	11.2		
20.0	12.8	12.2		
23.0	13.2	12.7		
25.0	13.3	13.0		
27.0	13.0	12.8		
29.0	13.0	13.4		
31.0	13.0	14.5		
33.0	13.0	15.0		